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PROTECTION AFFECTS THE ABUNDANCE AND ACTIVITY PATTERNS OF PUMAS IN THE ATLANTIC FOREST

AGUSTÍN PAVIOLO,* YAMIL E. DI BLANCO, CARLOS D. DE ANGELO, AND MARIO S. DI BITETTI

Consejo Nacional de Investigaciones Científicas y Técnicas de Argentina (CONICET), Yapeyú, 23, CP 3370 Puerto Iguazú, Misiones, Argentina (AP, CDDA, MSDB)
Asociación Civil Centro de Investigaciones del Bosque Atlántico (CeIBA), Yapeyú, 23, CP 3370 Puerto Iguazú, Misiones, Argentina (AP, CDDA, MSDB, YEDB)

Knowing the factors that affect the abundance and activity patterns of pumas (*Puma concolor*) in South American forests may help in their conservation. Using camera traps, we conducted 4 surveys in 3 areas with different levels of protection against poaching and logging within the biggest continuous fragment of the Upper Parana Atlantic Forest. We used capture–mark–recapture population models to estimate the density of pumas for each area. The core area of Iguazú National Park, with low poaching pressure and no logging for >60 years, had the highest density of pumas (between 1.55 and 2.89 individuals/100 km^2). Yabotí Biosphere Reserve, an area with the highest poaching and logging pressure, showed the lowest density (between 0.3 and 0.74 individuals/100 km^2). Areas with intermediate levels of poaching and logging pressure had densities between 0.66 and 2.19 individuals/100 km^2. Puma activity peaked during the 1st hours of morning in the most protected area, but became more crepuscular and nocturnal in areas with less protection. The lower abundance of pumas in the more degraded areas may be related to lower prey abundance. Differences in activity patterns of pumas among areas with different poaching pressures may be a direct response to poaching or to changes in the availability and activity patterns of primary prey. Conservation efforts should focus on decreasing poaching and logging pressures within protected areas to benefit pumas and other endangered species in the Atlantic Forest.

Key words: activity pattern, Atlantic Forest, camera traps, density estimate, jaguar, logging, poaching, prey abundance, protection, *Puma concolor*

The puma (*Puma concolor*) inhabits most of the American continent (Young and Goldman 1946). Although an extensive amount of information about the ecology of this species exists, 90% of the published studies were conducted in North America (Laundre 2005). Most of the existing information from South America focuses on the trophic ecology of pumas (Sunquist and Sunquist 2002). Studies related to other biological aspects affecting puma ecology are scarce and were conducted in temperate semidesert habitats (Franklin et al. 1999; Novaro and Walker 2005) or savannahs (Schaller and Crawshaw 1980; Scognamillo et al. 2003).

Important environmental and socioecological differences exist between North and South American countries. As a result, the management and conservation problems that pumas face are different in these 2 regions (Laundre 2005). Habitat loss and degradation are major threats to natural habitats in South America. The Upper Parana Atlantic Forest is a dramatic example of this process, with only 7% of its original surface remaining in isolated fragments (Di Bitetti et al. 2003). The biggest fragment of this ecoregion is known as the Green Corridor (about 10,000 km^2) and is located in Misiones Province of Argentina and neighboring areas of Brazil (Di Bitetti et al. 2003).

Most of these forest remnants suffered timber extraction of different intensities and reflect different states of degradation (Campanello et al. 2007). Habitat degradation caused by forest overexploitation in the Green Corridor has been identified as one of the possible causes of population decline in other predators such as ocelots (*Leopardus pardalis*—Di Bitetti et al. 2008a) and jaguars (*Panthera onca*—Paviolo et al. 2008). Puma populations also may be affected by this factor.

In addition to forest degradation by logging, these forests also are affected by poaching. In the Atlantic Forest, poaching is a common activity (Giraudo and Abramson 2000) and it negatively affects the abundance and behavior of some prey species of pumas (Chiarello 2000; Cullen et al. 2000; Di

* *Correspondent: paviolo4@gmail.com*

Bitetti et al. 2008b; Paviolo 2002). Therefore, variation in protection efforts against poaching and logging may affect the abundance and behavior of the primary prey species of pumas, and in turn puma abundance and behavior.

Kelly et al. (2008) found that the density of pumas is very low at Yabotí Biosphere Reserve in the Green Corridor, suggesting that it may be related to the high poaching pressure and intense logging activity suffered in the area. However, their study compared densities among areas located in different regions (Argentina, Bolivia, and Belize) where factors other than poaching may affect the abundance of pumas. The Green Corridor presents a variety of forest areas in different states of conservation, providing an ideal situation to test the hypothesis that human activities, such as poaching and logging, negatively affect the abundance of pumas.

In the Atlantic Forest, pumas are often in conflict with humans because they prey on domestic cattle (Conforti and Azevedo 2003; Mazzolli et al. 2002) or are potentially dangerous to humans, as was sadly confirmed by a fatal puma attack on a child at the visitor's area of Iguazú National Park in 1997. Information on patterns of puma abundance and activity might help to mitigate conflicts with humans, and to establish a baseline for the elaboration of conservation strategies for this species (Cougar Management Guidelines Working Group 2005).

The goal of this study was to compare the abundance and activity patterns of pumas in areas under different management and degradation conditions within the Green Corridor and assess the effect of these management practices on the ecology and behavior of the species.

Materials and Methods

Study area.—We carried out this study in 3 areas of the Green Corridor. This region is characterized by a semideciduous subtropical forest with no discernible dry season (Cabrera and Willink 1980). Average temperatures are around 22°C and 17°C during the warmest and the coldest months, respectively. Average annual precipitation is around 2,000 mm with 2 peaks in the spring and autumn (Crespo 1982).

One of the study sites was in Yabotí Biosphere Reserve (2,600 km^2; 27°S, 54°W). The surveyed area included part of Esmeralda Provincial Park (300 km^2; logged until 1990) and several private properties. At the time of the study, these private properties were being intensely exploited by logging companies with the exception of Miot's property, where logging was less intense (Di Bitetti et al. 2008a). Some of the results of the survey conducted at Yabotí Biosphere Reserve were presented by Kelly et al. (2008).

Another surveyed area was Urugua-í (25°58′S, 54°06′W). This area included Urugua-í Wildlife Reserve (32 km^2), part of Urugua-í Provincial Park (840 km^2), and Campo de los Palmitos (300 km^2), a property belonging to a logging company. The area was subject to selective timber extraction until 1990.

The Iguazú area (25°40′S, 54°30′W) was surveyed twice, 1st in 2004 and again between 2006 and 2007. During the 1st survey we covered the central area of Iguazú National Park (670 km^2) of Argentina. This park was subjected to selective logging until 1934 (Dimitri 1974). During the 2nd survey we expanded the study area, adding the western portion of Iguazú National Park, San Jorge Forest Reserve (174 km^2), and the western area of Iguaçu National Park of Brazil (1,850 km^2). Iguaçú National Park of Brazil was selectively logged until the decade of 1930 and the San Jorge Reserve until the end of the 1980s. A map of the study areas and surveys can be found in Paviolo et al. (2008).

Measurement of poaching intensity.—Hunting is an illegal activity in Misiones; therefore, we used indirect evidence to assess its intensity. We collected information on the evidence of poaching activities during our fieldwork. We recorded encounters with armed poachers or dogs, photographic records of dogs or people, hunting campsites, artificial salt licks, poaching platforms, gunshots heard, hunting trails, spent shotgun cartridges, and camera-trap stations robbed or destroyed. A detailed list of evidence of poaching intensity in the study areas can be found in Paviolo et al. (2008) and Di Bitetti et al. (2008b).

Poaching pressure was variable among the areas and depended mostly on the effort dedicated to controlling it and on the accessibility to different areas by poachers (Paviolo et al. 2008). Yabotí Biosphere Reserve suffered very high poaching pressure, although the pressure in Esmeralda Provincial Park and Miot's property was lower than in the rest of the surveyed area (Di Bitetti et al. 2008a; Paviolo et al. 2008). The Urugua-í area suffered a medium to high poaching pressure (Paviolo et al. 2008). Iguazú National Park suffered the lowest poaching pressure in the central area where we conducted the 1st survey (2004) but an intermediate poaching pressure in the areas added in the 2006–2007 survey (Paviolo et al. 2008).

Camera-trapping surveys.—We used records obtained by camera traps in combination with closed capture–mark–recapture population models to estimate animal densities (Karanth 1995; Karanth and Nichols 2002). Individuals were identified in the photographs by distinct pelage markings (Karanth 1995; Silver et al. 2004; Trolle and Kery 2003). Recently, Kelly et al. (2008) demonstrated that it is possible to identify individual pumas using photographs, which allows the estimation of the density of this species using this methodology if applied with caution and following certain protocols to evaluate the degree of confidence in the results.

Between 2003 and 2007, we conducted 4 surveys to estimate the absolute density of jaguars, pumas, and ocelots in different areas of the Green Corridor. At each study site, we placed between 34 and 47 sampling stations (Table 1). Each sampling station consisted of a pair of camera traps facing each other and operating independently. The stations were located on infrequently used dirt roads or small trails opened in the forest and were distributed at regular intervals with the purpose of evenly covering the entire surveyed area. We used

Table 1.—Dates and sampling effort of the different camera-trap surveys of pumas (*Puma concolor*) conducted in the Green Corridor of Misiones Province, Argentina.

Survey	Dates[a]	No. stations	Full survey duration (days)	Full survey effort (trap-days)	Total survey effort (trap-days)[a]
Iguazú 2004	April–December 2004	39	96	1.839	2.942
Iguazú 2006–2007	April 2006–January 2007	47	96	2.059	2.287
Urugua-í	May 2003–February 2004	34	90	1.495	2.611
Yabotí	March–December 2005	42	96	1.871	2.676

[a] Pilot + full surveys.

camera-traps of different brands and models. The equipment consisted of 2 Camtrakker (Camtrakker, Watkinsville, Georgia), 50 Leaf Rivers Trail Scan Model C-1 (Vibra Shine, Taylorsville, Mississippi), 30 TrailMACs 35mm Standard Game (Trail Sense Engineering, LLC, Middletown, Delaware), and 20 Trapacamera (CIETEC, São Paulo, Brazil) scouting cameras. Prior to the full survey period, we conducted pilot surveys with the purpose of identifying the best sites for the locations of the stations (Table 1). The full surveys consisted of a period of 90–96 days (Table 1). Because of the longevity and length of territory tenure of pumas, we assumed that a survey of this duration fulfilled the assumptions of a closed population (Karanth and Nichols 2002; Kelly et al. 2008).

We identified pumas following the protocol proposed by Kelly et al. (2008). Three of the authors independently classified the photographs of individuals, noting the distinguishing characteristics of each animal. After independent classifications, the 3 authors compared results and discussed their reasons for each classification, correcting discrepancies in cases when 1 of the authors could find evidence that the classification was incorrect. When the evidence was not clear the authors maintained their independent classifications. After this, we estimated the density of pumas using the classification of the 3 authors.

We estimated puma abundance using the program CAPTURE (Rexstad and Burnham 1991), which provides population estimates using several models (Otis et al. 1978; White et al. 1982). We present the results of the model Mh using jackknife estimates that assume heterogeneity in the capture probability among individuals. This model is the most appropriate because of the varying accessibility to the stations among individuals, product of the social structure of the population, and the location of the stations within each individual's home range (Karanth and Nichols 2002). We divided the survey into capture occasions of 6 consecutive days with the purpose of obtaining a capture probability >0.1 (Otis et al. 1978; White et al. 1982). Cubs (<1 year old) were not included in this analysis because their capture probability is related to the capture probability of their mothers (Karanth and Nichols 2002). Consequently, our density estimates refer to the population of adults and subadults.

To estimate density it is necessary to calculate the area surveyed. Most authors suggest that the area surveyed must be estimated by adding a buffer width equal to one-half the average of the maximum distance between captures of the individuals captured more than once during the survey (mean maximum distance moved [MMDM]) to each camera or the polygon that includes all the cameras (Karanth 1995; Silver et al. 2004; Trolle and Kery 2003). However, Maffei and Noss (2007) suggest that if the surveyed area covers <4 mean home ranges of the studied species, MMDM may be underestimated and in turn the area surveyed may be underestimated. In these situations, the appropriate buffer should be between one-half MMDM and MMDM (Maffei and Noss 2007). Because we lacked estimates of the size of puma home ranges for our study areas, we estimated density using 2 different calculations of the surveyed area: 1 was obtained by applying to each sampling station a buffer of one-half MMDM, and the other by applying a full MMDM buffer. We deducted those areas that are not suitable habitats for pumas, such as cities, annual crops, and airports. The value of MMDM was estimated as the average of the maximum distance of recapture for individuals captured at >1 station (Karanth 1995; Karanth and Nichols 2002), according to each investigator's classification. The values of MMDM and the surveyed areas were estimated using the program ArcView (version 3.2; Environmental Systems Research Institute, Inc., Redlands, California).

Some researchers have suggested that the photographic rate of a species is correlated with its absolute abundance (Carbone et al. 2001), especially when controlling for some confounding factors (Di Bitetti et al. 2008a). In order to validate the patterns observed using the density estimates, we compared different indices of relative abundance among surveys and the study areas. We used the recording rate of pumas (number of photographs of pumas/1,000 trap-days), the mean number of individuals recorded per station, and the percentage of stations with puma presence as relative abundance indices. Because the indices varied widely between roads and trails (see ''Results''), and because the number of stations located on trails at Yabotí (only 1) was insufficient to make a bifactorial analysis including this variable, we compared the abundance indices using only the values obtained from the stations located on roads. In the Iguazú 2006–2007 and Yabotí surveys we compared the relative abundance indices of pumas between the best-protected and the least-protected subareas. In addition, we compared the indices between the Iguazú 2004 survey and the same area of the Iguazú 2006–2007 survey to determine whether differences between years existed. Because the relative abundance data were not normally distributed, we used nonparametric statistics for these comparisons.

Activity pattern analysis.—To describe the activity pattern of pumas, we used the time printed on the photographs obtained during the pilot and full surveys (Table 1). We considered as independent records only those that were >1 h apart at the same station. We compared the activity pattern of pumas between the stations located in the best- and least-protected areas within the Iguazú 2006–2007 survey. We did not perform this analysis for Yabotí, because the number of records in the least-protected area was very low ($n = 11$). Additionally, we performed the same analysis considering the stations of all the surveys together (the well-protected central area of Iguazú National Park versus the rest of the areas). Finally, we compared the activity pattern in the central area of Iguazú National Park between the 2004 and 2006–2007 surveys to test whether there were differences between years. For these analyses we used the Mardia–Watson–Wheeler test (Batschelet 1981). During all procedures we followed guidelines approved by the American Society of Mammalogists for the use of wild animals in research (Gannon et al. 2007).

Results

Puma abundance.—At Yabotí we obtained 45 photographs of pumas during the survey, of which 5 were discarded because of their poor quality. The 3 investigators independently classified these photos as 6 or 7 different individuals and the MMDM value varied between 12,486 m and 13,986 m. The area surveyed varied between 1,082 and 2,006 km^2 according to the different methods and values of MMDM applied. In turn, density estimates for this area were between 0.3 and 0.74 individuals/100 km^2, respectively.

During the full survey at Urugua-í, we obtained 16 photographs of pumas that corresponded to 3 or 4 individuals according to the identification by the 3 investigators. The MMDM was 6,854 m and was the same for all investigators. The area surveyed was between 228 and 454 km^2 and the density of pumas was between 0.66 and 2.19 individuals/100 km^2.

During the Iguazú 2004 survey, we obtained 73 photographs of pumas, of which 5 were discarded because of their poor quality. The different investigators classified the photos as either 10 or 11 individuals. The MMDM was 8,100 m and did not vary among the investigators. The area surveyed was between 450 and 774 km^2 and puma densities were between 1.55 and 2.89 individuals/100 km^2.

During the Iguazú 2006–2007 survey, we obtained 78 photographs of pumas, of which only 1 was eliminated because of poor quality. The investigators identify between 11 and 16 different individuals. The estimates of MMDM varied between 7,800 and 9,154 m. In turn, the area surveyed varied between 750 and 1,295 km^2 and the population density was from 1 to 2.4 individuals/100 km^2.

The recording rate and the mean number of individuals recorded per station were higher on roads than on small trails (Mann–Whitney 1-tailed U-test, recording rate: $U = 2{,}074$, $P < 0.0001$; mean number of individuals: $U = 2{,}127$, $P < 0.0002$). The recording rate and the mean number of individuals recorded at stations located on roads were statistically higher for Iguazú 2004 than for the Urugua-í and Yabotí surveys. For the Iguazú 2006–2007 survey, these indices also were significantly higher than for the Yabotí survey but were not statistically different from those from Urugua-í and Iguazú 2004 surveys. Finally, the indices were not statistically higher for Urugua-í than for Yabotí (Kruskal–Wallis and all-pair comparisons test, recording rate: $H = 23.4$, $P < 0.0001$; mean number of individuals: $H = 23.81$, $P < 0.0001$).

In the Iguazú 2006–2007 survey, the recording rate was higher in the best-protected area than in the least-protected one (Mann–Whitney 1-tailed U-test, $U = 42$, $P = 0.009$; Fig. 1a), as was the number of individuals per station (Mann–Whitney 1-tailed U-test, $U = 52$, $P = 0.033$; Fig. 1b) and the probability of a station to record pumas (Fisher exact 1-tailed test, $\chi^2 = 6.17$, $d.f. = 1$, $P = 0.017$; Fig. 1c). On the other hand, the abundance indices for the surveys of Iguazú in 2004 and for the same area of the Iguazú in 2006–2007 were not different (Mann–Whitney 1-tailed U-test, recording rate: $U = 81$, $P = 0.89$; mean number of individuals: $U = 69.5$, $P = 0.46$), nor was the probability of a station to photograph pumas (Fisher exact test, $\chi^2 = 2.1$, $d.f. = 1$, $P = 0.265$).

The comparison between areas with different protection levels in Yabotí showed that the recording rate and the number of individuals recorded by station had a tendency to be higher in the best-protected area, but not statistically so (Mann–Whitney 1-tailed U-test, recording rate: $U = 167.5$, $P = 0.06$; Fig. 1a; mean number of individuals: $U = 170$, $P = 0.07$; Fig. 1b). Nevertheless, the probability of a station to photograph a puma was statistically higher in the best-protected compared to the least-protected area (Fisher exact 1-tailed test, $\chi^2 = 5.31$, $d.f. = 1$, $P = 0.022$; Fig. 1c).

Activity patterns.—In all the areas studied, pumas showed some level of activity around the clock. Nevertheless, pumas were more active during the 1st hours of the day in the well-protected area, whereas in the least-protected areas they showed 2 main activity peaks, 1 in the early morning and the other in the 1st hours of the night, remaining active during the night (Figs. 2a and 2b). These results were obtained when we considered the sampling stations of all the surveys together (Mardia–Watson–Wheeler test, $\chi^2 = 9.33$, $d.f. = 2$, $P < 0.011$; Fig. 2a) and when we considered only the stations of the Iguazú 2006–2007 survey (Mardia–Watson–Wheeler test, $\chi^2 = 6.85$, $d.f. = 2$, $P < 0.05$; Fig. 2b). On the other hand, the activity patterns in the well-protected area of Iguazú were not different between the 2004 and 2006–2007 surveys (Mardia–Watson–Wheeler test, $\chi^2 = 0.96$, $d.f. = 2$, $P = 0.607$; Fig. 2b).

Discussion

The abundance and behavior of pumas varied among areas with different levels of protection within the Green Corridor. Puma abundance was higher in the better-protected areas than in areas with less protection, and this was observed using indices of relative abundance and density estimates from capture–recapture population models.

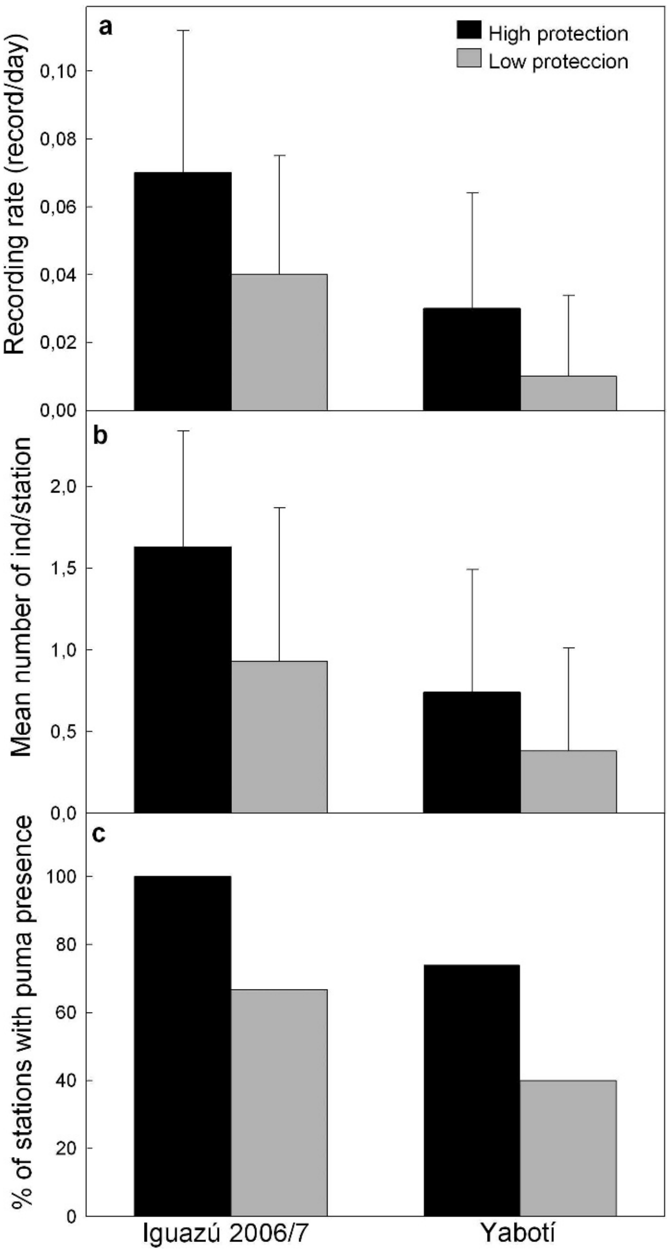

Fig. 1.—Indices of the relative abundance of pumas (*Puma concolor*) in areas with different levels of protection in Iguazú 2006–2007 and Yabotí surveys: a) recording rate (±*SD*), b) mean number of individuals (±*SD*), and c) percentage of stations with pumas present.

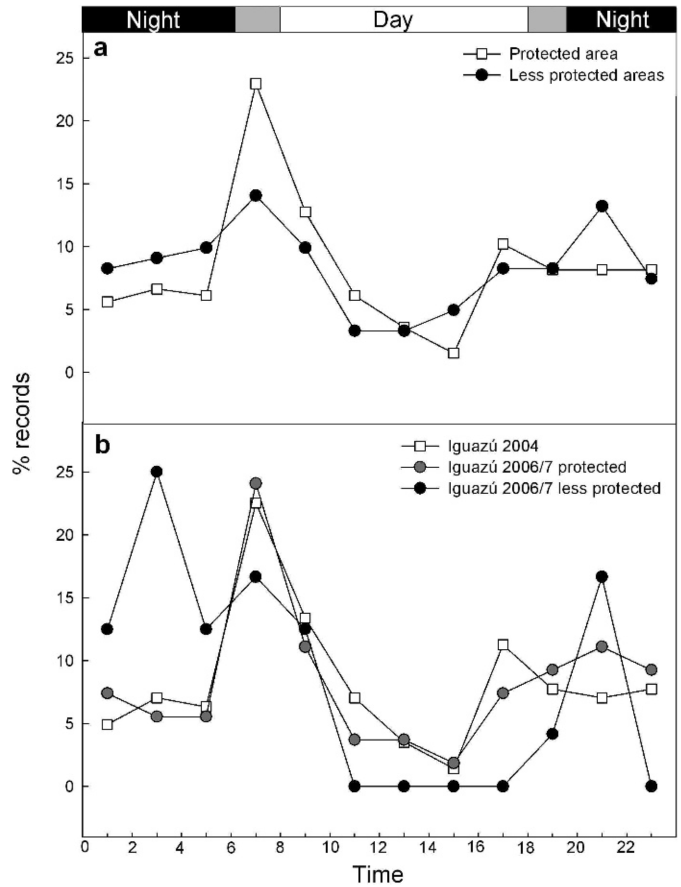

Fig. 2.—Activity patterns of pumas (*Puma concolor*) in areas with different levels of protection: a) including records from all study sites (n = 196 protected sites and n = 121 less-protected sites); and b) including records from the surveys Iguazú 2004 and Iguazú 2006–2007 in protected and less protected areas (n = 142, n = 54, and n = 24, respectively). The survey of Iguazú in 2004 included the same area as the survey of the protected area in Iguazú in 2006–2007.

This correlation between the abundance of pumas and the level of protection could result from several different factors. One of them is prey abundance, because in general the abundance of pumas depends mainly on the abundance of its prey (Logan and Sweanor 2001; Pierce et al. 2000). Three of the most important prey animals of pumas in this region are red brocket deer (*Mazama americana*), agoutis (*Dasyprocta azarae*), and collared peccaries (*Pecari tajacu*—Azevedo 2008; Crawshaw 1995). The relative abundance of these species was lower in less-protected areas as a consequence of poaching activity and habitat degradation due to the logging activities (Di Bitetti et al. 2008b; Paviolo et al., in press), which is consistent with the hypothesis that lower abundance of pumas in those areas could be caused by the lack of prey.

Human-induced mortality is another factor that may diminish puma populations (Hornocker 1970; Logan et al. 1986). In Florida, vehicle collisions were an important source of mortality (Maehr 1997). Nevertheless, most records of pumas killed on roads in the Green Corridor (at least 6 in the last 10 years) came from within the Iguazú area, which presents the highest densities of paved routes and pumas. On the other hand, the less-protected areas are crossed by few dirt roads and we do not have records of roadkills in those areas. Therefore, roadkills could not explain the differences in abundance among study areas.

Another cause of mortality is the sport and control hunting of pumas by humans. This is the main cause of puma mortality in areas where these kinds of hunting are allowed (Logan and Sweanor 2001; Sunquist and Sunquist 2002). In the Green Corridor pumas are occasionally killed because they prey on domestic animals, but puma attacks are usually attributed to jaguars (Conforti and Azevedo 2003). Unlike jaguars, pumas are not locally considered a trophy by poachers and are considered to be less dangerous (Conforti and Azevedo 2003). Therefore, pumas are not as systematically persecuted. However, lack of information on the number of pumas poached in our study areas prevents us from discarding this factor as a possible influence on puma abundance.

Another factor that could be limiting the population of pumas is the presence of competitor species. Interactions between feline species have been suggested as a possible cause for the decline of some cat species (Caro and Stoner 2003; Donadio and Buskirk 2006). In the Green Corridor, pumas live in sympatry with jaguars and are approximately one-third smaller. Some authors have suggested that jaguars can exclude pumas by competition (Crawshaw and Quigley 2002; Schaller and Crawshaw 1980). However, at present the abundance of jaguars is very low in the region (Paviolo et al. 2008), with jaguars being between 1.4 and 7 times less abundant than pumas in our study sites. In the Iguazú area, where the relative abundance of jaguar signs was higher than that of pumas some years ago (Crawshaw 1995; Crespo 1982), the situation has been reversed. This suggests that pumas are probably tolerating better some pressures that have decimated the jaguar population. On the other hand, jaguars, pumas, and ocelots present the same pattern of abundance across study sites, with lower densities in less-protected areas (Di Bitetti et al. 2006, 2008a; Paviolo et al. 2008), suggesting that the 3 predators are more affected by other factors than by competition among each other.

We believe that the differences in puma abundance among areas with different levels of protection in the Green Corridor are mainly caused by differences in prey availability. However, the absence of areas where poaching and logging were separate did not allow us to evaluate the relative direct and indirect effects of these 2 factors.

As suggested by Kelly et al. (2008), the cause of the low density of pumas found at Yabotí is likely related to high poaching pressure and intense logging activities. Puma density in this area is among the lowest reported in the literature (Anderson 1983; Sunquist and Sunquist 2002). On the other hand, densities in well-protected areas of the Green Corridor are similar to those found in the tropical forest of Belize and the places with high densities in North America (Hornocker 1970; Kelly et al. 2008; Logan and Sweanor 2001; Sunquist and Sunquist 2002), but lower than densities in the Bolivian Chaco (Kelly et al. 2008).

Activity patterns.—Pumas showed differences in their activity pattern in areas with different levels of protection. The same pattern was found when we analyzed data from all the surveys together and when we compared 2 areas with different levels of protection in the same year (Iguazú 2006–2007). Also, in the area for which we have data from >1 year, the activity pattern did not vary between surveys, which suggests that the observed patterns are not caused by interannual variation in ecological conditions.

Three hypotheses may explain these differences in the activity patterns of pumas. The 1st hypothesis is that pumas change their activity pattern to avoid periods when jaguars are more active. Some authors suggest that jaguars and pumas partition temporal and spatial activity (Emmons 1987) or that pumas actively avoid encounters with jaguars (Schaller and Crawshaw 1980). In Misiones, jaguars are predominantly nocturnal and more abundant at Iguazú than any other area in the Green Corridor (Paviolo et al. 2008). In Iguazú, the activity pattern of these 2 species is complementary, suggesting that time partitioning exists. On the other hand, jaguars live at very low densities at Urugua-í and Yabotí (Paviolo et al. 2008), so we would expect pumas could be more nocturnal in these areas because the probability of encounter with a jaguar is lower. Nevertheless, in the least-protected areas of the Iguazú 2006–2007 survey, jaguars were relatively abundant (Paviolo et al. 2008) and pumas also showed a more nocturnal pattern. The activity of pumas overlapped with that of jaguars, contradicting the hypothesis of temporal partitioning and suggesting that coexistence between jaguars and pumas may be altered by anthropogenic impacts, as proposed by Haines (2006).

Another hypothesis is that pumas are more nocturnal because they avoid periods of higher human activity. This has been observed in North America, where pumas were more nocturnal in areas with logging activity even years after these activities had ceased (Van Dyke et al. 1986). In other areas of the Atlantic Forest with cattle, pumas attacked domestic animals in hours of low human activity (Mazzolli et al. 2002). In our study, pumas were more nocturnal even in areas where logging activity had ceased more than 15 years previously. Nevertheless, in those areas where poachers were active during the day, pumas may have altered their activity pattern to avoid encounters with poachers and their dogs.

Finally, a 3rd hypothesis is that pumas change their activity patterns to improve their hunting success. Predators in general follow the activity period of their main prey (Curio 1976), a relationship reported for pumas in other areas (Beier et al. 1995; Maehr et al. 1990; Sunquist and Sunquist 2002). In our study sites, we found that red brocket deer were more nocturnal in less-protected areas (Di Bitetti et al. 2008b), presenting an activity pattern similar to that shown by pumas. Agoutis were active during the 1st hours of the day and in the afternoon and were very abundant at Iguazú area but scarce at Urugua-í and Yabotí. The change in activity pattern of red brocket deer and the scarcity of agoutis in the less-protected areas are probably contributing to the behavioral change in the activity pattern of pumas. However, this hypothesis does not exclude the previous ones, and the change in activity pattern in less-protected areas may bring several benefits for pumas.

Conservation of pumas in the Green Corridor.—The differences in density of pumas in the Green Corridor means that the 500 km^2 in the center of Iguazú National Park is supporting as many pumas as the entire Yabotí Biosphere Reserve of 2,600 km^2. In the Green Corridor, there is an extensive network of areas with some level of protection (nearly 6,000 km^2), but the areas also receive a high impact from poaching and logging and a great pressure from economic activities and urban areas. Under these conditions, we consider that the best strategy for conserving pumas in this region depends on strengthening the implementation of the existing protected areas through more effective protection against poaching activities and illegal logging, and consolidating corridors among those areas to allow the interarea exchange of individuals.

In the Green Corridor, pumas are present in a total area of 20,000 km^2 (De Angelo 2009). If we extrapolate our density values for areas with different levels of protection, we estimate a population of between 150 and 400 adult and subadult individuals. According to a general population viability model for pumas (Beier 1993), the population of pumas in the Green Corridor would not be threatened by extinction in the short term. Nevertheless, pumas, like other top predators, play a key role in the environment by regulating the populations of their prey and structuring the entire community (Logan and Sweanor 2001). If we consider that in areas with deficient protection other predators such as jaguars and ocelots also are at very low densities (Di Bitetti et al. 2006, 2008a; Paviolo et al. 2008), predation by top predators may be almost absent, with unpredictable consequences for the future of the Green Corridor.

Resumen

Conocer los factores que pueden afectar la abundancia y los patrones de actividad del puma (*Puma concolor*) en los bosques de Sudamérica es importante para la conservación de la especie. Utilizando cámaras-trampa realizamos 4 muestreos en 3 áreas con distinto nivel de protección contra la caza furtiva y explotación forestal en el mayor remanente continuo del Bosque Atlántico del Alto Paraná. Utilizamos modelos poblacionales de captura–marcado–recaptura para estimar la densidad de pumas en cada una de las áreas. El área central del Parque Nacional Iguazú, que tienen baja presión de caza furtiva y no ha sido explotado forestalmente por >60 años, tuvo la mayor densidad de pumas (entre 1,55 y 2,89 individuos/100 km^2). La Reserva de Biósfera Yabotí que sufre una alta presión de caza furtiva y fuerte explotación forestal tuvo la menor densidad de pumas (entre 0,3 y 0,74 individuos/100 km^2). Las áreas con niveles intermedios de caza furtiva y explotación forestal tuvieron densidades entre 0,66 y 2,19 individuos/100 km^2. Los pumas tuvieron el pico de actividad durante las primeras horas de la mañana en las áreas mejor protegidas mientras que en las áreas con menor protección mostraron mayor actividad crepuscular y nocturna. La menor abundancia de pumas en las áreas más degradadas podría estar relacionada con una menor abundancia de presas. Las diferencias en el patrón de actividad en áreas con distintos niveles de protección podría ser una respuesta directa a la presión de caza o a cambios en la abundancia y el patrón de actividad de sus presas principales. Los esfuerzos de conservación se deberían concentrar en disminuir los niveles de caza furtiva y explotación forestal lo que beneficiará al puma y otras especies amenazadas del Bosque Atlántico.

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