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Differential Responses to Hunting in Two Sympatric Species of Brocket Deer (*Mazama americana* and *M. nana*)

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ABSTRACT

Hunting by humans may affect the abundance and activity patterns of game species. We examined the effect of hunting on the abundance and activity patterns of sympatric red brocket deer *Mazama americana* and dwarf brocket deer *M. nana*. We conducted four camera-trap surveys (158 sampling stations, 10,244 trap-days, total area sampled 1200 km^2) in three areas within the Atlantic Forest of Misiones, Argentina, that differ in protection and hunting pressure. We used logistic regression and tests of independence to evaluate if protection, hunting pressure, and other independent variables affect the probability of recording each species and their recording rate. We used the Mardia–Watson–Wheeler test to examine if the daily activity pattern differs between species and changes with hunting pressure. Red brocket deer were more frequently recorded (397 records, 58% of stations) than dwarf brocket deer (100 records, 37% of stations). The probability of recording red brockets was higher in areas with better protection and increased with the distance to the main accesses used by poachers. The probability of recording dwarf brockets was higher in areas with low protection. Red brockets were more nocturnal than dwarf brockets, a difference that may reduce interspecific competition. However, red brockets were more diurnal in the best-protected areas, suggesting that they can adjust their activity to local hunting pressure. Hunting has opposite effects on the abundance of these deer and may facilitate their coexistence. Hunting should be carefully controlled or managed to ensure the conservation of these little known species.

Key words: abundance; Atlantic Forest; camera traps; conservation; daily activity pattern; protected area management; species coexistence.

HUNTING BY HUMANS IN TROPICAL FORESTS can have a strong effect on the abundance and behavior of game animals (Caro 1999, Peres 2000, Milner-Gulland *et al.* 2003). In tropical rain forests, hunting pressure is concentrated on large mammals, especially ungulates and primates (Bodmer 1995, Peres 2000, Fa *et al.* 2002). As a consequence, the structure of the mammal community changes, with a reduction in the relative abundance and total biomass of the larger species and sometimes even an increase in the absolute abundance of the smaller, less-hunted species (Lopes & Ferrari 2000, Peres 2000, Peres & Dolman 2000, Jerozolimski & Peres 2003, Wright 2003, Peres & Palacios 2007). Intense and prolonged hunting can even cause local extinctions of isolated large mammal populations (Chiarello 1999; Cullen *et al.* 2000, 2001; Lopes & Ferrari 2000; Peres 2001) and many tropical forests are now suffering from 'empty-forest syndrome' (Redford 1992). Cascade effects through the whole ecosystem, such as severe changes in the structure and composition of the forest, can also follow reductions in numbers of large ungulates (Wright & Duber 2001, Corlett 2007), although the long-term consequences of this phenomenon are still not clear (Wright *et al.* 2000, Wright 2003, Stoner *et al.* 2007). Thus, understanding the consequences of hunting on large ungulates has implications for forest conservation and management.

Brocket deer (*Mazama* spp.) are among the least studied species of deer (Weber & Gonzales 2003), and constitute some of the most sought after species by subsistence hunters in the Neotropics (Alvard *et al.* 1997, Escamilla *et al.* 2000, Peres 2000, Hurtado-Gonzales & Bodmer 2004, Gavin 2007). However, little is known on their habitat use, social behavior, conservation status and their response to human hunting pressure, and habitat fragmentation and degradation. In the Upper Paraná Atlantic Forest of Brazil, Argentina, and Paraguay, three species of brocket deer are found (Weber & Gonzales 2003). The red brocket deer *Mazama americana* Erxleben, and the dwarf brocket deer *M. nana* Hensel, are usually found in areas of dense forest, while the gray brocket deer *M. gouazoubira* Fischer (von Waldheim) is usually found in transitional zones with the more opened Chaco and Cerrado ecoregions (Crespo 1982).

Studies comparing habitat preferences of gray brockets and red brockets indicate that the latter prefer thicker and moister forests than the former (Redford & Eisenberg 1992, Juliá & Richard 2001, Rivero *et al.* 2005). Some evidence suggests that, in the Atlantic Forest, red brockets prefer more mature forests (Giraudo & Abramson 2000). Studies conducted in the Amazon (Bodmer 1995, Alvard *et al.* 1997, Hurtado-Gonzales & Bodmer 2004) and the Cerrado (Fragoso *et al.* 2000) indicate that red brockets are quite resilient to subsistence hunting, but studies conducted in the Atlantic Forest show the opposite (Hill *et al.* 1997; Cullen *et al.* 2000, 2001). The behavior and ecology of the dwarf brocket deer are still mostly unknown and most information available is anecdotal (Chebez & Varela 2001, Weber & Gonzales 2003). Some authors have suggested that the species prefers forests with dense bamboo thickets or that is more abundant in the rocky highlands of the southern portion of the Atlantic Forest (Duarte 1997, Emmons & Feer 1999, Chebez & Varela 2001). Anecdotal evidence also suggests that the dwarf brocket deer is less sensitive to hunting than the

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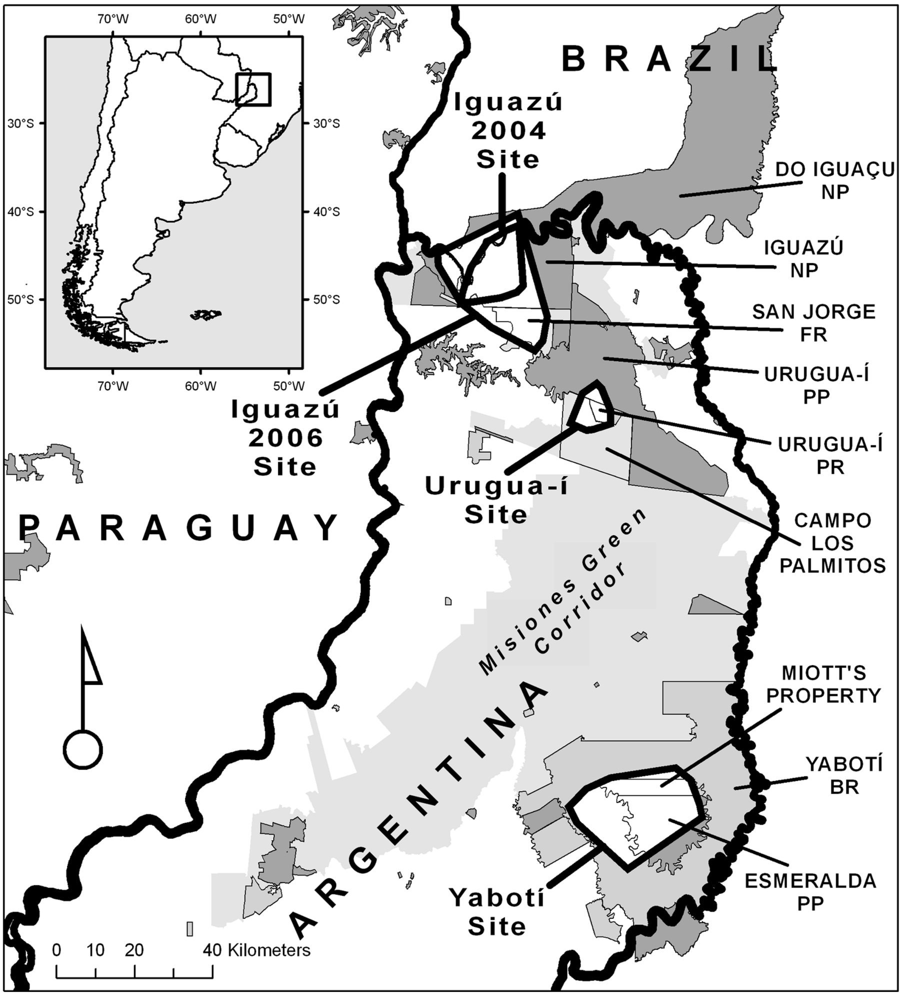

FIGURE 1. Study area and study sites.

red brocket deer (Giraudo & Abramson 2000). Here we use data from broad-scale and intensive camera-trapping surveys within the Atlantic Forest of Argentina to explore the responses of red brocket deer and dwarf brocket deer to the protection status of the area, hunting pressure, and other landscape features that may affect their abundance and daily activity patterns.

METHODS

STUDY SITES.—We conducted this study in the Green Corridor of Misiones province, NE Argentina, located in the most interior portion of the Atlantic Forests of South America, usually referred to as the Upper Paraná Atlantic Forest ecoregion (Di Bitetti *et al.* 2003, Galindo Leal & de Gusmão Câmara 2003; Fig. 1). The general climate, topography, vegetation, productivity patterns, history of exploitation, and protection status of the area have been described elsewhere (Crespo 1982, Placci 2000, Di Bitetti & Janson 2001, Galindo Leal & de Gusmão Câmara 2003, Campanello 2004, Di Bitetti *et al.* 2006b). Despite high human impact in these forests due to extractive activities (logging and hunting), the complete original mammal assemblage is still present in the Green Corridor, including large predators such as jaguars *Panthera onca* and pumas *Puma concolor*. One of the consequences of selective logging is the invasion of the forest gaps and understory by native bamboo species that preclude the immediate regeneration of the forest.

We conducted four camera-trap surveys at three different large forest areas within the Green Corridor. We carried out the first survey at Urugua-í (25°58′ S, 54°06′ W; Fig. 1), in an area that comprised a portion of a large timber company property (Campo Los Palmitos, *ca* 260 km^2), a portion of the Urugua-í Provincial Park (840 km^2), and most of the Urugua-í Private Reserve (32.4 km^2). About half of the area surveyed lies within the protected areas and half within Campo Los Palmitos (see Di Bitetti *et al.* 2006b for details on this study site). The Urugua-í Provincial Park and the Urugua-í Private Reserve have few park rangers and poaching of wild animals occurs in the study area. Most of the hunters come from rural communities that stretch along the East boundary of Urugua-í Provincial Park and concentrate their hunting along the Urugua-í River. Campo Los Palmitos, on the contrary, is regularly

TABLE 1. *Sampling effort at the three study sites.*

Variable	Iguazú 2004	Iguazú 2006	Urugua-í	Yabotí	Total or whole mean
Number of sampling stations	39	41*	34	44	158
Mean distance (± SD) among nearest stations (km)	2.1 ± 0.4	2.6 ± 0.6	1.3 ± 0.5	2.4 ± 0.8	2.1 ± 0.8
Area sampled (minimum convex polygon; km^2)	205	570	81.3	549	1200
Total sampling effort (days)	2942	2015	2611	2676	10,244
Mean sampling effort (days) per station (± SD)	75.4 ± 37.2	49.2 ± 16.1	76.8 ± 51.5	60.8 ± 22.9	64.8 ± 35.1

*Six other stations that were active only at night were not considered in this study.

patrolled by company personnel and we found less evidence of poaching here than within the protected areas. We conducted the survey at Urugua-í between 18 May 2003 and 25 February 2004.

Our second study site was the Iguazú National Park (25°40′ S, 54°20′ W, 670 km^2; Fig. 1) where we conducted two surveys, between 21 April and 7 December 2004, and 24 April 2006 and January 15 2007. The native forest has not been logged in this strictly protected area since its creation in 1934. A well-trained and equipped team of park rangers makes illegal poaching very rare within the core area of the park. The first survey at Iguazú (during 2004) was conducted in the best protected portions of the park. The second survey (2006) comprised a larger area and included two stations in the Iguaçu National Park of Brazil, four stations in the Iguazú Reserve of Argentina and 11 stations in the adjacent San Jorge Forest Reserve belonging to a timber company (where the forest has been selectively logged until 20 yr ago). These 17 stations were located in areas with relatively high presence of poachers.

Our third survey was conducted at Yabotí Biosphere Reserve (YBR, 26°55′ S, 54°00′ W), a 2742 km^2 sustainable use protected area in the SE portion of the Green Corridor. We conducted the survey between 18 March and 10 December 2005. The core area of the YBR is the Esmeralda Provincial Park, a recently created strictly protected area of 316 km^2 (Fig. 1). Most of YBR comprises private properties where, by law, the native forest can be selectively exploited for timber but cannot be converted to other land uses. Poaching is common, especially within the private properties and logging is intense in most of the private properties (even Esmeralda Provincial Park was intensively logged until its creation in 1997). A few dirt roads within YBR constitute the main access routes for hunters that come from the surroundings of the reserve. Our study area comprised the N sector of Esmeralda Provincial Park and several private properties. All of the stations at Yabotí (except one placed on a trail) were located along park or logging roads, most of them not open to the public. Table 1 summarizes our sampling effort during the surveys.

Sampling protocol and camera trapping.—We used camera traps (for details on the equipment used see Di Bitetti *et al.* 2006b) to estimate the relative abundance of brocket deer. Camera trapping has been used to describe mammal communities (*e.g.*, Trolle & Kéry 2005), or to get absolute density estimates of species with natural marks (*e.g.*, tigers *Panthera tigris*, Karanth & Nichols 1998). It has also been used to monitor brocket deer populations (Rivero *et al.* 2005). Our survey protocol was developed to estimate the absolute abundance of large felids (Di Bitetti *et al.* 2006b, Kelly *et al.* in press, Paviolo *et al.* in press), but the brocket deer data gathered are appropriate for the type of analyses conducted here.

Each sampling station consisted of two camera-traps operating independently and facing each other on both sides of existing dirt roads or trails. The roads were all similar in their width, frequency of use, and other physical characteristics. The distance to nearest stations (> 1 km) ensured that presence–absence records were statistically independent, since the probability of recording the same individual at more than one sampling station is extremely low given known information on home range size of brocket deer species (ranges are usually < 100 ha, see Duarte 1997, Maffei & Taber 2003, Vogliotti 2003, Rivero *et al.* 2005). We tested this assumption by checking whether the few individuals ($N = 7$) easily identifiable from natural marks and recorded more than once appeared at more than one station, none of which did.

We built a GIS of each study site using ArcView (version 3.2). We obtained the co-ordinates of each station with a GPS (Garmin® model e-trex Venture). We rated the structural characteristics of the vegetation (canopy cover and density of bamboo in the understory) at each station using a three-category ad-hoc index; for canopy: (1) no canopy layer or scattered trees; (2) open canopy; and (3) continuous canopy layer; for bamboo: (1) bamboo absent or scattered and clean understory; (2) bamboo present but not very dense; and (3) dense bamboo. Categories (2) and (3) were merged for the statistical analyses. We followed Ligier *et al.* (1990) to classify soil types into two categories according to their richness, using soil maps provided by Martín Pinazo (Instituto Nacional de Tecnología Agropecuaria, Montecarlo).

Measures of hunting pressure.—Hunting wildlife is illegal in Misiones but is socially accepted and widespread in the region (Giraudo & Abramson 2000). Most hunting in the study areas is practiced with guns either by settlers coming from the small towns and farms surrounding the protected areas (even from Brazil) or by workers of the logging companies (in YBR). In some analyses, we used the linear distance to the main access routes used by hunters in each study site (main unpaved roads at the three sites and the Urugua-í River at the Urugua-í site) as a proxy for hunting pressure

TABLE 2. *Evidence of protection and hunting pressure at the three study sites.*

Measure of protection and hunting pressure	Iguazú 2004	Iguazú 2006	Urugua-í	Yabotí
Law enforcement capacity				
Park rangers per 100 km^2.	3.73	2.60	0.80	0.22
Vehicles per 100 km^2.	0.60	0.33	0.27	0.095
Use of fire arms by rangers	Yes	Yes	No	No
Hunting evidence				
Number of independent signs of the presence of hunters observed during the surveys[a]	3	10[b]	36	> 20

[a]Signs include encounters with hunters or their dogs, photographic records of dogs or people, hunting camp sites, artificial salt lick stations or waiting devices, gunshot heard, hunter trails, shotgun shells or other devices used for hunting and camera traps robbed or destroyed. For a detailed list see Paviolo *et al.* in press.

[b]All these events occurred at stations located in the area of relatively low protection (Iguaçu National Park of Brazil, Reserve Iguazú and San Jorge Forest Reserve), none occurred in the core area of the Iguazú National Park of Argentina.

(see Hill *et al.* 1997, Caro 1999, Laurance *et al.* 2006, for a similar approach).

We used several measures of the level of protection and hunting pressure in the surveyed areas. First, three assessments of the protection status of protected areas in Misiones ranked them according to several quantifiable variables (Chalukian 1999, Cinto & Bertolini 2003, Giraudo *et al.* 2003). *Second*, we quantified the per-area number of park rangers and vehicles assigned to the protected areas when the surveys took placed as an indirect measure of law enforcement capacity (see Wright *et al.* 2000 for a similar approach). Third, we quantified all signs of hunting obtained during the surveys, including encounters with hunters or their dogs, pictures of people or dogs recorded in the camera traps, gunshot shells, gunshots heard, hunting structures found, etc. (Paviolo *et al.* in press). Finally, informal interviews with park rangers, wildlife biologists, and area managers provided additional information on the level of poaching in the surveyed areas. These four lines of evidence clearly indicate that the Iguazú National Park of Argentina is better protected and implemented than the other study sites and consequently has less-hunting pressure (Paviolo *et al.* in press; Table 2). Thus, we used two categories of protection, high (core area of Iguazú National Park) versus low (other surveyed areas), to characterize the study areas.

There is also some variation in protection and hunting pressure within surveyed areas. At Urugua-í, more poaching evidence was observed in the subarea of Urugua-í Provincial Park and the Urugua-í Private Reserve, which was not frequently patrolled by rangers, than within Campo Los Palmitos, where the company personnel regularly patrols the area. In Yabotí, poaching was less evident at the relatively inaccessible Esmeralda Provincial Park and at an adjacent property whose owner (Mr. Miott) does not allow hunting, than at other private properties that were being actively logged during this study. During the last survey at Iguazú, 17 stations were located in areas outside the core area of Iguazú National Park (see above) that are subjected to moderate hunting pressure (Table 2). Park rangers and wildlife biologists that work in these areas concur that these relative differences in protection and hunting pressure within the surveyed areas really exist. These contrasts in protection provided three independent within-survey comparisons to assess the effect of hunting pressure (comparatively high vs. low) on the relative abundance of the two brocket deer species.

IDENTIFICATION OF BROCKET DEER SPECIES.—To distinguish deer species we used features of the external morphology of the photographed individuals. Red brocket deer are particularly large and heavy at this location (30–50 kg; Vogliotti 2003, Weber & Gonzales 2003) while dwarf brockets are much lighter (10–13 kg; Weber & Gonzales 2003), shorter, and more slender. Dwarf brockets are generally uniformly red–brown. Red brockets show a brown–red trunk that contrasts with the grayish neck and the dark-gray, almost black, legs (Varela *et al.* in press). Red brockets have a distinguishable white coloration in the under tail and genital area, which is not as conspicuous or is absent in the dwarf brocket.

Four of the authors and a colleague (D. Varela) independently assigned the pictures to each species. We only included in the analysis those records that were unambiguously classified by the five evaluators. Assigning the unidentified *Mazama* sp. records ($N = 37$, 6.9% of records) to either red or dwarf brockets did not change the main results.

DATA ANALYSIS AND STATISTICAL PROCEDURES.—To avoid pseudoreplication, > 1 h had to pass for two consecutive photographs to be considered independent records. Due to the large fraction of stations with no records we were not able to normalize the frequency distribution of the number of records per station. Therefore, for most analyses, we used as the dependent variable, whether the species was recorded or not (1 or 0) at a sampling station. We refer to this dependent variable as the probability of recording a species or its recording probability, representing the proportion of stations where the species was recorded. With presence–absence data, we used logistic regression or independent tests to test for the effect of the independent variables, using sampling effort as a covariate in these tests. We also used nonparametric statistical tests (Kruskal-Wallis test) with recording rate (measured as the number of records per 100 d) as the dependent variable.

Other things being equal, the recording probability of the species should be positively correlated with their respective abundance. However, stations that were active for a longer period of time may have had a higher probability of records and differences in the local environmental conditions could also have caused a higher recording rate at some stations than others. For example, ocelots were recorded at higher rates by stations located along unpaved roads than by those along trails (Di Bitetti *et al.* 2006b). Some factors that may have affected the frequency of records (sampling

TABLE 3. *Frequency of records, recording probability and recording rate of red brocket deer and dwarf brocket deer at the four surveyed areas.*

	Iguazú 2004 ($N = 39$)	Iguazú 2006 ($N = 41$)	Urugua-í ($N = 34$)	Yabotí ($N = 44$)	Total or whole mean ($N = 158$)
Red brocket					
Number of stations with presence	36 (92%)	22 (54%)	14 (41%)	19 (43%)	91 (58%)
Total frequency	221	108	28	40	397
Mean frequency per station (± SD)	5.7 ± 5.9	2.6 ± 3.5	0.8 ± 1.3	0.9 ± 2.0	2.5 ± 4.1
Mean recording rate (records/ 100 days)	7.7 ± 7.0	6.3 ± 8.5	1.1 ± 1.8	1.5 ± 3.3	4.2 ± 6.5
Dwarf brocket					
Number of stations with presence (percentage)	11 (28%)	14 (34%)	16 (47%)	18 (41%)	59 (37%)
Total frequency	14	21	38	27	100
Mean frequency per station	0.4 ± 0.7	0.5 ± 0.9	1.1 ± 1.9	0.6 ± 0.8	0.6 ± 1.1
Mean recording rate (records/100 d ± SD)	0.5 ± 0.9	1.0 ± 1.8	1.3 ± 1.8	1.1 ± 1.5	1.0 ± 1.6

effort, location of a station on a trail vs. a road, year of survey) were statistically controlled for (see below independent variables). However, the frequency of records could have been affected by behavioral differences between the species, which cannot be accounted for in this study. For this reason, a higher probability of records for a given species does not necessarily imply greater abundance. Behavioral differences among years may have accounted for some variation and thus, year of survey was also included as an independent variable. Similarly, when variation in the key variables was present within sites and when the degrees of freedom allowed for them, we conducted within-site comparisons. Within-year comparisons were always consistent with the main results observed with the larger data set.

Ten independent variables were tested for effects on the probability of recording each species: (1) year of survey (= surveyed area); (2) protection status; (3) linear distance to the closest main route used by hunters; (4) distance to the closest main river; (5) forest cover; (6) bamboo density; (7) presence of other *Mazama* species as recorded by the station; (8) location of station (road or trail); (9) soil type; and (10) sample effort (in days) as a covariate.

The date and time was printed on the photographs, thus, each record was assigned to hourly intervals and used to describe the daily activity patterns of both deer species. We used the Mardia–Watson–Wheeler test (Batschelet 1981) to test two hypotheses: (1) the two species have different daily activity patterns; and (2) the daily activity patterns are influenced by the protection level of the site. All statistical tests were two-tailed. We set the alpha level to commit a type I alpha error at 0.05. For the noncircular statistical analysis we used program JMP (version 3.2).

RESULTS

FREQUENCY OF RECORDS, RECORDING PROBABILITY, AND RECORDING RATE.—The red brocket deer was, in general, more frequently recorded than the dwarf brocket, with 397 records at 91 stations (58% of stations) versus 100 records at 59 stations (37% of the stations; Table 3). We also obtained two records of the gray brocket deer, one in Campo Los Palmitos and the other in San Jorge Forest Reserve, both in areas close to pine plantations. The probability of recording red brockets was higher at stations located in Iguazú, particularly during the 2004 survey, than at those located in the other two surveyed areas ($\chi^2 = 27.0$, df = 3, $P < 0.0001$; Fig 2A). Recording rate was higher in Iguazú during both surveys (2004 and 2006) than in the other two surveyed areas ($\chi^2 = 41.2$, df = 3, $P < 0.0001$; Fig. 2B). The probability of recording dwarf brockets did not differ among surveyed areas ($\chi^2 = 3.2$, df = 3, $P = 0.364$; Fig. 2A) and recording rates were also similar among areas ($\chi^2 = 4.6$, df = 3, $P = 0.204$; Fig. 2B).

During the surveys in Urugua-í and Yabotí and during the 2006 survey in Iguazú, some stations were located in areas with different protection regimes, providing three independent contrasts of the effect of the relative protection status of the area on the probability of recording species. Red brockets showed a tendency to be more frequently recorded at stations located in the better-protected subareas, with one of the comparisons being statistically significant (Urugua-í: $\chi^2 = 3.4$, df = 1, $P = 0.0657$; Yabotí: $\chi^2 = 4.9$, df = 1, $P = 0.0262$; Iguazú 2006: $\chi^2 = 0.006$, df = 1, $P = 0.938$). Dwarf brockets showed the opposite trend, being more frequently recorded at stations in the less-protected subareas and also with one of the contrasts being significant (Urugua-í: $\chi^2 = 2.56$, df = 1, $P = 0.110$; Yabotí: $\chi^2 = 3.01$, df = 1, $P = 0.0827$; Iguazú 2006: $\chi^2 = 7.9$, df = 1, $P = 0.0050$; Fig. 3).

In an ANCOVA-like multiple logistic regression, the probability of recording red brockets increased with increasing distance to main access routes used by poachers, was higher during the 2004 survey than during other surveys, decreased with increasing bamboo density, was higher on roads than on trails, and increased with sampling effort (effect of distance to main entrances of poachers: Wald $\chi^2 = 16.3$, df = 1, $P = 0.0001$; effect of survey (year): Wald $\chi^2 = 21.5$, df = 3, $P = 0.0001$; bamboo density: two categories; low vs. medium + high, Wald $\chi^2 = 6.4$, df = 1, $P = 0.0111$; road vs. trail: Wald $\chi^2 = 5.9$, df = 1, $P = 0.0152$; sampling effort: Wald $\chi^2 = 4.5$, df = 1, $P = 0.0334$). Other independent variables had no significant effect on the recording probability either alone

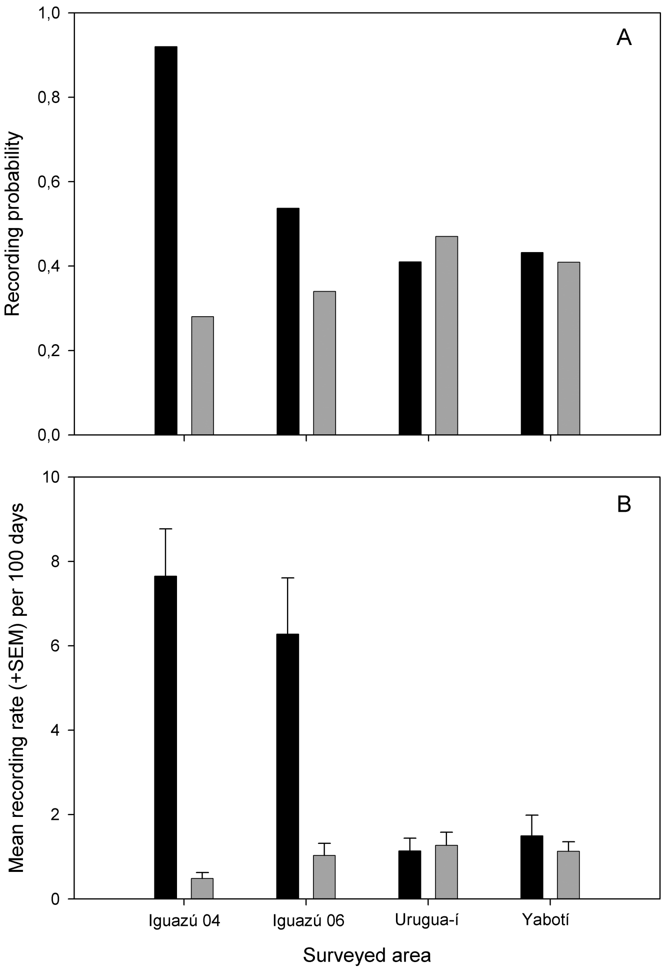

FIGURE 2. Recording probability, measured as the proportion of sampling stations where the species was recorded (A), and mean recording rate, measured as the number of records per 100 d (B), of red brocket deer (*Mazama americana*, black bars) and dwarf brocket deer (*M. nana*, gray bars) in the four surveyed areas. Number of stations in each area were: Iguazú 2004 = 39, Iguazú 2006 = 41, Urugua-í = 34, Yabotí = 44. The Iguazú surveyed area during 2006 includes stations from the Brazilian Iguaçu National Park ($N = 2$), the reserve area of Iguazú ($N = 4$), and the San Jorge Forest Reserve ($N = 11$), which were under relatively high hunting pressure.

or with other variables, with the exception of protection level, the effect of which disappeared when entered along with surveyed area. In within-survey analyses, the effect of distance to main access roads used by poachers on the probability of recording red brockets was significant in three of the four surveys (Urugua-í, Yabotí and Iguazú 2006), being the predictor variable with the largest statistical effect and with P values < 0.01 in all three cases.

The probability of recording dwarf brockets was lower in the best-protected sites (Wald $\chi^2 = 18.9$, df $= 1$, $P < 0.00001$), and increased with increasing soil quality (Wald $\chi^2 = 10.1$, df $= 1$, $P = 0.0015$), sampling effort (Wald $\chi^2 = 8.25$, df $= 1$, $P = 0.0041$), and increasing distance to a river (Wald $\chi^2 = 4.17$, df $= 1$, $P < 0.041$). Other independent variables had no effect on the probability of recording dwarf brockets.

ACTIVITY PATTERNS.—Red brockets were recorded more frequently during the night, with a bimodal pattern of activity, showing two nocturnal activity peaks at 1800–2200 h and 0100–0500 h. Dwarf brockets also showed a bimodal pattern, with a tendency to concentrate their activity during the morning (0600–1100 h) and the evening and early night (1800–2000 h). The hourly activity patterns of records of red brockets and dwarf brockets differed (Mardia–Watson–Wheeler test, $\chi^2 = 9.93$, df $= 2$, $P < 0.01$), with dwarf brockets being more diurnal than red brockets. However, the daily activity pattern of red brockets was affected by the level of protection of the site, being more diurnal at stations located in the more protected site (core area of Iguazú National Park) than at stations in sites with low protection ($\chi^2 = 32.6$, df $= 2$, $P < 0.001$; Fig. 4A). This same pattern was observed when comparing the activity of this species in the best-protected site surveyed during 2004 with the less-protected Urugua-í and Yabotí sites ($\chi^2 = 26.8$, df $= 2$, $P < 0.001$) and when comparing activity in the core area of Iguazú National Park versus the less-protected subareas simultaneously surveyed in 2006 ($\chi^2 = 6.55$, df $= 2$, $P < 0.05$). These similar but independent results, preclude the possibility that the observed pattern (Fig. 4A) results from among-year behavioral variation of the species. Dwarf brockets, in contrast, showed no difference in their daily activity pattern between better protected and less protected sites ($\chi^2 = 0.672$, df $= 2$, $P > 0.50$; Fig. 4B).

DISCUSSION

RELATIVE ABUNDANCE, HUNTING PRESSURE, AND OTHER LANDSCAPE FEATURES.—We have documented a contrasting pattern in the probability of recording two closely related species of brocket deer in relation to different levels of relative site protection and hunting pressure. The probability of recording red brockets and its recording rate was higher in the surveyed areas with better protection status and increased with increasing distance from the camera-trap station to the closest access point, probably due to decreased presence of poachers, an effect also noted in other studies assessing the effect of poaching on wildlife (*e.g.*, Caro 1999). The species showed a preference for forests with a low density of bamboo in the understory, a condition associated with more mature forests. Red brockets also tended to be recorded more frequently by stations along unpaved roads than by those along trails, probably due to easier access or greater mobility provided by the former, or because of vegetation changes resulting from a higher incidence of sunlight along roads.

As previously suggested by Giraudo and Abramson (2000), dwarf brockets were not affected by the protection status of the area, and their recording rate was higher in areas with relatively high hunting pressure and low protection. Contrary to previous suggestions (Duarte 1997, Emmons & Feer 1999, Chebez & Varela 2001), dwarf brockets were less frequently recorded at stations located on poorer soils, usually associated with rocky areas and steeper slopes

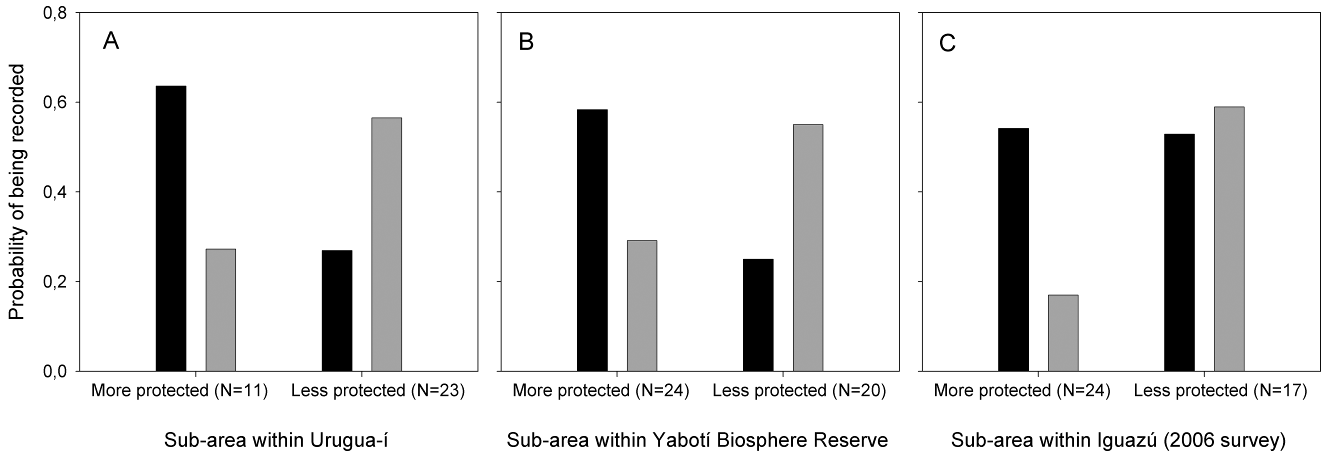

FIGURE 3. The probability of recording red brocket deer (black bars) and dwarf brocket deer (gray bars) in within-survey comparisons of areas with relatively high and relatively low protection. The probability of recording brocket deer represents the proportion of sampling stations where the species was recorded. Surveyed areas are: (A) Urugua-í Provincial Park, Urugua-í Private Reserve and Campo Los Palmitos, (B) Yabotí Biosphere Reserve, and (C) Iguazú National Park of Argentina, a small portion of Iguaçu National Park of Brazil and the San Jorge Forest Reserve (surveyed in 2006).

(Ligier *et al.* 1990), and showed no preference for forests with a dense bamboo understory. This species also showed a slightly higher recording probability at stations located far from rivers.

Since this was an observational study, it remains possible that some of the differences reported among surveyed areas are the result of pre-existing differences in the relative abundance of the species or the effect of variables that were not under our control. For example, the strong effect of survey year on the recording probability of red brockets (the higher probability of records in 2004 vs. 2006 in Iguazú) may be the result of among year variation in the abundance of resources that affect the mobility of the animals, an *ad hoc* and difficult to test explanation for a variable that we could not control for. Some of the differences in the relative abundance of the two brocket deer species may result from differences in the productivity of the areas or habitat preferences, as has been shown in other studies. For example, at sites across a large regional scale in Amazonia, mammal abundances are related not only to hunting pressure but also to habitat type (Peres 2000). At a landscape level, the relative abundance of some ungulate species in Southern Mexico was related to differences in habitat types and the interaction of the latter with hunting pressure (Reyna-Hurtado & Tanner 2005). In our study, some variables related to differences in the history of habitat use, habitat type or microhabitat type (forest cover, bamboo density, soil type, road vs. trails, distance to river), affected the probability of recording red brocket deer (preference for roads vs. trails, bamboo density) and dwarf brocket deer (soil quality, distance to river). However, none of these variables showed opposing effects in the two species as protection status did, further suggesting that protection and hunting pressure are the main drivers of the contrasting pattern of relative abundance in these deer species. The statistical effect of protection and hunting pressure was present after controlling for the potential effect of other variables, which indicates that a preference for certain habitat types does not constitute an alternative explanation for the effect of protection and poaching.

Activity patterns.—The two species differed in their daily activity patterns, red brockets being more nocturnal than dwarf brockets, which may facilitate their coexistence. Rivero *et al.* (2005) found differences in the daily activity of two sympatric brocket deer: red brockets are more nocturnal than gray brockets in Bolivia. In Bolivia, red brockets concentrate most of their activity between sunset and sunrise (Rivero *et al.* 2005), a pattern similar to the one we observed. Chebez and Varela (2001) suggested that the dwarf brocket is mostly nocturnal or crepuscular, but our study indicates that the species is mostly diurnal and crepuscular.

The red brocket seems able to accommodate its activity to become more nocturnal in areas with higher hunting pressure. This change in the daily activity pattern as a response to hunting pressure or human traffic has been documented in other deer species (Kilgo *et al.* 1998) and other mammals (Griffiths & van Schaik 1993, McClennen *et al.* 2001), which avoid time periods of intense human traffic or activity, usually becoming more nocturnal.

Differential effect of hunting on brocket deer species.—Brocket deer are among the preferred prey of subsistence hunters and poachers throughout their range in the Neotropics (Townsend *et al.* 2002, Hurtado-Gonzales & Bodmer 2004, Gavin 2007). Previous studies on the effect of hunting on brocket deer abundance indicate that they are relatively tolerant to hunting when compared with other mammals with lower reproductive rates (Alvard *et al.* 1997, Bodmer *et al.* 1997). Several studies have compared the abundance of brocket deer in areas with subsistence hunting and areas with little or no hunting and found no difference in abundance between sites (Bodmer 1995, Alvard *et al.* 1997, Fragoso *et al.* 2000, Hurtado-Gonzales & Bodmer 2004, Naranjo & Bodmer 2007, Reyna-Hurtado & Tanner 2007). Other studies have detected a negative effect of hunting on brocket deer abundance (Hill *et al.* 1997; Carrillo *et al.* 2000; Cullen *et al.* 2000, 2001; Lopes & Ferrari 2000; Dirzo *et al.* 2007; Nuñez-Iturri & Howe

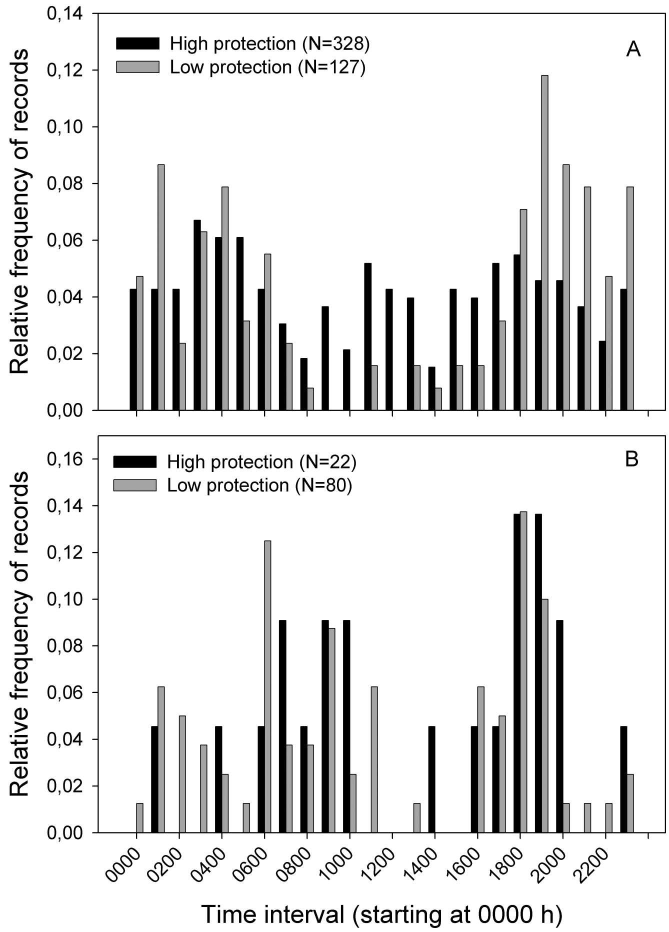

FIGURE 4. Daily patterns of records for red brocket deer (A) and dwarf brocket deer (B) discriminated according to the protection level of the area (black bars = best-protected site, gray bars = lower protection).

2007). The main difference between these two sets of studies is that most of the latter were conducted in fragmented areas surrounded by high human population densities. The populations of game animals in the hunting grounds of subsistence hunters are usually subsidized by the populations located in the nonhunted tracts of forests connected to them, acting as source–sink systems (Novaro *et al.* 2000, Peres 2001). Studies conducted in the Atlantic Forest have emphasized the dramatic effect of hunting in forest fragments (Chiarello 1999; Cullen *et al.* 2000, 2001), resulting from the absence of source populations that could replenish the hunting areas (see Novaro *et al.* 2000, Peres 2001). Therefore, it may be concluded that high hunting pressure reduces the abundance of brocket deer in fragmented areas. However, our study indicates that the response to hunting is species specific and while one brocket deer species (*M. americana*) is negatively affected, the other (*M. nana*) is unaffected or may even benefit from some level of hunting.

We envisage three possible causes for the contrasting response of red and dwarf brocket deer to hunting. First, the difference may reflect hunters' preference for larger prey (Jerozolimski & Peres 2003, Fa *et al.* 2005, Peres & Palacios 2007). Red brockets are heavier than dwarf brockets and, given a choice, hunters would prefer the larger species. However, due to the relatively low prey density characteristic of the area, hunters are not expected to be very selective (see Wright 2003, Fa *et al.* 2005). Second, the difference in relative abundance may be the result of different behavioral responses to hunting, particularly to hunting with dogs (M. Duarte, pers. comm.), which may make one species more vulnerable than the other. Finally, competition between species may be strong and red brockets might out-compete the smaller dwarf brockets when no top-down regulation forces are acting on them. In areas where hunting pressure reduces red brocket populations, dwarf brockets, being more tolerant to hunting, may benefit from this competitive release. Thus, dwarf brocket populations may be positively affected by the reduction of red brocket ones as a result of a compensatory change in abundance (see Peres & Dolman 2000, Wright 2003).

DWARF BROCKET DEER, AN ENDANGERED SPECIES?—The dwarf brocket deer is one of the least known species of deer (Weber & Gonzales 2003), being endemic to the southern portion of the Atlantic Forest, one of the most endangered ecoregions on Earth (Di Bitetti *et al.* 2003, Galindo Leal & de Gusmão Câmara 2003). Dwarf brockets are listed as vulnerable in Argentina (Diaz & Ojeda 2000) and as endangered by the Ministry of Environment of Brazil (Vogliotti 2003). Surprisingly, our results suggest that this endangered species is not negatively affected by current levels of hunting in Misiones, which affect several other species, including red brockets (this study), other large ungulates and large felids (Di Bitetti *et al.* 2006a, Paviolo *et al.* 2006, Kelly *et al.* in press, Paviolo *et al.* in press).

The fauna and flora of the Neotropics have coexisted with humans for the last 10,000 yr. Some species of mammals may have become extinct due to subsistence hunting by native people. However, for the most part, hunters have coexisted with present faunal assemblages, and species less tolerant to hunting had subsisted as a result of the patchy effect of hunting, with some areas acting as sources and refuges for fauna while others act as sinks (Novaro *et al.* 2000, 2005; Naranjo & Bodmer 2007). Some species may have benefited from this patchy effect of hunting as a spatiotemporal competitive release from larger ungulates, dwarf brockets being one of them.

The Green Corridor of Misiones province and nearby areas of Brazil contain large fragments of Atlantic Forest, and the potential to preserve almost intact mammal communities. However, no area within these fragments is currently out of reach of hunters, and populations of most large mammals are consequently being reduced (dwarf brockets are probably an exception), as a result of the lack of large and well-enforced protected areas, which could serve as population sources and support metapopulation source–sink dynamics. Active protection and law enforcement constitute effective ways to avoid empty forests (Redford 1992) in the Green Corridor and reduce the chances of local extinction of large predators (jaguars and pumas) that require vast areas of natural habitat with a good prey base (Paviolo *et al.* 2006, in press). For the near future, it is crucial to improve the implementation of the protected areas of the Atlantic

Forest, where hunting is still common. In the long term, effective implementation of the protected areas (sources) coupled with the implementation of hunting quotas for some game species in private forests and sustainable use protected areas (sinks), may provide recreational opportunities for hunters and facilitate the coexistence of brocket deer species (see Stoner *et al.* 2007 for other schemes).

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