Original Investigation

Daily activity patterns and habitat use of the lowland tapir (*Tapirus terrestris*) in the Atlantic Forest

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ABSTRACT

We studied the daily activity pattern and habitat use of the lowland tapir *Tapirus terrestris* and their relationship with environmental and anthropic variables. We used photographic records of tapirs obtained during five camera-trap surveys conducted in three areas of the Atlantic Forest of Argentina that differ in their protection against poaching. The daily activity pattern was analyzed with circular statistics and linear regression. The effect of protection against poaching and environmental variables on habitat use of tapirs was analyzed using occupancy modeling. Tapirs were nocturnal all year round, with 89% of the records between 1800 h and 0700 h. The proportion of nocturnal records and the recording rate did not change with mean daily temperature. The daily activity pattern of tapirs was not affected by the sex of the individuals, the lunar cycle or the protection level of the area. The probability of detecting tapirs increased with the distance to the nearest access points for poachers and decreased with the abundance of bamboo in the understory and increasing trail width. The probability of use of an area by tapirs increased with increasing protection against poaching and distance to the nearest access points for poachers. These results suggest that poaching is one of the factors with significant effect on habitat use by tapirs but not on their daily activity patterns.

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Introduction

The lowland tapir (*Tapirus terrestris*) is considered a keystone species as a result of its role as a seed disperser and ecosystem engineer (Bodmer, 1991; Fragoso, 1997; Chalukian et al., 2009). Globally it is categorized as vulnerable (VU) with a decreasing population trend (IUCN, 2010), while in Argentina it is considered endangered (EN; Chalukian et al., 2012).

Habitat loss, fragmentation and poaching (illegal hunting) have been identified as the main factors responsible for population declines of lowland tapirs throughout their range (Medici et al., 2007; Taber et al., 2008). In the Upper Paraná Atlantic Forest (UPAF) poaching of wild animals is culturally accepted and is widely practiced (Giraudo and Abramson, 2000; Cullen et al., 2001; Paviolo et al., 2009a). In the province of Misiones, Argentina, the hunting of tapirs is illegal, which makes it difficult to assess its magnitude (Di Bitetti et al., 2008).

Most animals do not use their habitats randomly but select areas that provide the resources and conditions necessary to satisfy their daily requirements, while avoiding areas of high predation risk and human threats (Manly et al., 1993). All tapir species show discernible habitat selection patterns although differences in habitat preferences have been observed among studies (Salas, 1996; Lizcano and Cavelier, 2000a; Foerster and Vaughan, 2002; Medici, 2010). Tapirs generally prefer riverine forests and avoid open areas, such as grasslands and crops (Salas, 1996; Medici, 2010), but, depending on the study site, may show preferences for either secondary forests, primary forests or both (Lizcano and Cavelier, 2000a; Foerster and Vaughan, 2002; Medici, 2010). Water bodies

are important as resting places, defecation sites, to avoid ectoparasites, to facilitate movement among foraging sites and for cooling off during the hottest hours of the day (Padilla and Dowler, 1994; Foerster and Vaughan, 2002). In the UPAF some environments have been shown to be avoided by the lowland tapir, such as areas with high density of bamboo (*Chusquea ramosissima*), probably due to the difficulty of movement (Gallardo et al., 2008). Furthermore, anthropic factors can also potentially influence habitat selection by tapirs (Licona et al., 2011).

Lowland tapirs have been described as nocturnal or crepuscular (Padilla and Dowler, 1994; Noss et al., 2003; Tobler, 2008; Medici, 2010; Wallace et al., 2012); however, several factors have been shown to affect the activity patterns of all tapir species. For lowland tapirs, increased diurnal activity was observed in humid months (Foerster and Vaughan, 2002; Medici, 2010). Mountain tapirs (*Tapirus pinchaque*) showed higher nocturnal activity during full moon in primary forest with dense canopy (Lizcano and Cavelier, 2000b), while lowland tapirs showed the opposite pattern (Medici, 2010). No response to the lunar phase has been reported around natural salt licks for the latter species (Coelho et al., 2008; Link et al., 2012). Finally, differences in the activity patterns between sexes have been reported in lowland tapirs, with females being active during a wider hourly range, probably as a result of their higher metabolic requirements, especially during late pregnancy and peak lactation (Medici, 2010). Considering the extensive gestation period (13–14 months; Barongi, 1993), and prolonged lactation phase (8–9 months; Padilla and Dowler, 1994) of tapirs, it is possible that females have higher year-round energetic requirements than males.

The use of remote cameras is a noninvasive technique that allows the study of nocturnal, rare or elusive animals, or those that inhabit areas of low visibility (Karanth and Nichols, 1998; O'Connell et al., 2011). Furthermore, remote cameras are an efficient tool to study the distribution, abundance, activity patterns and habitat use of large- and medium-sized mammals (Di Bitetti et al., 2006, 2008; Tobler, 2008; O'Connell et al., 2011). The elusive habits of lowland tapirs, combined with the relatively dense understory of most habitats within the UPAF make camera-trapping an appropriate methodology to study the species.

We used records of lowland tapir obtained during five intensive camera-trap surveys conducted in the Atlantic Forest of Argentina to analyze habitat use and daily activity patterns of the species. We employed circular statistics (Batschelet, 1981) and occupancy modeling (MacKenzie et al., 2006) to test hypotheses on how environmental (natural) and anthropic factors affect daily activity and the pattern of habitat use and detection of lowland tapirs in areas with differing levels of protection against poaching. We hypothesized that increasing distance from access points and higher levels of protection against poaching would positively affect habitat use by tapirs due to higher abundance and/or reduced avoidance, while tapirs would avoid areas with increasing amounts of bamboo. In addition we expected that decreasing distance from bodies of water would positively increase habitat use by tapirs. This study is aimed at elucidating the principal drivers of habitat use while incorporating incomplete detection through occupancy modeling.

Materials and methods

Study area

We conducted this study in three areas of the Green Corridor of Misiones, Argentina (Fig. 1). The Green Corridor constitutes one of the largest remnants of UPAF that still contains the complete regional native mammal assemblage (Giraudo and Abramson, 2000), and is considered one of the few areas in the
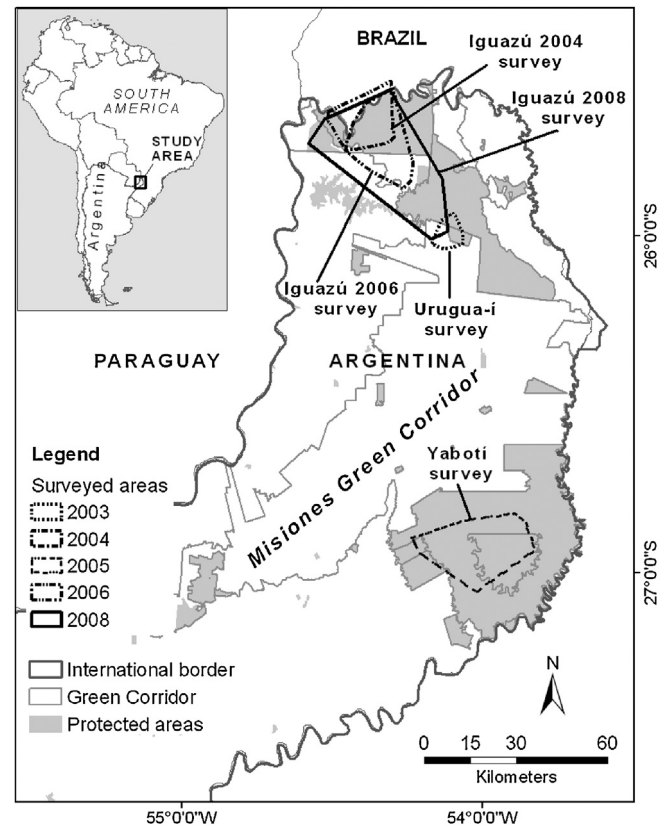

Fig. 1. Map of the Green Corridor of Misiones, Argentina including the main protected areas and the study sites.

ecoregion with high potential for long-term persistence of tapirs (Paviolo et al., 2008; Taber et al., 2008). The area has a wet subtropical climate with seasonality in temperature and day length, and with peak availability of resources for herbivores and frugivores during the spring-summer months (October–March, Agostini et al., 2010). Mean monthly temperatures vary between 17 and 22 °C and annual rainfall is about 2000 mm with no distinctive rainy season (Agostini et al., 2010).

One of the surveys was conducted during 2003 in the upper basin of the Urugua-í river (25°58′ S, 54°06′ W; Fig. 1), comprising a portion of the privately owned Urugua-í Wildlife Reserve (UWR), a portion of the Urugua-í Provincial Park (UPP), and a section of a private property (Campo Los Palmitos) belonging to a timber company. In both UWR and UPP timber was selectively extracted until the late 1980s, although native forest remained in relatively good condition (Di Bitetti et al., 2006).

Another study site was the Yabotí Biosphere Reserve (YBR), located in the southeastern portion of the Green Corridor (26°55′ S, 54°00′ W; Fig. 1), where we conducted a camera-trap survey in 2005. This multiple use reserve contains strictly protected areas, private lands with selective logging, and areas inhabited by indigenous people of the Mbya-Guaraní ethnic group who practice small scale agriculture and subsistence hunting. At this site camera-trap stations were located along old logging roads within the Esmeralda Provincial Park (EPP) and some private properties (Di Bitetti et al., 2008; Paviolo et al., 2008).

The third study site was Iguazú National Park (INP, 25°40′ S, 54°30′ W; Fig. 1), located in northern Misiones, bordering UPP in the south and Iguaçu National Park of Brazil in the north. INP was selectively logged until 1934 when the park was created. Three surveys were conducted in this area (in 2004, 2006 and 2008). The first survey (2004) was conducted in the central part of INP, while

the second survey (2006) also included the Iguazú National Reserve and the privately owned San Jorge Forest Reserve. The 2008 survey in INP included the previous surveyed areas but extended southward to the northern part of the Urugua-í survey site (Di Bitetti et al., 2010).

Protection against poaching

Poaching of wildlife is a relatively common recreational, although illegal, activity performed by both rural and urban people in Misiones. The most common hunting technique in the area is with firearms, either at stands (fruiting trees or artificial salt licks) or with the aid of dogs. Most poaching occurs during daylight hours and the first hours of the night. We used indirect evidence to estimate the level of poaching. First, we recorded signs of poaching activities (poaching campsites, spent cartridges, artificial saltlicks, etc.) during our field activities. Second, we conducted informal interviews with park rangers, biologists, and inhabitants of rural areas near our study sites about the modality and intensity of poaching in the area and the principal access points used by poachers to enter the study areas (roads, forest borders, rivers, etc.). Finally, we quantified the resources (personnel, infrastructure, etc.) invested in anti-poaching activities in each study area as an index of protection. Poaching pressure, as ascertained by the evidence found and interview information, was negatively associated with the resources invested in protection and with the distance to the nearest access points for poachers (DNAPP). Thus, we categorized the study areas into three relative levels of protection: "good" (Iguazú) "intermediate" (Urugua-i) and "poor" (Yabotí) (see details in Di Bitetti et al., 2008; Paviolo et al., 2008, 2009b). We also used the DNAPP for each survey station as another proxy of poaching intensity (Hill et al., 1997; Peres and Lake, 2003). We defined as "access points" all routes (vehicular roads, borders of forest and rivers) known to be used by poachers based on interview results and our field assessments.

Camera-trap surveys

Camera-trap surveys were designed to estimate jaguar densities using capture-recapture models (Paviolo et al., 2008). Each camera-trap station consisted of two camera-traps facing each other on both sides of rarely used unpaved roads (2–6 m wide) and small trails opened with a machete (1–2 m wide). These small trails were specifically opened for this study and do not constitute access roads used by poachers. Each survey had a preliminary or trial period and a systematic sampling period. During the preliminary period the location of the stations, the number of cameras per station and the duration the station was active did not follow standard protocols established for a capture-recapture survey (see Paviolo et al., 2008).

The systematic period was divided into two phases to increase the area surveyed with the camera-traps available. During the first phase camera-traps were located in half of the stations and were relocated to the remaining half during the second stage of the survey (Paviolo et al., 2008). The systematic period lasted 90–96 days (45–48 days each phase) during which we deployed 34–47 camera-trap stations (Table A.1). The mean distance between nearest camera-trap stations and its standard deviation during the systematic periods was 1960 ± 767 m. Cameras were active 24 h, except in stations with relatively frequent vehicular traffic during the day; these cameras were active only at night when traffic was almost nil (16 percent of the 2006 stations, and 15 percent of the 2008 stations).

For each camera-trap station we characterized the relative abundance of bamboo in the understory as being high, medium or low (following Di Bitetti et al., 2006). The location of each camera-trap station was geo-referenced and incorporated into a geographic information system (GIS) using ArcView 3.2 (ESRI, Redlands, U.S.A.). Using the GIS we measured the linear distance from each camera station to the closest body of water (rivers, streams and lakes) and the DNAPP.

Daily activity patterns

We used the photographic records of tapirs from both the preliminary and systematic periods only from those stations that were active 24 h to document the daily activity pattern of tapirs using the time printed on the photographs. To avoid pseudo-replication >1 h had to pass for two successive photographs of tapirs to be considered independent records, resulting in 703 independent detections (48 in Urugua-í, 324 in Iguazú 2004, 105 in YBR, 99 in Iguazú 2006 and 127 in Iguazú 2008). We classified photographs as diurnal or nocturnal based on day-to-day information on sunrise and sunset for this location (obtained at The Weather Channel web page; http://espanol.weather.com/climate/sunRiseSunSet-Iguazu-ARMS3370?month=2, accessed 15.01.12). To assess changes in the daily activity pattern in relation to the annual photoperiod we compared the observed activity pattern during the months with nights of shorter duration (10.15–11.22 h, November–February), the period where the availability of leaves and fruit that comprise tapir diet is highest (Agostini et al., 2010), with that observed during the months with longer nights (12.25–13.28 h, May–August) where the availability of food resources is lowest.

We analyzed the variation in the proportion of nocturnal records as a function of mean daily temperature to evaluate whether tapirs are more nocturnal in days with higher temperature. We also analyzed the variation of the mean rate of tapir records (number of records/number of days) in relation with the mean daily temperature to evaluate whether tapirs are less active during days of higher temperatures. We only used the values of temperatures (one degree intervals) that had at least fifteen days representing each interval (between 15 °C and 27 °C, $N = 493$ records). Temperature records were obtained from the National Meteorological Service station located at the Iguazú International Airport and, consequently, for this analysis we only used camera trapping data from the INP surveys due to its proximity to the meteorological station. To evaluate whether there was a relationship between the mean rate of tapir records and mean daily temperature, and also between the proportion of nocturnal records and mean daily temperature, we conducted linear regression analyses with the program InfoStat 2010 (Di Rienzo et al., 2010).

To analyze the daily activity pattern in relation to the lunar phase we used a moon calendar (Serrano, 2011) and considered the new moon day to be the first day of each lunar cycle and the full moon day as the fifteenth day. We divided the lunar cycle in two periods of ten or eleven days; the first, centered on the new moon, comprised days 1–5 and 25–29 or 25–30 and the second period, centered on the full moon, comprised days 10–20. Transitional days (6–9 and 21–24) were omitted from the analysis (following Di Bitetti et al., 2006).

To evaluate the effect of photoperiod, sex, lunar phase and protection against poaching (with two levels; good *vs.* poor protection) on the daily activity pattern we used the Mardia–Watson–Wheeler test, which assess whether two circular distributions differ (Batschelet, 1981).

Habitat use

We used occupancy modeling to estimate habitat use since it provides an unbiased estimate of the probability that a species occupies an area (ψ) when detection probability (p) is <1 while allowing modeling of the effects of covariates on p or ψ (MacKenzie et al., 2002, 2006). Since the distance between camera-trap

stations did not ensure that detections were spatially independent (we detected the same individual at two different stations) ψ should be interpreted as the probability of habitat use by tapirs rather than occupancy (MacKenzie et al., 2006). We defined habitat as an *n*-dimensional space which is a function of environmental and anthropic variables.

To compile a sufficiently large number of detections to produce robust estimates of ψ and p we pooled the survey data from Urugua-í 2003, Iguazú 2004 and Yabotí 2005 ($N = 117$ stations; total effort = 5205 camera-trap days) in a single analysis. A fundamental assumption of occupancy analysis is that populations are closed (MacKenzie et al., 2006), though this assumption could be relaxed if changes in a population occur at random (Kendall, 1999). In comparing data collected from three sites over approximately two years we assumed that the tapir population was stable during our sampling period with no violation of the closure assumption. We believe this is valid since longevity and generation time is long in tapirs (Barongi, 1993) and there were no unusual climatic events during the survey period that could have potentially altered tapir populations or behavior sufficiently to bias our results. Given the importance of poaching on other tapir populations (Cullen et al., 2001; Peres, 2000, 2001), comparing the three sites in one analysis (instead of performing one analysis per survey) allowed us to explicitly model the effect of the level of legal protection on tapir occurrence. Data from Iguazú 2006 and 2008 surveys were not included in the analysis to avoid pseudo-replicates, since several stations were located at the same sites during the three Iguazú surveys (Di Bitetti et al., 2010).

To reduce variance in parameter estimates it is necessary to maximize detection probabilities (MacKenzie and Royle, 2005). Thus, we combined every four consecutive trap days into trapping occasions, resulting in 10 sampling occasions. Since a fundamental assumption of the single-season occupancy model is that heterogeneity is accounted for through the inclusion of the effects of covariates (MacKenzie et al., 2002, 2006), we incorporated the effects of several covariates on ψ and p which we deemed important based upon our experience and the literature.

We included as covariates affecting ψ the distance to the nearest access point for poachers (DNAPP, continuous variable), the relative abundance of bamboo (BA, ordinal variable: low, medium, high), the distance to the nearest water body (DW, continuous variable), and the level of protection against poaching (PROTECT, ordinal variable: good, intermediate, poor). For p we included as covariates DNAPP, BA, PROTECT, and the width of the trail or road where the trap station was located (TW, categorical variable: narrow *vs.* wide). Since the survey was designed to maximize records of large felids, which make ample use of roads and wide trails (Harmsen et al., 2010; Tobler and Powell, 2013), a large proportion (50% on average) of camera-traps were placed on wide (2–6 m) roads. We included TW as a variable in the analyses because trail width may affect the detectability of a species (Weckel et al., 2006). Variables were *z*-transformed so their means were equal to 0 (Donovan and Hines, 2007).

We expected that DNAPP and PROTECT would positively affect detection because tapirs would be less elusive as these covariates increased in value: for example; in sites with high level of poaching animals may avoid camera-traps due to perceived signs of human activity, such as odors (Séquin et al., 2003; Séquin Larrucea et al., 2006). In areas with greater BA we expected that detection of tapirs would be reduced due to the density of vegetation, while we also expected that trail width (TW) would negatively affect detection due to avoidance of wider roads that are more used by humans.

Since the covariates could plausibly affect either ψ or p separately or in combination, we modeled all combinations of covariates using a single-species single-season occupancy model in program PRESENCE 3.1 (Hines, 2006), resulting in a candidate set of 128

models. Models were ranked using Akaike's Information Criterion (AIC) model weights. We employed model averaging, selecting those models with weights within 10 percent of the highest ranked model (Burnham and Anderson, 2002).

The significance of the effect of covariates on ψ and p was determined using the model averaged parameter estimates. Where the 95 percent confidence intervals of the parameter estimates did not include zero the effect of the covariate was considered to be significative (MacKenzie et al., 2006). One-tailed tests were used, establishing an overall alpha level of 0.05 for committing a type one error.

Results

Daily activity patterns

Tapirs were mostly nocturnal, with 89 percent of records occurring between sunset and sunrise (Fig. 2). Activity began around 1800 h and finished around 0700 h, with reduced nocturnal records between 2200 h and 0200 h (Fig. 2). The proportion of nocturnal records did not increase significantly with mean daily temperature ($R^2 = 0.07$, $P = 0.37$), and the mean rate of tapir records did not decrease significantly with mean daily temperature ($R^2 = 0.03$, $P = 0.61$). The daily activity pattern was not affected significantly by the annual photoperiod (Mardia–Watson–Wheleer test, $\chi^2 = 3.02$, df = 2, $P = 0.22$), the lunar cycle ($\chi^2 = 1.15$, df = 2, $P = 0.56$), the sex of the individuals ($\chi^2 = 1.16$, df = 2, $P = 0.56$), or the degree of protection of the area ($\chi^2 = 2.13$, df = 2, $P = 0.34$).

Patterns of habitat use

Nineteen models were selected for model averaging and all covariates used in the analysis were included in the best model set (Tables 1 and A.1). The ψ and p constant model ($\psi(*)$, $p(*)$), with an AIC weight of 0 and a $\triangle$AIC of 69.52 was not included within these 19 top models. Model fit was good with a value of c-hat for the global model of 1. Based upon the model averaged parameter estimates, both DNAPP and PROTECT had a significant positive effect on ψ, since zero was not included within the 95% confidence interval of the parameter estimates (Table 2, Fig. 3). Based upon the composite model from the model averaging, ψ was estimated to be 0.83 ($\pm$0.025) for the good protection level (Iguazú), 0.50 ($\pm$0.025) for the intermediate protection level (Urugua-í) and 0.40 ($\pm$0.062) for the poor protection level (YBR). Although DW and BA demonstrated the expected directional response, the effect of those covariates on ψ was not significant (Table 2, Fig. 3).

There was a significant negative effect of TW and BA, and a significant positive effect of DNAPP on p (Table 2).

Discussion

Daily activity patterns

In accordance with previous research, we found that lowland tapir activity is mostly nocturnal, where peak hours of movement are after sundown and before sunrise (Noss et al., 2003; Tobler, 2008; Medici, 2010; Wallace et al., 2012). This pattern has also been described for other tapir species (Lizcano and Cavelier, 2000b; Foerster and Vaughan, 2002; Holden et al., 2003). Tapir evidently remain active throughout the night, but reduce their displacements around midnight because it is the period when they concentrate their foraging activity (Tobler, 2008; Medici, 2010). Differential use of habitats between day and night has been documented for tapirs, with individuals resting in dense vegetation by day, and visiting foraging sites from sunset until sunrise (Padilla and Dowler, 1994;
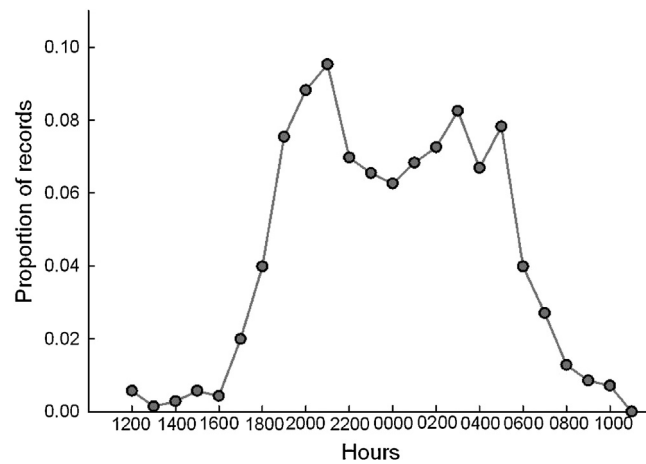
Fig. 2. Daily activity pattern of the lowland tapir in the Atlantic Forest of Argentina ($N = 703$). The proportion of records was calculated using the number of records per hour divided by the number of totals records. The data belong to the surveys conducted between 2003 and 2008.

Table 1
PRESENCE output with the top ranking models with ≤ 2 $\triangle$AIC value. Models were ranked using Akaike's Information Criterion (AIC). $\triangle$AIC and AIC weight are calculated from AIC.

Model[a]	$\triangle$AIC	AIC weight	Model likelihood	# Parameters
ψ(DNAPP, BA, PROTECT), p(DNAPP, TW, BA)	0	0.1475	1.000	8
ψ(DNAPP, DW, BA, PROTECT), p(DNAPP, TW, BA)	0.61	0.1087	0.7371	9
ψ(DNAPP, PROTECT), p(DNAPP, TW, BA)	0.98	0.0903	0.6126	7
ψ(DNAPP, DW, PROTECT), p(DNAPP, TW, BA)	0.98	0.0903	0.6126	8
ψ(DNAPP, BA, PROTECT), p(DNAPP, TW, BA, PROTECT)	1.96	0.0553	0.3753	9
ψ(BA, PROTECT), p(DNAPP, TW, BA)	2.04	0.0532	0.3606	7
ψ(DNAPP, BA, PROTECT), p(DNAPP, TW)	2.07	0.0524	0.3552	7

[a] ψ: probability of habitat use; p: detection probability; BA: relative abundance of bamboo; DNAPP: distance to the nearest access points for poachers; DW: distance to closest water body; PROTECT: relative level of protection against poaching; TW: trail or road width.

Tobler, 2008; Medici, 2010). It is possible that the activity pattern we observed reflects this same behavior.

Unlike most large mammals (>100 kg), which need to be active both diurnally and nocturnally to meet energetic needs (van Schaik and Griffiths, 1996), tapirs at our sites are strictly nocturnal. Tapirs may be nocturnal because their low surface to volume ratio makes body heat dispersal difficult (Randall et al., 1998; Foerster and Vaughan, 2002; Medici, 2010). If thermoregulation were the driving factor in determining daily movements, as for other mammal species (Morão and Medri, 2007), we would expect a seasonal shift in activity patterns in our study area given the variation in mean temperature between winter and summer. However, we did not find a relationship between either the proportion of nocturnal detections or the recording rate and the mean daily temperature.

Contrary to what has been reported by Lizcano and Cavelier (2000b) and Medici (2010), but in concordance with Coelho et al. (2008) and Link et al. (2012), lunar phase did not affect tapir activity in our study area. The differences among study sites may be due to higher levels of predation risk during the full moon in some regions (*e.g.* Medici, 2010). At our study sites predation risk is minimal since jaguar densities (probably the only important predator of tapirs besides humans in most of the Neotropics) are relatively low (Paviolo et al., 2008) and, consequently, the potential effect of predation on activity patterns is reduced. We also did not observe an effect of the degree of protection from poaching. Tapirs may fail to modify behavior regardless of poaching pressure because of a low plasticity to alter their circadian activity or because this conduct is a pre-adaptation (exaptation, sensu Futuyma, 1997), with the observed daily activity pattern being the best strategy to

Table 2
Model averaged beta values, standard errors, and 95% confidence intervals for the variables that affect the probability of habitat use (ψ) and the probability of detection (p) of lowland tapirs in the Atlantic Forest of Misiones, Argentina.

	Variable[a]	Parameter estimates	Standard error	95% confidence interval[b]	
				Lower limit	Upper limit
ψ	DNAPP	0.437	0.250	0.027	0.848
	DW	−0.116	0.123	−0.317	0.085
	BA	−0.238	0.177	−0.529	0.053
	PROTECT	0.881	0.387	0.246	1.515
p	DNAPP	0.430	0.089	0.284	0.576
	TW	−0.783	0.203	−1.117	−0.450
	BA	−0.154	0.082	−0.289	−0.020
	PROTECT	0.004	0.027	−0.040	0.048

[a] BA: relative abundance of bamboo; DNAPP: distance to the nearest access points for poachers; DW: distance to closest water body; PROTECT: relative level of protection against poaching; TW: trail or road width.
[b] Since the hypotheses are one-tailed (directional), the error is concentrated at one extremity.
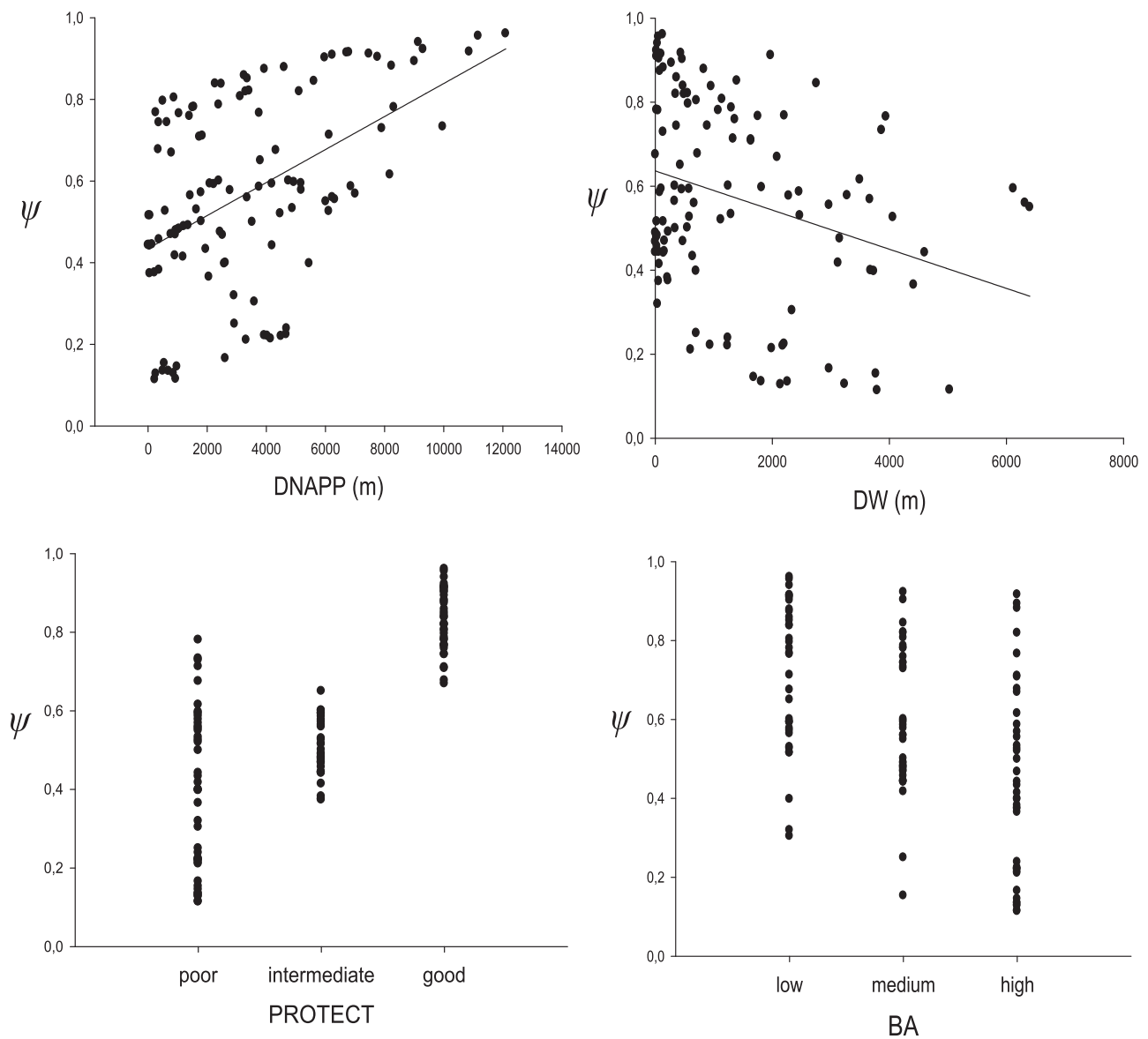
Fig. 3. The estimated probability of habitat use of tapirs (ψ) in relation to the distance to the nearest access points for poachers (DNAPP), the distance to closest water body (DW), the relative level of protection against poaching (PROTECT), and the relative abundance of bamboo (BA). ψ was estimated based on the composite model and the parameters estimates resulted from the model averaging.

minimize the risk of being killed by poachers. The similarity in the daily activity pattern among populations of lowland tapirs across the distribution of the species, as well as with other tapir species, suggests a lack of flexibility in this behavioral trait despite changing environmental conditions. It also suggests that the daily activity of tapirs may be phylogenetically constrained. Some morphological characteristics, such as poor vision and an acute sense of smell and hearing, indicate that tapirs are primarily adapted for nocturnal activity.

Patterns in habitat use

The occupancy modeling suggests that poaching is one of the factors with the greatest effect on habitat use by tapirs since both the level of protection and the distance to nearest access points for poachers (DNAPP) had significant positive effects on the presence of tapirs. Similar results were reported by Licona et al. (2011), who observed lower habitat use of tapirs in sites with higher human accessibility.

We found no effect of protection on detectability, suggesting that there were no large-scale effects on tapir behavior and any factors that affect detectability occur at more localized scales. This is supported by the observed reduction in detection related to increased accessibility and trail/road width which could result from active avoidance of areas frequently used by people or from evasive behaviors in response to camera-traps (probably associated to human activities).

Lowland tapirs have been shown to avoid closed understory areas with high density of the bamboo *Chusquea ramosissima* in the Upper Paraná Atlantic Forest, which potentially hinders their movements (Gallardo et al., 2008), as well as associated with areas close to water; a tendency that has been related to thermoregulation, ectoparasite avoidance and resting behaviors (Padilla and Dowler, 1994; Foerster and Vaughan, 2002). For our study area, however, the model averaged estimates for these covariates did not indicate a significant effect of either bamboo density or distance to water on site use by tapirs. As expected, however, we found a negative relationship between detection and bamboo abundance which

we potentially attribute to the dense bamboo layer decreasing the ability of cameras to detect tapirs.

The lower probability of habitat use of tapirs in less protected areas suggests a population response to poaching. The increase in habitat use and detection with the distance to access roads indicate differences in abundance and behavioral responses respectively in relation to differences in human activity. There is evidence that animals tend to avoid areas perceived as being of higher risk of predation or hunting (Laundre et al., 2010). Furthermore, if occupancy is interpreted as a surrogate for abundance (MacKenzie et al., 2004) we can infer that the negative relationship of distance to access points with the use of an habitat is a result of decreasing abundance of tapirs, which is consistent with previous research where tapir abundance and poaching level were negatively related (Cullen et al., 2001; Peres, 2000, 2001).

Medici et al. (2007) conducted a population and habitat viability analysis for lowland tapirs and found that poaching was one of the major threats for the species. Tapirs may be especially vulnerable to hunting, compared to other ungulates, because of their relatively low population density coupled with their life history traits (low reproductive rate; Bodmer et al., 1997). Poaching may not only negatively affect tapir populations but may also indirectly affect the composition and structure of the forest, since tapirs play an important ecological role, affecting the structure, composition, growth and regeneration of the vegetation (Bodmer, 1991; Dirzo and Miranda, 1991; Fragoso, 1997; Wright et al., 2000).

The Green Corridor of Misiones is one of the few areas of Upper Paraná Atlantic Forest with high probabilities of maintaining lowland tapir populations in the long term (Paviolo et al., 2008; Taber et al., 2008). However, a large portion of the Green Corridor suffers from medium to high poaching pressure; which, as our study suggests, negatively affects the abundance and the patterns of habitat use by tapirs. Thus, as a consequence of poaching most of the largest remnants of Upper Paraná Atlantic Forest contains no or very low densities of tapirs (Cullen et al., 2001; Paviolo et al., 2009a). To preserve an important and well preserved area of the Upper Paraná Atlantic Forest, where the ecological and evolutionary processes involving lowland tapirs persist, Argentinian, Brazilian and Paraguayan authorities should improve forest protection and reduce levels of poaching.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.mambio.2014.06.003.

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