

# Interspecific interactions between wild black and gold howler monkeys (*Alouatta caraya*) and other mammals in northeastern Argentina

Vanina A. Fernández<sup>1</sup> · Romina Pavé<sup>2</sup> · Silvana M. Peker<sup>3</sup> · Maria A. Pérez-Rueda<sup>3</sup>

Received: 25 January 2016 / Revised: 4 October 2016 / Accepted: 24 October 2016  
© Springer-Verlag Berlin Heidelberg and ISPA 2016

**Abstract** We studied the interactions between wild black and gold howler monkeys (*Alouatta caraya*) and other mammals at three sites with different human disturbance levels and forest structures in northeastern Argentina. The main goal was to evaluate the effects of the study site and type of interaction (agonistic or non-agonistic) on the rate of interaction. In addition, we also described the associations between interspecific interaction rate, species involved, howler monkeys' activity, and seasonality. We present 50 group-years for 14 groups, collected between 2003 and 2012. We registered a total of 29 interactions ( $0.22 \pm 0.26$  interactions/100 h). Most interactions (56.7%) were agonistic (12% of high intensity and 88% of low intensity), 41.9% were neutral, and 1.5% were affiliative. We found that both factors, site and type of interaction, have an effect on the rate of interaction. Interspecific interactions were more frequent at the two sites without human settlement than in the rural site. Interspecific interactions occurred during resting (46.73%), traveling (27.40%), and feeding (25.87%). Interactions occurred throughout the year but were concentrated in August (late winter) and September

(beginning of spring). Our results suggest that both site and type of interaction affected the rate of interaction between howler monkeys and other mammals in northeastern Argentina. Agonistic interactions were more frequent than non-agonistic ones, and monkeys reacted agonistically to several mammalian species, but these interactions were mainly of low intensity.

**Keywords** Agonistic interactions · Play · Tolerance · Community · Howler monkeys

## Background

Interspecific interactions are an underlying mechanism of the organization of ecological communities (Tilman 1977; Connell 1983). For example, predator–prey relationships can change the distribution and abundance of prey populations, and competition for shared resources can lead to niche differentiation (Pianka 1981, Connell 1983, Chesson 2000, Scheffer and van Nes 2006). Between primate and non-primate species, two categories of interspecific interactions are reported: agonistic interactions described as predator–prey interactions and competitive interactions, and non-agonistic interactions, which include affiliative and neutral interactions such as play and tolerance (Asensio and Gómez-Marín 2002; Rose et al. 2003; Resende et al. 2004; Miranda et al. 2005; Sushma and Singh 2006; Asensio et al. 2007; Gursky and Nekaris 2007; Haugaasen and Peres 2008; Desbiez et al. 2010; Cristóbal-Azkarate et al. 2015). Several factors may affect the occurrence and intensity of interactions, i.e., age and sex of interacting individuals, feeding niche overlap, food availability across seasons, breeding season of one or both species, and presence of immature individuals. For example, in the same community at São Paulo, Brazil, interactions

**Electronic supplementary material** The online version of this article (doi:10.1007/s10211-016-0243-2) contains supplementary material, which is available to authorized users.

✉ Vanina A. Fernández  
vanifer@gmail.com

- <sup>1</sup> Museo Argentino de Ciencias Naturales “Bernardino Rivadavia” (MACN-CONICET), Av. Ángel Gallardo 470, C1405DJR Buenos Aires, Argentina
- <sup>2</sup> Instituto Nacional de Limnología, CONICET-UNL, Ciudad Universitaria, Pje El Pozo s/n, 3000 Santa Fe, Argentina
- <sup>3</sup> Estación Biológica Corrientes (EBCo), CONICET, Ruta Provincial 8 Km 7 s/n, Corrientes, Argentina

between adult capuchin monkeys (*Cebus apella*) and coatis (*Nasua nasua*) are mainly agonistic, but young individuals of both species interact affiliatively through play (Resende et al. 2004). Because primates can share the same ecological niche with other taxa, a recent study suggested that interspecific interactions associated with competition are more frequent between primates and other taxa than among primate species themselves, indicating the importance of considering interspecific interactions between primates and other taxa to understand the structure of vertebrate communities (Beaudrot et al. 2012). However, reports of interactions between primates and other species are scarce, mainly because they are difficult to observe in the wild.

We studied the interspecific interactions of wild black and gold howler monkeys (*Alouatta caraya*), large-bodied and arboreal neotropical primates (weight, adult males  $6.42 \pm 1.15$  kg and adult females  $4.33 \pm 0.76$  kg) characterized by a folivorous–frugivorous diet (Milton 1980; Fernández 2014; Dias and Rangel-Negrín 2015). Non-agonistic and agonistic interactions have previously been reported between howlers and birds and other mammals (*Alouatta belzebul*: Camargo and Ferrari 2007; *A. caraya*: Miranda et al. 2005, 2006; Ludwig et al. 2007; *Alouatta guariba*: Boiniski and Scott 1988; Dias and Strier 2000; Miranda et al. 2006; Bianchi and Mendes 2007; *Alouatta palliata*: Asensio and Gómez-Marín 2002; Asensio et al. 2007; Gil-da-Costa 2007; *Alouatta puruensis*: Quintino and Bicca-Marques 2013; *Alouatta seniculus*: Sherman 1991). These studies suggest that most interactions occur as a consequence of food competition; however, most of the recorded cases are anecdotal and their rate in the communities and the effect of other factors, such as seasonality, are still unknown (Cristóbal-Azkarate et al. 2015). Here, we studied the interactions between wild black and gold howler monkeys (*A. caraya*) and other mammals. The main goal of this study was to evaluate the effects of the study site and type of interaction (agonistic or non-agonistic) on the rate of interaction. In addition, we also described the species involved, howler monkeys' activity, and seasonality in relation to interaction rate.

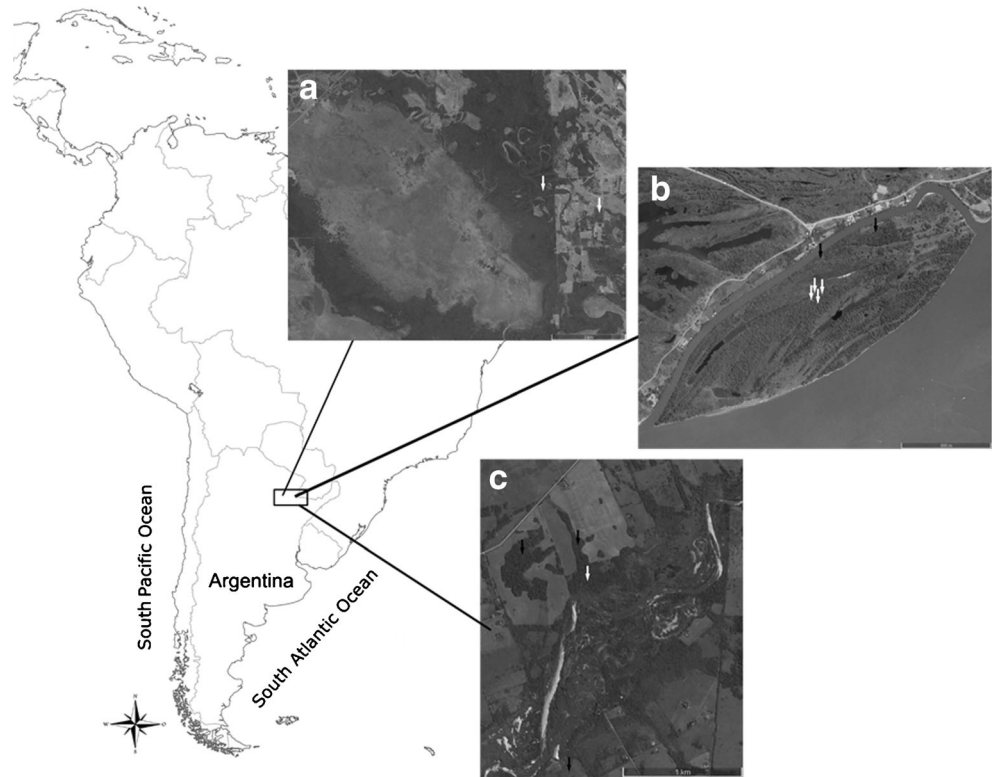
## Methods

We conducted this study at three sites located in two neighboring provinces of northeastern Argentina (Fig. 1). One site is Brasilera Island (BI) in Chaco Province ( $27^{\circ} 18' \text{ S}$ ,  $58^{\circ} 38' \text{ W}$ ), with an area of 292 ha near the confluence of the Parana and Paraguay rivers. This site is characterized by a continuous flooded forest without permanent human settlements, with an ecological density of howlers of 3.25 ind/ha (Kowalewski and Zunino 2004). The second site, located in the same province, is the Chaco National Park (CNP;  $26^{\circ} 48' \text{ S}$ ,  $59^{\circ} 40' \text{ W}$ ), a protected area of 15,000 ha without human settlements,

characterized by continuous upland and riparian forests, open lowlands with palm trees, wetlands, and lakes. At CNP, the ecological density of howlers is unknown. The third site includes the fragmented forests surrounding the Parque Provincial San Cayetano and Estación Biológica Corrientes, in Corrientes Province, Argentina (EBCo;  $27^{\circ} 30' \text{ S}$ ,  $58^{\circ} 41' \text{ W}$ ). EBCo vegetation is characterized by semi-deciduous upland and riparian forests, open lowlands with palm trees, and grasslands. EBCo is a rural site, i.e., there are permanent human settlements and livestock surrounding the forest fragments occupied by howlers. The ecological density of howlers at EBCo is 1.04 ind/ha (Zunino et al. 2007). A complete description of the sites can be found elsewhere (Burkart et al. 1999; Kowalewski and Zunino 2004; Zunino et al. 2007; Pavé et al. 2012). There are no other primate species inhabiting these sites, and we do not have quantitative data on the composition of the other mammal species. In Table 1, we show a list of the wild mammalian species that interacted with the howler monkeys during our study present at the study sites, and those that have been reported in any kind of interactions with howlers elsewhere (Asensio and Gómez-Marín 2002; Miranda et al. 2005; Asensio et al. 2007; Bianchi and Mendes 2007; Camargo and Ferrari 2007; Ludwig et al. 2007; Cristóbal-Azkarate et al. 2015). The study sites do not have large raptors that may hunt howlers (Cristóbal-Azkarate et al. 2015). However, BI and CNP have yellow anaconda (*Eunectes notaeus*), which may hunt howlers (Quintino and Bicca-Marques 2013), but we never observed a howler monkey being attacked by an anaconda or by any other predator (mammal, raptor, or reptile). Although howler monkeys are arboreal primates, they sometimes descend to the ground for certain activities, such as drinking water in lagoons, crossing forest patches, pursuing solitary individuals that approach the group, and playing (mainly older infants and juveniles) (Bianchi and Mendes 2007; Camargo and Ferrari 2007; Kowalewski 2007; Dias and Rangel-Negrín 2015), making themselves vulnerable to terrestrial predators.

We recorded interspecific interactions from 14 well-known habituated groups (6 at BI, 2 at CNP, and 6 at EBCo). Each group was studied for 1–5 days per month from dawn to dusk. Data were collected over 1–8 years depending on the group (50 group-years) between 2003 and 2012. The interactions were recorded during long-term studies on the ecology and behavior of black and gold howler monkeys (Kowalewski 2007, Peker et al. 2009; Fernández 2014; Pavé et al. 2015). At each study site, the howler groups occupied forest fragments that were similar in floristic composition and vegetation structure (Kowalewski 2007; Fernández 2014; Pavé et al. 2015). During the study period, all groups had one or more juveniles and/or infants. On average ( $\pm$ SD), we obtained  $936 \pm 1185.86$  observation hours per study group at BI (range = 56–2740.6 h;  $n = 6$ ), 288 observation hours per study group at CNP ( $288 \pm 0$  h per group;  $n = 2$ ), and

**Fig. 1** Map showing the locations of the three study sites: *a* CNP = Chaco National Park, *b* BI = Brasileria Island, and *c* EBCo = Estación Biológica Corrientes. *White arrows* point out the groups where interspecific interactions occurred



**Table 1** Mammalian species (possible predators and interacting species) present at three study sites in northeastern Argentina

Interacting species	Brasileria Island	Chaco National Park	Estación Biológica Corrientes	Previous studies <sup>a</sup>
<b>Canidae</b>				
Crab-eating fox ( <i>Cerdocyon thous</i> )	x	x	x	
Pampas fox ( <i>Pseudalopex gymnocercus</i> )		x	x	
<b>Felidae</b>				
Geoffroy's cat ( <i>Leopardus geoffroyi</i> )	x	x		
Ocelot ( <i>Leopardus pardalis</i> )		x		x <sup>b</sup>
Jaguarundi ( <i>Puma yagouaroundi</i> )	x	x	x	x <sup>c</sup>
Puma ( <i>Puma concolor</i> )		x		x <sup>d</sup>
<b>Mustelidae</b>				
Tayra ( <i>Eira barbara</i> )	x		x <sup>c</sup>	
<b>Procyonidae</b>				
South American coati ( <i>Nasua nasua</i> )	x	x		x <sup>c, e</sup>
<b>Myrmecophagidae</b>				
Southern tamandua ( <i>Tamandua tetradactyla</i> )	x	x		
<b>Cervidae</b>				
Gray brocket ( <i>Mazama gouazoubira</i> )	x	x	x	

*Note* The species cited in the table at the study sites were observed by the authors or cited in Soria (2000)

<sup>a</sup> Mammal species that interact with different howler species in previous studies

<sup>b</sup> Miranda et al. (2005), Bianchi and Mendes (2007)

<sup>c</sup> Cristóbal-Azkarate et al. (2015)

<sup>d</sup> Ludwig et al. (2007)

<sup>e</sup> The coati species cited in the revision of Cristóbal-Azkarate et al. (2015) is *Nasua nasua*

564.57 ± 411.88 observation hours per study group at EBCo (range = 197.5–1143.6 h;  $n = 6$ ), with a total of 9584.8 observation hours (5621.4 h at BI, 576 h at CNP, and 3387.4 h at EBCo). The observation hours were similarly distributed across seasons: 2814.61 h in spring (September to November), 1964.7 h in summer (December to February), 2262.8 h in autumn (March to May), and 2542.6 h in winter (June to August). We used the all-occurrences technique (Altmann 1974) to record the interactions that occurred within a radius of 30 m allowing visual and/or auditory contact between the howlers and the interacting species (Sushma and Singh 2006). We classified the observed interactions into three types: agonistic, affiliative, and neutral. Following Cristóbal-Azkarate et al. (2015), agonistic interactions were further divided into low- and high-intensity interactions. Low-intensity interactions included different combinations of alarm vocalizations (i.e., barking, throat rumble, howl), branch shaking, chases or rapid approaches, supplantations (when an individual replaces another individual in the same spatial position), and/or piloerection (when the fur is fluffed up). High intensity included the above behaviors plus physical contact between species, such as biting, grabbing, and pulling. Affiliative interactions referred specifically to play (when animals showed soft physical contact such as pulling the tail, pushing, and slapping). Neutral interactions were divided into two categories: tolerance, when two species rested or fed in the same tree or neighboring trees (less than 30 m) for a period of time equal to or greater than 10 min, and ignore (Rose et al. 2003), when a non-primate mammal walked by howler monkeys (which were resting or feeding), both species made visual contact, but the non-primate mammal walked away. Finally, to describe the context in which interactions occurred, we also recorded the activity in which the howler monkeys were engaged before the occurrence of the interaction, i.e., traveling, feeding, or resting.

We estimated the interaction rate per group as the number of interactions divided by the corresponding observation hours obtained per group. For comparative purposes, the rate was expressed as the number of interactions/100 observation hours. We used a linear mixed-effects model (LMM) to analyze potential effects of the site and type of interaction (independent variables) on the rate of interaction (dependent variable). We used “group” as a random factor (nested in site). We performed a logarithmical transformation (base 10) on the interaction rate. We based the choice of best model using the Akaike information criterion (AIC) (Akaike 1978). We used Fisher’s LSD test for “a posteriori” comparison of means. The level of significance was set to 0.05. We used InfoStat2011 (Di Rienzo et al. 2011) to perform the statistical analyses.

## Results

We registered a total of 29 interactions between howlers and other mammals ( $0.22 \pm 0.26$  interactions/100 h). The interaction rate was  $0.35 \pm 0.32$  interactions/100 h at IB,  $0.35 \pm 0$  interactions/100 h at CNP, and  $0.04 \pm 0.11$  interactions/100 h at EBCo. These interactions occurred in 50% ( $n = 7$ ) of the howler groups studied (IB = 4, CNP = 2, and EBCo = 1). In this sense, we observed 24 interactions (82.76%) during 5621.4 h at BI, three interactions (10.34%) during 3387.41 h at EBCo, and two interactions (6.9%) during 576 h at CNP. Considering only groups in which we observed interactions, the average rate of interactions per group was higher at BI and EBCo ( $0.29 \pm 4$  and  $0.25 \pm 1.5$  interactions/100 h, respectively) than at CNP ( $0.15 \pm 1.6$  interactions/100 h) (Table 2, LMM: AIC = 3.11,  $\sigma = 9.2 \times 10^{-05}$ ).

Regarding the type of the 29 interactions recorded, 56.7% ( $n = 17$ ) were agonistic (12% of high intensity and 88% of low intensity), 41.9% ( $n = 10$ ) neutral (50% ignore and 50% tolerance), and 1.5% affiliative ( $n = 2$ ) (see Table 3 and Electronic supplementary material). Agonistic interactions occurred more frequently ( $0.52 \pm 4.6$  interactions/100 h) than neutral or affiliative interactions ( $0.17 \pm 3.55$  and  $0.13 \pm 5.13$  interactions/100 h, respectively) (Fig. 2, Table 2, LMM: AIC = 3.11,  $\sigma = 9.2 \times 10^{-05}$ ) and were recorded at the three study sites. However, no interaction ended in a predation event. Neutral interactions occurred at BI and EBCo ( $n = 9$  and 1, respectively) and the two affiliative interactions were registered in one group (X) at BI (Table 3).

With respect to the species involved in the interactions, at BI, the most common species interacting with howlers were South American coatis (71.43% of the interactions,  $n = 17$  interactions, average  $0.45 \pm 0.25$  interactions per group/100 h) followed by jaguarundis (19.05%,  $n = 5$  interactions), crab-eating foxes (4.76%,  $n = 1$  interaction), and southern tamanduas (4.76%,  $n = 1$  interaction) (Table 3). Among interactions with coatis, 80% ( $n = 12$ ) were with solitary adults (females, males, and undefined sex) and only 20% ( $n = 5$ ) with groups of several individuals (1–2 adult males, 2–3 adult females, and 2 immature individuals). Of coati interactions, 57% were agonistic ( $0.54 \pm 0.59$  interactions/100 h,  $n = 8$ ), 39% neutral ( $0.42 \pm 0.49$  interactions/100 h,  $n = 7$ ), and 4% affiliative ( $0.15$  interactions/100 h,  $n = 2$ ). Of jaguarundi interactions, 78.6% were agonistic ( $0.28 \pm 0.16$  interactions/

**Table 2** Total number and rate of agonistic and non-agonistic interactions among howler groups and other mammals (\*  $P < 0.05$ )

Source of variation	Numerator <i>df</i>	Denominator <i>df</i>	<i>F</i> value	<i>p</i> value
Intercept	1	11	12.69	0.0044*
Type of interaction	2	11	294.28	<0.0001*
Site	2	4	64.97	0.0009*

**Table 3** Statistical results of LMM for the rate of interaction in 100 observational hours

Site and howler group	Interacting species	Type of interaction	Rate of interaction (no. of interactions/100 h)	Category of interaction	Season	Previous activity	Presence of infants (<1 year old)	Case number of additional file 1
BI-G	South American coati	Agonistic	0.18	HI	Spring	Resting	No	1
				LI	Autumn	Feeding	No	–
				LI	Spring	Traveling	1 (6 months)	–
BI-X	South American coati	Agonistic	0.2	HI	Autumn	Resting	No	7
				LI	Spring	Traveling	1 (1 month)	–
				LI	Winter	Resting	No	–
				LI	Winter	Feeding	3 (2 months, 10 months, 10 months)	–
BI-G	Jaguarondi	Agonistic	0.2	LI	Winter	Resting	1 (4 months)	2
				LI	Spring	Traveling	No	3
				LI	Autumn	Feeding	No	4–6
				LI	Autumn	Traveling	No	4–6
BI-X	Southern tamandua	Agonistic	0.08	LI	Winter	Resting	No	–
BI-X	South American coati	Affiliative	0.08	–	Autumn	Resting	2 (0 month, 0 month)	–
				–	Autumn	Feeding	2 (0 month, 0 month)	–
BI-G	Crab-eating fox	Neutral	0.23	IG	Winter	Resting	2 (0 month, 0 month)	–
BI-G	Jaguarondi	Neutral	0.23	IG	Winter	Resting	2 (0 month, 0 month)	–
BI-M	South American coati	Neutral	1.44	IG	Spring	Resting	no	–
BI-G	South American coati	Neutral	0.14	IG	Spring	Resting	No	–
				T	Winter	Feeding	2 (0 month, 0 month)	–
				T	Spring	Resting	2 (2 months)	–
BI-X	South American coati	Neutral	0.52	T	Spring	Resting	No	–
BI-E	South American coati	Neutral	0.7	T	Autumn	Feeding	2 (0 month)	–
				T	Winter	Resting	1 (0 month)	–
EBCo-T	Pampas foxes	Agonistic	0.59	HI	Spring	Feeding	2 (6 months, 6 months)	8
				LI	Summer	Resting	2 (6 months, 6 months)	–
EBCo-T	Gray brocket	Neutral	0.19	IG	Spring	Resting	2 (8 months, 5 months)	–
CNP-Mo	Pampas foxes	Agonistic	0.35	LI	Summer	Traveling	1 (4 months)	–
CNP-Re	Crab-eating fox	Agonistic	0.35	LI	Winter	Traveling	2 (0 month, 2 months)	–

BI Brasileria Island, EBCo Estación Biológica Corrientes, CNP Chaco National Park, HI high-intensity agonistic interaction, LI low-intensity agonistic interaction, IG ignore, T tolerance

\**p* value <0.05 (i.e., significant difference)

100 h  $n = 4$ ) and 21.4% were neutral (0.23 interactions/100 h,  $n = 1$ ). The only interaction recorded with a crab-eating fox was neutral, and we recorded one agonistic interaction with a tamandua. At EBCo, most interactions involved pampas foxes (66.7%,  $n = 2$  interactions) and all interactions were agonistic. Also, we recorded a neutral interaction with gray brockets (33.3%). Finally, at CNP, we recorded two agonistic interactions: one with pampas foxes and one with crab-eating foxes (Table 3, see [Electronic supplementary material](#)).

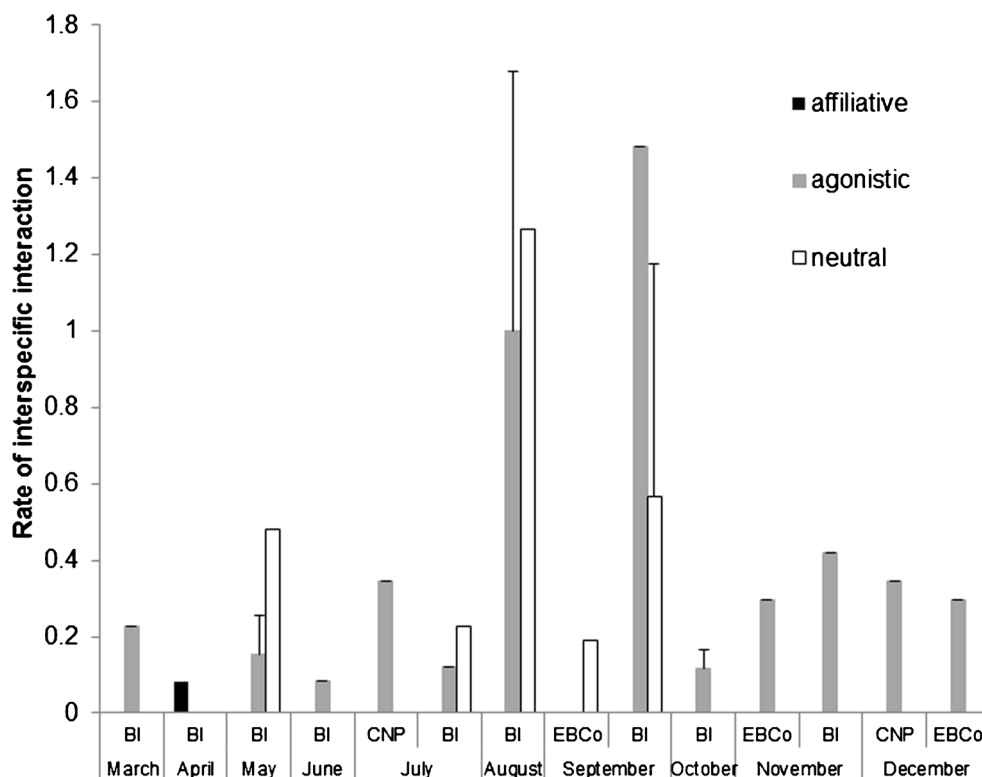
Concerning howler monkey activity, interspecific interactions occurred mainly during resting (46.73%), then during traveling (27.40%), and finally during feeding (25.87%) (Table 4). Agonistic interactions, the most common

interspecific interaction type, occurred mainly during howler monkey traveling (48.32%), then during feeding (33.69%), and finally during resting (19.99%) (Table 4). We also evaluated howler activity patterns during agonistic interactions only with coatis because howlers interacted the most with and overlap in diet with coatis (Gompper and Decker 1998). Agonistic interactions between howlers and coatis occurred mostly during traveling (43.8%) and feeding (39.4%) and less frequently during resting (16.8%).

Finally, regarding seasonality, interspecific interactions at BI ( $n = 24$ ) occurred throughout the year but concentrated in August (late winter, 32.1%,  $1.09 \pm 0.5$  interactions/100 h) and September (beginning of spring, 36.8%,  $0.75 \pm 0.7$



**Fig. 2** Rate of interspecific interactions, type of interactions, and seasonality by study site. BI = Brasileria Island, CNP = Chaco National Park, EBCo = Estación Biológica Corrientes



interactions/100 h) and were principally with coatis (Table 3, Fig. 2). The four interactions with jaguarundis were in March (autumn). Of these, three were with an adult (sex unidentified) and one was with two adults (sex unidentified). At EBCo, interspecific interactions ( $n = 3$ ) only occurred in spring. Finally, at CNP ( $n = 2$ ), one interaction occurred in winter and one at the beginning of summer (Table 3, Fig. 2).

## Discussion

This is the first study focused on interactions between black and gold howler monkeys and other mammals near the southernmost limit of *A. caraya*'s distribution. We recorded  $0.22 \pm 0.26$  interactions/100 h from three sites in northeastern Argentina. Our rate is lower than those recorded in previous studies of other neotropical

primates (*A. palliata*: Asensio et al. 2007; *Brachyteles hypoxanthus*: Dias and Strier 2000; *Cebus* spp.: Rose et al. 2003; Resende et al. 2004). Capuchin monkeys and potential predators at three sites in Costa Rica showed  $4.8 \pm 1.54$  interactions/100 h (Rose et al. 2003) and howler monkeys (*A. palliata*) and coatis (*Nasua narica*) in Los Tuxtlas, Mexico, showed 3.21 interactions/100 h (Asensio et al. 2007). In contrast, at Brasileria Island, we registered  $0.45 \pm 0.25$  interactions per group/100 h. According to the review by Cristóbal-Azkarate et al. (2015), howler monkeys have a low frequency of interactions with other vertebrates throughout their geographical distribution, compared to other neotropical primates (for example, capuchin monkeys: Rose et al. 2003; Resende et al. 2004). The low frequency of interactions between primates and other mammals generally may be partly attributed to the fact that field primatologists, who invariably follow habituated study groups for hundreds of hours, may inadvertently repel unhabituated mammals. Therefore, the occurrence of interactions between primates and other mammals may be underestimated (Haugaasen and Peres 2008; Cristóbal-Azkarate et al. 2015). The low rate of interactions registered in our study populations may be because our sites are located in subtropical areas, and therefore, there is a lower diversity of mammalian species compared to tropical forests (Ojeda 2013). Also, our study sites, except CNP, are mainly non-protected

**Table 4** Context of the interspecific interactions recorded between black and gold howler monkeys and other mammals

Previous activity of the howler groups	Agonistic (%)	Affiliative (%)	Neutral (%)
Traveling	27.40	0	0
Feeding	19.11	0.72	7.98
Resting	10.20	0.72	33.88

areas with or without human settlements, where people modify the forest and hunt different mammals.

We found an effect of site on the rate of interactions, with more frequent interactions at BI and CNP. BI consists of two types of forest: tall and continuous forest in the center and northwest of the island and low forest on the coast (González et al. 2002). All encounters were recorded in the four groups inhabiting the tall forest in the center of the island. Groups living on the coast are more exposed to humans (e.g., fishermen) and dogs (see Fig. 1). Although CNP is a protected area with higher mammal species richness compared to the other two sites, the home ranges of both howler study groups were near tourists' trails, where human activities may have deterred other wildlife. Finally, many of the forest fragments surrounding EBCo were modified and replaced by secondary forest due to selective logging (Zunino et al. 2007). The three interactions observed at EBCo occurred in one group (T), although we also studied a neighboring group (S) for a similar number of hours with no interactions observed (T = 1143 observation h, S = 1034 observation h). The main difference between these groups is that the S home range was adjacent to a farm and therefore more exposed to dogs and humans. In summary, we propose that the higher rate of interactions recorded in the groups at BI compared to the other sites is due to several factors, including the tall and continuous forest at the center of the island that facilitates movement of wildlife within the area, the lower exposure to humans and dogs, and the continuous presence of coati groups that interact with howlers.

Agonistic interspecific interactions were more frequent than non-agonistic ones (neutral and affiliative). Similarly, Rose et al. (2003) found that mantled howler monkeys (*A. palliata*) and white-faced capuchins (*Cebus capucinus*) were involved in more agonistic interactions (45%) than other interaction types (i.e., affiliative, vigilance, ignore, co-feeding) at two sites in Costa Rica. They also found that agonistic interactions (75.57%) between white-faced capuchins and coatis (*N. narica*) were more frequent than other types (i.e., alarm, ignore) at three sites in Costa Rica (Rose et al. 2003). The agonistic interactions we observed between howlers and coatis occurred mainly when howlers were traveling (i.e., they were not feeding encounters) and during winter and spring, months characterized by low fruit availability at BI (Kowalewski and Zunino 2004; Pavé et al. 2012). We did not observe co-feeding/co-foraging behavior nor aggression in a feeding context, and therefore, we do not have evidence for considering feeding competition as a major cause of agonism between these species, as previously suggested (Asensio et al. 2007;

Cristóbal-Azkarate et al. 2015). For example, Asensio et al. (2007) found that 65% of the interactions observed between howlers and coatis were at the end of the dry season when there is high fruit availability and the breeding season of coatis begins. These interactions were feeding encounters over fig trees, and 52% of them were with solitary adult coatis. In one case, the interaction ended when an adult male howler attacked the coati, who then left the tree (Asensio et al. 2007).

The most intense agonistic interactions recorded at our study sites were those with adult pampas foxes at EBCo and with adult male coatis at BI. Although agonistic interactions between howlers and foxes have not been previously reported, howlers reacted aggressively to adult foxes probably because they pose a threat, especially to immature howler individuals. Interactions with pampas foxes also showed the active role played in group defense by adult female howlers (case 8 in the [Electronic supplementary material](#)) as they engaged in ambush behaviors to repel the foxes. Asensio and Gómez-Marín (2002) reported a similar behavior by adult *A. palliata* females in repelling adult tayras (*Eira barbara*) in Los Tuxtlas, Mexico. Similar ambush behavior has been observed in BI in conspecific interactions in which both adult female and male howlers react to extra-group individuals (Kowalewski 2007). All of these observations suggest that both adult female and adult male howlers engage in group defense.

Neutral interactions occurred principally during resting and were equally divided between tolerating and ignoring behaviors. Tolerance interactions occurred exclusively with coatis, but ignoring involved two potential predators (jaguarundi and crab-eating fox). It is striking that monkeys responded by ignoring these potential predators and at the same time showed aggressive behavior (low intensity) towards a southern tamandua that should not pose a threat to them. Regarding of the first case (ignoring a potential predator), there are no previous reports on this type of behavior. One possibility is that the monkeys try to avoid the attention of potential predators. We have noted on several occasions that when groups of humans pass under the monkeys without noticing them, howlers remain silent and immobile. Therefore, this reaction may be the same with the neutral interactions recorded with jaguarundis and foxes. Regarding showing aggressive behavior to non-predators, a previous study on the interactions between capuchin monkeys and other species reported "harass to neutral species" and suggested that this may be for "(1) practice and learning, (2) testing unfamiliar allospecifics, and (3) a generalized trait of pugnacity that reflects underlying temperament" (see Rose et al. 2003 for details). Alternatively, when we observed howlers barking at the tamandua, it is possible that

howlers were testing the response of an unfamiliar animal, as howler–tamandua interactions are rare in our study sites.

Affiliative interactions, particularly interspecific play, involved almost exclusively young individuals (juveniles and subadults) of monkeys and coatis. There are several reports on playing among different species of primates or between primates and other mammals (Rose et al. 2003; Resende et al. 2004; Cristóbal-Azkarate et al. 2015). For example, Resende et al. (2004) reported play between *Cebus apella* and *Nasua nasua*. Observed play interactions occurred in the presence of adults of both species while resting, indicating a degree of “social tolerance” between species. In the sense of more general “social tolerance,” there are previous reports of howler monkeys (*A. caraya* and *A. palliata*) feeding in the same tree with coatis (*N. nasua* and *N. narica*) in Mato Grosso do Sul, Brazil, and Los Tuxtlas, Mexico (Asensio et al. 2007; Rímoli et al. 2008).

Interspecific interactions occurred throughout the year but were more frequent in August (winter) and September (spring). The highest frequency of interactions during these two months occurred at BI with coatis. This mammalian species was the only interacting species that shares a feeding niche with the howlers, i.e., both species are partially frugivorous (Dias and Rangel-Negrín 2015; Gompper and Decker 1998) and may compete for food (Asensio et al. 2007; Cristóbal-Azkarate et al. 2015). At BI, August (late winter) and September (beginning of the spring) are months with low fruit availability (Kowalewski and Zunino 2004; Pavé et al. 2012), and for this reason, there is a low probability that the interactions between coatis and howler monkeys were due to competition for fruits. Therefore, we suggest that the concentration of interactions in August and September may be associated with the reproductive biology of the interacting species. At BI, two howler groups have overlapping home ranges with at least one coati group and we observed a coati nest adjacent to a howler sleeping site. The interactions with coatis occurred mainly between May and September (autumn–spring) with coati groups or solitary adult individuals (males and sex unidentified). Though we do not know the breeding season of coatis at BI, the same species breeds in August (late winter) and September (beginning of spring) in southeastern Brazil (Beisiegel 2001; Beisiegel and Mantovani 2006) and females give birth between October and November (spring) in northeastern Argentina and southeastern Brazil (Hirsch 2007a). During the mating season, coati groups are often followed by several solitary males that mate with resident females (Hirsch 2007a). We recorded interactions between howlers and groups of coatis mainly in August and September, and interactions between

howlers and solitary coatis during the coati nesting period (September to November), indicating that interspecific interactions may be partially dictated by coati reproductive behavior. From December to February, coatis forage mainly on the ground (Beisiegel and Mantovani 2006; Hirsch 2007b) and probably for this reason we observed a lower number of interspecific interactions during this period. With respect to the interactions with pampas foxes at EBCo, we observed two in November (spring) and, during one of these, we observed cubs in a den under a tree close to the interaction. This fox species forms a breeding pair that stays together until the cubs leave the natal den, which occurs between September and December (spring–summer) in central Argentina (Lucherini et al. 2004), indicating a potential connection between fox reproductive behavior and likelihood of interspecies interaction.

## Conclusions

Our results suggest that both factors analyzed, site and type of interaction, had an effect on the rate of interaction between howler monkeys and other mammals in northeastern Argentina. We registered more interactions in groups inhabiting tall continuous forest without permanent human settlement at Brasilera Island. In general, agonistic interactions were more frequent than non-agonistic interactions and monkeys reacted agonistically to several mammalian species, but these interactions were mainly of low intensity. In addition, the type of interaction between two species is not necessarily the same throughout the year. Seasonal variation may be associated with the biology of the interacting species (which, for example, leads to seasonal changes in group numbers) and perception of danger across months. Although our data do not allow us to make conclusions about the ultimate causes of these interspecies interactions, our findings provide some support for an anti-predator adaptation (mainly for foxes and felids) but no support for interspecific food competition as suggested in previous studies (Asensio and Gómez-Marín 2002; Miranda et al. 2006; Asensio et al. 2007; Gil-da-Costa 2007; Quintino and Bicca-Marques 2013; Cristóbal-Azkarate et al. 2015). Finally, our results suggest that habitat transformation also affects the interaction patterns between howlers and other species (see Cristóbal-Azkarate et al. 2015). Habitat reduction and human presence may result in a lower presence of wildlife with which monkeys can interact. Future ecological studies on howler monkeys and other neotropical primates are necessary to understand how primates share their habitats with other animal species, especially in



changing anthropogenic environments. Future studies can also shed light on the role of food competition and predation as important forces that organize the vertebrate community structure in the neotropics.

**Acknowledgments** We are grateful to all the field assistants who helped us with data collection, as well as to the collaborators, local people at Isla del Cerrito and San Cayetano, and technicians from Estación Biológica Corrientes (MACN-CONICET). MAPR thanks Administración de Parques Nacionales for allowing fieldwork within the Chaco National Park. We specially thank Martín Kowalewski who provided valuable information for this manuscript on interspecific interactions among howler monkeys and other species at Brasilera Island. We are thankful for the constructive comments of the two anonymous reviewers that improved this manuscript. We thank Nicoletta Righini and Margaret Bryer for their kind help with the English version of this manuscript. This research complied with the current laws and permission of Argentina and also adhered to the American Society of Primatologists Principles for the Ethical Treatment of Primates. This study was supported by grants and fellowships of the American Society of Mammalogists (VAF, RP), American Society of Primatologists (SMP), Consejo Nacional de Investigaciones Científicas y Técnicas de Argentina (VAF, RP, SMP, MAPR), Idea Wild (RP, SMP), International Primatological Society (VAF), The Scientific Research Society (VSF), and Zoo of Barcelona (RP).

**Authors' contributions** VF, RP, SP, and MPR conceived and designed their studies and obtained the data. VF and RP analyzed the data and wrote the manuscript. VF, RP, SP, and MPR interpreted the results. All the authors read, made suggestions, and approved the final manuscript. Informed consent was obtained from all individual participants included in the study.

#### Compliance with ethical standards

**Conflict of interest** The authors declare that they have no competing interests.

## References

- Akaike H (1978) A Bayesian analysis of the minimum AIC procedure. *Ann Inst Stat Math* 30(1):9–14
- Altmann J (1974) Observational study of behavior: sampling methods. *Behaviour* 49:227–267
- Asensio N, Gómez-Marín F (2002) Interspecific interaction and predator avoidance behavior in response to tayra (*Eira barbara*) by mantled howler monkeys (*Alouatta palliata*). *Primates* 43:339–341
- Asensio N, Arroyo-Rodríguez V, Cristóbal-Azkarate J (2007) Feeding encounters between a group of howler monkeys and white-nosed coatis in a small forest fragment in Los Tuxtlas, Mexico. *J Trop Ecol* 23:253–255
- Beaudrot L, Struebig MJ, Meijaard E, Van Balen S, Husson S, Young CF, Marshall AJ (2012) Interspecific interactions between primates, birds, bats, and squirrels may affect community composition on Borneo. *Am J Primatol* 75:170–185
- Beisiegel BM (2001) Notes on the coati, *Nasua nasua* (Carnivora: Procyonidae) in an Atlantic Forest area. *Braz J Biol* 61:689–692
- Beisiegel BM, Mantovani W (2006) Habitat use, home range and foraging preferences of the coati *Nasua nasua* in a pluvial tropical Atlantic forest area. *J Zoology* 269:77–87
- Bianchi RC, Mendes SL (2007) Ocelot (*Leopardus pardalis*) predation on primates in Caratinga Biological Station, Southeast Brazil. *Am J Primatol* 69:1173–1178
- Boinski S, Scott PE (1988) Association of birds with monkeys in Costa Rica. *Biotropica* 20:136–143
- Burkart R, Bárbaro NO, Sánchez RO, Gómez DA (1999) Ecoregiones de la Argentina. Administración de Parques Nacionales, Buenos Aires, Argentina
- Camargo CC, Ferrari SF (2007) Interactions between tayras (*Eira barbara*) and red-handed howlers (*Alouatta belzebul*) in eastern Amazonia. *Primates* 48:147–150
- Chesson P (2000) Mechanisms of maintenance of species diversity. *Annu Rev Ecol Sys* 31:343–366
- Connell JH (1983) On the prevalence and relative importance of interspecific competition: evidence from field experiments. *Am Nat* 122:661–696
- Cristóbal-Azkarate J, Urbani B, Asensio N (2015) Interactions of howler monkeys with other vertebrates: a review. In: Kowalewski MM, Garber PA, Cortés-Ortiz L, Urbani B, Youlatos D (eds) *Howler monkeys: behavior, ecology, and conservation*. Springer Press, New York
- Desbiez A, Rocha FL, Keuroghlian A (2010) Interspecific association between an ungulate and a carnivore or a primate. *Acta Ethol* 13:137–139
- Di Rienzo JA, Balzarini MG, Gonzalez L, Tablada M, Robledo CW (2011) InfoStat versión 2011. Grupo InfoStat, FCA, Universidad Nacional de Córdoba
- Dias PAD, Rangel-Negrín A (2015) Diets of howler monkeys. In: Kowalewski MM, Garber PA, Cortés-Ortiz L, Urbani B, Youlatos D (eds) *Howler monkeys: behavior, ecology, and conservation*. Springer, New York, pp. 21–56
- Dias LG, Strier KB (2000) Agonistic encounters between miquis, *Brachyteles arachnoides hypoxanthus* (primates, Cebidae), and other animals at the Estação Biológica de Caratinga, Minas Gerais, Brazil. *Neotropical Primates* 8:138–141
- Fernández VA (2014) Ecología nutricional del mono aullador negro y dorado (*Alouatta caraya*) en el límite sur de su distribución. Dissertation, Universidad de Buenos Aires
- Gil-da-Costa R (2007) Howler monkeys and harpy eagles: a communication arms race. In: Gursky SL, Nekaris KAI (eds) *Primate anti-predator strategies*. Springer, USA, New York
- Gompper ME, Decker DM (1998) *Nasua nasua*. *Mamm Species* 580:1–9
- González V, Zunino GE, Kowalewski M, Bravo SP (2002) Densidad de monos aulladores (*Alouatta caraya*) y composición y estructura de la selva de inundación en una isla de Río Paraná Medio. *Rev Mus Argentino Cienc Nat* 4:7–12
- Gursky SL, Nekaris KAI (2007) *Primate anti-predator strategies*. Springer, Verlag, Berlin
- Haugaasen T, Peres CA (2008) Associations between primates and other mammals in a central Amazonian forest landscape. *Primates* 49:219–222
- Hirsch BT (2007a) Spoiled brats: is extreme juvenile agonism in ring-tailed coatis (*Nasua nasua*) dominance or tolerated aggression? *Ethology* 113:446–456
- Hirsch BT (2007b) Within-group spatial position in ring-tailed coatis (*Nasua nasua*): balancing predation, feeding success, and social competition. Dissertation, Stony Brook University
- Kowalewski MM (2007) Patterns of affiliation and co-operation in howler monkeys: an alternative model to explain social organization in non-human primates. Dissertation, University of Illinois
- Kowalewski M, Zunino GE (2004) Birth seasonality in *Alouatta caraya* in northern Argentina. *Int J Primatol* 25:383–400

- Lucherini M, Pessino M, Farias AA (2004) Pampas fox. *Pseudalopex gymnocercus*. In: Sillero-Zubiri C, Hoffmann M, Macdonald DW (eds) Canids: foxes, wolves, jackals and dogs, IUCN/SSC Canid Specialist Group, UK
- Ludwig G, Aguiar LM, Miranda JMD, Teixeira GM, Svoboda WK, Malanski LS, Shiozawa MM, Hilst CLS, Navarro IT, Passos FC (2007) Cougar predation on black-and-gold howlers on Mutum Island, southern Brazil. *Int J Primatol* 28:39–46
- Milton K (1980) The foraging strategy of howler monkeys: a study in primate economics. Columbia University Press, New York
- Miranda JMD, Bernardi IP, Abreu KC, Passos FC (2005) Predation on *Alouatta guariba clamitans* Cabrera (primates, Atelidae) by *Leopardus pardalis* (Linnaeus) (Carnivora, Felidae). *Rev Bras Zool* 22:793–795
- Miranda JMD, Bernardi IP, Moro-Rios RF, Passos FC (2006) Antipredator behavior of brown howlers attacked by black hawk-eagle in southern Brazil. *Int J Primatol* 27:1097–1101
- Ojeda RA (2013) Diversity and conservation of neotropical mammals. In: Levin SA (ed) Encyclopedia of biodiversity, vol 2, 2nd edn. Academic Press, Waltham, MA, pp. 582–594
- Pavé R, Kowalewski MM, Garber PA, Zunino GE, Fernandez VA, Peker SM (2012) Infant mortality in black-and-gold howlers (*Alouatta caraya*) living in a flooded forest in northeastern Argentina. *Int J Primatol* 33:937–957
- Pavé R, Kowalewski MM, Zunino GE, Giraudo AR (2015) How do demographic and social factors influence parent-offspring conflict? The case of wild black and gold howler monkeys (*Alouatta caraya*). *Am J Primatol* 77:911–923
- Peker SM, Kowalewski MM, Pavé R, Zunino GE (2009) Births in wild black and gold howler monkeys (*Alouatta caraya*) in northern Argentina. *Am J Primatol* 71:261–265
- Pianka E (1981) Resource acquisition and allocation among animals. In: Townsend CR, Calow P (eds) *Physiol. Ecol. An Evol. Approach to Resour. use.* Blackwell, Oxford, pp. 300–314
- Quintino EP, Bicca-Marques JC (2013) Predation of *Alouatta puruensis* by *Boa constrictor*. *Primates* 54:325–330
- Resende BD, Mannu M, Izar P, Ottoni EB (2004) Interaction between capuchins and coatis: nonagonistic behaviors and lack of predation. *Int J Primatol* 25:1213–1224
- Rímoli AO, Valdivino EM, Rímoli J, Ferrari SF (2008) Behavior patterns of a group of black howler monkeys *Alouatta caraya* (Humboldt, 1812) in a forest fragment in Terenos, Mato Grosso do Sul: a seasonal analysis. In: Ferrari SF, Rímoli J (eds) *A Primatologia no Brasil 9*, Sociedade Brasileira de Primatologia–UFS
- Rose LM, Perry S, Panger MA, Jack K, Manson JH, Gros-Louis J, Mackinnon KC, Vogel E (2003) Interspecific interactions between *Cebus capucinus* and other species: data from three Costa Rican sites. *Int J Primatol* 24:759–796
- Rumiz DM (1990) *Alouatta caraya*: Population density and demography in Northern Argentina. *Am J Primatol* 21(4):279–294
- Scheffer M, van Nes EH (2006) Self-organized similarity, the evolutionary emergence of groups of similar species. *Proc Natl Acad Sci U S A* 103(16):6230–6235
- Sherman PT (1991) Harpy eagle predation on a red howler monkey. *Folia Primatol* 56:53–56
- Soria A (2000) *Especies de valor especial de los Parques Nacionales Chaqueños*. Biblioteca DTRNEA, Administración de Parques Nacionales
- Sushma HS, Singh M (2006) Resource partitioning and interspecific interactions among sympatric rain forest arboreal mammals of the Western Ghats, India. *Behav Ecol* 17:479–490
- Tilman D (1977) Resource competition between planktonic algae: an experimental and theoretical approach. *Ecology* 58:338–348
- Zunino GE, Kowalewski MM, Oklander LI, González V (2007) Habitat fragmentation and population size of the black and gold howler monkey (*Alouatta caraya*) in a semideciduous forest in northern Argentina. *Am J Primatol* 69:966–975