UNUSUAL BEHAVIORAL RESPONSES OF THE SOUTH AMERICAN COATI *(NASUA NASUA)* TO THE HOODED CAPUCHIN *(SAPAJUS CAY)* IN THE PARAGUAYAN UPPER PARANÁ ATLANTIC FOREST

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Abstract

In eastern Paraguay, the South American coati *Nasua nasua* and hooded capuchin *Sapajus cay* are sympatric across most of their range. Both species are diurnal, arboreal, omnivorous mammals and have similar diets consisting of fleshy fruits and insects and are therefore potential competitors. In this article, we report three observations of unusual behavioral responses of coatis to the presence of hooded capuchins. On two occasions groups of coatis elected to show avoidance behavior by hiding from capuchin groups, despite the much closer proximity of human observers. On another occasion coatis and capuchins were seen to feed side by side in a fruit tree without antagonism for over half an hour. We also review the literature to begin the process of identifying the factors that may influence the frequency and outcome of such encounters.

Key Words: Atlantic Forest, Behavior, Cebidae, Interspecific competition, Paraguay, Procyonidae

Resumen

En el oriente de Paraguay, el coatí sudamericano *Nasua nasua* y el capuchino encapuchado *Sapajus cay* son simpátricos en la mayor parte de su rango. Ambas especies son mamíferos diurnos, arbóreos y omnívoros y tienen dietas similares que consisten en frutos carnosos e insectos y, por lo tanto, son competidores potenciales. En este artículo, reportamos tres observaciones de respuestas de comportamiento inusual de los coatíes a la presencia de capuchinos encapuchados. En dos ocasiones los grupos de coatíes eligieron mostrar un comportamiento de evasión escondiéndose de los grupos de capuchinos, a pesar de la proximidad mucho más cercana de los observadores humanos. En otra ocasión se vio que los coatíes y los capuchinos se alimentaban uno al lado del otro en un árbol frutal sin antagonismo durante más de media hora. También revisamos la literatura para comenzar el proceso de identificación de los factores que pueden influir en la frecuencia y el resultado de tales encuentros.

Palabras Clave: Bosque Atlántico, Comportamiento; Cebidae, Competición interespecífica; Paraguay; Procyonidae

Introduction

Interspecific interactions are an important and yet frequently overlooked part of wild animal ecology (Jones et al., 1994), and they may vary in nature depending on the ecological relationships between those species involved (Resende et al., 2004; Fack et al., 2019). The most commonly reported interspecific interactions between primate and non-primate species include agonistic interactions (predator–prey and competitive interactions) and non-agonistic interactions (affiliative and neutral interactions) (Asensio and Gómez-Marín, 2002; Rose et al., 2003; Resende et al., 2004; Cristóbal-Azkarate et al., 2015; Fernandez et al., 2017).

The hooded capuchin (*Sapajus cay:* Illiger, 1815) is found in sympatry with the coati throughout eastern Paraguay, south-east Bolivia, northern Argentina, and Brazil (states of Goiás, Mato Grosso, Mato Grosso do Sul and marginally into Rondônia) (Stallings, 1985; Lynch Alfaro et al., 2012; Wallace, 2015). Hooded capuchins live in large multi-male, multi-female groups (Pinto, 2006; Fernandes Jr., 2013; Smith and Briggs, 2015), however the only interspecies interactions that we are aware of include feeding associations with collared peccary *Pecari tajacu* in the Brazilian Pantanal (Tortato et al., 2014), sleeping, and sometimes feeding, in the same area as black-and-gold howler monkeys (*Alouatta caraya*) in Nueva Gambach, Paraguay (Rebecca L. Smith, *pers. obs.*) and an observation of predation of a black tailed marmoset (*Mico melanurus*) in the Brazilian Pantanal (Porfilio et al., 2017). In general, very little is known about the behavioral ecology of the hooded capuchin, with very few studies, and no long-term studies, published from any part of its range (Brown and Zunino, 1990; Smith and Briggs, 2016; Smith, 2017; Smith and Payne, 2017; Smith *et al.*, 2018; da Costa et al., 2020).

The South American coati *Nasua nasua* Linnaeus, 1766 is widely distributed from Venezuela and Colombia, south to Uruguay and northern Argentina (Alves-Costa et al., 2004, Emmons and Helgen, 2016). Coatis are mainly found in forested areas, both humid and dry, including in Paraguay gallery forest, Atlantic Forest, palm savannas, Cerradón and xeric Chaco forests (Emmons, 1990; Gompper and Decker, 1998; Beisiegel, 2001; Trovati et al., 2010). They are a social procyonid, living in large groups made up of adult females and their offspring, with males typically being solitary (Russell, 1981; Haugaasen and Peres, 2008; Hirsch, 2011). Adult males will occasionally associate with groups of females (Hirsch, 2011), though usually only one male per group (Hirsch, 2006). Coatis have been reported as forming feeding associations with birds (Booth-Binczik et al., 2004, Beisiegel, 2007), peccaries *Pecari tajacu* (Desbiez et al., 2010), tapirs *Tapirus bairdii* (Overall, 1980), and primates (Haugaasen and Peres, 2008, Desbiez et al., 2010).

The coati occurs in sympatry over much of its South American range with several other species of capuchin monkeys (*Sapajus* and *Cebus* species) with which feeding associations have also been reported (Resende et al., 2004, Haugaasen and Peres, 2008). Coatis, in common with many Neotropical primates (including capuchins), are diurnal omnivores that forage mainly on mature fruits and invertebrates (Izar, 2004; Resende et al., 2004; Costa et al*.,* 2009; Hirsch, 2009; Hirsch et al., 2013; de Almeida et al., 2018), creating potential for interaction at feeding sites (Alves-Costa et al., 2004; Cristóbal-Azkarate et al., 2015; Fernandez et al., 2017). In several publications that have commented on interactions between coati and primate species, interactions were apparently either mutualistic or commensal (Haugaasen and Peres, 2008, Desbiez et al., 2010), yet others resulted in conflict (Fragaszy et al., 2004; Resende et al., 2004; Fack et al., 2018), Gracile capuchins (genus *Cebus*) have even been reported to predate coati pups (Newcomer and de Farcy, 1985; Fedigan, 1990; Perry and Rose, 1994). Though we are unaware of published reports of robust capuchins (genus *Sapajus*) predating coatis, they are known to consume vertebrate prey (Izawa, 1978; Terbourgh, 1983; Galetti, 1990; Resende et al., 2003; Sampiao and Ferrari, 2005; Carretero-Pinzón et al., 2008; Rebecca L. Smith, *pers. obs.*).

Frequencies of coati-primate encounters are likely mitigated by movement patterns, with most Neotropical monkeys foraging in the trees and coatis usually foraging on the ground (Hirsch et al., 2013). Capuchins additionally show a largely lineal foraging pattern in the canopy, while coatis follow a more circuitous route on the ground, often visiting the same fruiting tree more than once a day (Hirsch et al., 2013). However, the existence of cross-site differences in foraging behavior in capuchins is well known, even in geographically proximate populations (Panger et al., 2002).

Here we provide descriptions of new observations of interactions between South American coatis and hooded capuchins from eastern Paraguay, and through reviewing the published literature we attempt to identify what factors may influence the frequency and outcome of such encounters.

Methods

The observations described here were obtained at two study sites in eastern Paraguay. Rancho Laguna Blanca (RLB) is an 804 ha property in San Pedro department, eastern Paraguay, including an isolated and disturbed 243 ha fragment of Upper Paraná Atlantic Forest. This fragment is home to two groups of hooded capuchins: O Group (18 individuals) (Smith and Briggs, 2015) and F Group (21 individuals). The population size of coatis in this fragment was unknown. Encounters between the monkeys and other mammalian species were observed occasionally. At the time we recorded our observations, the capuchins were in the process of being habituated to researcher presence. A typical response to human presence was for them to alarm call and flee.

"Área para Parque" San Rafael is a 73,000 ha patch of near pristine Upper Paraná Atlantic Forest (BAAPA) in departments Itapúa and Caazapá in the south of Paraguay. San Rafael the largest remaining tract of BAAPA left in Paraguay and consists of more than 50 private properties. Nueva Gambach is the southernmost property with 15 ha of forest connecting at its northern end to the rest of San Rafael. Nueva Gambach is home to four groups of hooded capuchins (20-25 individuals per group) and an unknown number of coatis.

Observations were obtained during daily monitoring (from 2013 to 2017 at RLB, and from 2017 to present at Nueva Gambach) as part of the Para La Tierra Capuchin Research Project. Data were collected six days per week at RLB and for 15 days per month at Nueva Gambach. The capuchins were followed for as long as possible between dawn and dusk and all social behavior was recorded using one-minute scan sampling (Altmann, 1974), including interspecific interactions.

Previous studies have reported that when groups of coatis are disturbed in the trees they come to the ground and escape on the ground (Gompper and Decker, 1998). Coatis are hunted by people at both sites and it was not the normal response to either approach humans, or to remain close and keep still, in the presence of human observers. Normally, observer encounters with solitary individuals or larger groups of coatis in the absence of capuchins resulted in the coatis either moving into the forest canopy and hiding from observers or fleeing on the ground while vocalizing loudly. Retreating higher into the canopy was more commonly observed for solitary individuals than for groups at both sites.

Results

Rancho Laguna Blanca: On 16 July 2014 at 08:14, a presumed adult male coati (solitary) was observed while the authors were following O Group (RLB: –23.829444, –56.294722). The coati had pushed its body underneath a large mass of woody vines on a tree trunk approximately 1 m above the ground. The capuchin group was located 8 m laterally from the coati and between 5 to 7 m higher up in the canopy, while the human observers were approximately 2 m from the coati. Rather than fleeing on the ground (as is habitual), the coati slowly tried to move higher into the tree, freezing whenever the alarm call of the monkeys could be heard. Three adult male monkeys then began to threaten the observers by vocalizing loudly and breaking branches, but the coati remained completely still and silent. Despite the closer proximity of the humans, the coati's gaze remained directed towards the monkeys as they vocalized, switching the gaze back to the human observers during the pauses. The coati remained in this position for 11 minutes until the capuchins travelled out of sight; at that point, the coati moved higher into the tree apparently to increase the distance from the human observers.

On 2nd September 2014 at 08:30, three adult coatis were encountered sitting silently on an exposed branch at a height of 5 m from the ground, just below the canopy of a mid-canopy tree (RLB:–23.829814, –56.296003). The coatis remained still and watched the human observers for around four minutes. The coatis then shifted their gaze eastwards through the canopy and did not return their gaze to the observers on the ground. Without vocalizing, the coatis then moved slowly and quietly into the denser leafy vegetation of the tree top branches, approximately 9 m high and out of sight of the observers. Once the coatis were out of sight observers spotted the O Group capuchins approximately 50 m southeast of the tree in which the coatis hid, in the same direction that the coatis had been looking prior to hiding in the treetop.

Nueva Gambach: On the 17th August 2017, a group of capuchins (around 20 individuals) was encountered feeding in a *Ficus enormis* at 15:55 (–26.62128, –55.66998). Also feeding in the same tree, there was a large group of coatis (around 15 individuals) and a group of Paraguayan howler monkeys (*Alouatta caraya*) (four individuals). At 16:15, an adult coati of undetermined sex approached an adult male capuchin while he was feeding. The capuchin turned his back on the coati and continued to feed and the coati travelled past him. All of the animals fed in close proximity to one another with no obvious aggression for 31 minutes before the capuchins and the coatis left the tree at 16:26 in opposite directions, the feeding patch apparently depleted.

Discussion

There are conflicting published reports on interactions between capuchins and coatis in the wild (Table 1). As a result of their belligerent natures, capuchin species can frequently behave aggressively towards competitors (Freese, 1978; Rose, 1997; Dias and Strier, 2000; Rose et al., 2003; Resende et al., 2004; Buchanan-Smith et al., 2013). The most commonly observed interactions between capuchins in two areas of São Paulo, Brazil (*Sapajus spp.* in Tiete Ecological Park and *Sapajus nigritus* in Carlos Botelho State Park) and coatis were attacks and threats by the capuchins (Resende et al., 2004). The same study also recorded both interspecific playing and four capuchin attacks on coati nests (though there was no definitive evidence of consumption of coatis by the monkeys) (Resende et al., 2004). Haugaasen and Peres (2008) however reported "*Cebus apella*" (probably *Sapajus macrocephalus* Spix, 1823) in the Purus region of Amazonian Brazil feeding side by side with coatis for prolonged periods with no interaction or aggression; this was similar to what we observed between the hooded capuchins and the coatis in Nueva Gambach. Clearly interactions between capuchins and coatis are more complex than fixed interspecific antagonism or indifference, and many other factors may also influence the outcome of these interactions, including, but not restricted to context, age or status of individuals involved, levels of threat posed, resource availability, and environmental conditions.

The differential response of coatis to humans in the presence or absence of capuchins at RLB suggests that they may be assessing risk in deciding how to respond. It is clear from the flight reaction in the absence of capuchins that humans are viewed as a threat, yet the presence of capuchins significantly alters this response. The apparent reluctance of the Rancho Laguna Blanca animals to draw the attention of the capuchins to their presence might suggest that interspecific reactions between the two species at this site are potentially agonistic, and the differential response to the presence of human observers when the capuchins are also present could indicate that the coatis perceive the monkeys to represent a greater risk. However, in reality the risk being assessed is rather more complex.

The observations in which coatis adopted a cautious response to the presence of monkeys involved a small number of individuals, greatly outnumbered by the capuchins. On the other hand, the peaceful foraging situation observed at Nueva Gambach involved similar-sized troops of both species (~20 and ~15 individuals respectively). Previous studies have discovered that both coatis and capuchins are individually less vigilant when they are in larger groups than in smaller groups (Burger and Gochfeld, 1992; Burger, 2001; Di Blanco and Hirsch, 2006). Similar interactions between small groups of coatis and primates present in larger groups have been reported perhaps indicating that primates are most likely to respond with aggression when they outnumber the competitor (capuchins: Fragaszy et al., 2004; Resende et al., 2004; Asensio et al., 2007; woolly monkeys (*Lagothrix flavicauda*): Fack et al., 2018).

Table 1. Summary of interactions between coatis and capuchins.

Capuchin species	Coati species	Type of Interaction	Behavior	Study site	Reference
Sapajus cay	*Nasua nasua*	Avoidance	Coati hid close to human observers until capuchin group had moved away	Rancho Laguna Blanca, San Pedro, Paraguay	**This study**
Sapajus cay	*Nasua nasua*	Avoidance	Stayed silent in the presence of human observer until capuchins had moved away	Rancho Laguna Blanca, San Pedro, Paraguay	**This study**
Sapajus cay	*Nasua nasua*	Neutral	Feeding in same tree with no aggression (howler monkeys also present)	Nueva Gambach, Itapúa, Paraguay	**This study**
"*Cebus apella*" (*Sapajus macrocephalus)*	*Nasua nasua*	Neutral	Feeding in same area with no aggression	Purus region of Amazonian Brazil	Haugaasen and Peres, 2008
Cebus capucinus	*Nasua narica*	Neutral	Drinking together at a waterhole with occasional threat from capuchins towards coatis	Santa Rosa National Park, Costa Rica	Freese, 1978
Sapajus spp. (Tiete Ecological Park) & *Sapajus nigritus* (Carlos Botelho State Park)	*Nasua nasua*	Affiliative	Playing together	Tiete Ecological Park and Carlos Botelho State Park in São Paulo, Brazil	Resende et al., 2004
Sapajus libidinosus	*Nasua nasua*	Agonistic	Capuchins directed threats and attacks towards coatis	Tiete Ecological Park and Carlos Botelho State Park in São Paulo, Brazil	Resende et al., 2004
Cebus capucinus	*Nasua narica*	Agonistic	Capuchins predating on coati nestlings	Santa Rosa National Park/ Lomas Barbudal, Costa Rica	Rose et al., 2003
Cebus capucinus	*Nasua narica*	Agonistic	Capuchins chasing larger coati pups and drowning of larger pups	Santa Rosa National Park/ Lomas Barbudal, Costa Rica	Rose et al., 2003
Sapajus spp. (Tiete Ecological Park)	*Nasua nasua*	Agonistic	Nest attacks	Tiete Ecological Park, São Paulo, Brazil	Resende et al., 2004

Resource availability may play an important role in how species interact. It has been hypothesized that robust capuchins will prey on coati nestlings under certain ecological conditions such as food shortages for capuchins coinciding with coati birth season, high population densities or high home range overlapping (Resende et al., 2004). Affiliative behavior between capuchins and coatis was never observed at RLB, though neither was direct predation on coatis. Both capuchin groups at RLB were observed to aggressively mob other large mammals including tayra (*Eira barbara*) (three observations), Paraguayan howler monkeys (*Alouatta caraya*) (six observations), and puma (*Puma concolor*) (one observation). In forest fragments competition can play a much greater role in regulating the abundance of species within different niches (Kozakiewicz, 1993). As coatis and capuchins show dietary overlap (Resende et al., 2004) it may be that the capuchins in Laguna Blanca presented a greater threat to the coatis, not solely as potential predators but as a result of increased competition for more limited resources in a poorer quality forest.

Though different taxa are involved in these observations, we suggest that it oversimplifies the complexity of interactions of highly cognitive species such as the coati and the capuchin if we assume that such interactions are fixed at the interspecific level rather than multi-factorial, ecologically-influenced or learned (Romero and Aureli, 2008; Hirsch et al., 2012; Gasco et al., 2016). No systematic investigation of interspecific interactions of large mammals has been carried out in the Paraguayan Atlantic Forest and there is little information regarding the hooded capuchin in general across its entire range. Further studies are required to identify the potentially multiple and complex factors that may determine such behaviors.

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