

First records of Brazilian three-banded armadillo (*Tolypeutes tricinctus*, Mammalia, Cingulata, Chlamyphoridae) predation by jaguar (*Panthera onca*, Mammalia, Carnivora, Felidae)

Rodolfo Assis Magalhães^{1,2}; Liana Mara Mendes de Sena^{1,3} & Flávio Henrique Guimarães Rodrigues^{1,4}

¹ Universidade Federal de Minas Gerais (UFMG), Instituto de Ciências Biológicas (ICB), Departamento de Genética, Ecologia e Evolução (DGEE), Laboratório de Ecologia de Mamíferos. Belo Horizonte, MG, Brasil.

² ORCID: <http://orcid.org/0000-0002-6876-8521>. E-mail: rodolfoassismagalhaes@gmail.com

³ ORCID: <http://orcid.org/0000-0002-1364-1769>. E-mail: lianamms@gmail.com

⁴ ORCID: <http://orcid.org/0000-0002-4797-0085>. E-mail: rodriguesfhg@gmail.com

Abstract. The jaguar *Panthera onca* and the Brazilian three-banded armadillo *Tolypeutes tricinctus* are two threatened mammals that coexist in the Caatinga dry forests and the Cerrado savannas of Brazil. Yet, to the best of our knowledge, interactions between these species have not been reported in the literature. Here, we present the first records of *P. onca* predation on *T. tricinctus* from two different areas in the Caatinga in northeastern Brazil. We showed that *P. onca* can pierce the hard carapace of *T. tricinctus*, which may be possible due to its distinctly strong bite and associated predation behavior. We argue that *P. onca* may be the most adapted non-human predator to feed on *T. tricinctus*, and that the smaller body sizes of *P. onca* individuals in the Caatinga may increase their likelihood to feed on smaller prey, including *T. tricinctus*. Thus, the originality of our records is probably more related to insufficient research in the areas where these species coexist than to the rarity of this interaction.

Keywords. Bahia; Diet; Predator-prey interaction; Serra da Capivara National Park; Seasonally Dry Tropical Forest.

INTRODUCTION

The jaguar *Panthera onca* (Linnaeus, 1758) and the Brazilian three-banded armadillo *Tolypeutes tricinctus* (Linnaeus, 1758) are two threatened mammals that coexist in the Caatinga and Cerrado domains in Brazil (Bocchiglieri *et al.*, 2010; Astete *et al.*, 2017). *T. tricinctus* is one of the two species of the genus *Tolypeutes*, along with *Tolypeutes matacus* (Desmarest, 1804) (Wetzel *et al.*, 2008). These species are among the smallest Brazilian armadillos and are unique in presenting the ability to roll up their bodies into a ball (Wetzel *et al.*, 2008). When rolled up, *Tolypeutes* protect their softer tissues with their hard, ossified tegument, thereby providing protection against predation (Wetzel *et al.*, 2008; Superina & Loughry, 2012).

Tolypeutes tricinctus is the only armadillo endemic to Brazil and is restricted to the Caatinga and Cerrado domains (Feijó *et al.*, 2015). The species is facing a significant decline in its populations due to hunting and habitat loss, which led it to be classified as Endangered in Brazil (Reis *et al.*, 2015).

Nevertheless, little is still known about its biology (Superina *et al.*, 2014; Reis *et al.*, 2015). For instance, as far as we know, there is no published study that presented evidence of *T. tricinctus* predation by other native predators, although it has been considered a potential prey for larger felids (Astete *et al.*, 2017). This scenario led *T. tricinctus* to be classified as a top-priority armadillo species for research and conservation initiatives (Superina *et al.*, 2014).

Panthera onca is the largest felid in America, occurring from south to north of the continent, where it inhabits numerous ecosystems (Sanderson *et al.*, 2002; Morato *et al.*, 2013). In Brazil, *P. onca* is found in almost all domains, including the Caatinga, where the species is classified as Critically Endangered as a result of habitat loss and hunting (Morato *et al.*, 2013).

The diet of *P. onca* comprises more than a hundred species, with a preference for larger prey (Hayward *et al.*, 2016). However, prey selection by *P. onca* depends on abundance and herd size more than body mass (Hayward *et al.*, 2016). Armadillos, such as *Dasybus novemcinctus* Linnaeus, 1758 and

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Euphractus sexcinctus (Linnaeus, 1758) (\approx 3–6 kg; Medri et al., 2011) can be the most consumed prey (Foster et al., 2010; Miranda et al., 2018), whereas smaller armadillos, such as *Tolypeutes* spp. (\approx 1.5 kg; Medri et al., 2011) are rarely documented in the literature (Hayward et al., 2016). Nevertheless, *T. matacus* has been found in *P. onca* diet (Taber et al., 1997; McBride et al., 2010), while *T. tricinctus* has not. Here, we present the first records of *T. tricinctus* predation by *P. onca* from two areas in northeastern Brazil, thereby providing evidence of a predator-prey relationship between these two threatened species and contributing to the knowledge on *P. onca* diet and *T. tricinctus* natural predators.

MATERIAL AND METHODS

The records presented here were obtained in two areas situated in the Caatinga, a semiarid phytogeographical domain predominantly covered by Seasonally Dry Tropical Forests (SDTF) distributed throughout northeast Brazil (Silva et al., 2017). We recorded the interaction once in the municipality of Brotas de Macaúbas (hereaf-

ter, BdM), state of Bahia (Fig. 1), while monitoring threatened felids between August and September 2017. At the occasion, we placed 20 camera traps in pairs at 10 sites throughout a 53-km² area composed of shrubby-arboreal SDTF, former croplands in regeneration covered by ruderal vegetation, roads, and a complex of three adjacent wind farms. The sampling lasted 15 days, and we set cameras to operate 24 hours a day, with one-minute intervals between consecutive 15-second-long videos.

The other record was opportunistically obtained at the Serra da Capivara National Park (hereafter, SCNP), a 1,291-km² Protected Area located in the state of Piauí, Brazil (Fig. 1), during field activities to document the distribution of armadillos. The SCNP houses an important remnant of conserved Caatinga, comprising from sparse, bushy formations rich in cacti and bromeliads to dense arboreal SDTF (Olmos, 1992).

RESULTS AND DISCUSSION

The record from BdM was obtained on September 1st, 2017, at 06:49 pm (Fig. 2). The camera trap site was in a

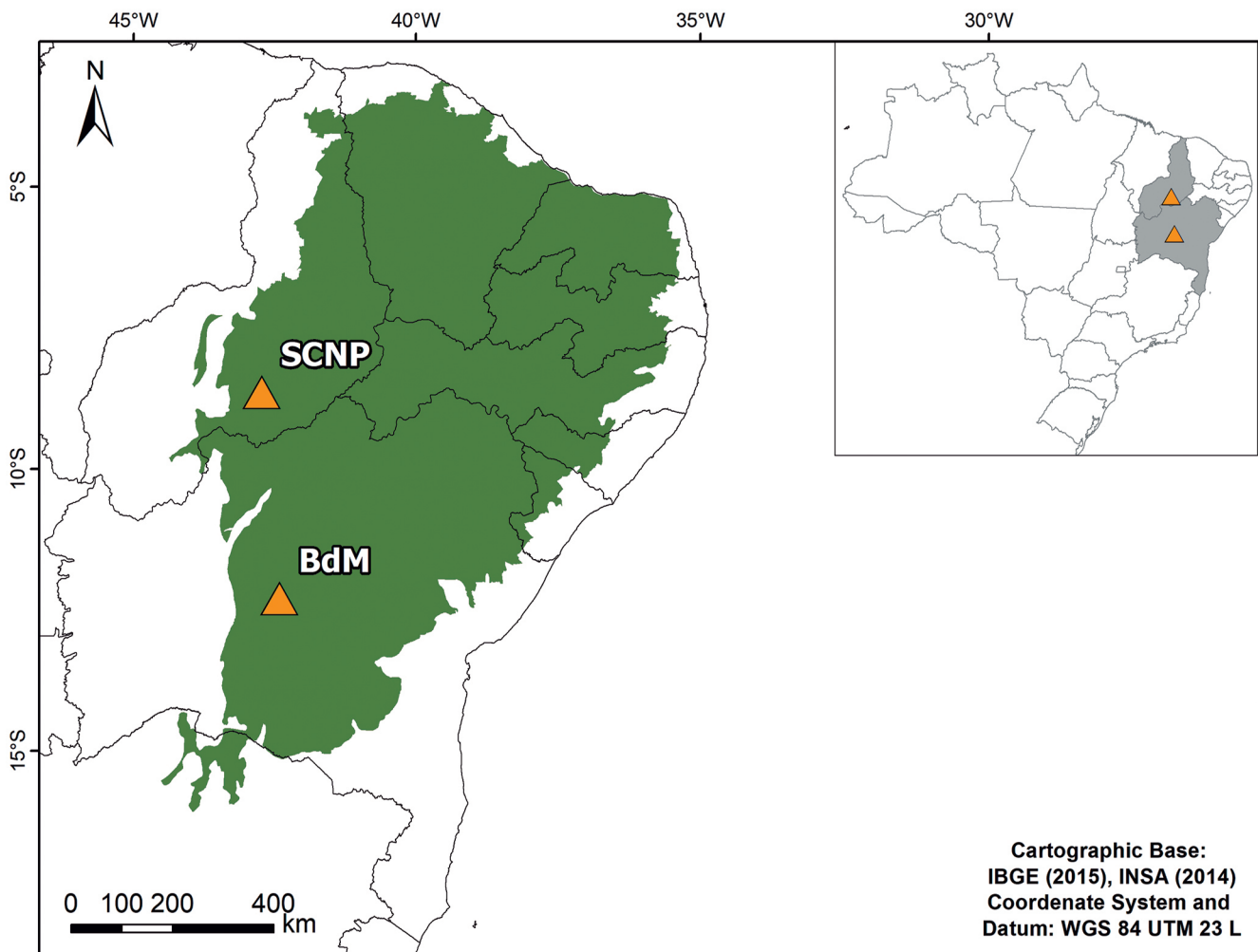


Figure 1. Location of the two areas (orange triangles) where the predation of Brazilian three-banded armadillo (*Tolypeutes tricinctus*) by jaguar (*Panthera onca*) was recorded in the Caatinga domain (green shaded area) in northeastern Brazil: Serra da Capivara National Park (SCNP) and an unprotected rural area in the municipality of Brotas de Macaúbas (BdM). The inset shows the two areas in relation to Brazilian states (gray shaded states refer to those in which the areas are located). The state divisions are from IBGE (2015), and the distribution of the Caatinga is from INSA (2014).



Figure 2. Record of a jaguar (*Panthera onca*) carrying a Brazilian three-banded armadillo (*Tolypeutes tricinctus*) in its mouth in the municipality of Brotas de Macaúbas, state of Bahia, Brazil. This photo is from a 15-second-long video recorded by camera trapping.

small trail sometimes used by local people, covered by shrubby vegetation and close to roads and wind turbines (12°17'26.94"S, 42°21'45.84"O). The video shows a *P. onca* individual carrying a *T. tricinctus* individual in its mouth. *T. tricinctus* was completely rolled up in its defensive position, and *P. onca* was holding it by the left canines.

The record from SCNP consists of a damaged *T. tricinctus* carapace (Fig. 3A) collected on June 9th, 2017, in a densely forested site, at the Serra Branca locality, in the south portion of SCNP (08°38'13.08"S, 42°42'46.66"O). The material was deposited in the collection of mammals of the Federal University of Minas Gerais, Brazil, under the accession number 4394.

Different factors led to the differential diagnosis for *P. onca* predation for the damaged carapace. Some scutes of the scapular shield were broken (Fig. 3B), and they fit the canines of *P. onca* (Fig. 3C). When the carapace was collected in the field, these scutes constituted the only damaged region of the scapular shield; the other missing scutes were probably accidentally removed by posterior manipulation and transport or deterioration of the material. More distinct, the perforation in the pelvic shield fits *P. onca* canines (Fig. 3D), although some scutes are also missing. When the carapace is positioned half-rolled (simulating the defense mechanism) against a *P. onca* skull, the jaws fit both damaged areas while respecting the maximum mandibular opening (Fig. 3E).

Furthermore, *P. onca* has one of the strongest bites and the most robust canine teeth among the extant felids for their body sizes (Christiansen & Adolfsen, 2005; Christiansen, 2007; Meachen-Samuels & van Valkenburgh, 2009). These features are considered adaptations to prey on larger animals (Hayward *et al.*, 2016), but also to attack by biting hard tissues, such as by braincase piercing or by cracking open the shells of tortoises (Meachen-Samuels & van Valkenburgh, 2009). Hence, they allow *P. onca* to prey on species that rely on armor as a defense mechanism (Miranda *et al.*, 2016), which is the case of chelonians (Brito *et al.*, 2018) and *Tolypeutes* spp. Consequently, *P. onca* is the most probable predator that could use a bite on the hard carapace of these armadillos to feed on them. In other words, while the hardness of *Tolypeutes* carapace may be efficient to avoid predation

by other predators, it should be less efficient in avoiding predation by *P. onca*.

Such armor inefficiency is considered a possible reason why armadillos can be avoided by *Puma concolor* (Linnaeus, 1771), while not by *Panthera onca* where these predators coexist (Novack *et al.*, 2005), which is the case of SCNP (Astete *et al.*, 2017). Besides, armadillos are significantly more consumed by *Panthera onca* than by *Puma concolor*, probably for the same reason (Miranda *et al.*, 2016). Nevertheless, *T. matacus* remnants have already been found in *Puma concolor* scats (Taber *et al.*, 1997). Therefore, even though predation by other animals might occur, *Panthera onca* seems to be the most adapted predator to feed on *Tolypeutes* spp. and the most probable predator responsible for the perforations in the carapace that we found at SCNP (Fig. 3).

The two records we presented are complementary. The *T. tricinctus* individual in the video obtained in BdM was completely rolled up and thus, it may still be alive. Although this record does not show how and whether the predator fed on the prey or not, it demonstrates that *P. onca* exerts predation risk for *T. tricinctus*. The effects of predation risk should affect *T. tricinctus* population dynamics through the costs of antipredator behavioral responses (or risk effects), which can result in reduced survival, growth, or reproduction (Creel & Christianson, 2008). The record from SCNP presents the actual removal of *T. tricinctus* individuals from its population, and the record from BdM indicates that *P. onca* may capture *T. tricinctus* individuals at one place to feed on them at another.

The consumption of *Tolypeutes* by *P. onca* has already been reported through the presence of *T. matacus* remnants in *P. onca* scats (Taber *et al.*, 1997; McBride *et al.*, 2010). Thus, the records we obtained add to previously available information on this interaction, by demonstrating that it also occurs with *T. tricinctus* and how it may occur for both *Tolypeutes* species. We believe that the *P. onca* predation behavior we reported here should be valid for both *T. tricinctus* and *T. matacus*, as these armadillos share similar biology (Medri *et al.*, 2011).

Panthera onca individuals tend to present smaller body sizes in areas where the mean weight of its consumed prey is lower (Hoogesteijnt & Mondolf, 1996). This appears to be the case of the Caatinga, where *P. onca* individuals present lower body mass than in floodplains and rainforests (Cláudia Bueno de Campos, personal communication; Hoogesteijnt & Mondolf, 1996), as it is the mean weight of their consumed prey (Miranda *et al.*, 2018). Although *P. onca* tends to avoid species as small as *Tolypeutes* spp. (Hayward *et al.*, 2016), the smaller sizes of *P. onca* individuals in the Caatinga should reduce the individual's energy requirement, allowing them to feed more frequently (but not solely) on smaller species, especially if larger prey are less available (Miranda *et al.*, 2018). Those individuals might also be less capable of successfully slaughtering larger prey.

Armadillos are shown to be consumed by *P. onca* according to their abundance (or availability) (Hayward *et al.*, 2016). This might explain why *T. matacus* has already been found in higher frequency than *D. novemcinctus* and *E. sexcinctus* in *P. onca* scats (Taber *et al.*, 1997; McBride

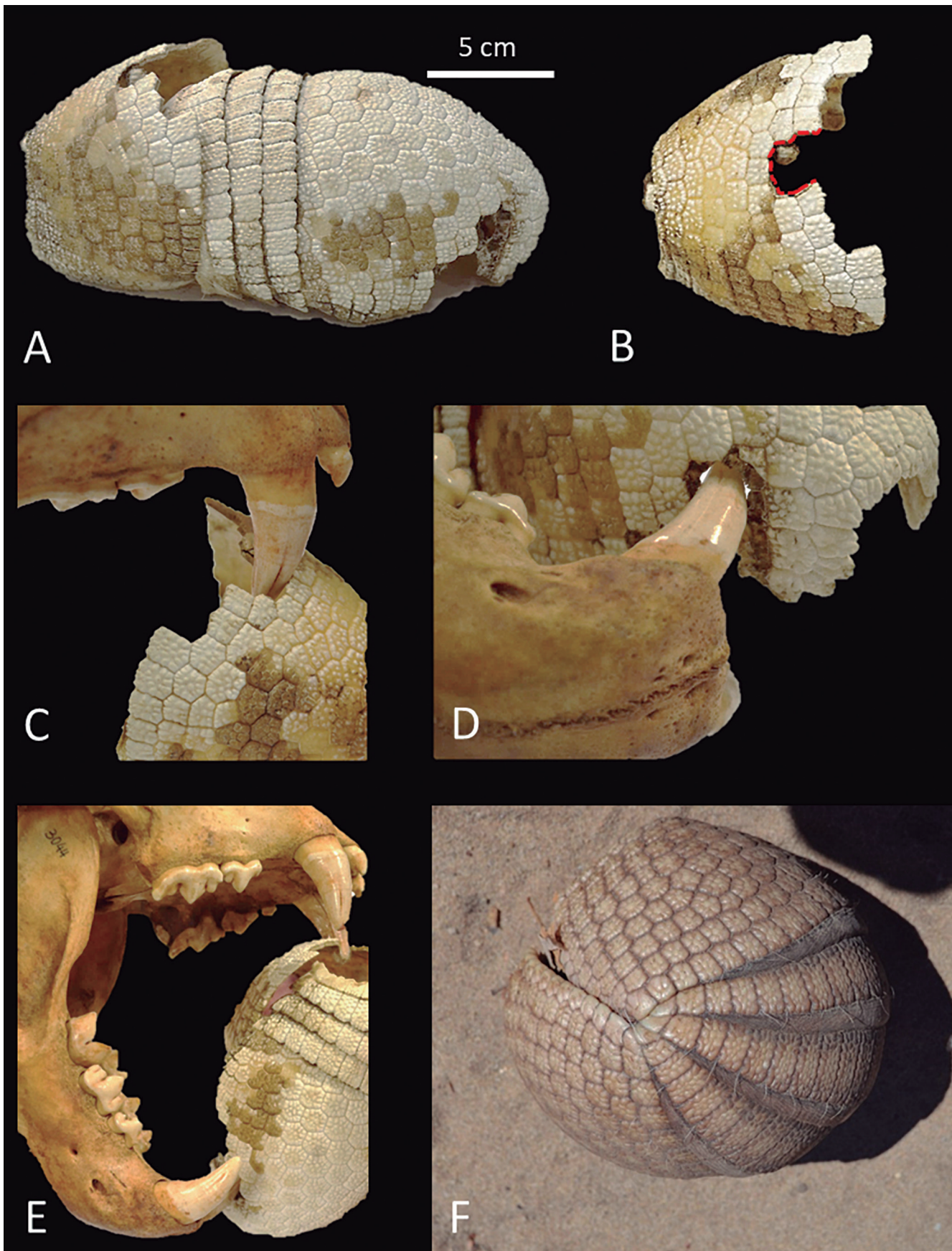


Figure 3. The carapace of an individual of Brazilian three-banded armadillo (*Tolypeutes tricinctus*) attacked by a jaguar (*Panthera onca*). (A) An overview of the carapace. (B) A close-up of the damaged scapular shield (broken scutes are circled in red). (C) The fitting of a *P. onca* canine tooth into a broken scute of the scapular shield. (D) The fitting of a *P. onca* canine tooth into the perforation in the pelvic shield. (E) The probable disposition of *P. onca* jaws during the bite, while respecting the maximum mandibular opening. (F) An individual of *T. tricinctus* rolled up parallel to the ground, demonstrating a possible position of the individual in which the bite could have occurred.

et al., 2010). But, while it could be due to the higher availability of *T. matacus*, it could also be a consequence of the easiness for *P. onca* to prey on *Tolypeutes* spp., which is derived from its capacity to prey on armored animals (Meachen-Samuels & van Valkenburgh, 2009; Miranda *et al.*, 2016; Brito *et al.*, 2018).

The inefficiency of *Tolypeutes* defense mechanism against *P. onca* predation might also make slaughtering these armadillos less energetically costly for *P. onca* individuals than other armadillos that rely on fleeing and digging burrows to escape predation. Depending on the relative availability of these prey, *P. onca* predation on *Tolypeutes* spp. could be expected not to be uncommon, and especially on *T. tricinctus* in the Caatinga.

In conclusion, the originality of the records we obtained is more likely to be a result of the negligence-driven scarceness of scientific research in the Caatinga (Santos *et al.*, 2011) as well as in areas of the Cerrado where *P. onca* and *T. tricinctus* coexist than the rarity of this interaction. However, different factors may influence its occurrence, such as the population densities of these species, which may decrease due to overexploitation and habitat loss, even leading to local extinctions (Morato *et al.*, 2013; Reis *et al.*, 2015). Overall, our findings allow this interaction to be assessed in future research on the ecology of *P. onca* and *T. tricinctus* without further uncertainty about its existence.

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AUTHORS' CONTRIBUTIONS

RAM: Conceptualization, Funding acquisition, Investigation, Methodology, Project administration, Resources, Software, Validation, Visualization, Writing – original draft, Writing – review & editing. LMMS: Conceptualization, Funding acquisition, Investigation, Methodology, Project administration, Resources, Validation, Writing – review & editing. FHGR: Conceptualization, Funding acquisition, Investigation, Methodology, Project administration, Resources, Supervision, Validation, Writing – review & editing.

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