UNIVERSIDADE FEDERAL DE MINAS GERAIS
Instituto de Ciências Biológicas
Programa de Pós-Graduação em Ecologia, Conservação e Manejo da Vida Silvestre

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Ocupação, atividade e efeito da caça de tatu-bola *Tolypeutes tricinctus* na Caatinga, Nordeste do Brasil

Belo Horizonte, Minas Gerais, Brazil
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Liana Mara Mendes de Sena

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Orientador: Prof. Dr. Flávio Henrique Guimarães Rodrigues

Co-orientador: Dr. Rodrigo Lima Massara

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“Por toda parte a natureza fala com o ser humano numa voz que é familiar à sua alma”.

Alexander Von Humboldt

À todas as mulheres que, antes de mim,
suportaram, persistiram, enfrentaram,
não se calaram, não se curvaram,
abriram caminhos, e conquistaram o lugar de fala
e o direito de ser(tão) mulher na ciência.

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RESUMO

Tatu-bola *Tolypeutes tricinctus* é a única espécie endêmica do Brasil, encontrada predominantemente na floresta seca da Caatinga e em algumas áreas do Cerrado. Possui a habilidade de flexionar sua carapaça assumindo a forma de uma bola, o que o torna mais vulnerável à captura humana, uma prática que impacta todas as espécies de tatus. Devido à caça ilegal e à perda de habitat, essa espécie é classificada como ameaçada de extinção. Além disso, aspectos da biologia do tatu-bola são pouco conhecidos, com escassas informações sobre sua ecologia e distribuição. Neste estudo, nós investigamos a frequência de apreensão de tatus e outros mamíferos nos relatórios de crimes ambientais no estado do Piauí, nordeste do Brasil. Além disso, assumindo que a caça está entre as principais ameaças ao tatu-bola e o maior problema em Unidades de Conservação na Caatinga, investigamos como fatores ambientais e antrópicos influenciam a ocupação, detecção e o padrão de atividade de *T. tricinctus* no Parque Nacional Serra da Capivara, uma área prioritária para conservação da Caatinga. Para atingir essas metas, avaliamos os relatórios de autos de infração dos órgãos ambientais federais no estado do Piauí, entre 2008 e 2018. Realizamos também uma amostragem com armadilhas fotográficas entre janeiro e setembro de 2018 para obter dados de presença-ausência e horários de atividade da espécie e de outros mamíferos. Também descrevemos os padrões de atividade de *T. tricinctus* e testamos a sua sobreposição com a atividade temporal de seus potenciais competidores e predadores, usando estatística circular. Os autos de infração revelaram que os tatus são as espécies mais caçadas, representando 89,2% dos mamíferos apreendidos. *Dasypus novemcinctus* e *T. tricinctus* são os alvos principais. As apreensões foram mais concentradas na capital Teresina e no sul do Piauí, onde se encontram importantes áreas protegidas do domínio Caatinga. Através de um esforço amostral de 9.801 armadilhas-dias, obtivemos 118 registros independentes de *T. tricinctus* no PNSC, resultando em uma proporção de ocupação de 49% dos sítios amostrais. Entre as variáveis testadas, apenas a cobertura vegetal apresentou efeito significativo, com influência positiva na ocupação do tatu-bola (NDVI, $w_+ = 0,61$). Além disso, encontramos uma relação positiva entre a probabilidade de detecção e o número de dias que as câmeras funcionaram ($w_+ = 0,82$), assim como uma maior detecção da espécie ($w_+ = 0,72$) na estação seca. *T. tricinctus* apresentou padrão de atividade noturno-crepuscular e sua atividade noturna diminuiu na presença de predadores (grandes felinos). Nossos resultados confirmam a alta pressão de caça sobre tatus no Piauí e maior intensidade próximo à Unidades de Conservação no sul do Estado. *T. tricinctus* ocupa ambientes com cobertura vegetal densa, onde encontra melhores recursos, tais como refúgio em temperaturas elevadas e abrigo contra predadores. Além disso, a espécie parece tolerar moderada influência antrópica, como proximidade de estradas, assentamentos humanos e presença de caça. No entanto, novas pesquisas em áreas com diferentes impactos antrópicos em paisagens heterogêneas, bem como áreas não protegidas, podem complementar conhecimento ecológico de *T. tricinctus* e desvendar mecanismos de persistência a longo prazo da espécie.

Palavras-chave: Cingulata. Modelo de ocupação. Habitat. Espécies ameaçadas. Semiárido.

ABSTRACT

Among armadillos, the Brazilian-three-banded-armadillo *Tolypeutes tricinctus* is the only endemic species of Brazil, found predominantly in the Caatinga dry forest and some areas of the Cerrado savanna. *T. tricinctus* can flex its carapace assuming the shape of a ball, which provide protection against natural predators, but it makes it more vulnerable to human capture. Due to illegal hunting and habitat loss, the species is classified as endangered. Also, is a poorly known armadillo, with scarce scientific information about its ecology and occurrence. In this study, we investigated the frequency of seized of armadillos and other wild mammals in the environmental notices of violation reports in the state of Piauí, northeastern Brazil. Assuming that hunting is one of the main threat to the armadillo and the biggest management challenge for protected areas in the State of Piauí, we conducted a camera trap survey between January and September 2018 at Serra da Capivara National Park, a priority area for conservation of the Caatinga. We aimed to investigate how environmental and anthropic factors influence the occupation, detection and activity pattern of *T. tricinctus*. To achieve these goals, we evaluated environmental notices of violations reports from the federal agencies about seizure mammals in the Piauí State, from 2008 to 2018. Using absence-presence data, we evaluated how environmental and anthropic factors affect the occupancy and detectability probabilities based on the Akaike Information Criterion. Also, we describe the daily activity patterns of *T. tricinctus* and test the overlap in daily activity between their potential competitors and predators using circular and overlapping analyses. Armadillos were the most poached species, representing 89,2% of seized mammals. *D. novemcinctus,* followed by *T. tricinctus* are the main target. We obtained 118 independent records of *T. tricinctus* resulting in a naïve occupancy of 0,49 from 9,801 camtrap-days. *T. tricinctus* occupancy was positively influenced by vegetation cover (NDVI, w+=0,61). Also, we found a positive relationship between the probability of detection and effort (w+=0,82) and detection was higher (w+=0,72) in the dry season than in rain season. The temporal patterns of *T. tricinctus* was crepuscular and nocturnal, and its nocturnality decreased in the presence of large felids. This results indeed the high pressure of poaching on armadillos, evident pattern throughout the Teresina capital and southeastern pf State of Piauí. The occupancy modeling showed that *T. tricinctus* occupies environments with denser forest cover, and that it tolerates moderate anthropic influence in a forest landscape. We emphasize the need for future research for better planning of local conservation interventions involving poaching, subsistence, and illegal trade, in order to guarantee the long-term persistence of *T. tricinctus*.

Keywords: Cingulata. Occupancy model. Habitat. Endangered species. Tropical dryforest.

SUMÁRIO

1 INTRODUÇÃO GERAL

No mundo, as espécies têm enfrentado expressivo declínio populacional e extinção, principalmente em função de modificações e perda de habitat, além da caça exploratória, introdução de espécies exóticas e doenças (Young et al., 2016; Dirzo et al., 2014). A resposta às ameaças pode refletir mudanças no padrão espacial e temporal das espécies, e afetar a sua persistência (Aronson et al. 1993). Esse contexto é particularmente desafiador para espécies endêmicas, uma vez que estas possuem populações pequenas e, tendo poucos locais para intervenção em conservação, são inerentemente vulneráveis à extinção (Loyola et al., 2007). Portanto, entender como variáveis antrópicas afetam a ocupação de habitat e o padrão de atividade das espécies é essencial para entendimento das dimensões de nicho e para implementação de estratégias de conservação eficientes, especialmente espécies ameaçadas e endêmicas (Ceballos et al., 2015).

Os tatus (Cingulata: Chlamyphoridae) são parte de um grupo com uma história evolutiva única na América do Sul, conhecido como Xenarthra, do qual também fazem parte os tamanduás e preguiças (Wetzel, 1985). Esses animais estão entre os mais antigos mamíferos placentários, que divergiram dos outros mamíferos há cerca de 103 milhões de anos atrás (Delsuc et al., 2004), e são encontrados desde a Argentina até o sul dos Estados Unidos (Vaughan et al., 2015; Wetzel et al., 2008). As características mais marcantes dos tatus são a carapaça óssea, que protege as partes moles do corpo, e o hábito de escavar o solo para a construção de tocas (McDonough et al., 2000).

Os tatus desempenham um papel fundamental no funcionamento dos ecossistemas neotropicais, atuando como engenheiros do ecossistema, no controle de insetos e dispersão de sementes (Rodrigues et al., 2019). Além disso, esses animais coexistem com seres humanos há milhares de anos (Fig. 1) e historicamente são utilizados como alimento, uso medicinal, artesanato e fabricação de instrumentos musicais (Noss et al., 2008; Peredo, 1999). No Brasil, os tatus têm grande importância para a subsistência em zonas rurais e urbanas como fonte direta de proteína (Bonifácio et al., 2016; Alves et al., 2012, 2009). Entretanto, apesar da caça desses animais ser ilegal no país, a economia local é movimentada pelo comércio da carne e das ferramentas envolvidas na captura dos animais, como as armadilhas e cachorros (Alves et al., 2016; El Bizri et al., 2015).

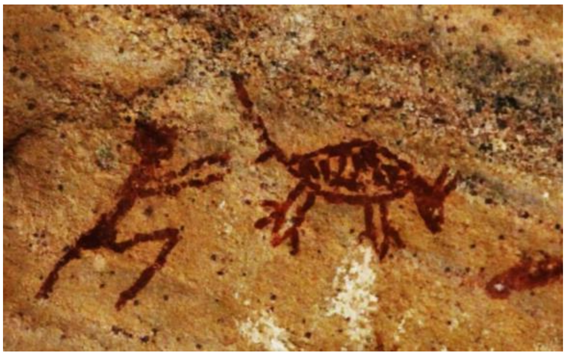

Figura 1. Pintura rupestre retratando uma cena de caça a um tatu, no Parque Nacional da Serra da Capivara, Piauí, Nordeste do Brasil. Foto Liana Sena.

Existem nove gêneros e 20 espécies reconhecidas de tatus e 12 espécies existentes são encontradas no Brasil (Quintela et al., 2020). Entre estas, a única exclusivamente brasileira é o tatu-bola *Tolypeutes tricinctus* Linnaeus 1758 (ICMBio, 2018). A espécie, juntamente com o congênere *Tolypeutes matacus*, é conhecida pela habilidade de curvar a carapaça assumindo o formato de uma bola (Fig. 2). Essa flexibilidade é viabilizada por cintas de tecido conjuntivo no dorso da carapaça, que possibilitam a curvatura do corpo até o encaixe entre o escudo encefálico e a cauda, protegendo totalmente o ventre (Eisenberg e Redford, 1999; Sanborn, 1930; Nowak, 1999). Esta estratégia parece ser eficiente contra predadores naturais, como felinos de grande porte, porém torna a espécie vulnerável a predação humana (Silva e Oren, 1993).

Figura 2. Posição de defesa do tatu-bola (*Tolypeutes tricinctus*). À esquerda, o encaixe entre o escudo encefálico e a cauda; à direita, destaque para as cintas de tecido conjuntivo que conferem flexibilidade a carapaça óssea, protegendo as partes moles do corpo. Fotos Liana Sena.

Após alguns anos sem registros pela comunidade científica, o tatu-bola foi considerado extinto na natureza (Cole et al., 1994). Entretanto, na década de 1990, pesquisadores redescobriram a espécie na Caatinga, domínio do qual era considerada endêmica (Santos et al., 1994; Silva e Oren, 1993), e em 1996 foi encontrada em uma região do Cerrado (Marinho-Filho et al., 1997), no oeste do estado da Bahia. A sua distribuição inclui registros entre nos estados do Maranhão, Piauí, Ceará, Paraíba, Rio Grande do Norte, Pernambuco, Alagoas, Bahia, Goiás e Tocantins (Santos et al., 2019; (Feijó et al., 2015). Estima-se que nos últimos 30 anos, a espécie tenha sofrido pelo menos 50% de redução nas suas populações, principalmente devido à caça para consumo da carne e a perda do habitat – desmatamento e lenha na Caatinga e expansão da agricultura no Cerrado (Reis et al., 2016). Esse cenário contribuiu para a espécie ser considerada “vulnerável” a extinção (VU) pela União Internacional para a Conservação da Natureza, pelo critério A2cd (Miranda et al., 2014) e “Em Perigo” na Lista Nacional de Espécies Ameaçadas de Extinção do Ministério do Meio Ambiente (CONABIO, 2021).

O Plano de Ação Nacional para Conservação do Tatu-bola (PAN Tatu-bola) elencou 38 ações distribuídas em 06 objetivos que abordam vários aspectos de geração de conhecimento científico, proteção e diminuição das ameaças à espécie (ICMBio, 2014). Em 2014, a espécie foi escolhida como mascote da Copa do mundo de futebol, realizada pela FIFA no Brasil. Desde então, o tatu-bola tem sido considerado como espécie bandeira para conservação da biodiversidade da Caatinga. Entretanto, apesar da sua importância e seu grau de ameaça de extinção, existem poucos estudos a respeito de sua ecologia e como a espécie responde às alterações do ambiente.

Entretanto, a amostragem de espécies não consideram a probabilidade de detecção menor do que 1 (<1) ou seja, menor do que 100%) e estão sujeitas a falhas na detecção, o que pode levar a falsas ausências (Mackenzie and Royle, 2005). Essas falhas na detecção ou detecções imperfeitas, tanto devido as falhas amostrais como baixa densidade populacional, são comuns para mamíferos tropicais de médio e grande porte, especialmente espécies crípticas e de difícil detecção.

Nesse sentido, a modelagem de ocupação proposta por Mackenzie et al. (2002) vem sendo bastante utilizada em estimativas de ocorrência das espécies por considerar a probabilidade de detecção imperfeita para corrigir falsas ausências (Mackenzie and Royle, 2005). Esta abordagem permite calcular a probabilidade de ocupação (ψ, probabilidade da espécie ocupar um sítio específico em uma determinada janela de tempo) e a probabilidade de detecção (p, probabilidade da espécie ser detectada, quando presente). A análise é feita utilizando dados de presença e ausência obtidos, por exemplo, por armadilhas fotográficas em função de covariáveis que representam hipóteses biológicas avaliadas através de modelos hierárquicos que consideram uma detecção imperfeita (p<1) (Mackenzie et al., 2002; MacKenzie et al., 2006).

Para abordar essas questões, a Tese tem como objetivo geral investigar os fatores ambientais e antrópicos que influenciam a ocupação e o padrão de atividade de *T. tricinctus* em uma área prioritária para conservação da Caatinga, o Parque Nacional Serra da Capivara

(PNSC), sudoeste do estado do Piauí, Brasil. O PNSC foi criado em 1979 e tem cerca de 130 mil hectares, sendo a área de maior concentração de sítios pré-históricos do continente americano e pinturas rupestres do mundo (Guidon et al., 2007). A extensa cobertura vegetal e diversidade de habitats contribuem para elevada biodiversidade. A área é reconhecida como Patrimônio Cultural Mundial pela UNESCO e área prioritária de conservação da Caatinga pelo Ministério do Meio Ambiente (MMA, 2016) e está inserida no contexto do Corredor Ecológico Capivara-Confusões, que se conecta ao Parque Nacional Serra das Confusões, formando um mosaico de quase um milhão de hectares (Oliveira et al., 2007).

Os objetivos deste trabalho estão alinhados com o cumprimento de metas definidas no PAN Tatu-bola (ICMBio, 2014) e buscam contribuir com as seguintes ações: “elencar elementos preditores de hábitats para ocorrência das espécies e conciliar com a modelagem de sua distribuição potencial passada, presente e futura” e “caracterizar a utilização de recursos alimentares, espaciais e temporais das espécies (*T. tricinctus* e *T. matacus*)” (ICMBio, 2014). Este estudo recebeu autorização (nº 53500-4) do Instituto Chico Mendes de Conservação da Biodiversidade (ICMBio) e do Instituto do Patrimônio Histórico e Artístico Nacional (Iphan).

A Tese está dividida em três capítulos. O primeiro capítulo quantifica a caça de mamíferos no estado do Piauí, através da compilação de dados de autos de infração entre 2008 e 2018. O segundo capítulo investiga as variáveis preditoras da ocorrência de *T. tricinctus*, como fatores ecológicos (vegetação, solo e declividade) e fatores antrópicos (assentamentos humanos, caça e estradas) usando modelos de ocupação. O terceiro capítulo investiga o padrão de atividade temporal de *T. tricinctus* e sua sobreposição com predadores e potenciais competidores, bem como a influência de variáveis espaciais no padrão de atividade da espécie.

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CAPÍTULO 01 - CAÇA ILEGAL DE MAMÍFEROS SILVESTRES NO ESTADO DO PIAUÍ, NORDESTE DO BRASIL ATRAVÉS DE AUTOS DE INFRAÇÃO

Resumo

A caça é uma atividade amplamente difundida no Brasil, inclusive em áreas protegidas. No entanto, a informação sobre a caça é escassa, principalmente devido à proibição desta atividade na maioria das situações. Analisamos os dados dos autos de infração relatados pelos órgãos ambientais federais brasileiros de 2008 a 2018 no estado do Piauí, nordeste do Brasil. Nosso objetivo foi fornecer uma visão geral das atividades de caça ilegal, identificando as espécies mais caçadas e a distribuição dos registros em áreas protegidas federais. Identificamos 935 autos de infração relacionados a caça. Os mamíferos foram as espécies-alvo entre as apreensões (n = 662, 70,8%). Aproximadamente 1.824 (~ 4,5 toneladas) carcaças de mamíferos apreendidos foram citadas, representando 17 espécies e 10 famílias, sendo sete espécies ameaças de extinção. O grupo mais caçado foi o dos tatus, seguido pelos roedores, ungulados e tamanduás. *Dasypus novemcinctus* representou 54,7% (~ 1.700 kg) de todas as espécies apreendidas. Cerca de 53% dos animais não foram identificados. Em geral, as espécies de porte pequeno e médio foram as mais caçadas. A maioria dos autos de infração de caça foi realizado dentro de áreas protegidas, indicando prioridade nos esforços de fiscalização. Nossos achados destacam a importância dos dados fornecidos pelos órgãos ambientais federais com grande poder informativo sobre atividades ilegais. Entretanto, para beneficiar sua aplicação em ações preventivas e de conservação, eles devem ser padronizados, melhorando a qualidade dos dados fornecidos e futuras análises de monitoramento em áreas protegidas.

Palavras-chave: Tatus. Espécies cinegéticas. Autos de infração. Fiscalização. Crimes ambientais.

CHAPTER 01 – POACHING PATTERNS ON WILD MAMMALS IN NORTHEASTERN BRAZIL BASED ON NOTICES OF VIOLATIONS RECORDS

Abstract

Poaching is a widespread activity in Brazil. including in protected areas. However, poaching information is scarce mainly due to the prohibition of this activity in most situations. We analyzed data from environmental notices of violation reported by Brazilian federal environmental agencies from 2008 to 2018 in Piauí, northeastern Brazil. We aimed to provide an overview of poaching activities, identifying patterns of the most poached animals and categories of federal protected areas. We found 935 reports of poaching activities. Mammals were the target species (n = 662, 70,8%). Approximately 1,824 (~4.5 ton) seized wild mammals' carcasses were cited, representing 17 species and 10 families. Seven species are in threatened lists. The most poached group were armadillos, *Dasypus novemcinctus* representing 54.7% (~1,700kg), followed by rodents, ungulates, and anteaters. About 53% of the animals were not identified. Most of the poaching records were obtained within federal protected areas. Our findings highlight the importance of the data provided by the environmental federal agencies in given great informative about poaching. Although, to help improve conservation policies, these data must be standardized improving the quality of data provided and the analysis of monitoring protected areas.

Keywords: Armadillos. Hunting species. Notes of violation; Environmental crimes.

1 Introduction

Hunting has been practiced over two million years and is one of the oldest ways of meat acquisition by humans (Bunn et al., 2017). Usually, game mammals are essential to maintain mechanisms of biological diversity and structure such as herbivory, seed dispersal and predation (Jorge et al., 2013; Peres, 1997). In tropical areas, for example, many rural and urban human populations hunt as a way of food acquisition (Bodmer et al., 1997; Parry et al., 2014), representing an important source of incomes.

Hunting and gathering wildlife are part of traditional people livelihood (Van Vliet, 2011). Currently, hunting transcends food subsistence (bushmeat nutritional) and monetary benefits (Nunes et al., 2019), and has many social values, including recreation, heritage, social and cultural identification (Castilho et al., 2018; Kahler and Gore, 2012). Game species are pursued for many purposes, including food, pet trade and medical and magical-religious activities (Alves et al., 2016a; Alves et al., 2012; Castilho et al., 2017; Nielsen et al., 2017; Souto et al., 2018), resulting in a varied range of human-wildlife interactions. Also, poaching is one of most important drivers to biodiversity loss (Dirzo et al., 2014; Young et al., 2016). The impacts of overharvesting include declines in wildlife populations's, local extinction of species (Benítez-López et al., 2017; Ripple et al., 2016), decreases in the abundance of medium and large mammals (Cullen et al., 2001, 2000; Galetti et al., 2016), as well as in their densities (Wilkie et al., 2011). In addition to the direct impacts caused by the removal of specimens from natural environments, bushmeat consumption has been associated with emergent zoonotic diseases, evidencing a risk in terms of human heath (Karesh et al., 2005; Kurpiers et al., 2015; Van Vliet et al., 2017). Therefore, understanding of role of game populations is a subject of high social concern.

Several countries have banned on the exploitation of wildlife, aiming at mitigating the increasing effects of poaching (Nasi, 2008). In Brazil, for example, activities involving persecution, capture or killing of wild animals are prohibited since 1967 (Brasil, 1967) and non-compliance results in severe penalties and include prison sentences and fines (Brasil 1998; 2008). There are few exceptions, such as subsistence hunting, allowed in Indigenous Lands and for poor rural areas to ensure food security and livelihood (Bragagnolo et al., 2019). Meanwhile, poaching, the illegal taking of wildlife in violation of laws or rules, is widely practiced throughout the Brazil (de Azevedo Chagas et al., 2015; El Bizri et al., 2015), either in surrounding or inside protected areas (Bertrand et al., 2018; Castilho et al., 2017; Constantino, 2018).

Nevertheless, as any other prohibited practice, obtaining reliable information on poaching practices is a difficult task, particularly when informants are aware of the illegality of this activity (Castilho et al., 2018). Methods to access poaching tend to be site-specific and expensive, thus, methods adequate to regional data is scarce (Swan, 2017). An alternative to this scenario has been the acquisition of official data provided by environmental authorities. In Brazil, irregularities framed according to Environmental Crimes Law - Brazil (Brasil, 1998) are framed in environmental notice of violation reports. Although there are limitations regarding the performance of the environmental agencies, this approach allows extracting fundamental information to identify patterns of poaching activities.

In this study, we provided an overview of poaching activities, in State of Piauí, northeastern of Brazil. We used data based on environmental notices of violation registered by Brazilian federal environmental agencies. We aimed to investigate the representativeness of wild mammals and discuss the implications for species conservation, especially threatened and endangered species. Also, we describe the spatial pattern of apprehension withing and off federal protected areas.

2 Methods

2.1 Study area

The state of Piauí is in the northeastern Brazil and covers an area of 251,616 km^2 (~the United Kingdom area, see Fig. 1). Piauí has a population of approximately 3.2 million people and, population density of 12.4 hab/km² (IBGE, 2010).

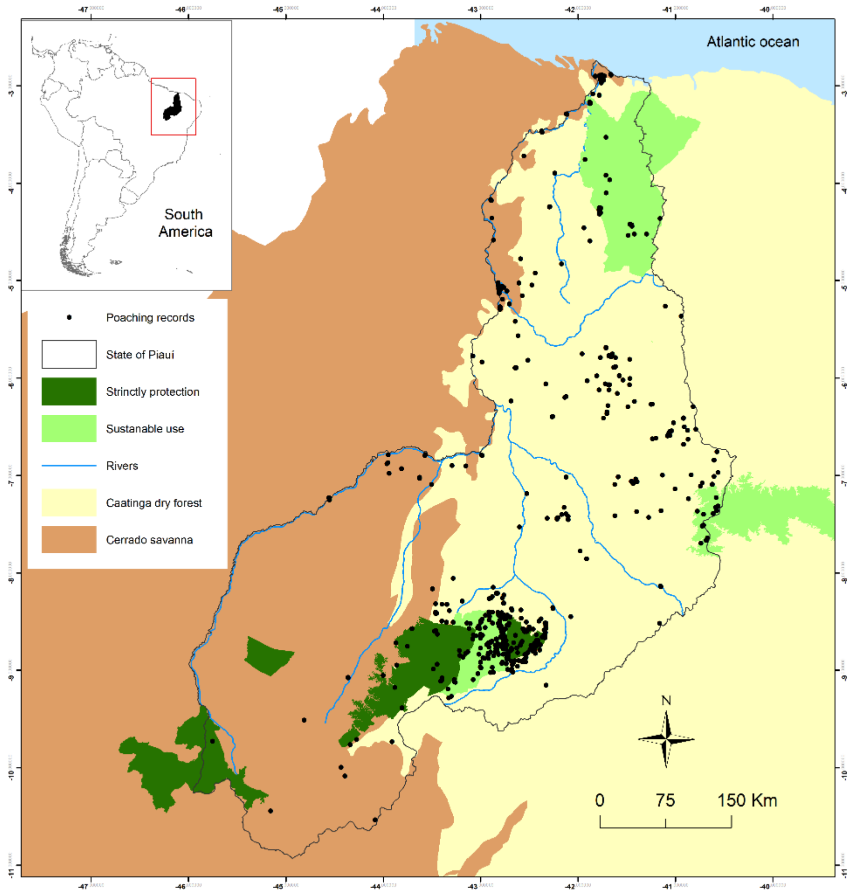

Figure 1. Location of state of Piauí, Northeastern of Brazil. Caatinga (yellow) and Cerrado (brown) vegetation cover; rivers (blue lines); federal protected areas (lighter green - sustainable use and dark green - strictly protected); poaching records from 2008 to 2018 (black points).

Among 224 municipalities, only three have more than 80,000 inhabitants, the capital Teresina, and the cities of Picos and Parnaíba. The climate is tropical and semiarid (IBGE, 2010) and harbors two biomes: tropical dry forest (Caatinga) and savanna (Cerrado) (Brasil, 2019).

2.2 Data collection

We analyzed 2,944 environmental notices of violations reported from 2008 to 2018 to extract data on poaching activities (Figure 2). The database was available by the Brazilian federal environmental agencies: Instituto Chico Mendes de Conservação da Biodiversidade (Icmbio) and Instituto Brasileiro do Meio Ambiente e dos Recursos Naturais Renováveis (Ibama). We found 935 notice of violation reports on poaching in the state of Piauí along the 10 sampling years (2008-2018), of which 662 were related to wild mammals (see fig. 2 for more details). We identified the popular names and organized species according to their taxonomic groups. For each mammal record, were counted all animals reported, the locations and periods. For the corrected database, we used the scientific name of species according to Abreu et al. (2021). However, some animals were not identified in the species level; therefore, we kept them into the genus or family level, and considered as “unconfirmed”.

2.3 Data analysis

We extracted, when possible, the number of individuals of each species recorded in each record and estimated total seized biomass per event based on literature (Abreu et al., 2021). The conservation status of each species was based on the lists of the International Union for Conservation of Nature (IUCN, 2020), the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES, 2020) and the Official National List of Fauna

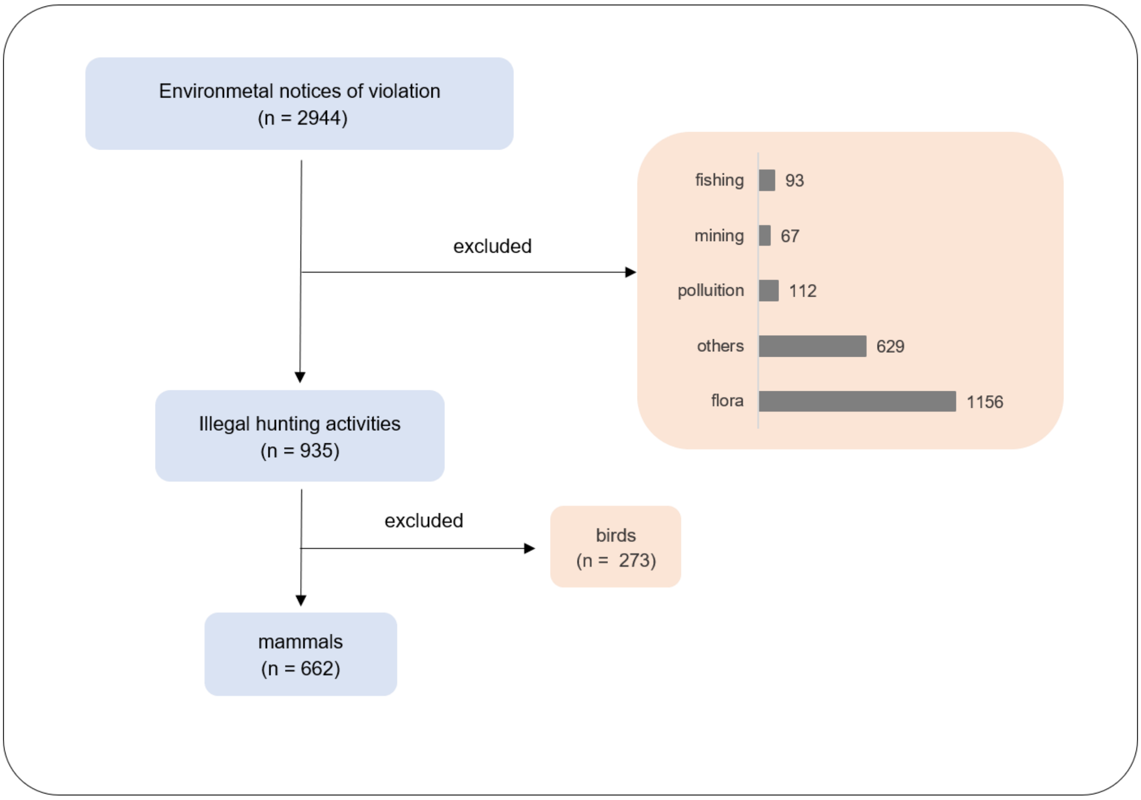

Figure 2. Data treatment of environment notices of violations reports from 2008 to 2018, in Piauí, Northeastern Brazil. The flowchart shows all illegal activities (pink) excluded from the database of environmental notice of violation, and the remaining records that reported seized mammals, totalizing 662 reports.

Endangered Species (CONABIO, 2021). When possible, we estimated the total seized biomass per event separated in three groups: small (<1.5kg); medium (>1.5 <30kg) and; large (>30kg) according to Paglia et al.(2012). Notices of violation were framed according to Federal Decree 6,514 (Brasil, 1998), which deals with administrative environmental infractions and penalties (Environmental Crimes Law - Brazil, 2008). Finally, we extract geographic coordinates of each notice of violation to investigate the density of poaching records in the studied areas, we used a point-based pattern analysis (kernel). The geographic information system (GIS) environment was created in ArcGIS 10.2 (ESRI, 2011).

3 Results

Poaching was the second most often activity cited in the environmental notices of violation reports in the state of Piauí, Brazil, between 2008 to 2018. The environmental notices of violation reports showed 875 seized wild mammals, representing 17 species and approximately 4,5 ton of carcasses (Table 1; Fig. 3). Armadillos were the most seized group (n = 656; 70.2%), followed by rodents (n = 92; 9.8%), ungulates (n = 56; 5.9%) and anteaters (n = 41; 4.4%). Unfortunately, 967 of the animals were not specifically identified by the environmental agents, and, therefore, were not included in the analysis.

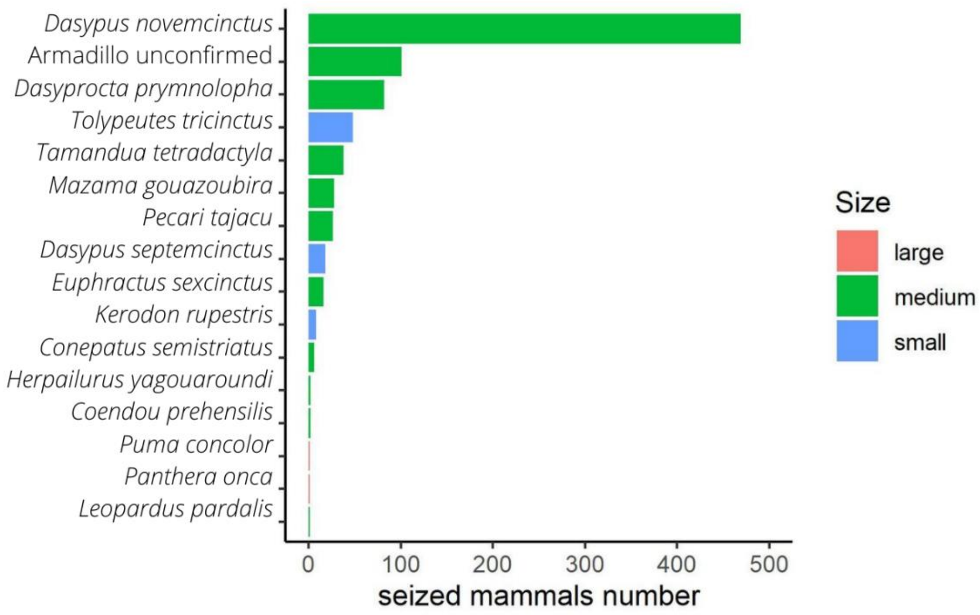

Figure 3. Number of wild seized mammal species reported in the environmental notices of violation from 2008 to 2018, in Piauí, Northeastern Brazil.

Table 1. Total and biomass of seized mammals in state od Piauí, northeastern Brazil, from 2008 to 2018. Threat categories according to IUCN (2020), CITES (2020), and Brazilian Ministry of Environment (2014). Legend: VU - Vulnerable; NT - Near Threatened; LC - Least Concern; EN – Endangered.

Specie	Popular name (English/Portuguese)	MMA	CITIES*	IUCN	Current population trend IUCN	Seizured animals	Biomass harvest (kg)
Dasypus novemcinctus	Nine-banded Armadillo / Tatu verdadeiro	-	-	LC	Stable	469	1711.85
Dasypus septemcinctus	Seven-banded Armadillo / tatuí	-	-	LC	Unknow	18	27
Euphractus sexcinctus	Yelow Armadillo / tatu-peba	-	-	LC	Stable	16	86.4
Tolypeutes tricinctus	Brazilian Three-banded Armadillo / tatu-bola	EN	-	VU	Decreasing	48	73.44
Armadillo unconfirmed	Armadillo / Tatu	-	-	-	-	101	303
Dasyprocta sp	Agouti / Cutia	-	-	LC	Unknow	82	246
Coendou prehensilis	Brazilian porcupine / coendu	-	-	LC	Stable	2	8.5
Kerodon rupestris	Rocky cavy / mocó	VU	-	LC	Stable	8	6.4
Mazama gouazoubira	Gray Brocket / Veado-catingueiro	-	-	LC	Decreasing	28	588
Blastocerus dichotomus	Marsh deer / cervo-do-pantanal	VU	II	VU	Decreasing	3	360
Pecari tajacu	Collared Peccary / caititu	-	II	LC	Stable	26	676
Tamandua tetradactyla	Southern Tamandua / tamanduá-mirim	-	-	LC	Unknow	38	197.6
Anteater unconfirmed	Anteater / tamanduá	-	-	-	-	3	
Herpailurus yagouaroundi	Jaguarundi / gato-mourisco	VU	II	LC	Decreasing	2	9
Leopardus pardalis	Ocelot / gato-maracaja	-	I	LC	Decreasing	1	9.5
Puma concolor	Cougar / onça-parda	VU	II	LC	Decreasing	1	46
Panthera onca	Jaguar / onça-pintada	VU	I	NT	Decreasing	1	109.5
Conepatus semistriatus	Striped Hog-nosed Skunk / cangambá	-	-	LC	Unknow	6	14.4
Saimiri sp	Squirrel Monkey / macaco-de-cheiro*	-	-	-	-	1	
Canis lupus familiaris	domestic dog / cachorro	-	-	-	-	248	
Bos taurus	cattle / gado	-	-	-	-	13	

*CITES (Convention on International Trade in Endangered Species of Wild Fauna and Flora); I - endangered species that are or potentially could be affected by trade. Trade in these species shall be authorized only after careful consideration and under exceptional conditions; II includes those species which, although not currently in danger of extinction, will fall into this category if their trade is not subject to strict regulations in order to avoid exploitation above the carrying capacity of the populations; III: Species included in Annex III of CITES through a declaration from any country, those whose exploitation needs to be restricted or prevented and which requires cooperation in their control, and may be allowed to be commercialized, by means of a license or certificate, by the Administrative Authority.

unfilled cells and were lacking the essential information on the seizures and species identification. Thus, the data are limited and do not completely reflect the reality of the activity or the depletion of individuals in the natural environment.

Among armadillos, *Dasypus novemcinctus* was the species with higher number of apprehensions (n = 469) followed by *Tolypeutes tricinctus* (n = 48), *Dasypus septemcinctus* (n = 18), and *Euphractus sexcinctus* (n = 16). We observed 98 citations only as "armadillo", probably because it is composed of species that receive more than one popular name in the same region, making an analysis by species imprecise.

Among rodents, *Dasyprocta* sp. (n = 82) was the most represented species. Among ungulates, two species were more frequently slaughtered: deer (*Mazama gouazoubira*) and pecary (*Pecari tajacu*). Anteaters were just represented by *Tamandua tetradactyla* (n = 38). The carnivores, which are generally vulnerable to hunting and comprise many threatened species, represented only 1.3% of the poached mammals recorded in the notices of violation. Nonetheless, carnivores were the group with the highest number of species: *Leopardus pardalis*, *Puma concolor*, *Panthera onca*, *Herpailurus yagouaroundi*, *Conepatus semistriatus*.

Seven species are in the Brazilian threatened List (see table 1). One species is considered as Endangered, the Brazilian three-banded armadillo *Tolypeutes tricinctus*, and six are considered Vulnerable: *Kerodon rupestris*, *Blastocerus dichotomus*, *Herpailurus yagouaroundi*, *Puma concolor*, and *Panthera onca*. Threatened species correspond to 10% of the total animals registered. Jaguar (*P. onca*) and ocelot (*L. pardalis*) are listed in CITES Appendix I, granting them the maximum protection from exploitation. *Blastocerus dichotomus*, *Pecari tajacu*, *Herpailurus yagouaroundi* and *Puma concolor* are listed in CITES Appendix II that includes species not necessarily threatened with extinction, but in which trade must be controlled in order to avoid utilization incompatible with their survival (CITES, 2020).

An average of 2.5 mammals were apprehended per notification (range: 1-30) and, in 85.7% of the apprehensions, up to 3 individuals not necessarily of the same species were apprehended (considering only notifications that reported the quantity of animals). The most recurrent human criminal conducts in the records were poaching, shooting, or killing (Table 2), followed by maintenance-related conducts, such as keeping in captivity. Additionally, we found 248 records of apprehension of hunting dogs (Table S2).

Table 2 – Quantity of environmental notices of violation according to human conduct and seized mammals' groups from 2008 to 2018 in Piauí, Northeastern Brazil.

Human conduct	**N**
Market /expose the sale	3
Carry	38
Stores maintain on deposit /saving / Keep in captivity	79
To practice ill-treatment	0
To hunt /Shoot /kill	223
To chase / catch / purchase	4
Use	7

Most of the poaching records (61.5%) occurred in protected areas. Our kernel density map showed a higher density of poaching activities in the north, northwestern (near capital Teresina) and mainly in the southeast region (Fig. 4). The southern region concentrated most of the poaching records, including two National Parks and one Ecological Corridor that covers more than 10,000 km² (see Table S1). Recently created Protected Areas and private reserves showed fewer records, except for Nascentes do Rio Parnaíba National Park.

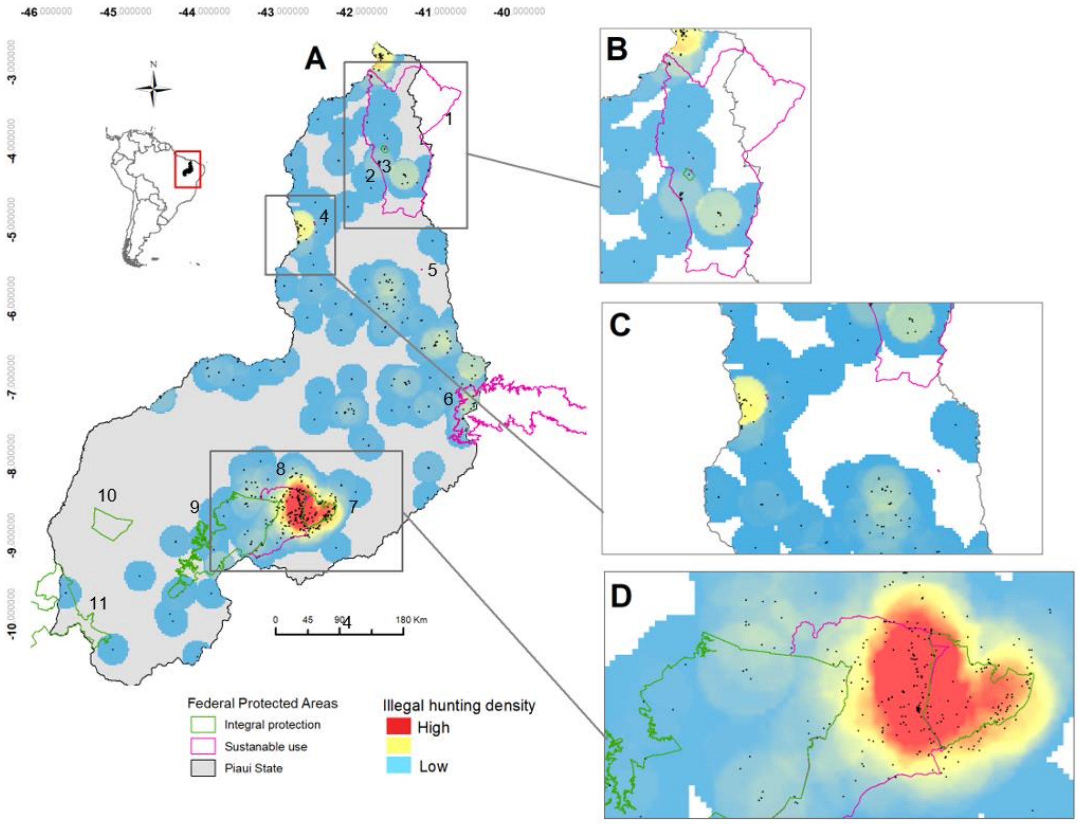

Figure 4. Density of illegal hunting records within state of Piauí, northeastern Brazil. Integral protected areas are in green and sustainable use reserves in pink (**a**). The inserts show locations with high number of poaching records in the North region (**b**), near the State capital (**c**), and south region (**d**). The black points represent each notice of violation records between 2008 and 2018. The numbers represent the protected areas: Ibiapaba Environmental Protected Area (1); Sete Cidades National Park (2); Recanto da Serra Negra Private Reserve (3); Palmares National Forest (4); Dunas Douradas Private Reserve (5); Chapada do Araripe Environmental Protected Area (6); Serra da Capivara National Park (7); Capivara-Confusões Ecological Corridor (8); Serra das Confusões (9); Uruçuí-Una Ecological Station (11).

4 Discussion

Poaching activities were the second most important from the environmental notices of violation reported in state of Piauí, Brazil, from 2008 to 2018. Mammals were the target species (n=662, 62.4%), representing 17 species and 10 families. We found 3 species of them being threatened according to IUCN, 6 cited by the Brazilian red list, and 6 being listed in CITES appendices.

Armadillos were the most hunted animals. Factors such as taste preferences, perception of good quality of the meat, and the fact that it is relatively common and easy to capture may have contributed to the poaching status (Alves et al., 2016a). Because some species are relatively more disturbance tolerant, armadillos are relatively abundant in many areas of the Caatinga (Marinho et al., 2018; Campos et al., 2019), however, poaching pressure has already caused the decline of populations or their local extinction in other areas of the domain (Bezerra et al., 2014).

Armadillos presented the highest number of seized individuals. Only *Dasypus novemcinctus* represented 54.7% (~1,700kg) of seized mammals. The main target species reported here are the same as those affected by subsistence hunting and trade by rural populations in northeastern Brazil (Almeida et al., 2018; Alves et al., 2016b; 2012; Barboza et al., 2016; de Azevedo Chagas et al., 2015; El Bizri et al., 2015; Dantas-Aguiar et al., 2011; Miranda and Alencar, 2007), as well as for sport or leisure (Barboza et al., 2011). In the Amazon, target species is consistently skewed towards larger body size, yielding the greatest amount of meat per unit of energy or time allocated (Jerozolimski and Peres, 2003). In the Caatinga, persecutions seem less selective, with many game vertebrates weighing less than 3 kg (Fernandes-Ferreira, 2014), possibly as a result of strong historical defaunation, and not of hunters' preference (Albuquerque et al., 2018; Fernandes-Ferreira and Alves, 2017). This may explain the low number of ungulates, and high number of rodents in the notice of violation reports in this study.

Some game vertebrates are already threatened according to the MMA, IUCN and CITES (see Table 1). Species that have declining population trends, as species with fewer puppies per litter and long intervals between reproductive cycles, are more susceptible to extinction (Bodmer et al., 1997). Hunting seems to be the main cause of extinction of *Priodontes maximus,* the giant armadillo, in the Serra da Capivara National Park (Olmos, 1995). This fact highlights the need to estimate the possible impacts of poaching on wildlife, for example, *T. tricinctus,* an endemic and threatened armadillo, that draw more attention to conservation strategies, since it has poor scientific knowledge available on its biology.

Most apprehensions had 3 individuals or less. However, one half (48%) of the notification's reports were not clear in reporting the number of carcasses or live animals. Many reports were related to the illegal transportation of tools or hunting instruments, and illegal possession of weapons. Additionally, the notification forms do not have a specific field for identifying the species seized and their quantity. Therefore, filling in this information is not a duty. We believe that it explains the several unfilled cells and the lack of essential information on the seizures. Domestic dogs were widely used for hunting in our study area, which reinforce the sociocultural importance of these animals' in hunting and chasing armadillos (Neto-Vasconcelos et al., 2012). Furthermore, we found a variety of apprehended tools that are used in the pursuit of digging animals, such as shovels, hoes, or tools developed to capture animals in burrows, corroborating a tendency to specialize in the practice of hunting of these animals (Barboza et al., 2011). Probably because the armadillo bushmeat consumption supports a profitable commercial chain, including the market of specialized tools, traps, weapons, and the market of hunting dogs.

Our results show that the occurrences of poaching records were unevenly distributed within state of Piauí. Most of the records were in or around protected areas. However, as pointed out by Constantino (2018), these results should be interpreted with caution. The amount of seizures depends on enforcement effort, and the proximity of environmental agencies offices (Constantino, 2018; Swan, 2017). This fact can explain the high concentration of notices of violation in these areas and is possibly a reflection of the prioritization by federal environment agencies in monitoring this region. An example is the Serra da Capivara National Park, that until 2016, had an internal policing system, which means budget for vehicles, fuel, and park rangers, essential to improve federal policing planning. Moreover, we noticed that protected areas that have had few records do not have a management plan. Without this document, PAs do not have their priorities defined and, consequently, planning for resource allocation. The management plan is also a document that facilitates raising funds for purchasing equipment and acquisition of infrastructure, which are fundamental actions for the implementation of protection actions (ICMBio and WWF-Brasil, 2015).

Prehistoric rupestrian paintings show humans with deer, armadillos, and peccaries in hunting scenes, demonstrating the presence of this game mammals in the diet of these human populations in region (Cavalcante et al., 2017; Guidon et al., 2007). Still, they are an important source of food, commercial ends (illegal markets), or sport (leisure and entertainment) (Barboza et al., 2011; Souto et al., 2019). Armadillos, rodents and ungulates present high resilience to anthropized environments, but many of them play important roles in maintaining mechanisms of biological diversity and structure such as herbivory, seed dispersal and predation (Cullen et al., 2000; R. Dirzo et al., 2014; Guimarães et al., 2008; Redford, 1992). Thus, despite the economic and cultural significance of game vertebrate for the people in the State of Piauí, their depletion can cause the loss of important ecological services. Moreover, the bushmeat consumption of armadillos, especially *D. novemcinctus* and *E. sexcinctus*, has been associated with the transmission of zoonosis of public health relevance. Handling or just the contact with contaminated biological fluids and soil particles can increase the risk of contamination of zoonotic diseases, such as Hansen´s disease (Antunes et al., 2006; da Silva et al., 2018; Ferreira et al., 2020), Chagas´s disease (Capellão et al., 2016), and pulmonary mycosis (Eulalio et al., 2001).

Furthermore, it is necessary to investigate why people have difficulty in obeying the rules related to fauna legislation. Remaining gaps related to drivers, such as population density, deforestation, roads, and social vulnerability need to be clarified. This understanding is crucial to efficient allocation of resources in inspection. Additionally, we recommend standardization of federal databases on environmental crimes, to allow the detailing of information related to species identification, quantities and enable the use of better estimators. This information can be used by local managers, who are fundamental decisions-makers about the monitoring and prevention of fauna-related crimes in their territories. The official data can be used to improve planning and prevention among urban and rural zones and around the Protected Areas.

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Appendix A – Federal protected areas

Table S1. Summary of federal protected areas included in the analysis. Overall information and absolute number of poaching activities in Piauí, Northeastern Brazil.

Protected area class	Protected area Category	Name	IUCN	State	Biome	Management plan	Area* (km²)	poaching (n)**
Strictly protected	National Park	Serra da Capivara	II	PI	Caatinga	no	1,353.9	195
	National Park	Serra das Confusões	II	PI	Caatinga, Cerrado	yes	8,238.4	79
	National Park	Nascentes do Rio Parnaíba	II	PI, MA, BA	Cerrado	no	2,580.4	3
	National Park	Sete Cidades	II	PI	Caatinga, Cerrado	yes	63.0	1
	Ecological Station	Uruçui-Unã	Ia	PI	Cerrado	no	1,351.2	0
Sustainable use	Environmental Protection Area	Serra da Ibiapaba	V	PI, CE	Caatinga	no	12,647.4	50
	Environmental Protection Area	Chapada do Araripe	V	PI, CE, PE	Caatinga	no	1,479.6	39
	National Forest	Palmares	VI	PI	Caatinga, Cerrado	no	1.7	1
	Ecological Corridor	Capivara Confusões	V	PI	Caatinga	no	4,012.3	208
	Private Reserve	Dunas Douradas		PI	Caatinga, Cerrado	no	0.9	0
	Private Reserve	Recanto da Serra Negra		PI	Caatinga	no	1.7	1

*corresponding area in Piauí.
** Inside a 5km buffer zone.

Appendix B – Poaching tools

Table S2 – Summary of hunting tools poaching reported in the environmental notices of violation from 2008 to 2018, in Piauí, Northeastern Brazil.

Poaching tools	**N**
Fire arms	153
Fire arms for armadillos	341
Digging tools (hoe / scythe / shovel)	148
Trap for armadillos (jequi)	45
Trap for médium size mammals (aratraca)	24
Hunting dogs	248

CAPÍTULO 02 – FATORES QUE INFLUENCIAM O USO DO HABITAT POR TATU-BOLA TOLYPEUTES TRICINCTUS NA CAATINGA, NORDESTE DO BRASIL

Resumo

Compreender como as espécies são influenciadas pelas condições ambientais e pelos distúrbios causados pelo homem continua sendo uma questão central em ecologia e conservação. O tatu-bola *Tolypeutes tricinctus* é a menor e única espécie endêmica de tatu no Brasil. Nesse estudo buscamos entender fatores que influenciam a probabilidade de ocupação e a detecção de *T. tricinctus* usando dados de armadilhas fotográficas de 47 sítios de amostragem localizados no Parque Nacional Serra da Capivara (PNSC), nordeste do Brasil, entre janeiro e setembro de 2018. Medimos 12 covariáveis locais que presumimos afetar a ocupação (ex: solo, vegetação, caça ilegal) e detecção (ex: esforço amostral e estação seca ou chuvosa). Obtivemos 118 registros independentes nos locais (ocupação naive = 0.49), com 9.801 armadilha/dia. A ocupação de *T. tricinctus* aumentou com densidade de cobertura vegetal (w_+ = 0.62) e nenhuma outra variável afetou esse parâmetro. A detecção de *T. tricinctus* foi positivamente influenciada pelo esforço amostral (número de dias que as câmeras funcionaram, w_+ = 0.82) e foi maior na estação seca. A densa cobertura vegetal representa habitat de maior qualidade para a espécie, por representar proteção contra temperaturas extremas e ainda maior disponibilidade de recursos. Apesar da forte pressão de caça na área de estudo, as ações de proteção e fiscalização parecem beneficiar a persistência de *T. tricinctus*.

Palavras-chave: Cingulata. Modelos de ocupação. Armadilhas fotográficas. Caça.

CHAPTER 02 – HABITAT USE OF THE ENDANGERED BRAZILIAN THREE-BANDED-ARMADILLO IN THE CAATINGA DRYLANDS, BRAZIL.

Abstract

Understanding how species is influenced by environmental conditions and human-caused disturbances remains a central question in ecology and conservation. The Brazilian three-banded-armadillo *Tolypeutes tricinctus* is a small, threatened, and the only endemic living armadillo in Brazil. Here, we explore how *T. tricinctus* occupancy and detectability probability are affected by habitat. We conduced camera traps survey and modeled factors affecting occupancy and detection for *T. tricinctus* at 47 sites in Serra da Capivara National Park (SCNP), northeastern Brazil, during January-September 2018. We measured 12 covariates at camera sites presumed to affect occupancy (*i.e*. soil, vegetation, poaching), and detection (*i.e.* effort and season). We obtained 118 records at 23 sites (naïve occupancy = 0,49) thought 9,801 camera trap-days of effort. *T. tricinctus* occupancy increased as dense vegetation cover (w_+ = 0,62). *T. tricinctus* detection was positively affected by effort (camtrap-days w_+ = 0,82) and was higher in the dry season than in the rainy season. Our results showed that dense vegetation cover may represent higher-quality habitats for *T. tricinctus*, and protection against extreme temperatures and high availability of resources. Despite the strong hunting pressure in the study area, the protection and inspection actions seem to benefit the persistence of *T. tricinctus*.

Keywords: Cingulata. Occupancy models. Camera traps. Poaching.

1 Introduction

Species distribution is driven by landscape patterns and amount of suitable habitat. Habitat is usually defined by the suite of resources (food and shelter) and environmental conditions (abiotic and biotic) where survival and reproduction of a population, and fitness can be found (Gaillard et al., 2010). However, these set of conditions usually vary across the landscape (Anacleto et al., 2006), thereby providing a gradient between suitable habitat (the species is present) and unsuitable habitat (the species is not present). Worldwide, forests are under increasing pressure because demands on agriculture and forest products, urbanization, and infrastructure development (Bestelmeyer et al., 2015; Leberger et al., 2020), which have implications for animal persistence. This highlights the importance of understanding the species distribution and their responses to threats are essential for realistic species conservation strategies (Mace et al., 2008).

The armadillos (Cingulata: Clamyphoridae) are the most widespread xenarthrans distributed throughout South America. These mammals are semi-fossorial, present a typical carapace, and are poor thermal regulators (McNab, 1985; Superina et al., 2014). In general, spatial distribution of armadillos is influenced by climate, topography, vegetation cover, and land uses changes (Abba et al., 2015; Feng et al., 2016; Zimbres et al., 2013, 2012). Soil has important direct effects on armadillos through its role as a foraging substrate (McDonough et al., 2000) and has indirect effects as a primary driver of vegetation structure (Arteaga and Venticinque, 2012). Additionally, the association between armadillos and human dates back to ancient times (Superina and Abba 2020). Recent studies showed that human activities directly and indirectly affect the distribution of armadillos, causing population decline or local extinctions (Peres and Nascimento, 2006).

The emblematic Brazilian three-banded-armadillo *Tolypeutes tricinctus* Linnaeus, 1758 is the only armadillo endemic to Brazil (Carmignotto and Astúa, 2018; Gutiérrez and Marinho-Filho, 2017). The two *Tolypeutes* spp. species have the unique ability to roll their bodies into an almost perfect ball as a defense mechanism (Wetzel et al., 2008; Eisenberg and Redford, 1999; Sanborn, 1930). The species occur in the Caatinga dry forest and Cerrado of Brazil (Silva and Oren, 1993; Santos et al., 1994; Feijó et al., 2015). It also plays an important role as flagship species for conservation efforts, especially after it was chosen as a mascot of the FIFA World Cup 2014 in Brazil (Bernard and Melo, 2019; Melo et al., 2014). However, despite this famous campaign, there is a limited number of studies on *T. tricinctus* (Magalhães et al 2020; Martins et al., 2020; Attias et al., 2016; Bocchiglieri et al., 2010; Marinho-Filho and Guimarães 2010; Santos et al., 1994; Guimarães, 1997) and many gaps remain about their ecology.

T. tricinctus population has declined more than 50% in the last 30 years (Reis, et al., 2016), which led the species to be classified as Vulnerable by the International Union for Conservation of Nature (IUCN, Miranda et al., 2014) and as Endangered by the Brazilian Ministry of Environment (CONABIO, 2021). Ongoing habitat loss and degradation and exploitation have been considered the main threats to *T. tricinctus*. In the Brazilian Caatinga dry forests, main occurrence domain, half of its the original cover has been modified due to human activities (Antongiovanni et al., 2018). The remaining fragments are exposed to extensive anthropogenic disturbance (Ribeiro et al., 2015), such as agriculture and cattle ranches, poaching, charcoal production and exploitation of non-timber products, practices that remains since during since colonization periods in the XVI century (Leal et al., 2005). Despite these threats, the Caatinga has only 7% of its territory within protected areas, and 1.7% are under strict protection (Antongiovanni et al., 2020).

Therefore, a crucial goal is to identify the set of predictors that can promote or decrease the occurrence of this species within a specific location.

We addressed this challenging by applying a presence/absence modelling framework to estimate site occupancy and detection probabilities of *T. tricinctus*). The occupancy analysis allows counting patches or sites potentially occupied by species instead of counting animals, which is useful for cryptic and non-identifiable species (Mackenzie et al., 2006; Mackenzie et al., 2002). We conducted a camera trapping survey in one large remnants of Caatinga dry forest and a priority area for biodiversity conservation, the Serra da Capivara National Park, in southern state of Piauí, Brazil, (MMA, 2016) to determine the environmental, anthropic, and methodological variables that predicted the occupancy (Ψ) and detection (p) probabilities of *T. tricinctus*.

We believe that, due to its small body size, the burrow building activity would be even more challenging for *T. tricinctus* (Attias et al., 2016). Thus, we hypothesized that *T. tricinctus* would prefer locations with physical characteristics that reduce its effort expended to digging burrows, such as sandy soils (Abba et al., 2015) and sloping terrain (Arteaga and Venticinque, 2008), where armadillo use less energy than they would to excavate a flat area. Therefore, we expected a positive relationship between the *T. tricinctus* Ψ and sandy and less dense soil, and sloping terrain sites. Vegetation cover can provide microhabitats that would make temperature regulation easier, especially in an semiarid environment (Attias et al., 2018; Maccarini et al., 2015), and constitute a greater availability of shelters and foraging sites (Anacleto and Diniz, 2008). We expected a positive relationship between the *T. tricinctus* Ψ and more complex habitats (*e.g.*, high NDVI and density of larger trees). Additionally, we evaluated if the presence of other insectivorous species (*Tamandua tetradactyla*, *Myrmecophaga tridactyla* and *Dasypus* *novemcinctus*) would negatively influence the *T. tricinctus* Ψ, as the species may adopt a spatial segregation strategy to avoid competition.

In relation to human-related features, accessibility and proximity to human settlements has been identified as a predictor for illegal activities within protected areas (Ferreguetti et al., 2018; Xavier da Silva et al., 2018), and has been shown to be a strong threat to armadillos (Abra, 2019; Ascensão et al., 2019; Ribeiro et al., 2017). Thus, we predicted that the *T. tricinctus* Ψ would be higher in areas far from human settlements and roads, because these areas are subjected to lower disturbance to the fauna (Marinho et al., 2018). Hunting of wildlife has been prohibited by law in Brazil since 1967, except for subsistence or under specific circumstances (Bragagnolo et al., 2019). Because it is an illegal activity, hunting, hereinafter, will be referred as poaching. Assuming that *T. tricinctus* is sensitive to poaching, we expected its occupancy probability to be negatively influenced by the poaching activity (Ferreguetti et al., 2016).

We also explored variables that may cause changes in the *T. tricinctus* detection probability (Mackenzie et al., 2006) among site locations. Because armadillos may use trails to move throughout the landscape (Attias et al., 2018), we expected a higher *T. tricinctus* detection in camera traps installed on trails compared to those installed off trails. Finally, we predicted a positive relationship between the number of days the camera operates (i.e., sampling effort) and the *T. tricinctus* detection probability. These *a priori* hypotheses were conducted to attend goals of the National Action Plans of *Tolypeutes* spp. (ICMBio, 2014). as well as to subsidize decision-makers responsible for conservations policies in Brazil.

2 Methods

2.1 Study area

This study was conducted in Serra da Capivara National Park (acronym, SCNP, Fig. 1), in southern state of Piauí, Brazil, which is a protected area of 129,953 hectares of seasonally tropical dry forest, managed by the Brazilian environmental agency. The climate is classified as tropical hot and dry and receives approximately 689 mm of precipitation annually, most falling between October and April (Pessis et al., 2014). The elevation varies between 280 and 600 m and the topography consist of a main plateau (*Chapadas* in Portuguese), intersected by steep cliffs, with deep, long canyons (*Boqueirões* in Portuguese). The vegetation structure is a mosaic from deciduous thorn scrubs and semideciduous dense forest with tall canopy cover.

The vegetation in these canyons is composed of semi-deciduous and mesic forests with tall canopy cover. The pedological survey identified the following soil classes: Red Latosol, Red-Yellow Latosol, Yellow Latosol, Bruno Latosol, Haplic Cambisol, Litosol Latosol and Quartzarenic Latosol (Santos, et al., 2012). Inside the SCNP there are no natural water bodies, but a system of artificial water channels and ponds built to provide water to wild animals by the Park administration.

The SCNP harbors the most important archaeological sites in the Americas, recognized as World Heritage site by UNESCO, and is also located in a large forest fragment of Caatinga. Nevertheless, a federal highway BR-020 cuts the park, facilitating access to poachers and road kills, both are the main threats to medium and large mammals.

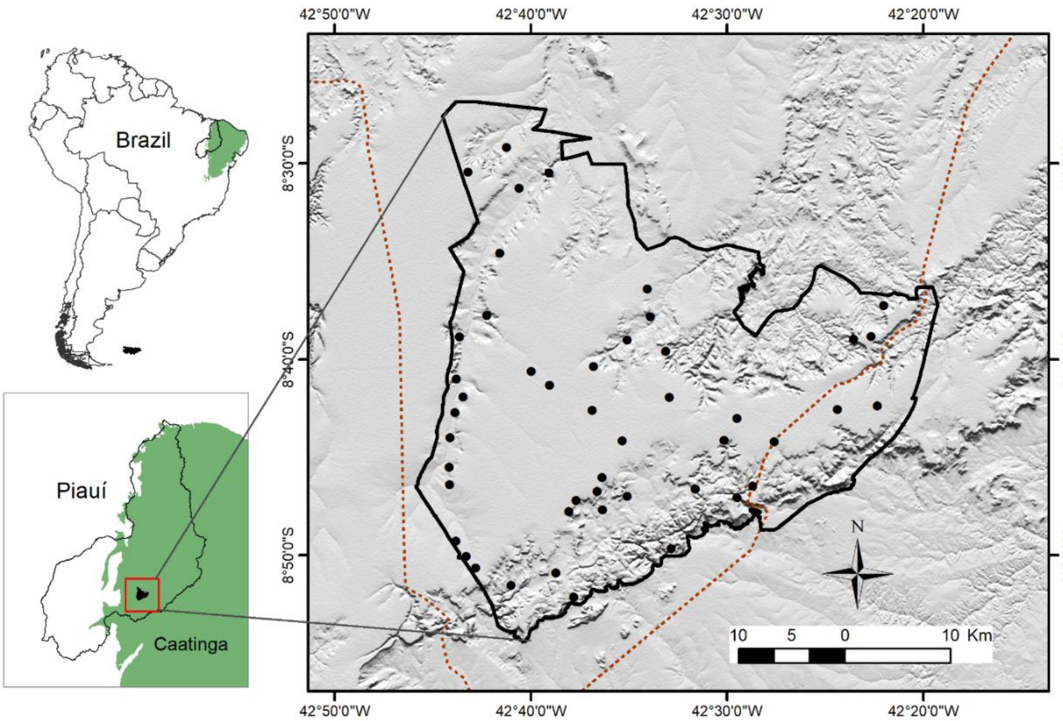


Figure 1. Serra da Capivara National Park within the Caatinga domain (green area in the insert map of Brazil), state of Piauí, northeastern Brazil. Location of the 47 camera trap sites (black dots) for sampling *T. tricinctus* and paved roads (brown dotted line).

2.2 Sampling design and covariates selection

We randomly selected 53 sampling sites within the SCNP limits. Due to the lack of roads or geographic barriers, some points were relocated to places where access was possible, considering the shortest distance from the previously selected point. To calculate the sampling effort, we excluded and discontinued camera traps units that were stolen or did not operate (n = 6), remaining 47 sites (Fig. 1). To collect data on *T. tricinctus* occurrence, one camera trap (Bushnell®) was installed at each sampling site with a mean distance of 2.68 km (range: 1.23 – 6.33 km) between adjacent traps. Cameras were placed either on (n=25) or off (n= 22) trails approximately 30-40 cm above the ground, and no baits were used. The camera traps were programmed to operate for 24 hours using a passive infra-red motion sensor. We set the cameras to record three photos every 1-minute interval. When the option was video, it was 10 seconds long. For each image or video, we saved the date and time of the record. The study period encompassed 240 days of sampling, being 120 days in each of the rainy (January to April) and dry seasons (May to September) 2018. For the following analyses, only images taken one hour apart were considered as 487 independent records to minimize pseudoreplication (Lucherini et al., 2009). They were 488 checked every 30-45 days for memory card and battery replacement.

2.3 Data analyses

We used hierarchical occupancy models and maximum likelihood estimator (Mackenzie et al., 2002; MacKenzie et al., 2006) to estimate the probabilities of occupancy (ψ, the probability that a sample site is occupied by a target species) and detection (p, the probability of detecting a target species at sampling site *i* at time or survey *t*, given the site is occupied). In these models, detection (1) and non-detection (0) histories are built over multiple surveys (or sampling occasions) for each sampling units and model parameters (ψ and p) can be modeled as function of predictor variables (Mackenzie et al., 2002). Occupancy models account for imperfect detection ($p < 1$) or false absences.

We selected *a priori* 15 covariates we believed would influence the occupancy and detection of *T. tricinctus* in the Caatinga drylands based on previous knowledge about this and other related armadillo species. To estimate soil physical characteristics, we dig out a trench (approximately 1 × 1 × 1 m) in each sample site using a spade. Soil samples were collected from layers above 40 cm deep (surface layers) and placed in appropriate containers for moisture conservation and transportation. To estimate percentage of particle-size fractions (clay, silt, and sand) in each soils layer, we performed the pipette and sodium hydroxide method according to Santos et al. (2005). To estimate bulk density, we collected sample soil of each layer using a manual cylinder and analyzed the samples with volumetric-flask method (Santos et al., 2005). We considered soil density as dry soil mass and total volume (g/m^3) including spaces occupied by air and water (Santos et al., 2005). To determine density of large trees, we counted plants with >5 cm circumference at 1 meter above ground in plots of 10 m × 5 m at each site. We used the Normalized Difference Vegetation Index (NDVI) as a vegetation biomass cover predictor, derived from Landsat 5 TM images with 30-m spatial resolution using software ArcGis 10.2. The declination of terrain at each sampling site in percentage was obtained through Shuttle Radar Topographic Mission data (SRTM) with 90 m of horizontal resolution and 1 m of vertical resolution (http://srtm.csi.cgiar.org). To create the declination map (percentage), we used the *slope* function in the software ArcGis 10.2.

To investigate the influence of potential competitors (*Dasypus novemcinctus*, *Mirmecophaga tridactyla* and *Tamandua tetradactyla*) on *T. tricinctus* occupancy probability, we estimated the conditional occupancy probability ($\psi_{conditional}$) of all competitors combined for each site using the single-season occupancy model in Program Presence (Hines, 2006). The $\psi_{conditional}$ here was used as a probability of potential competitors were present at a site given it was sampled; if any potential competitor were detected at a site, $\psi_{conditional} = 1$ (MacKenzie et al., 2006).

To investigate the influence of anthropogenic features on the *T. tricinctus* occupancy probability, we used linear distance (Euclidean) to the nearest human settlements considering agrarian and rural communities (http://www.ibge.gov.br/home; http://www.incra.gov.br/), and the linear distance to the nearest roads using software

ArcGis 10.2. For poaching activities, we considered either (1) records of poachers and dogs from camera traps or (2) records obtained by active searches (firecamps, poachers footprints, hunting tools and robbery) within a 1 km buffer surrounding each sampling site. Then, we combined the presence/absence records from camera traps and the active searches at each site to estimate the $\Psi_{\text{conditional}}$ of poaching in Program Presence (Hines, 2006). Given that approximately one-half of the cameras were deployed on trails, which is used for tourism or maintenance of the SCNP, we considered whether the camera was installed on (1) or off (0) "trail" as a site predictor variable that may have influenced the *T. tricinctus* detection probability. Finally, we recorded the number of days the cameras operated at each sampling site to explore the effect of this predictor variable on the *T. tricinctus* detection probability.

Then, we performed a Pearson's correlation test in software R version 3.5.1 (R Development Core Team 2016) to investigate for strong correlated predictor variables ($|r| \geq 0.70$). We found highly correlated predictor variables and decided to exclude soil particle density, soil porosity, clay, silt, and distance from the park edge (see Supplementary Information S1). This final set of 11 covariates were divided into environmental, anthropogenic, and methodological variables, and all were measured at each sampling site (Table 1).

2.4 Occupancy and detection probabilities

We combined the *T. tricinctus* detections during the 240 days of sampling into ten-day periods (occasions) to compose detection histories for each site and season (rainy and dry). Specifically, we recorded whether the camera detected *T. tricinctus* (1) or not (0) during each of the ten-day occasions. Using these data, we first explored possible changes in occupancy state between seasons (i.e., evaluated the closure assumption) using a dynamic occupancy model (MacKenzie et al., 2003). We fit two models, where the dynamic parameters (local colonization, γ and extinction, ε) were either estimated (i.e., occupancy state is dynamic between seasons) or fixed to zero (i.e., occupancy state is static between seasons).

Table 1. Predicted variables used to model occupancy (Ψ) and detection probabilities (p) of *T. tricinctus* in Serra da Capivara National Park, Northeastern Brazil. The mean and range (minimum-maximum) are presented for each covariate and its expected positive (+) or negative (-) effects are given for each parameter. Legend: NA - not applied.

Predicted variables	**Code**	**Mean and range (minimum-maximum)**	**Ψ**	***P***
Methodological				
Season	seas	1 (rainy) or 0 (dry)		
Effort (days) in the rainy and dry season	days	111 days (50 - 120) 102 days (0 - 120)	NA	+
Trail	trail	1 (on-trail) or 0 (off-trail)	NA	+
Environmental				
Percentage of sand	sand	80.59% (37.95 - 93.59)	+	NA
Soil density	soil	1.50 g/m³ (0.64 - 1.65)	-	NA
Declination of terrain	slope	6.34% (1.06 - 39.24)	+	NA
Normalized Difference Vegetation Index	ndvi	0.4984 (0.1206 - 0.6055)	+	NA
Density of larger trees	tree	20.75 (12.59 - 34.6)	+	NA
$\Psi_{conditional}$ of competitors	comp	0.69 (0 to 1)	-	NA
Anthropogenic				
Distance to human settlements	hum	8.05 km (1.98 - 16.19)	-	NA
Distance to roads	road	8.56 km (0.27 – 21.25)	-	NA
$\Psi_{conditional}$ of poaching	poach	0.45 (0 to 1)	+	NA

Using Akaike's Information Criterion adjusted for small sample size (AICc) (Burnham et al., 2011), the model with a dynamic occupancy between seasons was best supported (ΔAICc = 7.32; for the model with the dynamic parameters fixed as zero). Because our original sampling design was not focused on factors influencing the dynamic parameters (γ and ε) and our main goal was to investigate variables influencing the *T. tricinctus* occupancy probability, we did not use a dynamic occupancy approach. Instead, we used a single-season occupancy model (Mackenzie et al., 2002) with 12 occasions (for each season) and evaluated for seasonality effects on *T. tricinctus* occupancy and detection in our subsequent analysis.

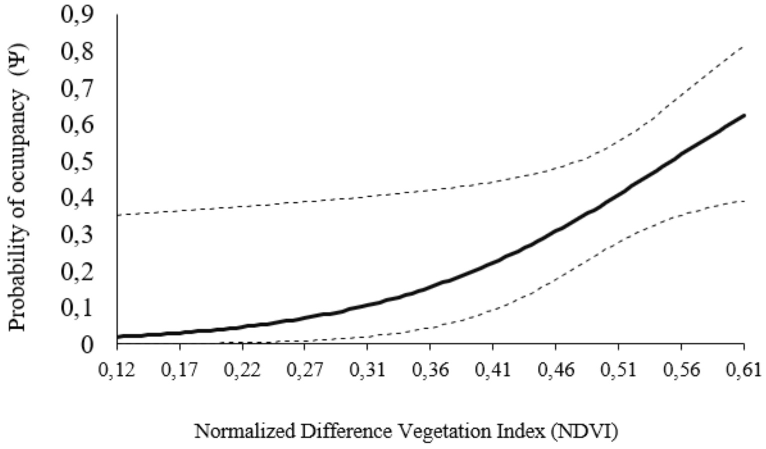
The single-season occupancy model was ran in Program MARK (White and Burnham, 1999) to determine the influence of the selected predictor variables on the probabilities of occupancy and detection of the *T. tricinctus* in our study area. As our primary objective was the identification of the predictor variables that have the greatest effect or influence on the probabilities of occupancy and detection, we adopted a model selection strategy based on all possible combinations contemplated by our *a priori* hypotheses. Specifically, we built 1093 models (see Table S2) based on all the possible additive predictor variable combinations for occupancy and detection probability. This approach resulted in a set of balanced models (Doherty et al., 2012), which allowed us to calculate the accumulative AICc weights (w_+) of each covariate and evaluate which were the most likely ($w_+ \geq 0.50$) to influence the occupancy and detection probabilities of the *T. tricinctus* (Burnham and Anderson, 2002).

We checked for a possible lack of independence (overdispersion) among sites using the goodness-of-fit test in Program PRESENCE version 2.12.20 (Hines, 2006). Then, we used the estimates from the occupancy probabilities models to generate prediction maps for the *T. tricinctus* distribution in the study area using the *Kriging* function in the software ArcGis 10.2.

3 Results

We obtained 118 records of *T. tricinctus* in a total effort of 9,801 camera trap-days. The goodness of fit test revealed no evidence of overdispersion ($\hat{c}$ = 0.3092; χ^2 = 19563.9736; p = 0.33) 0.0001). *T. tricinctus* was observed in 23 of the 47 sampling sites (*naïve* occupancy = 0.49) and occupancy probability of 0.38 (95% CI = 0.25 - 0.53). Consistent with our *a priori* hypothesis, the *T. tricinctus* occupancy probability showed a strong positive relationship with NDVI (w_+ = 0.61; Fig. 2a; Table 2), indicating that the species occupy with dense vegetation cover sites. All other covariates had w_+ <0.30 and did not influence the *T. tricinctus* occupancy probability (Table 2). The *T. tricinctus* detection probability was influenced by season (w_+= 0.72), being higher in the dry season (p = 0.15; 95% CI = 0.08 - 0.25) than in the rainy season (p = 0.08; 95% CI = 0.03 - 0.14). Also, the *T. tricinctus* detection probability was positively influenced by the number of days on that camera were operational (w_+ > 0.80; Fig.2b), but whether or not the cameras were installed on trails did not influence species detection (Table 2).

a)



b)

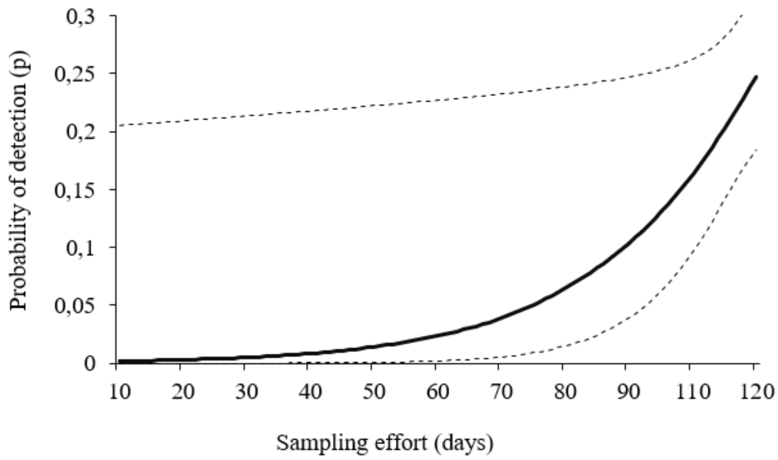


Figure 2. *T. tricinctus* occupancy and detection probability at 47 sample sites within the Serra da Capivara National Park, Northeastern Brazil. a) occupancy probability as function of the Normalized Difference Vegetation Index, and b) detection probability as function of the sampling effort (*i.e.*, the number of days the camera operates). Estimates are from the most parsimonious model that included the covariates. The black line indicates the estimated covariate relationship and the black dash indicate the upper and lower 95% CI.

Table 2. Cumulative AICc weights, beta coefficient estimates (*β*) and their respective standard errors (SE) and 95% confidence intervals (CI) for the covariates used to model the probabilities of occupancy (Ψ) and detection (*p*) of *T. tricinctus* in the Serra da Capivara National Park, Northeastern Brazil. The estimates of the effects of the covariates (*β* parameters) were obtained from the most parsimonious model that included each covariate. The Ψ was modeled as a function of season (seas), sand percentage (sand), soil density (soil), slope (slope), NDVI (ndvi), density of larger trees (tree), distance from nearest human settlements (hum), distance from nearest roads (road), $\Psi_{conditional}$ of competitors (comp) and $\Psi_{conditional}$ of poaching (poach). The *p* was modeled as a function of season (seas), trail (trail) and effort (days, the number of days on which the cameras were operational).

Covariate	Cumulative AICc Weights	*β* parameters			
		Estimate	**Standart error**	**Lower 95% CI**	**Upper 95% CI**
Ocuppancy (Ψ)					
ndvi	0,61	9,08	4,12	0,85	17,31
slope	0,34	-0,06	0,04	-0,16	0,02
hum	0,22	0,09	0,06	-0,02	0,21
sand	0,13	0,02	0,02	-0,02	0,07
soil	0,12	-0,64	1,73	-4,04	2,74
road	0,11	-0,06	0,05	-0,17	0,04
poach	0,11	-0,24	0,68	-1,57	1,09
tree	0,10	0,00	0,02	-0,04	0,05
comp	0,11	0,40	0,57	-0,72	1,52
psi-seas	0,10	0,27	0,60	-0,91	1,45
Detection (*p*)					
days	0,81	0,04	0,02	0,00	0,09
p-seas	0,72	-0,76	0,32	-1,40	-0,12
trail	0,15	-0,37	0,31	-0,97	0,23

Our predictive maps generated from the most parsimonious model show that the *T. tricinctus* has few sites with high occupancy probability, and moderate probability in the western and central portion of the study area (Fig. 3).

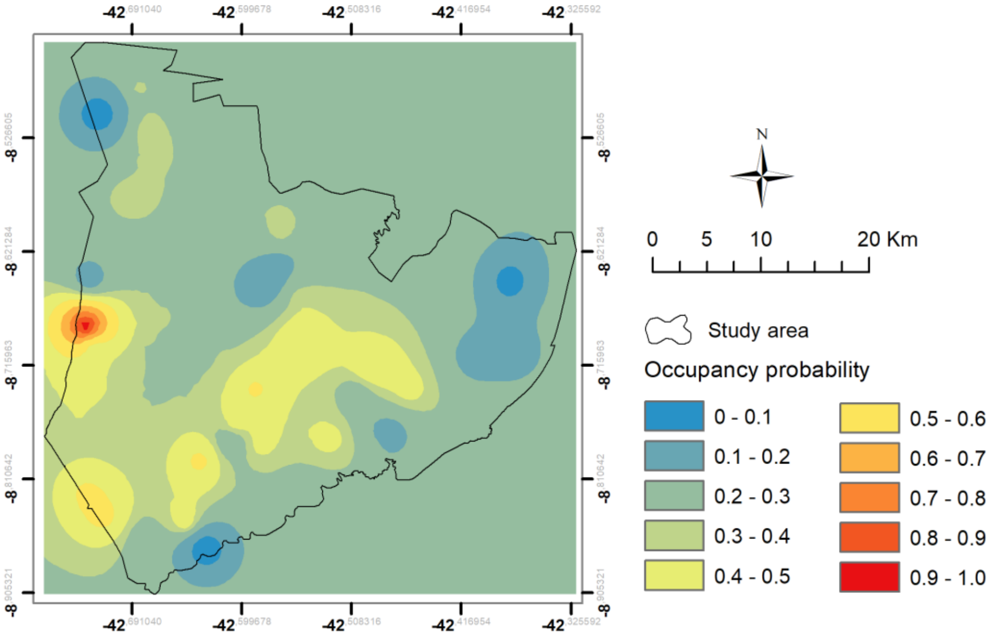


Figure 3. Predicted estimates of *T. tricinctus* occupancy probability in the Serra da Capivara National Park, Caatinga dry forest, Northeastern Brazil; the most parsimonious occupancy model: Ψ (NDVI + hum) *p* (seas + days) was used.

4 Discussion

Our findings support the hypothesis that dense vegetation cover favors the occurrence of the *T. tricinctus*. Research have shown the positive relationship between the amount of native forest cover and occurrence of armadillos within and off protected areas (Abba et al., 2016; Ferreguetti et al., 2016; Rodrigues and Chiarello, 2018). In a semiarid environment, areas where plants remain green (or lost their leaves lately) throughout periods of drought create a soft microclimatic condition that may act as thermal and humidity shelters for animals with low metabolic rates. In the SCNP, temperatures can range 50°C in hottest days (Figueiredo and Puccioni, 2006), an air temperature breadth outside the armadillo´s thermoneutral zones (Maccarini et al., 2015).

Moreover, sites with dense vegetation cover indicates better habitat quality and invertebrate's availability (Oliveira et al., 2017; Ribeiro-Neto et al., 2016; Vasconcellos et al., 2010; Viana et al., 2014). Invertebrates are widespread in semiarid environments, even under different levels of anthropogenic disturbance, been a resource rarely lack in the Neotropical region. However, in the rainy season, it could be expected *T. tricinctus* to behave as expected for generalist species, when the species must broad the diet and opportunistically feeding on roots of tuber plants, due to high availability of this items (Bolković et al., 1995). This could explain *T. tricinctus* occurrence in areas with different density of larger trees. Additionally, sites with low density of larger trees generally had a thorny shrub stratum difficult to penetrate. A small armadillo that roll up into a ball as self-defense strategy, it is probably benefited by thorny scrub vegetation to protect itself from natural predators, such as jaguars and pumas (Taber, 1997). Thus, this finding reflects the importance of the amount of suitable habitat for *T. tricinctus*, since they can exploit a range of resources or behavior needs in dense vegetation cover of arboreal and in shrub caatinga.

The lack of influence of the sand content and soil density on the occupancy probabilities of *T. tricinctus* may be related to the characteristic of the soils of our study area. In our sampling sites, latosols were predominant, with high clay content and low soil density (1.25 to 1.60 g/cm^3). This soil characteristics facilitates the excavation of burrows. *T. tricinctus* can also find shelter in shallow excavations, leaf-litter, and bromeliads, that does not depend on physical soil attributes, such as density. *T. tricinctus* builds small burrows (burrow entrances 10.5 ± 1.4 cm high, 14 ± 2.9 cm wide, and depth of over 30 cm, Attias et al., 2016), therefore, they are less dependent on deep burrows (Rotondi, 2016). On the other hand, soil physical characteristics variables may need a wide scale to present greater variation in characteristics.

In Caatinga, sandy soils are typical of shrubby plants adapted to drought, with tuberous roots (*e.g.* cassava), or corn and bean crops (Embrapa, 1997). These soils are often used for rudimentary agricultural practices, such as slash-and-burn agriculture (Costa et al., 2016; Pinheiro et al., 2013; Salviano et al., 2016). These practices are historically carried out across the semiarid region. In general, Xenarthra species are susceptible to brush fires, probably because the inability to move quickly (Prada and Marinho-filho, 2008; Rodrigues et al., 2008). For example, local communities have identified local extinction of *T. tricinctus* after fires, in western of Piauí (Sena, 2017). This is of great concern, because periodic burning may repeatedly reduce the population to low numbers and might then lead to an eventual loss of evolutionary potential (Rodrigues et al., 2008).

Surprisingly, our results did not show a negative influence of anthropic activities on the occupancy probability of the *T. tricinctus*. Armadillo bushmeat consumption dates to ancient time and is still an important part of the culture of the people who live in the Caatinga region (Alves 2016; Barboza 2016; Albuquerque et al. 2018). The centuries of hunting for subsistence, poaching and illegal trade likely contributed to the extinction of species or declines in extant populations (Superina and Abba 2018; Cione et al. 2003). The SCNP is the most policed protected area in the state of Piauí (see Chapter 01) and the management practices might mitigate the currently poaching pressure and logging (Miranda and Alencar, 2007) contributing to the persistence of *T. tricinctus*. Alternatively, this apparent lack of poaching effect would be a bias in our sampling. Because we had eight stolen camera traps (tow of then were replaced), this fact reflects in a considerable number of missing historic of detection of poaching activities among those sites. Therefore, effects of poaching may be underestimated here.

During our sampling, we recorded one roadkill event of *T. tricinctus* in SCNP (Júlio F. Bastos, pers. comm. Fig. S1c), but that does not mean that roadkill is not a potential threat to the species in the region. Perhaps, game vertebrate carcasses are quickly removed by drivers to use of the meat (Abra, 2019). We assume that *T. tricinctus* has similar biology with its congener *T. matacus*, presenting low population growth and long generation length, with one and sometimes two cubs per gestation (Wetzel et al., 2008). Thus, the removal of just one individual, by poaching or roadkill, can have a major impact on its population, as expected for other armadillos (Fontes et al., 2020).

Previously studies have shown the *T. tricinctus* occurrence in anthropogenic gradients both in the Caatinga (Campos et al., 2019; Magalhães, 2020; Santos et al., 1994) and in some areas of the Cerrado (Bocchiglieri et al., 2010; Guimarães, 1997; Marinho-Filho et al., 1997). However, due to the biological traits of the species, the accelerated change in the landscape in the Caatinga and Cerrado can drastically affect its persistence. According to Santos et al. (2019), in a data paper that compiled the largest data set on abundance and occurrence of Neotropical Xenarthrans, for example, Ceará, Paraíba and Sergipe States have no longer recent records of *T. tricinctus*. Modeling research suggest that *T. tricinctus* is far from being adequately protected, due to the small number of reserves in their distribution (Zimbres et al., 2012), probably because Caatinga dry forest has been historically neglected by conservation efforts (Fonseca et al., 2018). The importance of protected areas for conservation of biodiversity are critical in face of climate change and increasing in land uses, which are expected to expand in Caatinga (Oliveira et al., 2012). New approaches to measure chronic anthropogenic disturbance in Caatinga revels that strictly protected areas functions as repositories of native fauna in a human modified landscape context (Alves et al., 2020; Antongiovanni et al., 2020). However, the expansion of protected areas has been a challenge given its high costs and inefficiency in achieving its objectives. Therefore, to improve *T. tricinctus* conservation throughout its distribution, our results support the need for maintenance in forest cover and encourage coexistence between people and wildlife, considering that armadillos in general are much appreciated for bushmeat consumption.

Our models suggested that the detection probability was higher in the dry season. In this critical period, many wild mammals tend to increase their activity and travels to explore a wider range of places in search of food resources that are scarcer, so they might be more detected (Marinho et al., 2020). *T. tricinctus* was the most recorded armadillo in the SCNP, followed by *Dasypus novemcinctus* and *Euphractus sexcinctus*. The number of days the camera operates among sampling sites was the most important covariate for detection probability of *T. tricinctus*. Semi-fossorial habits, mainly nocturnal and solitary behavior (Wetzel et al., 2008) may contribute to low detectability of *T. tricinctus* in the wild. This result reinforces the need to maximize the number of sampling days to ensure reliable modelling using camera traps, especially if other methods that are also effective, such as active search (Magalhães et al, 2020), are not available.

In summary, our study suggests that the occurrence of *T. tricinctus* was higher in areas with dense vegetation cover, and the species inhabiting sandy neosoils and latosols, and a moderate level of anthropogenic pressures is tolerated. This represent a step forward for little known endemic and threatened armadillo in the Caatinga dry forest. Thereby, we stress the need of identifying more suitable areas for better understanding of habitat requirements and anthropic responses. Also, we believe that the persistence of the *T. tricinctus* broad distribution can be better explained by local scale variables, such as agricultural management practices and human-wildlife interactions.

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Appendix A – Predicted variables correlation matrix

Table S1 – Predicted variables correlation matrix used in occupancy models of *T. tricinctus* in the Serra da Capivara National Park, Northeatern, Brazil.

Predicted variables	days	soil density	particle soil density	porosity	clay	sand	silt	slope	ndvi	tree	human	road	edge	competitor	poaching
days	1														
soil density	-0.06	1													
particle soil density	0.06	0.10	1												
porosity	0.05	-0.90	0.26	1											
clay	0.13	-0.03	-0.11	-0.10	1										
sand	-0.14	0.01	0.07	0.10	-0.98	1									
silt	0.14	0.04	0.07	-0.10	0.76	-0.87	1								
slope	0.16	-0.33	-0.01	0.38	-0.12	0.10	-0.03	1							
ndvi	0.02	-0.11	-0.06	0.05	0.08	-0.08	0.06	-0.04	1						
tree	0.06	-0.02	0.15	0.17	-0.21	0.18	-0.06	0.25	-0.31	1					
human	0.04	0.26	0.26	-0.22	0.16	-0.18	0.21	-0.29	-0.14	-0.14	1				
road	0.00	0.21	0.17	-0.21	-0.04	0.00	0.11	-0.25	0.16	-0.31	0.63	1			
edge	0.10	0.27	0.27	-0.21	0.21	-0.26	0.35	-0.31	0.13	-0.02	0.69	0.70	1		
competitor	0.38	0.21	-0.15	-0.27	0.19	-0.15	0.04	-0.26	-0.08	-0.08	0.27	0.10	0.21	1	
poaching	-0.27	-0.15	-0.12	0.12	-0.22	0.24	-0.27	-0.11	-0.15	-0.10	-0.21	-0.28	-0.35	-0.16	1

Appendix B – Model selection results

Table S2 - Model selection results for the top 10 models consisting of the probabilities of occupancy (Ψ) and detection (*p*) of *T. tricinctus* in the Serra da Capivara National Park, state of Piauí, Brazil.

Model	AICc	Delta AICc	AICc Weights	Num. Par	Deviance
psi(ndvi+hum) p(seas+days)	**433.5012**	**0**	**0.05973**	**6**	**420.5357**
psi(days+slope+ndvi) p(seas)	**433.5874**	**0.0862**	**0.05721**	**6**	**420.6219**
psi(ndvi) p(seas+days)	**434.0513**	**0.5501**	**0.04536**	**5**	**423.3695**
psi(ndvi}) p(seas+days+trail)	**434.9364**	**1.4352**	**0.02914**	**6**	**421.9709**
psi(sand+ndvi) p(seas+days)	**435.2627**	**1.7615**	**0.02475**	**6**	**422.2972**
psi(slope) p(seas+days)	435.7946	2.2934	0.01897	5	425.1128
psi(ndvi+poach) p(seas+days)	435.8388	2.3376	0.01856	6	422.8733
psi(seas+ndvi) p(seas+days)	436.1271	2.6259	0.01607	6	423.1616
psi(soil+ndvi) p-seas+days	436.1835	2.6823	0.01562	6	423.218
psi(soil+slope) p(seas+days)	436.2032	2.702	0.01547	6	423.2377

Appendix C – *Tolypeutes tricinctus* pictures

Supplementary Figure 1. *Tolypeutes tricinctus* records between January to September 2018 in Serra da Capivara National Park, Piauí, Brazil: (a) Individual foraging in latosol and arboreous vegetation cover site, (b) Individual in sandy soils and scrub vegetation site, (c) record of a roadkill in PI-140 highway (Foto: Júlio Filho).

CAPÍTULO 03 - PADRÃO DE ATIVIDADE DE TATU-BOLA TOLYPEUTES TRICINCTUS EM UMA ÁREA PROTEGIDA DE CAATINGA, NORDESTE DO BRASIL.

Resumo

Fatores que influenciam os padrões de atividade temporal da maioria dos Xenarthra, especialmente os tatus, são negligenciados. Esse trabalho busca estimar o padrão de atividade do tatu-bola, uma espécie pouco conhecida, endêmica e ameaçada no Brasil. Avaliamos se a partição de atividade temporal pode ser um possível mecanismo por trás da coexistência de *Tolypeutes tricinctus*, um competidor subordinado, com competidores dominantes e simpátricos (*Dasypus novemcinctus*, *Euphractus sexcinctus*, *Myrmecophaga tridactyla e Tamandua tetradactyla*) e se o *T. tricinctus* exibe segregação temporal com seus principais predadores (*Panthera onca* e *Puma concolor*). Adicionalmente, avaliamos se fatores ambientais e antrópicos que afetam o padrão temporal do tatu-bola. Nossos resultados mostraram que a atividade dessa espécie é predominantemente noturna e crepuscular, com sobreposição temporal com competidores, exceto *E. sexcinctus*, e predadores. Nossa análise também sugere que o tatu-bola se tornou mais noturno na presença de predadores, uma possível estratégia de comportamento para evitar predadores. Nosso estudo contribui para entender a ecologia comportamental de um pequeno tatu ameaçado, sobre suas interações interespecíficas.

Keywords: Ciclo circadiano. Armadilha fotográfica. Estatística circular. Tatus.

CHAPTER 03 - ACTIVITY PATTERNS OF THE BRAZILIAN THREE-BANDED ARMADILLO (*Tolypeutes tricinctus*) IN PROTECTED AREA ON CAATINGA DRY FOREST, NORTHEASTERN BRAZIL

Abstract

Although the patterns of temporal activity in most mammal species are well known, factors that influence the patterns of temporal activity in most Xenarthra, especially armadillos, are neglected. This work aims to estimate the activity pattern of *Tolypeutes tricinctus*, a little known, endemic, and endangered species. We used camera trap data from 47 sample sites in the Serra da Capivara National Park, northeastern Brazil, collected between January of September 2018. We assessed whether the partition of temporal activity could be a possible mechanism behind the coexistence of *T. tricinctus*, a subordinate competitor, with dominant and sympatric competitors (*D. novemcinctus*, *E. sexcinctus*, *M. tridactyla* and *T. tetradactyla*) and whether the armadillo exhibits temporal segregation with its main predators (*Panthera onca* and *Puma concolor*). Additionally, we evaluated if environmental and anthropic factors would affect the temporal pattern of *T. tricinctus*. Our results showed that the *T. tricinctus* is predominantly nocturnal and crepuscular, with temporal overlap with competitors, except E. sexcinctus, and predators. Our analysis also suggests that this armadillo constrained its activity in the presence of predators, adjusting its pattern by becoming more nocturnal, as a way of avoiding predator behavior. Our study contributions to understand behavioral ecology of a threatened small armadillo on its interspecific interactions.

Keywords: Circadian rhythms. Temporal partitioning. Camera trapping. Temporal overlap. Armadillos.

1 Introduction

The activity patterns represent temporal strategies of the species to deal with environmental conditions, regulate their interspecific interactions and maximize foraging (Ashby, 1972; Hazlerigg and Tyler, 2019). Several factors can modify activity patterns, such as abiotic (e.g. lunar cycle, temperature) and biotic factors (e.g. exploitative competition, agonistic interaction, predation risk) (Prugh and Golden, 2014). The expansion of human activities can also influence the temporal pattern of animals. For example, species may have a more concentrated period of activity as a reaction to human persecution, becoming more nocturnal (Benítez-López, 2018; Gaynor et al., 2018).

Ecological differentiation generally involves aspects of habitat, feeding and climate, or a combination of them (Kronfeld-Schor and Dayan 2003; MacArthur, 1958). Temporal segregation is a mechanism that species ecologically similar can use to avoid competition (Kronfeld-Schor and Dayan, 2003). When dietary separation could not be a strategy to decrease competition between species, temporal or spatial segregation may contribute to reduction in interspecific competition (Schoener, 1974) and thus favor their long-term coexistence. Additionally, species may have anti-predator behaviors, adjusting their activity patterns to avoid presence those of species (Foster et al., 2013; Harmsen et al., 2011; Huck et al., 2017; Pratas-Santiago et al., 2017; Soria-Díaz et al., 2016).

Nevertheless, activity patterns are poorly understood in many species due to the logistical constraints involved in measuring activity when animals are elusive, constraints which limit the accuracy and resolution of activity data across space and time (Zhang et al 2015). Such constraints have limited the knowledge available on the activity patterns of a symbolic threatened species as *Tolypeutes tricinctus* (Brazilian three-banded armadillo). *T. tricinctus* is a small and the endemic armadillo known for its ability of rolling its body into an almost perfect ball. It typically occurs in Caatinga dry tropical forest, in the semiarid of northeastern Brazil, and Cerrado savannas of central region (Gutiérrez and Marinho-Filho, 2017).

To date, information on activity patterns of the *T. tricinctus* is limited to studies conducted in the 1980s and 1990s (Santos, 1993; Silva and Oren, 1993). These earlier studies reported that *T. tricinctus* was crepuscular (active at dawn and dusk), nocturnal in Caatinga and Cerrado savannas, except for Bocchiglieri (2010), which found cathemeral pattern (active between dusk and dawn) in Cerrado. However, in general, the activity period of *T. tricinctus* was detected with low number of observations and the non-correlation with habitat features.

Our study is the first to use camera trap data on an analysis on temporal niche of *T. tricinctus.* Our objectives were (i) to describe activity patterns, (ii) to examine patterns of segregation or temporal overlap among potential competitors and predator’s species, and (iii) the relationships with ecological and anthropogenic factors at SCNP. Due to its small body size (1 to 1.5 kg), we assume *T. tricinctus* as subordinate competitors (Anacleto, 2007; Guimarães, 1997), thus, we hypothesized that it would show significant differences in the temporal activity with dominant competitors (*D. novemcinctus*, *E. sexcinctus*, *M. tridactyla* and *T. tetradactyla*) that present different temporal pattern (Attias et al., 2018), but their daily cycle are poorly studied in the Caatinga domain.

Also, we tested if activity patterns of *T. tricinctus* segregate with their main predators (*Panthera onca* and *Puma concolor* (Taber et al., 1997), that are typically nocturnal in the Caatinga (Astete et al., 2017; Dias et al., 2019) .Additionally, we investigated predictor variables that would affect the temporal activity of *T. tricinctus* at the Serra da Capivara National Park (SCNP), a protected area in the Caatinga dry forest of state of Piauí, Northeastern Brazil. We expected the crepuscular-noctural activity of *T. tricinctus* to be enhanced in areas with a high occupancy probability of predators and competitors. Likewise, we expected *T. tricinctus* to be more nocturnal in areas closer to anthropic disturbance (human settlements and roads), and poaching pressure. These features are surrogates of human presence, and thus *T. tricinctus* may use these areas only during the night hours when human activities are presumably lower.

2 Methods

2.1 Study area

The Serra da Capivara National Park (SCNP) is a protected area of 129,953 hectares established in 1979 in Southeastern state of Piauí, in Northeast Region of Brazil (Figure 1). The local climate is hot and semiarid with summer rains (Ayoade, 1996). The average annual temperature is 28°C, maximum of 50°C and minimum of 10°C. The rainy season extends from October to April, characterized by an irregular rainfall regime (concentrated in 3-4 months) with an average annual precipitation of approximately 689 mm (Pessis et al., 2014). In the SCNP prevails a caatinga deciduous and arboreal forest and the vegetation structure varies from shrublands to relatively dense forests (Emperaire, 1984).

2.2 Sampling design

Armadillos' records were obtained through camera trapping between January and September 2018, totaling a sampling effort of 9,801 camera-days along a total of 47 sampling units. In each sampling unit was installed one camera trap (model Bushnell®), approximately 30-40 cm above the ground, either on or off trails, without the use of baits. Camera traps remained active in the field programmed to operate continuously for 24 h using passive infra-red motion sensor. We set the cameras to record three photos every 1-minute interval. When the option was video, it was 10 seconds long. For each image, we saved the date and time of the record. For the following analyses, only images taken one hour apart were considered as independent records to minimize pseudoreplication (Lucherini et al., 2009). They were checked every 30-45 days for memory card and battery replacement.

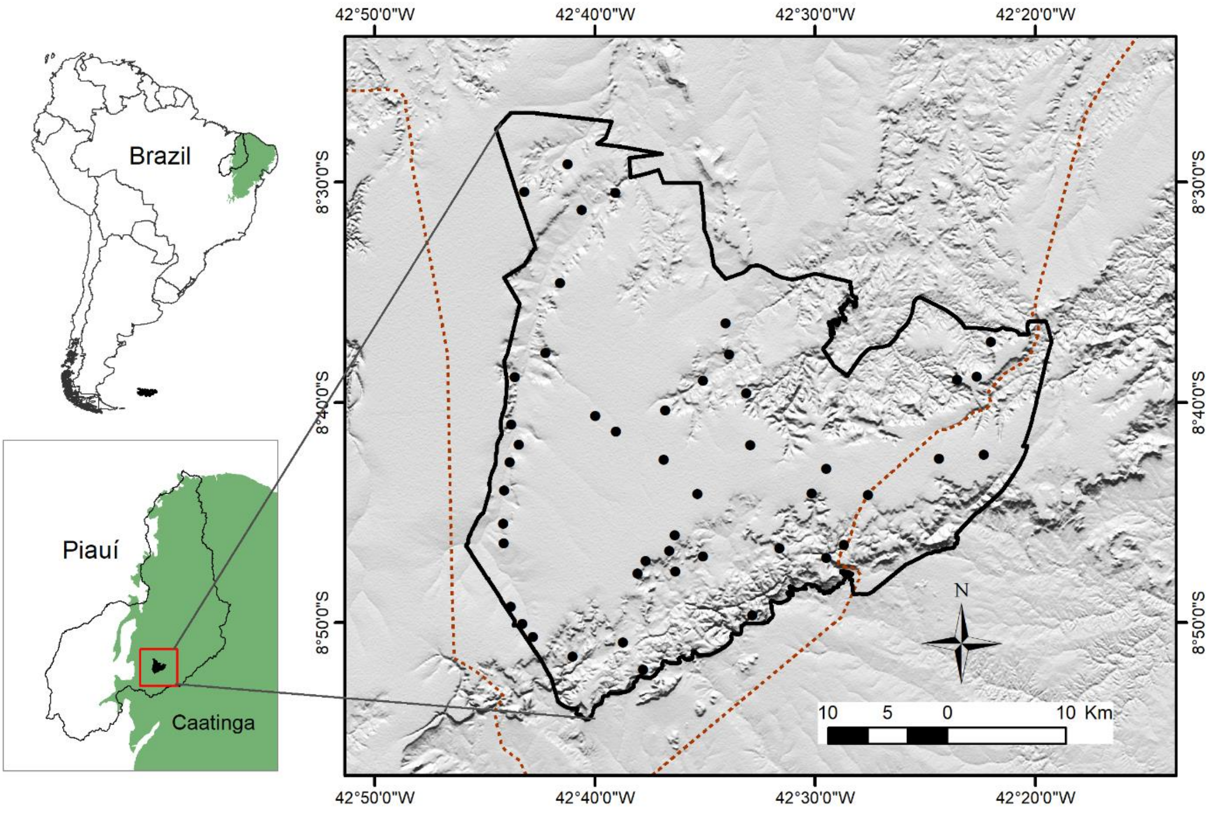

Figure 1. Serra da Capivara National Park (08°26’50” S and 08°36’34” W) within the Caatinga domain (green area in the insert map of Brazil), state of Piauí, northeastern Brazil, from January to September 2018. Location of the 47 camera trap sites (black dots) for sampling *T. tricinctus* and paved roads (brown dotted line).

2.3 Data analyses

The temporal activity patterns of the species were defined based on the timing of independent records obtained from the camera traps, separated by 1 (one) hour apart (Harmsen et al., 2011). To define the exact time of sunrise and sunset, we used the software Tropsolar 5.0 (Cabús, 2015). For sunrise the average value was 05:54 am, while for sunset, the average value was 06:14 pm. Daytime was defined in between 06:55 am to 05:14 pm (one hour after the sunrise and one hour before the sunset); nighttime from 07:15 pm to 04:54 am (one hour after the sunset and one hour before the sunrise); crepuscular time in between 04:55 to 06:54 am and 05:15 to 07:14 pm (Monroy-Vilchis et al., 2011).

We used the Rayleigh test to assess whether the activity of the species is homogeneous throughout the circadian cycle or directed to some period of the day, using the Oriana v.4 software (Kovach Commuting Services, Wales, UK). Completely, activity of *T. tricinctus* and the competitors and predators were classified into four categories: diurnal, when < 15% of the observations were at night; nocturnal, when > 85% of the observations at night; mostly diurnal, when 15-35% of the observations at night; mostly nocturnal, when 65-85% of the observations at night; crepuscular, when 50% of the observations during the crepuscular period; and cathemeral, peaks of activity through the diurnal and nocturnal period (Porfirio et al., 2016).

We estimated the density of the activity of each species by kernel density, a nonparametric approach that evaluates the probability function of the density of a random variable (Worton, 1989), using the R package overlap (Meredith and Ridout, 2018; R Development Core Team 2012). Then, to investigate the temporal overlap between three-banded-armadillo and its competitors and predators, we calculated the most adequate overlap coefficient (Δ), which varies from 0 (no overlap) to 1 (complete overlap) (Meredith and Ridout, 2018). We used the Δ_1 estimator, indicated for small samples ($n \leq 75$; (Meredith and Ridout, 2018; Ridout and Linkie, 2009). The strength of the temporal interaction between the species of interest was classified as low overlap ($\Delta \leq 0.5$), moderate overlap ($0.5 < \Delta \leq 0.75$), and high overlap ($\Delta > 0.75$) (Monterroso et al., 2014). To complement the coefficient of overlap, we used the Mardia-Watson-Wheeler Test to compare the 24 h cycles between *T. tricinctus* and potential competitors and predators species in the software Oriana v.4 (Kovach Computing Services, Anglesey, UK), following Monterroso et al., 2014).

Additionally, we explore the direct spatial influence of biotic, environmental, and anthropic on the temporal activity of *T. tricinctus* (Table 1). We estimated the conditional occupancy probability ($\Psi_{conditional}$) of top predators (puma and jaguar) and competitors (armadillo and anteaters) for each camera site using the single-season occupancy model in program PRESENCE (Hines, 2006). The $\Psi_{conditional}$ is defined as the probability of a target species were present at a site given it was sampled (MacKenzie, 2006). To explore the influence of vegetation cover, we used the Normalized Difference Vegetation Index (NDVI), derived from Landsat 5 TM images with 30-m spatial resolution using software ArcGis 10.2. To investigate the influence of anthropogenic features on the *T. tricinctus*' activity pattern, we used linear distance (Euclidean) to the nearest human settlements considering agrarian and rural communities (http://www.ibge.gov.br/home; http://www.incra.gov.br/), and the linear distance to the nearest roads, using software ArcGis 10.2. Additionally, we estimated the $\Psi_{conditional}$ of poaching activities by combining the (1) records of poachers and dogs from camera traps and the (2) records obtained by active searches (firecamps, poachers footprints, hunting tools and robbery) within a 1 km buffer surrounding each sampling site. We tested for correlation among these variables, but none was highly correlated ($r \leq 0.60$, Table S1).

We first tested for overdispersion and we did not found extra-binomial variation (*c-hat* = 0,85), so we compared candidate models using Akaike Information Criterion AICc because our small sampled size (Burnham and Anderson, 2002). We considered the variables from the top-ranked models (i.e., models with ΔAICc ≤ 2) as the most likely to explain the activity of *T. tricinctus* (Burnham and Anderson, 2002). Then, we used these variables as predictor variables in a generalized liner model (GLM) with a binomial distribution, where the response variable was the proportion of nocturnal *T. tricinctus* registers (*i.e.*, registers between 1 h after the sunset and 1 h before the sunrise) at each site (Table S1). The GLM analysis was performed in R using the package AICcmodavg (Mazerolle, 2020).

Table 1. Variables expected to influence the temporal activity of *T. tricinctus* in Serra da Capivara National Park, northeastern Brazil. Mean and range (minimum–maximum) of each variable are given. NDVI are given within a 1-km-radius buffer around each camera site. Distances from the camera sites to the nearest human settlements and paved road. Psi (Ψ) conditional is the probability that predators (puma and jaguar), competitors (armadillos and anteaters) or poaching were present at a site given it was sampled.

Covariate	**Mean and range (minimum-maximum)**
Normalized Difference Vegetation Index	0.53 (0.38 – 0.61)
Distance to human settlements	11.6 km (4.6 – 21.66)
Distance to roads	8.26 km (0.27 – 21.25)
$\Psi_{\textbf{conditional}}$ of competitors	0.67 (0.04 – 1)
$\Psi_{\textbf{conditional}}$ of predators	0.49 (0.02 – 1)
$\Psi_{\textbf{conditional}}$ of poaching	0.54 (0.02 – 1)

3 Results

We obtained 118 independent records of *T. tricinctus.* The results of Rayleigh's uniformity test (Table 2) indicated that the activity of *T. tricinctus* did not have a uniform distribution (Z = 30.363; p < 0.001), presenting clear preferences for a specific portion of the circadian cycle, being predominantly nocturnal (Fig. S1, Fig 2). It concentrated most of its activity during the night (65.6% of the records), with higher peak between 19:00 pm and 03:00 am (Fig. 2), with greater activity during the first half of the night (19:00 to 00:00 h). We also detected activity around sunset period, at 17 to 19h, and around sunrise, at 05 to 07h.

D. novemcinctus also presented nocturnal activity peak pattern (Z = 26.343, p < 0.001), with activity after midnight peak at 02:00 but with short periods of diurnal activity, while *E. sexcinctus* presented 100% diurnal activity (Z = 19.439, p < 0.001), with peak activity at 13:00 usually the hottest time of day. *M. tridactyla* and *T. tetradactyla* were both cathemeral (Fig 2).

Table 2. Results of Rayleigh's uniformity test (Z) for the frequency of records; P-values based on the number of independent records (N) collected for each species in the Serra da Capivara National Park, northeastern Brazil.

Species	Rayleigh Test (Z)	Rayleigh Test (p)	N
Tolypeutes tricinctus	30.363	< 0.001	118
Dasypus novemcinctus	26.343	< 0.001	61
Euphractus sexcinctus	19.439	< 0.001	24
Tamandua tetradactyla	1.665	0.191	20
Myrmecophaga tridactyla	0.455	0.641	16
Puma concolor	18.298	< 0.001	75
Panthera onca	12.543	< 0.001	54

The temporal overlap between *T. tricinctus* and competitors varied among species. *D. novemcinctus* showed high overlap, but with significantly different distributions (Δ_1 = 0.78, p = 0.038) and *E. sexcinctus* showed low overlap (Δ_1 = 0.10, p = <0.001), due to its exclusively diurnal activity (Fig. 2). *M. tridactyla* and *T. tetradactyla* showed moderate overlap (Δ_1 = 0.71, p = 0.03 and Δ_1 = 0.60, p = 0. 02, respectively). Among predators, *P. onca* and *P. concolor* showed high temporal overlap coefficient and synchrony in activity distributions (Δ_1 = 0.89, p = 0.959 and Δ_1 = 0.82, p = 0.111, respectively) with *T. tricinctus* (Table 3).

Table 3. Temporal overlap coefficient between *T. tricinctus* and their potential predators and competitors. The strength of the temporal interaction ($\Delta_{1)}$ was classified as low overlap ($\Delta \leq 0.5$), moderate overlap ($0.5 < \Delta \leq 0.75$), high overlap ($\Delta > 0.75$) 95% confidence intervals (95% CI) (following Monterroso et al., 2014). The Mardia–Watson–Wheeler test (W) and its p-value were used as complement.

Species	Δ_1	95% CI	*W*	*p*
T. tricinctus				
Dasypus novemcinctus	0.78	0.65 - 0.88	6.546	0.038
Euphractus sexcinctus	0.10	0.02 - 0.19	51.559	< 0.001
Myrmecophaga tridactyla	0.71	0.53 - 0.87	7.013	0.03
Tamandua tetradactyla	0.60	0.42 - 0.77	7.19	0.027
Panthera onca	0.89	0.78 - 0.97	0.084	0.959
Puma concolor	0.82	0.71 - 0.91	4.389	0.111

The only variable that influenced the proportion of three-banded-armadillo nocturnal activity was the conditional occupancy of top predators (Table 4). The presence of pumas and jaguars was negatively correlated with the proportion of nocturnal records of this armadillo (Figure 3).

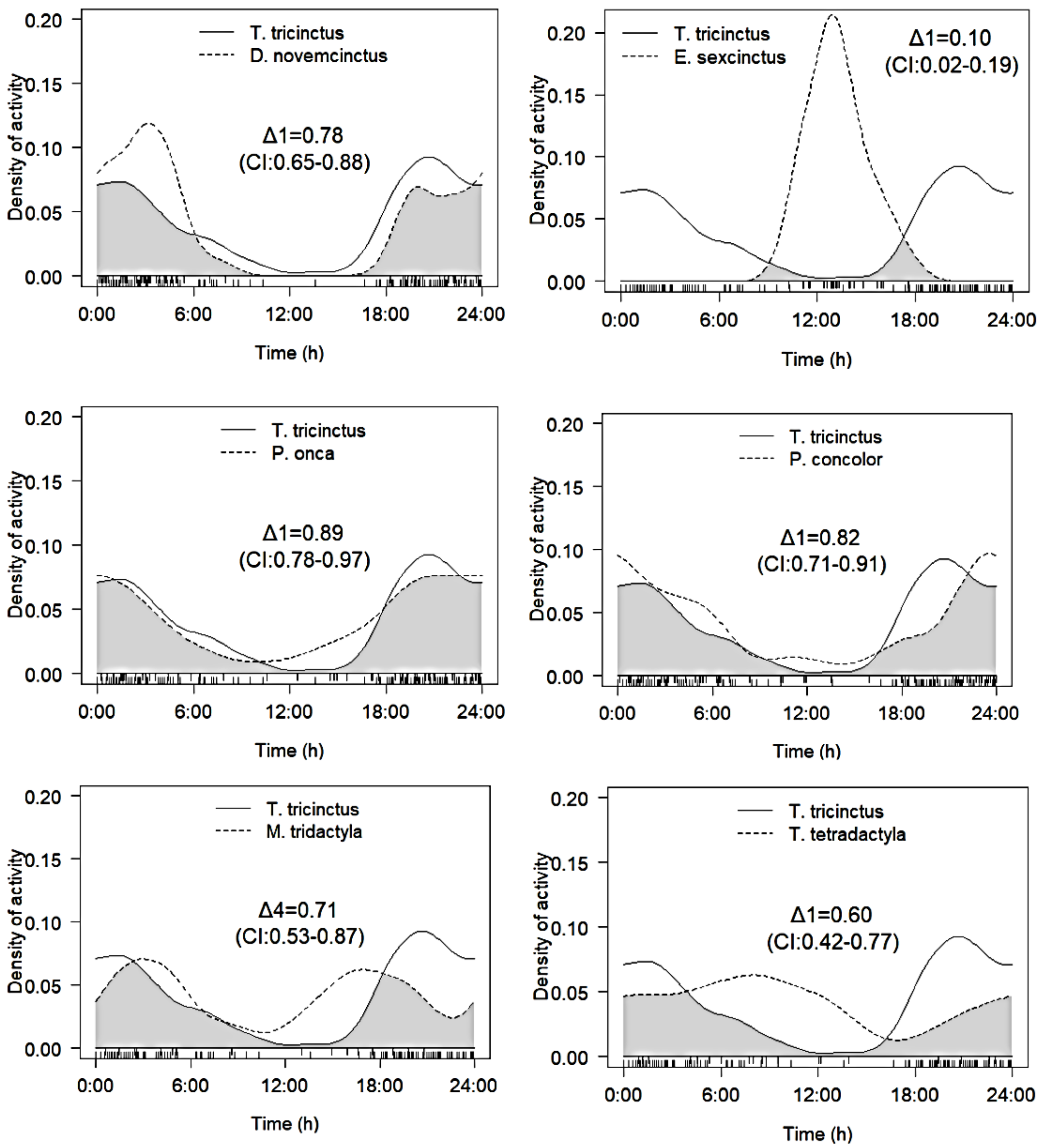

Figure 2. Temporal activity of *T. tricinctus* (continuous curves) and its competitors and predators (dashed curves) in the Serra da Capivara National Park, Brazil, during 2018 survey. The coefficient of overlap corresponds to the shaded grey area below both curves. The time of the records is shown as ticks in the bottom of the figures. For sunrise the average value was 05:54 am, while for sunset, the average value was 06:14 pm.

Table 4. Model selection results from the GLM analysis performed to investigate variables that may influence the temporal activity of *T. tricinctus*, in Serra da Capivara National Park, northeastern Brazil.

	K	AICc	Delta AICc	AICcWt	Cum.Wt
$\Psi_{conditional}$ of predators	2	48.55	0.00	0.80	0.8
$\Psi_{conditional}$ of competitors	2	52.84	4.28	0.09	0.9
Distance from human settlements	2	54.47	5.91	0.04	0.94
$\Psi_{conditional}$ of poaching	2	54.98	6.42	0.03	0.97
Intercept	1	56.42	7.86	0.02	0.99
Distance from nearest road	2	58.26	9.71	0.01	0.99
NDVI	2	58.64	10.09	0.01	1.00

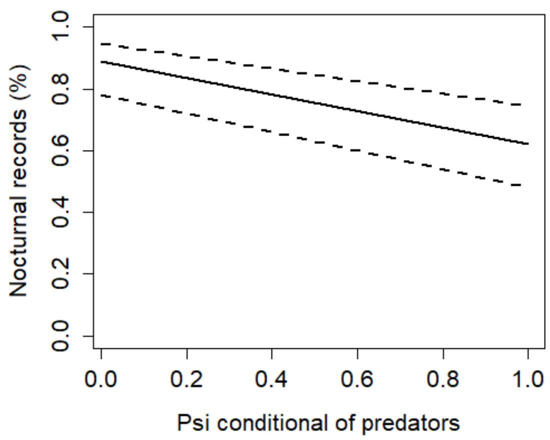

Figure 3. Proportion of nocturnal *T. tricinctus* registers (±95% CI) in Serra da Capivara National Park, Northeaster Brazil, as a function of Psi $_{conditional}$ of predators (puma and jaguar).

4 Discussion

Our study provides the first view of activity patterns of *T. tricinctus*, a poor known and threatened species, and of its main competitors and predators in a dry tropical forest of Brazil. The observed activity pattern indicates that *T. tricinctus* have crepuscular and nocturnal habits in the Caatinga dry forest. Bocchiglieri (2010) found equivalence between daytime and nighttime, with two peaks of activity: one in the afternoon, between 2:00 pm and 6:00 pm and another between 8:00 pm and 11:00 pm in Cerrado savanna. The congener *T. matacus* is also active throughout the night (Attias et al., 2018; Cuéllar 2002; Schaller, 1983). The pattern of activity of *T. tricinctus* may be due to the feeding habit of the main prey, since termites are more active at night (Coles de Negret and Redford 1982), as reported in other studies with armadillos (McDonough et al. 2000).

Also, the activity pattern may be a response to changing in temperature during day and nighttime (Breece and Dusi, 1985; McDonough and Loughry, 2003; Superina and Boily, 2007), as an alternative to thermoregulation. For example, the activity pattern of *T. matacus* tends to increase gradually as air temperature decreases before sunset (Attias et al., 2018). We were unable to determine the air temperature per sampling site, which made it impossible to evaluate the effect of temperature on species activity. However, according to our field records, the temperature amplitude ranged from 10 to 43°C during dry season (May to September). The nocturnal and crepuscular pattern thus represent an efficient evolutionary mechanism to avoid extreme air temperatures.

Our study shows that *T. tricinctus* presents temporal overlap with the insectivorous *D. novemcinctus* and *M. tridactyla*. Mechanisms related to the intrinsic behavior of the species, such as prey selection, may allow coexistence between these species. Ants, termites, and other invertebrates also have nocturnal habits, and this can modulate the foraging strategy necessary to obtain resources by *T. tricinctus* and other insectivorous species studied here. The exception was *E. sexcinctus*, which presented low temporal overlap because its exclusively diurnal activity and eating habit essentially omnivorous. On the other hand, competitor's occupancy probability did not influence the proportion of nocturnal records of *T. tricinctus*.

The activity pattern of *T. tricinctus* overlapped the predator's activity pattern during the nighttime. The extremely high temperatures during daytime also represents a constraint for felids which have limited ability to thermo-regulate (Penido et al., 2017) and the species may be forced to concentrate activity in nocturnal period, but also to synchronize your activity with prey (Astete et al., 2017; Marinho et al., 2020). On the other hand, prey species may be less active, with less foraging effort, due to the increased risk of predation, particularly from vertebrates (Vasquez, 1994; Clarke et al., 1996; Skutelsky, 1996). Additionally, our work shows that the nocturnal activity of *T. tricinctus* is lower in places where the occupancy probability of jaguar and puma are high, which can be a strategy to improve the capacity of not being detected and thus reduce the chances of predation. Armadillo are the main item of the jaguar's diet in Caatinga (Miranda et al., 2018), and the predation of *T. tricinctus* by jaguar has already been documented through camera trapping at 18:49 pm in Caatinga area (Magalhães et al., 2020). Contrary to our expectations, we did not find influence of vegetation cover or anthropic variables (poaching, roads, distance to human settlements) on the proportion of nocturnal records of *T. tricinctus.* Perhaps, our sampling sites may not reflect enough spatial variation and heterogeneity to express such effect.

Our results contribute to the understanding of the ecology of *T. tricinctus*, intraguild interactions, and predator-prey relationships in a protected area in Caatinga dry forest. In summary, our results corroborate the nocturnal-crepuscular activity of *T. tricinctus*. It is possible that *T. tricinctus* activity pattern is mainly regulated by temperature, predation and feeding habitats. Further studies should investigate how the

T. tricinctus activity respond to seasonality and prey availability. However, the high overlap between predators and the high nocturnality in the presence of these species, indicates *T. tricinctus* may have developed strategies to avoid encounters with these species, to the point of allowing their coexistence.

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Appendix A - Correlation matrix for predictor variables

Table S1 - Correlation matrix for predictor variables used in generalized linear models to investigate predict variables that may influence the temporal activity of *T. tricinctus* in Serra da Capivara National Park, northeastern Brazil. NDVI are given within a 1-km-radius buffer around each camera site. Distances from the camera sites to the nearest house (human) and road. Psi (Ψ) conditional is the probability that predators (puma and jaguar), competitors (armadillos and anteaters) or poaching were present at a site given it was sampled.

	ndvi	**human**	**road**	**competitor**	**hunter**	**predator**
ndvi	1	-0.37542	0.337725	0.046949	0.250776	0.319803
human	-0.37542	1	0.190409	-0.01979	-0.1836	-0.00902
road	0.337725	0.190409	1	0.094508	-0.10578	0.269939
competitor	0.046949	-0.01979	0.094508	1	-0.23228	0.141686
hunter	0.250776	-0.1836	-0.10578	-0.23228	1	0.400065
predator	0.319803	-0.00902	0.269939	0.141686	0.400065	1

Appendix B - Daily activity patterns

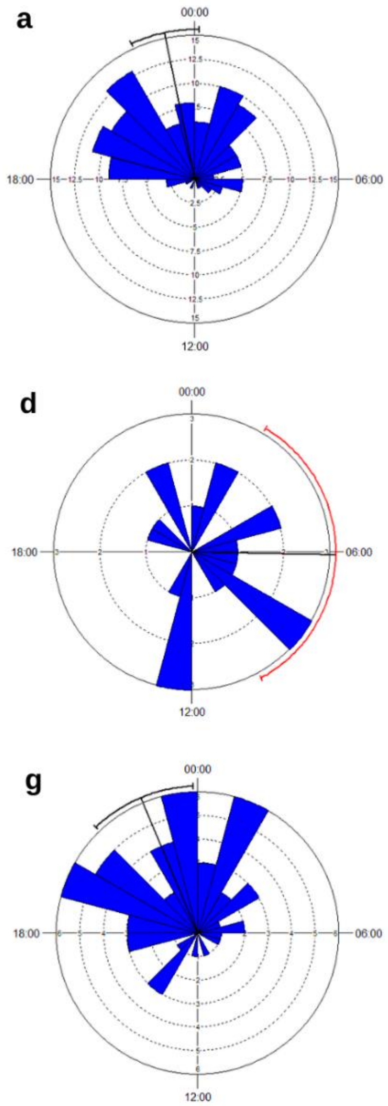

Figure S1 – Daily activity patterns of target species in Serra da Capivara National Park, northeastern Brazil, during 2018. Each circular histogram is divided into 24 intervals of 60 min, and their bars represent the number of records by camera-trap at the corresponding hour of the circadian cycle, while the external line indicates the standard error. Species are (a) *T. tricinctus*, (b) *D. novemcinctus*, (c) *E. sexcinctus*, (d) *T. tridactyla*, (e) *M. tridactyla*, (f) *P. concolor*, and (g) *P. onca*.

5 CONSIDERAÇÕES FINAIS

Nossos resultados indicam que entre os mamíferos, os tatus são os animais mais citados nos relatórios de autos de infração (Capítulo 1). A espécie mais caçada foi *D. novemcinctus*, seguida do endêmico e ameaçado *T. tricinctus*. O consumo desse grupo está amparado em uma complexa e profissionalizada cadeia de comércio, com armadilhas e utensílios específicos para sua captura. A caça ilegal pode ser encontrada em áreas com baixa densidade populacional, em áreas rurais pequenas e esparsas e no entorno de áreas protegidas. Apesar de serem reconhecidas como repositório de vida silvestre, abrigando espécies de hábitat mais restrito e florestais, por outro lado, as áreas protegidas enfrentam um desafio complexo referente aos crimes ambientais relacionados à fauna. De forma geral, um problema evidenciado neste estudo foi a falta de campo específico para relato da espécie de animal apreendida, nos relatórios de auto da infração. E, quando mencionadas, nomes populares ou genéricos foram empregados; o que dificulta uma tabulação precisa sobre a fauna apreendida. Nesse sentido, recomenda-se treinamento dos profissionais da fiscalização quanto à identificação das espécies e padronização do preenchimento dos relatórios de infração com informação mais precisa possível em relação a espécies e quantidades.

Esse trabalho contribuiu para entender o uso de hábitat do tatu-bola como a espécie responde a variáveis antrópicas. O principal fator determinante da probabilidade de ocupação pelo tatu-bola foi a cobertura vegetal (Capítulo 2), com florestas e densas sendo mais adequadas para a espécie. Portanto, a perda de hábitats mais florestados e densos pode ser um fator limitante para espécie. Diante do cenário de mudanças climáticas, as florestas secas como a Caatinga tendem a enfrentar maior variação de temperatura, diminuição da disponibilidade de água e aceleração nos processos de desertificação. Nesse dilema, os remanescentes florestais se tornam imprescindíveis para manutenção de populações de tatu-bola, e assim devem ser prioritariamente protegidos e /ou recuperados. A ocupação do tatu-bola ocorreu em classes de solos (neossolos e latossolos) que geralmente tem maior proveito para agricultura do semiárido, principalmente para culturas de sequeiro, como milho, mandioca e feijão. Frequentemente, o manejo dessas culturas envolve o uso de queimadas na etapa de preparação da terra, que eventualmente podem perder o controle e se tornar incêndios florestais. Apesar do tatu-bola ser uma espécie prioritária para conservação dada o seu status de ameaça a extinção e endemismo, é inviável propor a criação de áreas protegidas em toda a área de distribuição da espécie. Por isso, estratégias que promovam a coexistência entre pessoas e a espécies em paisagens exploradas por atividades antrópicas devem ser desenvolvidas e implementadas.

O padrão de atividade do tatu-bola (Capítulo 3) sugere que a espécie prioriza estar ativa durante a noite e o crepúsculo, provavelmente como uma adaptação para o forrageio e evitação das altas temperaturas diurnas. Na presença de grandes felinos, a noturnalidade do tatu-bola foi menor. proteção contra predadores. De fato

O Parque Nacional Serra da Capivara tem papel fundamental na conservação do tatu-bola e de outros mamíferos ameaçados de extinção. As ações de manejo, proteção, fiscalização e prevenção a incêndios florestais tem surtido efeito positivo em manter populações de tatu-bola e demais espécies na região. Entretanto, em um mundo em constante mudanças, com o aumento de paisagens modificadas pelo homem, a necessidade de coexistência harmônica entre humanos e vida silvestre é cada vez mais uma realidade que os tomadores de decisão e pesquisadores devem considerar.

Apesar do efeito da caça não ter sido evidenciado no padrão espacial e temporal do tatu-bola, recomendamos o monitoramento de longo prazo das populações de *T. tricinctus* em nossa área de estudo - bem como em outras áreas-chave ao longo da distribuição da espécie - incorporando padrões dinâmicos de populações, para estimar mudanças no *status* da população ao longo do tempo e determinar o uso de recursos em áreas fragmentadas e cercadas por diferentes tipos de habitat. Nesse sentido, a compreensão dos aspectos culturais e socioeconômicos da coexistência tatus-humanos é essencial, de forma a contribuir no planejamento para conservação de espécies alvo de caça, como o tatu-bola, principalmente diante da importância desses animais para saúde pública, como hospedeiros e reservatórios naturais de diversas zoonoses.