



SUSANE XAVIER BRAS

**EFEITOS DA URBANIZAÇÃO NA PERSONALIDADE ANIMAL: UM EXPERIMENTO
CONTROLADO EM CALANGOS *TROPIDURUS HISPIDUS***



SÃO LUÍS

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Dissertação apresentada ao Programa de Pós-Graduação em Biodiversidade e Conservação / UFMA como parte dos pré-requisitos para obtenção de créditos

Orientadora: Prof^a Dr^a Ana Catarina Sequeira Nunes Coutinho de Miranda

Coorientadora: Prof^a Dr^a Gilda Vasconcellos de Andrade

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Dissertação apresentada ao Programa de Pós-Graduação em Biodiversidade e Conservação da Universidade Federal do Maranhão para obtenção do título de mestre em Biodiversidade e Conservação.

Apresentada em ___ / ___ / ___

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“Somos privilegiados em viver entre pessoas brilhantes e passionalmente inquiridoras, e em uma época em que a procura do saber é, em geral, recompensada.”

Carl Sagan

Dedico essa dissertação aos meus pais,
Rosa e Tony, por todo sacrifício e fé. Eu amo
vocês.

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RESUMO

Mudanças antropogênicas estão ocorrendo a nível global e têm efeitos significativos na vida selvagem. Estudos vêm buscando entender em que medida a urbanização causa alterações na ecologia de diferentes espécies. Tais estudos demonstraram animais urbanos podem mudar seu comportamento para se adaptar a essas novas condições. Indivíduos de uma mesma espécie apresentam diferença no comportamento entre habitats urbanos e rurais. Apesar de estudos sobre urbanização terem se tornado comum na literatura, no Brasil, há uma escassez de estudos com evidências empíricas dos mecanismos subjacentes responsáveis pelas relações entre a urbanização e a estrutura da comunidade animal. Diante disto, essa dissertação teve como objetivo testar se a urbanização influencia o comportamento do lagarto tropical *Tropidurus hispidus*, no âmbito da personalidade animal. Nós capturamos lagartos machos de habitats rurais e urbanos na Ilha do Maranhão-MA. Mantivemos os lagartos em terrários individuais e, após um período de aclimação, realizamos três testes para avaliar os comportamentos de imobilidade tônica, distância de iniciação de fuga e agressividade. Cada teste foi repetido três vezes para medir a consistência intraindividual no comportamento. Encontramos evidências que *T.hispidus* apresenta traços de personalidade envolvendo os comportamentos de imobilidade tônica, distância de iniciação da fuga e agressividade. Esses comportamentos não pareciam diferir entre os indivíduos rurais e urbanos, mas os indivíduos urbanos tendiam a ter comportamentos mais flexíveis enquanto os rurais apresentavam comportamentos mais consistentes. Nossos resultados são a primeira evidência de personalidade animal em *T. hispidus* e sugerem que essa espécie pode ser mais flexível nas populações urbanas.

Palavras-chave: consistência intra-individual, repetibilidade, urbanização, *Tropidurus*, trópicos, comportamento animal.

ABSTRACT

Anthropogenic changes are occurring globally and have significant effects on wildlife. Studies have sought to understand the extent to which urbanization causes changes in the ecology of different species. Such studies have shown that urban animals can change their behavior to adapt to these new conditions. Individuals of the same species differ in behavior between urban and rural habitats. Although studies on urbanization have become common in literature in Brazil, there is a paucity of studies with empirical evidence of the underlying mechanisms responsible for the relationships between urbanization and the structure of the animal community. In view of this, this dissertation had as objective to test if the urbanization influences the behavior of tropical lizard *Tropidurus hispidus*, within the animal personality. We captured male lizards from rural and urban habitats on the Island of Maranhão-MA. We kept the lizards in individual terrariums and, after a period of acclimatization, we performed three tests to evaluate the behavior of tonic immobility, distance of initiation of escape and aggressiveness. Each test was repeated three times to measure intra-individual consistency in behavior. We found evidence that *T.hispidus* presents personality traits involving tonic immobility, distance of initiation of escape and aggressiveness. These behaviors did not appear to differ between rural and urban individuals, but urban individuals tended to have more flexible behaviors while rural individuals had more consistent behaviors. Our results are the first evidence of animal personality in *T. hispidus* and suggest that this species may be more flexible in urban populations.

Key words: intra-individual consistency, repeatability, urbanization, *Tropidurus*, tropics, animal behavior.

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1. CAPÍTULO I

1.1. APRESENTAÇÃO GERAL

O mundo tem passado por um acelerado processo de urbanização nos últimos séculos (ZHOU et al., 2015). Atualmente, mais de metade da população humana mora em cidades, e a perspectiva é que se chegue a 60% até 2050 (UNITED NATIONS, 2016). Esse acelerado processo de urbanização tem transformado drasticamente a paisagem natural (ZHOU et al., 2015) e tem despertado o interesse dos ecólogos em entender como as espécies estão lidando com o novo ambiente (ALBERTI, 2015).

No ambiente urbano, os animais enfrentam condições diferentes das encontradas em seus habitats originais, tais como poluição sonora (CAORSI et al., 2017; DOMINONI et al., 2016; FULLER; WARREN; GASTON, 2007), iluminação artificial (RAAP; PINXTEN; EENS, 2015; SWADDLE et al., 2015), tráfego (KOLBE; BATTLES; AVILÉS-RODRÍGUEZ, 2016; LOWRY; LILL; WONG, 2013), espécies não nativas (DUGUAY; EIGENBROD; FAHRIG, 2007) e alimentação antropogênica (PRANGE; GEHRT; WIGGERS, 2004; RILEY et al., 2003; SCHULTE-HOSTEDDE et al., 2018). Esse novo cenário ecológico exige que os animais se ajustem ao ambiente para terem sucesso (ALBERTI, 2015). De fato, espécies que habitam áreas urbanizadas estão apresentando mudanças em traços fisiológicos, morfológicos e comportamentais (ver revisão de literatura em ALBERTI; MARZLUFF; HUNT, 2017). Porém, na Ecologia, ainda é um desafio entender por que alguns animais são capazes de lidar com as novas condições urbanas, enquanto outros não são (LAPIEDRA; CHEJANOVSKI; KOLBE, 2017).

O comportamento contribui para que os animais lidem com as mudanças no ambiente (DUCKWORTH, 2009). Alguns estudos têm demonstrado que indivíduos que habitam áreas urbanizadas estão apresentando diferenças comportamentais em relação a indivíduos que vivem em ambientes não antropizados (MIRANDA, 2017; TUOMAINEN; CANDOLIN, 2011; WONG; CANDOLIN, 2015). Os animais que habitam ambientes urbanos podem ter diferenças em vários traços comportamentais como, por exemplo, ter maior agressividade (e.g. WOLF; WEISSING, 2012), maior ousadia (e.g. ATWELL et al., 2012) e mais atividade (e.g. LAPIEDRA; CHEJANOVSKI; KOLBE, 2017), entre outros (MIRANDA, 2017).

No ambiente urbano, eventuais alterações comportamentais podem ser benéficas para os indivíduos se forem capazes de aumentar sua aptidão sob as novas pressões seletivas (WONG; CANDOLIN, 2015). No entanto, se as respostas comportamentais forem inadequadas, podem reduzir a aptidão para ter sucesso no ambiente urbano, podendo até levar ao declínio das populações (TUOMAINEN; CANDOLIN, 2011).

Em lagartos, a maioria dos estudos de comportamento tem mostrado que, quando comparados com indivíduos rurais ou florestais, indivíduos urbanos tendem a ser mais ousados (AMO; LÓPEZ; MARTÍN, 2006; PROSSER; HUDSON; THOMPSON, 2006), mais agressivos (LAPIEDRA; CHEJANOVSKI; KOLBE, 2017), mais ativos e mais exploratórios (BATABYAL; BALAKRISHNA; THAKER, 2017; LAPIEDRA; CHEJANOVSKI; KOLBE, 2017; MOULE et al., 2016).

Recentemente, estudos têm abordado as diferenças individuais de comportamentos em populações conhecidas pelo termo personalidade animal (BIRO; STAMPS, 2008). A personalidade animal pode ser definida por dois critérios: (i) consistência comportamental ao longo do tempo a nível do indivíduo e (ii) correlação entre comportamentos em diferentes contextos (BELL, 2007). Espera-se que componentes de personalidade animal (e.g. ousadia, atividade, exploração e agressividade) influenciem e modifiquem os processos ecológicos e evolutivos, pois apresentam uma variação intraespecífica e são moderadamente hereditários (Dingemanse & Réale, 2005). Na presença de traços de personalidade hereditários, os indivíduos cujo comportamento é consistente e adequado para lidar com os desafios do novo ambiente urbano deverão ser favorecidos neste ambiente, tendo maior probabilidade de passar os seus traços comportamentais para as gerações sucessivas. Por outro lado, indivíduos cujas respostas comportamentais consistentes não sejam adequadas às condições urbanas podem não ser tão bem sucedidos neste novo ambiente, podendo conseqüentemente diminuir a sua frequência nas populações urbanas (MIRANDA et al., 2013; SIH et al., 2004).

Estudos comportamentais em ambiente urbano no âmbito da personalidade animal se concentram, principalmente, em aves e mamíferos (GRAVOLIN; KEY; LILL, 2014; MIRANDA et al., 2013; RIYABI et al., 2017; VINES; LILL, 2015). Poucos são os estudos que investigam tanto a existência de personalidade animal em lagartos (CARTER et al., 2013; LAPIEDRA; CHEJANOVSKI; KOLBE, 2017; MCEVOY et al., 2015; MICHELANGELI; CHAPPLE; WONG, 2016; MOULE et al., 2016), quanto as diferenças no comportamento em

geral e na personalidade animal entre lagartos urbanos e rurais (LAPIEDRA; CHEJANOVSKI; KOLBE, 2017; MOULE et al., 2016; PROSSER; HUDSON; THOMPSON, 2006).

O presente estudo tem como objetivo principal verificar a existência e investigar eventuais diferenças na personalidade animal de populações rurais e populações urbanas no lagarto territorial neotropical *Tropidurus hispidus* (Spix, 1825). Aqui testamos as hipóteses de que *Tropidurus hispidus* (i) apresenta consistência intra-individual nos comportamentos distância de fuga, agressividade e imobilidade tónica e correlações entre esses comportamentos, (ii) *T. hispidus* rurais e urbanos apresentam diferenças na consistência intra-individual dos comportamentos distância de fuga, agressividade e imobilidade tónica e (iii) *T. hispidus* rurais e urbanos apresentam diferenças nas médias dos comportamentos distância de fuga, agressividade e imobilidade tónica.

1.2. REVISÃO BIBLIOGRÁFICA

À medida que urbanização global cresce, a necessidade de entender o seu impacto na vida selvagem também aumenta (ALBERTI; MARZLUFF; HUNT, 2017; SETO; GUNERALP; HUTYRA, 2012). A urbanização é um processo que leva a mudanças em ambientes naturais, criando uma nova cobertura terrestre (DELCOURT; DELCOURT, 1988), gerando mudanças no ambiente como, por exemplo, ruído e iluminação artificial (CAORSI et al., 2017; DOMINONI et al., 2016; FULLER; WARREN; GASTON, 2007), e criando tanto novas assembleias bióticas quanto novas associações entre os organismos (e.g. parasitismo e predação) (BAKER et al., 2005; COOK et al., 2012). Nesse ambiente, os animais têm contato com diferentes estressores, por exemplo, exposição a poluentes (BURGER et al., 2004; CHATELAIN; GASPARINI; FRANTZ, 2016), tráfego de veículos (BAUTISTA et al., 2004; CAORSI et al., 2017), passagem de humanos (FERNÁNDEZ-JURICIC, 2002) e presença de predadores não naturais (BAKER et al., 2005, 2008; FLUX, 2017; HOLDERNESS-RODDAM; MCQUILLAN, 2014).

Essas condições têm gerado pressões sobre diferentes tipos de organismos (ver revisão em MCDONNELL; HAHS, 2015). Muitos destes organismos, incluindo artrópodes, aves, peixes, e mamíferos estão alterando sua fisiologia, morfologia e comportamentos face ao novo ambiente urbano (ALBERTI; MARZLUFF; HUNT, 2017). Por exemplo, o ruído artificial pode afetar drasticamente espécies de aves (DOMINONI et al., 2016; FULLER; WARREN;

GASTON, 2007). Espécies de aves, diante ao ruído artificial, têm alterado o horário de atividade de canto a fim de evitar a sobreposição com o ruído artificial (DOMINONI et al., 2016; FULLER; WARREN; GASTON, 2007). Fuller; Warren e Gaston (2007) descobriram que o pisco-de-peito-ruivo *Erithacus rubecula* (Lineu, 1758) canta mais no período noturno em áreas afetadas com poluição sonora no período diurno. O efeito da poluição sonora no comportamento vocal também se aplica a outros taxa (CAORSI et al., 2017; ZOLLINGER et al., 2017). O mesmo tem ocorrido com espécie de anuro, havendo, por exemplo, um efeito do ruído antropogênico na vocalização de anuros e no mascaramento da mesma (CAORSI et al., 2017).

Mudanças comportamentais são propostas como importantes para a ocupação áreas urbanas pelas espécies animais (LOWRY; LILL; WONG, 2013). Uma revisão realizada por Sih et al. (2011) enquadra os ajustes comportamentais ao ambiente modificado pelo homem, sugerindo que estes são importantes em vários aspectos, como evitar ou lidar com novos competidores, utilizar novos recursos ou habitats, evitar ou enfrentar novos estressores abióticos (SIH; FERRARI; HARRIS, 2011). Algumas espécies persistem no ambiente urbano, e algumas parecem até obter algumas vantagens ao viver neste novo habitat (FICETOLA et al., 2007). Lagartos *Urosaurus ornatos* (Baird & Girard, 1852) se aclimataram a estressores urbanos repetitivos, ou que, o aumento ao acesso a alimentos urbanos e aos recursos hídrico, escassos no ambiente rural, podem ter atuado para diminuir os níveis de corticoides (FRENCH; FOKIDIS; MOORE, 2008). Outras diferenças comportamentais entre indivíduos urbanos e rurais têm sido demonstradas em diferentes táxons (aves, mamíferos, anfíbios, artrópodes, artrópodes, répteis e peixes). Principalmente em comportamentos agressivos, comportamento antipredatório, comportamento de risco, exploração do ambiente, neofilia e neofobia (MIRANDA, 2017; ROYAUTÉ; BUDDLE; VINCENT, 2015; SANTOSTEFANO et al., 2016).

Tal como nos outros táxons, em lagartos, a maioria dos estudos de comportamento no contexto da urbanização focam comportamento de fuga (AMO; LÓPEZ; MARTÍN, 2006; PROSSER; HUDSON; THOMPSON, 2006), a atividade, a exploração (BATBYAL; BALAKRISHNA; THAKER, 2017; LAPIEDRA; CHEJANOVSKI; KOLBE, 2017; MOULE et al., 2016) e a agressividade (LAPIEDRA; CHEJANOVSKI; KOLBE, 2017). Os estudos em lagartos encontraram diferenças comportamentais entre indivíduos urbanos e não urbanos, tendo os indivíduos urbanos tendência a correr mais ou menos riscos (BATBYAL; BALAKRISHNA; THAKER, 2017a; PROSSER; HUDSON; THOMPSON, 2006b). Espécies de lagartos estão se tornando mais ousados, mesmo na presença de predadores, outros mais

agressivos, e também foram encontradas mudanças morfológicas (Ver revisão em FRENCH et al., 2018)

Embora muitas pesquisas se tenham centrado na ideia de que os indivíduos podem modificar seus comportamentos para lidar com mudanças ambientais (WONG; CANDOLIN, 2015), estudos recentes apoiam a existência de diferenças em comportamentos consistentes, repetíveis, (BIRO; ADRIAENSSENS, 2013; SIH et al., 2012). Essas diferenças individuais no comportamento são agora conhecidas como personalidade animal (BIRO; ADRIAENSSENS, 2013). Tal abordagem surgiu como consequência de estudos sobre a personalidade humana, sendo usada para indicar a individualidade observada em diferentes indivíduos em populações. Por exemplo, os indivíduos podem ter uma tendência a serem mais ousados, amistosos ou mesmo agressivos, independente do contexto em que se encontram (GOSLING, 2001). Estes padrões foram identificados em animais domésticos, roedores de laboratório e primatas (GOSLING, 2001, 2008). Assim, o termo personalidade ganhou uma maior abrangência, não se limitando apenas aos humanos, mas também englobando outros animais (GOSLING, 2001). Alguns pesquisadores de animais usaram termos como "temperamento" (RÉALE et al., 2007) ou "síndromes comportamentais" (SIH et al., 2004) em vez de "personalidade" para designar essa variação no comportamento. O termo temperamento muitas vezes descreve diferenças na emotividade ou descreve traços que são demonstrados muito cedo na vida (RÉALE et al., 2007), enquanto as "síndromes comportamentais" são referidas mais comumente como conjuntos de comportamentos correlacionados em situações ou contextos diferentes dentro da população (SIH et al., 2004). Apesar da ligeira variação de significados, esses diferentes termos se referem à mesma classe de fenômenos (GOSLING, 2008).

Segundo BELL (2007), dois critérios são importantes no estudo da variação comportamental em animais e definem a personalidade animal: (i) Os indivíduos podem variar consistentemente entre si nas respostas comportamentais ao longo do tempo, (ii) os comportamentos podem estar correlacionados entre diferentes contextos, o que pode também ser definido como síndrome comportamental. Por exemplo, a ousadia muitas vezes está associada a agressividade (EVANS; BOUDREAU; HYMAN, 2010; LAPIEDRA; CHEJANOVSKI; KOLBE, 2017), e a um maior nível de atividade e exploração (LAPIEDRA; CHEJANOVSKI; KOLBE, 2017).

A personalidade animal tem sido comumente descrita usando principalmente cinco componentes: (i) ousadia - a reação de um indivíduo a qualquer situação arriscada, mas não nova; (ii) exploração - a reação de um indivíduo a uma nova situação; (iii) atividade - o nível geral de locomoção e uso do espaço pelo indivíduo; (iv) agressividade - a reação agonística de um indivíduo em relação a coespecíficos ou predadores e competidores; e (v) sociabilidade - a relação social entre um indivíduo e os seus coespecíficos (excluindo o comportamento agressivo) (RÉALE et al., 2007).

Do ponto de vista ecológico e evolutivo, as componentes da personalidade animal são importantes porque representam indivíduos respondendo de forma consistente de diferentes maneiras e em diferentes contextos em uma mesma população (BIRO; STAMPS, 2008). Por exemplo, nos peixes da espécie *Lepomis macrochirus* (Rafinesque, 1810), antes considerados predadores generalistas (WILSON, 1998), sabe-se hoje em dia que muitos indivíduos desta espécie têm tendência a ser especialistas: enquanto que alguns deles ficam consistentemente em águas abertas, outros indivíduos ficam consistentemente nas margens de corpos d'água, e um número menor alterna entre os dois microhabitats (WERNER; MITTELBACH; HALL, 1981). Adicionalmente, este último estudo identificou que a preferência em forragear em determinado microhabitat está relacionada com outros comportamentos, tais como atividade, ousadia e tendências exploratórias, e que estratégias individuais especialistas tinham maior sucesso em ambientes estáveis, enquanto que estratégias individuais generalistas tinham mais sucesso sob mudanças ambientais.

Estudos de personalidade animal geralmente identificam tanto a consistência dos comportamentos quanto a correlação entre eles (CARRETE; TELLA, 2017; LAPIEDRA; CHEJANOVSKI; KOLBE, 2017; MYERS; HYMAN, 2016; SCHUSTER et al., 2017), mas tem sido comum também encontrar somente um desses aspectos (HURTADO; MABRY, 2017; MCEVOY et al., 2015; MOULE et al., 2016). Por exemplo, Mcevoy et al. (2015) descobriram no lagarto australiano *Liopholis whitii* (Lacépède, 1804) consistência intra-individual em comportamentos relacionados com agressividade, ousadia e exploração, mas não encontraram correlação entre nenhum dos comportamentos estudados, não havendo portanto evidências de uma síndrome comportamental (MCEVOY et al., 2015). Já Moule et al. (2016) encontraram correlação entre atividade e exploração no lagarto australiano *Lampropholis delicata* (De Vis, 1888), mas não encontraram repetibilidade individual no comportamento desse lagarto. Isto pode sugerir que algumas pressões seletivas podem moldar tanto a repetibilidade quanto a

formação de síndromes comportamentais (MCEVOY et al., 2015). Ambientes com diferentes pressões podem ser importantes não só ao favorecer indivíduos com determinado tipo comportamental, mas também formando consistência individual nos comportamentos e correlações entre estes (TÜZÜN et al., 2017).

Estudos indicam que componentes da personalidade animal podem ser hereditários (DINGEMANSE et al., 2002; RIYAHY et al., 2017). Diferentes traços de personalidade podem ser favorecidos em ambientes urbanos. De facto, dado um traço de personalidade hereditário, indivíduos com comportamentos consistentemente mais adequados para lidar o ambiente urbano poderão ter maior chance de sucesso reprodutivo do que outros (SIH et al., 2004, 2012). Por exemplo, estudos com vertebrados têm sugerido que os indivíduos urbanos são em geral mais ousados do que os seus coespecíficos em áreas rurais, por exemplo tendo geralmente maiores tolerâncias à presença de seres humanos (CARRETE; TELLA, 2017; GRAVOLIN; KEY; LILL, 2014; MIRANDA, 2017; MYERS; HYMAN, 2016; VINES; LILL, 2015). Padrões de predação, diferentes entre áreas urbanas e áreas rurais podem moldar componentes da personalidade em algumas espécies animais (FISCHER et al., 2012). Estudos manipulativos com peixes da espécie *Brachyrhaphis rhabdophora* (Regan, 1908) mostraram que indivíduos desta espécie são menos ousados na presença de predadores do que na ausência destes (RASMUSSEN; BELK, 2017), e que esta mostrou que diferenças comportamentais induzidas por predação em *B. rhabdophora* tem uma base genética (JOHNSON, 2001)). Assim, pode-se concluir que tanto a experiência individual como a história evolutiva da predação podem afetar a expressão de componentes de personalidade (DINGEMANSE et al., 2009).

Além de moldar componentes de personalidade, padrões de predação também podem moldar a existência ou não de correlações entre esses componentes (KLAAS-DOUWE B. DIJKSTRA; RICHARD LEWINGTON, 2006). Tüzün et al (2017) mostraram que larvas de libélulas da espécie *Coenagrion puella* (Linnaeus, 1758), bem adaptadas a lagoas urbanas na Europa, apresentam padrões de atividade e ousadia consistentes tanto em indivíduos de áreas rurais quanto em indivíduos de áreas urbanas. No entanto, a correlação entre a atividade e a ousadia foi encontrada apenas em indivíduos urbanos (TÜZÜN et al., 2017). Notavelmente, quando expostas a pesticidas, as larvas rurais apresentaram uma correlação positiva entre atividade e ousadia, indicativo de que esta espécie, a correlação entre atividade ou ousadia, ou a síndrome comportamental, é mais propensa a ocorrer em condições estressantes (TÜZÜN et al., 2017). Carrete e Tella (2017) descobriram que as corujas *Athene cunicularia* (Molina, 1782)

urbanas eram, em geral, menos ousadas, menos exploradoras e menos agressivas do que as corujas urbanas. Estes comportamentos não variavam independentemente apenas nos indivíduos rurais, que ao contrário dos urbanos apresentavam correlações significativas e positivas entre alguns dos comportamentos analisados (CARRETE; TELLA, 2017). Os autores sugerem que as pressões de seleção que atuam durante a colonização do ambiente urbano podem estar rompendo as correlações comportamentais que existiam no ambiente natural (CARRETE; TELLA, 2017).

Em lagartos, alguns estudos evidenciam a existência de efeitos da urbanização na personalidade de algumas espécies (LAPIEDRA; CHEJANOVSKI; KOLBE, 2017; MOULE et al., 2016). Lapedra; Chejanovski e Kolbe (2017), ao realizaram experimentos replicados na natureza e em cativeiro em lagartos *Anolis sagrei* (Duméril & Bibron, 1837) rurais e urbanos. O estudo encontrou tanto na natureza como em cativeiro consistência intra-individual e correlação entre os comportamentos, e uma diferença entre lagartos urbanos e florestais no comportamento de escape, na exploração e na ousadia. Adicionalmente, verificou-se que, na ausência de predadores, *A. sagrei* de locais urbanos apresentavam maior tendência a explorar novos recursos alimentares quando comparados com *A. sagrei* urbanos na presença de predadores.

Um outro estudo, realizado por Moule et al. (2016), não encontrou diferenças significativas entre populações urbanas e florestais do lagarto *Lampropholis delicata* para os comportamentos de atividade e exploração, embora os lagartos de uma das populações urbanas fossem mais ativos e mais exploratórios do que os indivíduos das outras populações urbana e rurais. Neste estudo foi encontrada a correlação entre atividade e exploração no lagarto *Lampropholis delicata* em áreas urbanas, mas não em áreas florestais. Os autores sugerem que a menor densidade de predadores nas áreas urbanas pode ter favorecido lagartos com tais traços comportamentais, principalmente na busca de alimento (MOULE et al., 2016).

Ainda são raros os estudos dos efeitos da urbanização no comportamento de lagartos (AMO; LÓPEZ; MARTIN, 2006; CHEJANOVSKI et al., 2017; PROSSER; HUDSON; THOMPSON, 2006; MACMILLAN et al 2010, BLOCH; IRSCHICK, 2006), principalmente no âmbito da personalidade animal (LAPIEDRA; CHEJANOVSKI; KOLBE, 2017; MOULE et al., 2016). Assim, é importante o desenvolvimento de mais pesquisas nesse grupo para um melhor entendimento da influência da urbanização sobre o comportamento animal neste táxon.

1.3. HIPÓTESES

O presente estudo pretende testar as seguintes hipóteses:

- i. *Tropidurus hispidus* apresenta consistência intra-individual nos comportamentos distância de fuga, agressividade e imobilidade tónica;
- ii. *Tropidurus hispidus* apresenta correlações entre os comportamentos distância de fuga, agressividade e imobilidade tónica;
- iii. *Tropidurus hispidus* rurais e urbanos apresentam diferenças na consistência intra-individual nos comportamentos distância de fuga, agressividade e imobilidade tónica;
- iv. *Tropidurus hispidus* rurais e urbanos apresentam diferenças nas correlações entre os comportamentos distância de fuga, agressividade e imobilidade tónica.

1.4. OBJETIVO GERAL

O objetivo geral do presente estudo é verificar o efeito da urbanização no comportamento do calango *Tropidurus hispidus*.

1.5. OBJETIVOS ESPECÍFICOS

Os objetivos específicos do presente estudo são:

- i. Investigar em *Tropidurus hispidus* a existência de consistência intra-individual nos comportamentos distância de fuga, agressividade e imobilidade tónica;
- ii. Investigar em *Tropidurus hispidus* a existência de correlações entre os comportamentos distância de fuga, agressividade e imobilidade tónica;
- iii. Investigar se *Tropidurus hispidus* rurais e urbanos apresentam diferenças na consistência intra-individual nos comportamentos distância de fuga, agressividade e imobilidade tónica;
- iv. Investigar se *Tropidurus hispidus* rurais e urbanos apresentam diferenças nas correlações entre os comportamentos distância de fuga, agressividade e imobilidade tónica.

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3. **CAPÍTULO II**

Individual consistency in behavior in urban and rural Peter Lava Lizards

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Individual consistency in behavior in urban and rural Peter Lava LizardsBRAS, S X^{1,2}, OLIVEIRA, K C², ANDRADE, G V^{1,2}; MIRANDA, A C^{1,2}

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Abstract

Urbanization is rapidly creating new environments and generating new selective pressures on animal populations worldwide. In urban areas, animals need to cope with novel challenges such as non-natural predators, traffic, noise pollution, and light pollution. Behavior is a crucial factor determining how animals interact with the new and rapidly evolving urban environment. Across different taxa, studies show differences in behavior between urban and rural conspecifics, and some of these studies suggest that these might result not only from phenotypic plasticity, but also from microevolution. In lizards, few studies have studied behavior in the context of urbanization. Although tropical areas have some of the biggest cities and the highest diversity of lizards in the planet, knowledge about the effect of urbanization on tropical lizards is specially scarce. To test whether urbanization influences the behavior of the tropical lizard *Tropidurus hispidus*, we captured male lizards from rural and urban habitats in a tropical region. We kept the lizards in individual terraria and, after a period of acclimation, we conducted three behavioral tests to assess the behaviors tonic immobility, flight initiation distance and aggression. Each test was repeated three times in order to measure intra individual consistency in behavior. We found high intra-individual consistency in tonic immobility, in flight initiation distance and in aggression. These behaviors did not seem to differ in mean between rural and urban individuals, but rural individuals tended to show higher repeatabilities. Our results are the first evidence of animal personality in *T. hispidus*, and suggest that it may be more flexible in urban populations.

Keywords: animal personality, behavioral syndromes, lizard, tropics, *Tropidurus hispidus*, urbanization.

Introduction

The world is currently undergoing an accelerated urbanization process (CHEN et al., 2014), where the new urban environments are thought to generate new selective pressures on animal populations (SIH; FERRARI; HARRIS, 2011). But while some species are unable to persist in cities, others seem to be able to cope with the challenges of the new urban environment, and even thrive thereof, others (ALBERTI, 2015; LUCAS; FRENCH, 2012). Several studies in the last decades have shown that species inhabiting urban areas show changes in physiological, morphological and behavioral traits (but see Alberti *et al.*, 2017 for a revision on the theme).

Behavior is a crucial factor determining how animals interact with the new and rapidly evolving urban environment (SIH; FERRARI; HARRIS, 2011; WONG; CANDOLIN, 2015). When facing environmental changes such as urbanization, inadequate behavioral responses can reduce the fitness of individuals and may even lead an entire population to decline (TUOMAINEN; CANDOLIN, 2011). Contrarily, adequate behavioral responses might increase individuals' fitness under the new urban selective pressures (WONG; CANDOLIN, 2015). Across different taxa, studies in the last decades have shown that urban and rural conspecifics behave differently (MIRANDA, 2017). Some data suggest that these differences in behavior might result not only from phenotypic plasticity, but also from microevolution (Atwell *et al.*, 2012; Miranda, 2013).

Recent research on animal behavior has shown that individual animals consistently vary in sets of behavioral traits usually known as animal personalities (Biro, 2013). Animal personality can be defined by two criteria: (i) behavioral consistency over time at the individual level, and (ii) correlation between behaviors in different contexts (BELL, 2007). For example, *Anolis sagrei* lizards that are more explorative in an unfamiliar environment are also bolder in relation to predators (Lapiedra *et al.*, 2017). Individuals behaving in different ways can play different ecological roles (Sih et al., 2011). Individuals whose personality type is appropriate should increase the probability of successfully occupying and persisting in urban environments (Sih et al., 2011). Recently, studies have addressed the effect of urbanization on animal personality (Lapiedra, Chejanovski & Kolbe, 2017; Miranda, 2013; Riyahi *et al.*, 2017,).

In lizards, some studies have reported effects of urbanization in morphology (Prosser, Hudson & Thompson, 2006; Iglesias *et al.*, 2012; Kolbe, Battles & Avilés-Rodríguez, 2016; Winchell *et al.*, 2016, Hall 2017) and physiology (FRENCH et al., 2017; LUCAS; FRENCH,

2012), and behavioral traits (Prosser *et al.*, 2006; Moule *et al.*, 2016; Chejanovski *et al.*, 2017; Lapedra *et al.*, 2017, Batabyal *et al.* 2017, Pellitteri-Rosa *et al.*, 2017, Kwiatkowski *et al.* 2008, Winchell *et al.*, 2018, Macmillan *et al.* 2010, Bloch *et al.* 2006). Recent studies in two different species of lizard found that animal personalities differ between urban and rural skins *Lampropholis delicata* and between urban and rural *Anolis sagrei* (LAPIEDRA; CHEJANOVSKI; KOLBE, 2017; MOULE *et al.*, 2016a). For example, Moule and collaborators (2016a)

The present study main objective is to verify the existence and to investigate possible differences in animal personality between urban and rural populations of the neotropical lizard *Tropidurus hispidus* (Spix, 1825). Here we test the hypothesis that *T.hispidus* presents intra-individual consistency in flight initiation distance, aggressiveness, and tonic immobility behaviors, and correlations between these behaviors. We further investigated whether *T.hispidus* differs in the intraindividual consistency of the behaviors studied.

Methods

Study species

Tropidurus hispidus is an iguanid neotropical ground lizard native to South America, distributed from Venezuela to Argentina (DE CARVALHO, 2013). This lizard is a generalist species in terms of habitat (DIAZ-URIARTE, 1999), although it seems to have a preference for open areas (DE CARVALHO, 2013). It is common in the urban habitat, where it seems to be well succeeded (Díazuriarte, 2000; Díazuriarte, 1999; Abreu *et al.*, 2002).

Animal collection and maintenance in captivity

From October 2016 to January 2017, we collected 20 urban and 20 rural *T. hispidus* males in Maranhão Island, State of Maranhão, Northeastern Brazil. The urban lizards were collected in the city center of São Luís (U1-2°32'40"S 44°17'36"W), while the rural lizards were collected in two rural locations (R1: 02° 37' 17" S, 44° 6' 28" W and R2: 02° 38' 8" S, 44° 8' 51" W) at a linear distance of, respectively, 5 km and 6 km of the external perimeter of São Luís. The rural habitat refers to sites that visually resemble wilderness area in terms of their structure, with the absence of paved surfaces or buildings and with rare vehicle traffic. São Luís is the city with the largest urban population of the Brazilian state of Maranhão and one of oldest cities of this state with 405 years of foundation (IBGE, 2013). In the urban center, the lizards mainly occupied human structures as walls, while rural lizards were mostly found on trees, fallen barks, rocks or bare soil.

We captured the lizards mostly with the aid of a “lizard fishing pole”, where we attached one end of a nylon string to a stick, making a slipknot at the other end of the string that

allowed us to “fish” the lizards. In some cases, we caught the lizards by hand. Immediately after capture, the lizards were measured for Snout to Vent Length (SVL), and their sex was determined (as males possess conspicuous black spots on the ventral part of the body (Ribeiro; Freire, 2009)). Only male adults (SVL >69 mm, Ribeiro; Freire, 2009) were included in the study.

Lizards were individually housed at the Federal University of Maranhão in equal terraria covered with 150 x 150 x 70 cm length x width x height. Urban and rural lizards were intercalated to avoid effects of potential environmental gradients on the treatments (Hurlbert, 1984). Each terrarium was covered with a screen to prevent predator attacks or the escape of individuals (see figure S1 in supplementary material). Each terrarium contained a brick, with wooden planks and straw placed on its top serving as a refuge (see figure S1 b) in supplementary material). Water and food (living termites *Nasutitermes coxipoensis*) were provided daily. Before the experimental tests started, the lizards had a time of acclimation to the terraria of around 3 months (mean \pm se =65.43 \pm 3.06 days). After the end of the study, we returned the lizards to their original environments.

During the study, 6 out of 40 lizards died (5 rural and 1 urban). The deaths occurred all in the same day, after a flight initiation distance test. Although the lizards that died did not show altered behaviors in the flight initiation test (statistics maintaining or removing these individuals provided similar results), we decided from that event on to reduce the time we retained the lizards in a cardboard box before and after this experiment. The other 34 lizards remained healthy during the entire period in captivity.

Behavioral tests

Between December 2016 and June 2017, we subjected the lizards to three different behavioral tests: tonic immobility (TI), Flight Initiation Distance (FDI) and Simulated Territory Intrusion (STI). Subjects were tested individually in three repeated trials of each behavioral test to determine the intra-individual consistency in behavior. There was a minimum interval of two weeks between subsequent trials of the same test.

Tonic Immobility

The tonic immobility test was adapted from the methodology by Maximino, Carvalho & Morato (2014) for *Tropidurus oreadicus*. These tests were performed in the individual terraria from 9 a.m. to 1 p.m. To assess tonic immobility, the lizard was placed on its back on the terrarium floor and gentle pressure was applied to the thorax and pelvis for 12 seconds, eliciting the voluntary immobilization that usually follows a predator attack. After this time, the lizard was released from the pressure and the time until resumption of the usual posture was

registered as a measure of tonic immobility. Each of the three trials of this test was conducted by a different experimenter, with similar clothing, to avoid the habituation of the lizards to the experimenter. All the recorded tonic immobility measures were above zero (minimum = 5 seconds, max = 7260 seconds).

Flight Initiation Distance

Ca 60 minutes (mean \pm se = 64.2 ± 5.7 minutes) before its individual test, we removed the lizard from its' individual terrarium and placed it alone in a cardboard box with breathing holes. In the beginning of the test, the lizard was individually placed under another cardboard box (20 x 12 x 7) with the opening facing the floor at a specific point at the end of the room. A human experimenter stood motionless 5 meters away from the box containing the lizard during a period of acclimation of 3 minutes. After the 3 minutes, the human experimenter slowly lifted the box through an attached thread and directly but slowly approached the lizard. Similarly, to the tonic immobility rest, a different experimenter to avoid the habituation of the lizards to the experimenter performed each of the three trials of this test. The experimenters were standardized regarding clothing and approach velocity. Flight Initiation Distance was considered the distance at which the lizard began to move away from the experimenter

We returned the lizards to the terraria ca 50 minutes (mean \pm se = 47.7 ± 5.3 minutes) after their individual experiment.

Simulated Territory Intrusion

We conducted Simulated Territorial Intrusion tests to quantify the aggressive behavior of *T. hispidus*. The tests were performed in the individual terraria from 10 a.m. to 4 p.m. Behavior displays were captured by a video camera (Motorola phone G3-Xt1543 and Sony Handycam Hdr-cx220). To elicit aggressive behavior, we adapted the methodology by Baxter and collaborators (2001) for the genus *Anolis*. The lizard was captured and placed under a cardboard box (20 x 12 x 7) in its individual terrarium, and centrally positioned in front of a mirror (56 cm L \times 50 cm H) placed against the wall. Before the test, we removed the brick, the wood and the straw from the terrarium. After 3 minutes, a line lifted the box, allowing the researcher to remove it from the terrarium. Each subject was recorded for 30 min.

After the video analysis, for each subject in each of the three trials of this test, aggression was quantified as the sum of the number of aggressive displays. This included the behaviors (i) head bobbing (a series of sequential up and down head movements), (ii) push-up (an up and down movement of the body by flexing the front legs), (iii) arching of the back (an upward bending of the spine forming an arch), (iv) complete gular extension, (v) open-mouthed threat display, (vi) trunk elevation (an elevation of the front legs and trunk after which

the individual remains immobile for a period of time) on the substrate, and (vii) attack (an attack where the lizard touched the mirror).

Statistical analyses

The data were analyzed using the software *R* (3.4.3). Statistical significance was assigned at $\alpha = 0.05$. The variables tonic immobility, escape distance and aggressiveness were log transformed in order to verify the assumptions of normality of the models' residuals.

For each behavior of interest, we used linear mixed effects models (LMM; package *lme4*: BATES et al., 2015) to determine whether there were any differences in behavior between origins (rural origin, including the 2 rural areas, vs urban origin) or trials (trial 1, trial 2 and trial 3). We included individual ID in the models as a random effect to account for repeated measures of each individual. Initially, the models included the interaction between origin and trial, but we allowed this to be eliminated from the model through a backward stepwise procedure (package *LmerTest*: KUZNETSOVA; BROCKHOFF; CHRISTENSEN, 2015). *P*-values for LMMs were calculated based on Satterthwate's approximations (package *LmerTest*: Kuznetsova, Brockhoff & Christensen 2015).

To assess intra-individual consistency in behavioral responses, we calculated for each behavior of interest LMM based repeatabilities and their standard errors (package *rptR* Nakagawa & Schielzeth, 2018). The *p*-values for the repeatability estimates were obtained from likelihood ratio tests. We investigated differences between repeatabilities in the rural and the urban population using Monte Carlo simulations performed on bootstrapping samples of the two repeatability estimates. We sampled 10 000 times with replacement from the bootstrapping samples and estimated the asymptotic two-tailed *P*-value for the difference in repeatabilities as twice the proportion of samples for which the difference ($R_{urban} - R_{rural}$) was equal or smaller than zero.

For each trial, both for the overall data and for each population, we calculated the Pearson coefficients of correlation between pairs of the three behaviors of interest.

Results

Overall, tonic immobility was significantly repeatable across different trials ($R = 0.25$, $CI = [0.033, 0.462]$, $p = 0.009$). Analyzing repeatability separately for each origin, we found that the significant overall repeatability seems to be driven by the relatively high and significant repeatability of rural individuals ($R = 0.41$, $CI = [0.077, 0.650]$, $p = 0.005$), with urban individuals' repeatabilities being lower and non-significant ($R = 0.157$, $CI = [0, 0.437]$, $p = 0.156$), but with overlapping confidence intervals and without significant differences between the two origins ($P = 0.238$).

Flight initiation distance also showed a significant and relatively high overall repeatability across different trials ($R = 0.413$, $CI = [0.199, 0.594]$, $p < 0.001$). Performing the repeatability estimation separately for urban and rural individuals, we found this applied both for rural ($R = 0.404$, $CI = [0.075, 0.660]$, $p = 0.008$) and urban ($R = 0.372$, $CI = [0.046, 0.619]$, $p = 0.005$) individuals. Repeatability estimates were not significantly different between the two origins ($P = 0.810$).

Aggressiveness was significantly repeatable and with a relatively high point estimate ($R = 0.546$, $CI = [0.313, 0.697]$, $p < 0.001$). Although this behavior was repeatable both for rural and urban individuals, we found a much higher and more significant point estimate for rural individuals, with only a slight overlap of the confidence intervals (Rural: $R = 0.785$, $CI = [0.583, 0.897]$, $p < 0.001$; Urban: $R = 0.421$, $CI = [0.099, 0.654]$, $p = 0.002$), and a significant difference between point estimates for the two origins ($P = 0.016$).

Correlations between corresponding trials of different behavioral tests were always relatively low (r between 0.029 and 0.39) and non-significant (p values between 0.081 and 0.905) and, both overall and separately for rural and urban individuals (see appendix; table 1).

Tonic immobility and aggression did not seem to differ between rural and urban individuals or between the trials (see appendix; table 2; Fig.1 and 3), but flight initiation distance presented a marginally significant difference between urban and rural (see appendix; table 3, Fig.2)

Discussion

The present study shows that *T. hispidus* have high intra-individual consistence in different behaviors, and that this seems to be lower in the urban individuals. The fact that tonic immobility, flight initiation distance and aggression were highly repeatable is the first evidence of the existence of personality traits in the neotropical lizard *T. hispidus*.

Our results suggest a tendency for rural individuals to have greater or more significant repeatabilities than urban ones in aggression and tonic immobility. This may indicate a change in the structure of personalities in the urban environment, that could indicate an increase in behavioral plasticity in urban individuals. The difference in individual consistency in behavior, or animal personality, has been associated as having direct influence on individuals' physical fitness (Réale et al, 2007; Sih etl al 2012). This is because such differences are expressed in various contexts. Por example, bold individuals tend to show boldness in mating, foraging and risk-taking behavior (Dingemanse & Denis Réale, 2005). Individuals from a single population vary in responses to similar situations (Biro 2013, Réale 2007 and Sih 2004). In contrast, behavioral plasticity can cause immediate behavioral modifications to novel and potentially

risky stimuli (Lowry et al. 2013). Behavioral plasticity might be favored in urban individuals, as it potentially allows them to deal with a range of novel situations in the new urban environment (Shochat et al. 2006; Tuomainen & Candolin 2011). Lowry et al, 2013, suggest that these two factors can lead to behavioral changes in the urban environment. The species with behavioral plasticity may be particularly predisposed to inhabiting urban landscapes due to their ability to respond more rapidly to altered conditions. In contrast, animal personality implies in animals with limited flexibility in behavior. Thus, the urban environment may favor individuals or species with certain behavioral types, for example, boldness (Lowry et al., 2013).

Rodriguez-Prieto et al. (2011) found in a study with lizards a relation between exploration traits and plasticity in FID in relation to predator. Individuals that explored a new environment quickly also decreased their FID more quickly in response to the predator over time. Habituation capacity could provide benefits for individuals in urban areas with abundant low-risk predators. Colonization could be facilitated if the greater potential of exploratory individuals to habituate is coupled with their greater dispersion ability (Rodriguez-Prieto et al. 2011). Duckworth e Badyaev (2007) found a relationship between dispersion and aggressive behavior in birds in United States. Our study found no difference between FID repeatability in urban and rural individuals, but found for aggression. We suggest a similar process between flexibility in aggressive behavior and success in colonizing and persisting in urban environment.

In different taxa, aggressive behavior has been associated with boldness (DINGEMANSE; RÉALE, 2005; HURTADO; MABRY, 2017; LAPIEDRA; CHEJANOVSKI; KOLBE, 2017), but this is not always the case (review in Sih & Bell, 2008). In our study, we did not find any correlation between aggressive behavior and either tonic immobility or flight initiation distance, that are usually considered different contexts of behaviors related to boldness. Although we cannot completely exclude the possibility of having measured non-target behaviors, this lack of correlation might mean that boldness and aggression evolved as independent personality traits in *T. hispidus*, suggesting no strong selection for generate trait correlation. McEvoy et al, 2014 have suggested that behavioral traits that have the potential to affect survival and reproduction may require different adaptive responses, and their covariance between different contexts might be detrimental.

Urban and rural *T.hispidus* did not differ in tonic immobility or in aggression. Flight initiation distance showed a marginally significant difference between urban and rural individuals. This tendency is consistent with previous studies with lizards in the wild, that found shorter flight initiation distances in urban lizards when compared to their rural counterparts

(Batabyal et al., 2017; Sparkman et al., 2018). The studies attributed this difference to the habituation to human presence. Rural lizards tend to consider a real predatory threat showing less boldness and greater caution (Pellitteri-rosa et al., 2017). In urban environments, the ability to habituate to human presence could allow individuals to decrease the cost of fleeing and increase time for other activities, such as foraging or mating ((Rodríguez-Prieto et al., 2009).

Our experiments were conducted in captivity in order to standardize the environmental conditions, eliminating the intrinsic environmental differences between the urban and rural habitats, that could elicit differences in behavior independent of the urban or rural origin of the focal individuals. Moreover, experiments in captivity allowed us to eliminate the effects of possible interactions of the focal individuals with other individuals in the same environment. Our tests were performed after a fairly long acclimation period, in order to try to exclude the effects of eventual differences in the strength of reaction to captivity, or in the time of habituation to captivity. Moreover, we cannot exclude the hypothesis that our simulated behavioral challenges may not reflect the type of ecological problems faced in the wild. Thus, our results do not necessarily reflect the results we would have measured in the wild, or even in captive experiments without a period of acclimation. Additionally, even though our data suggest that urbanization creates a disruption in intra-individual consistency of behavior (and thus of the structure of personality traits), a generalization could only be made through studies focusing on multiple rural–urban population pairs.

Facing the continuous increase in urbanization at a global level, it is vital to understand how animals respond to this changing world. Here, for the tropical lizard *T. hispidus*, we show evidence for differences in the intra-individual consistency of personality traits between urban and rural populations.

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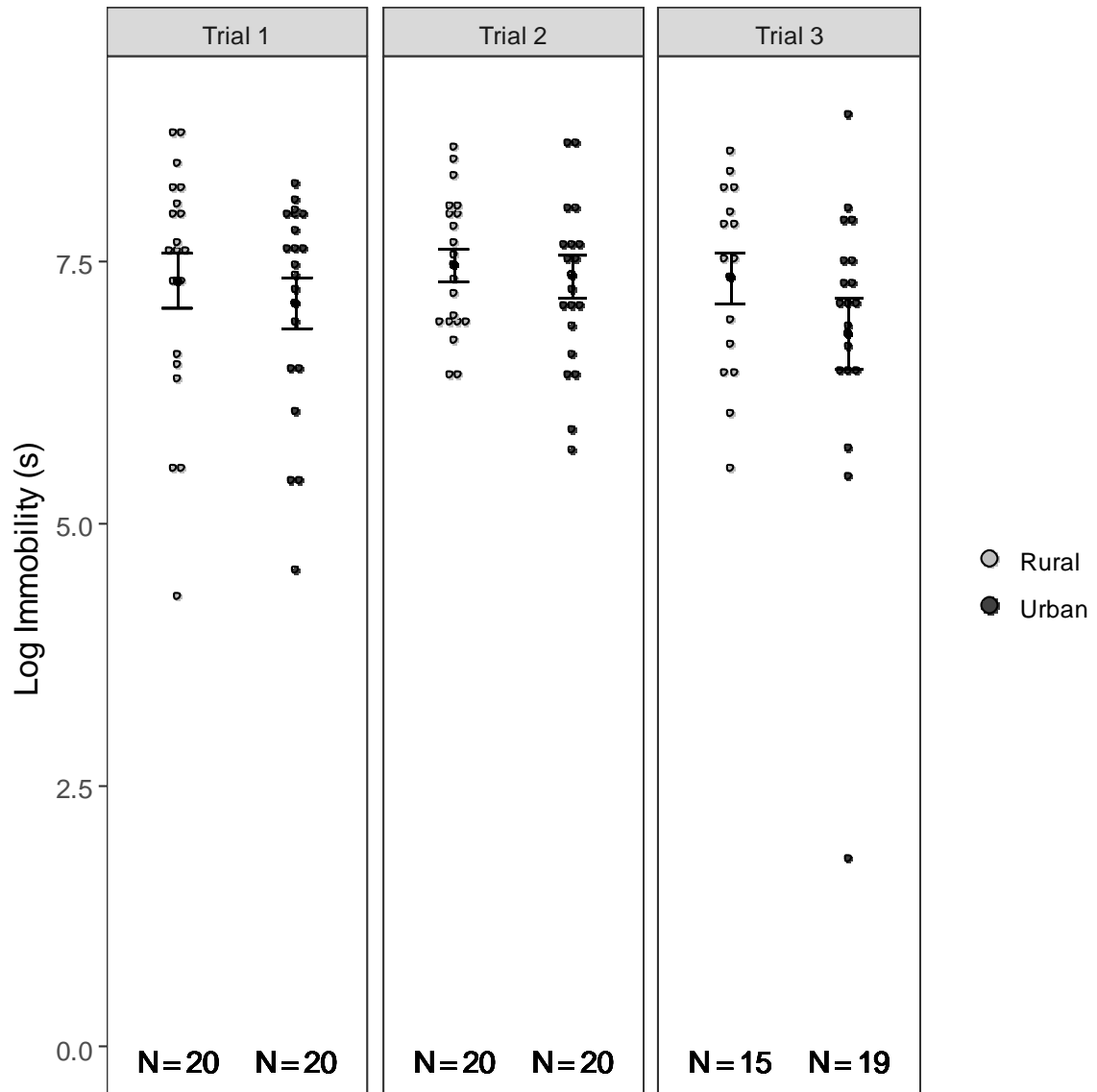
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4. CONSIDERAÇÕES FINAIS

A personalidade animal tem sido considerada um mecanismo importante para que animais persistam em ambientes urbanos. Neste estudo, encontramos a primeira evidência de personalidade animal no lagarto neotropical *T. hispidus*. Encontramos também diferença na personalidade em lagartos urbanos e rurais, sugerindo que *T. hispidus* apresente comportamento mais flexível. Como a urbanização aumenta consideravelmente com o crescimento da população humana, a compreensão de personalidade animal em animais que são capazes de lidar com as novas situações apresentadas nos ambientes urbanos é de grande importância para entender os mecanismos que permitem a persistência das espécies nesse ambiente. Estudos nesse âmbito podem servir de ferramenta para identificar espécies vulneráveis que podem não ser capaz de lidar com a urbanização e nos permitem intervir antes que a urbanização os afete.

APÊNDICES

Figures



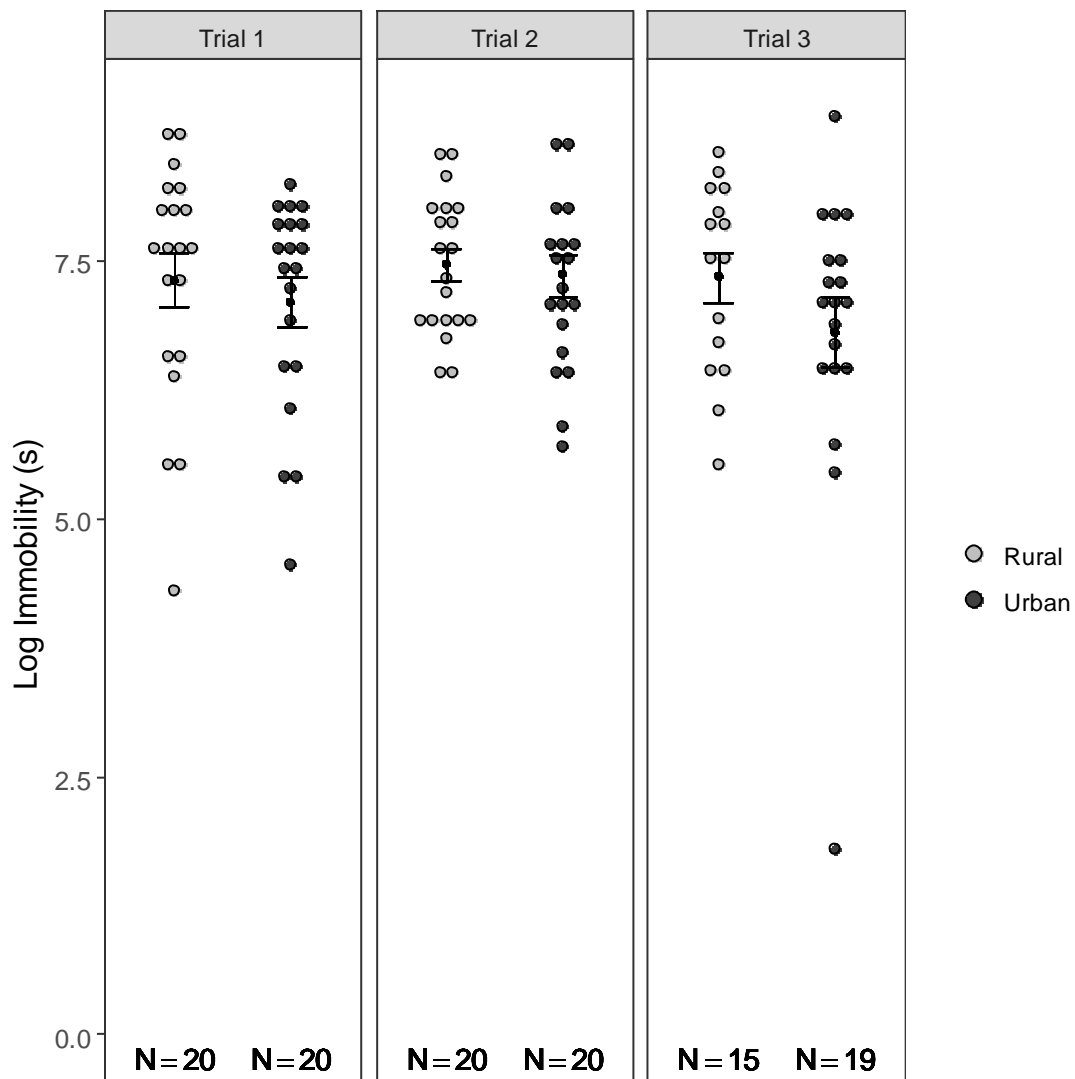


Figure1: Latency for to return to usual posture during tonic immobility test for rural (light grey) and urban (dark grey) *T. hispidus* in each trial. Points represent tonic immobility for each individual. Means \pm standard errors are shown. Latency (in seconds) was log-transformed.

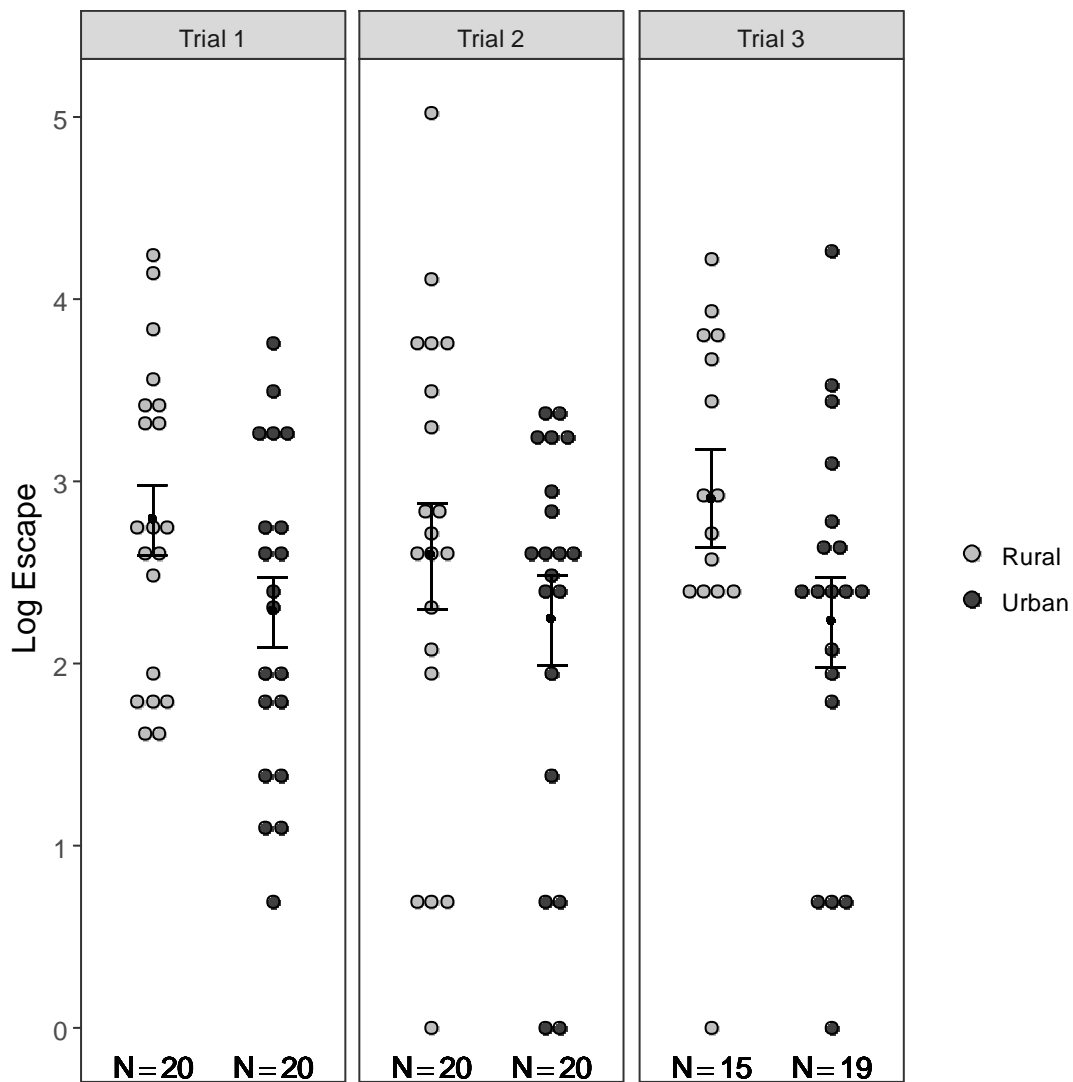


Figure 2: Flight initiation distance test for rural (light grey) and urban (dark grey) *T. hispidus* in each trial. Points represent flight initiation distance for each individual. Means \pm standard errors are shown. Flight initiation distance (in cm) was log-transformed.

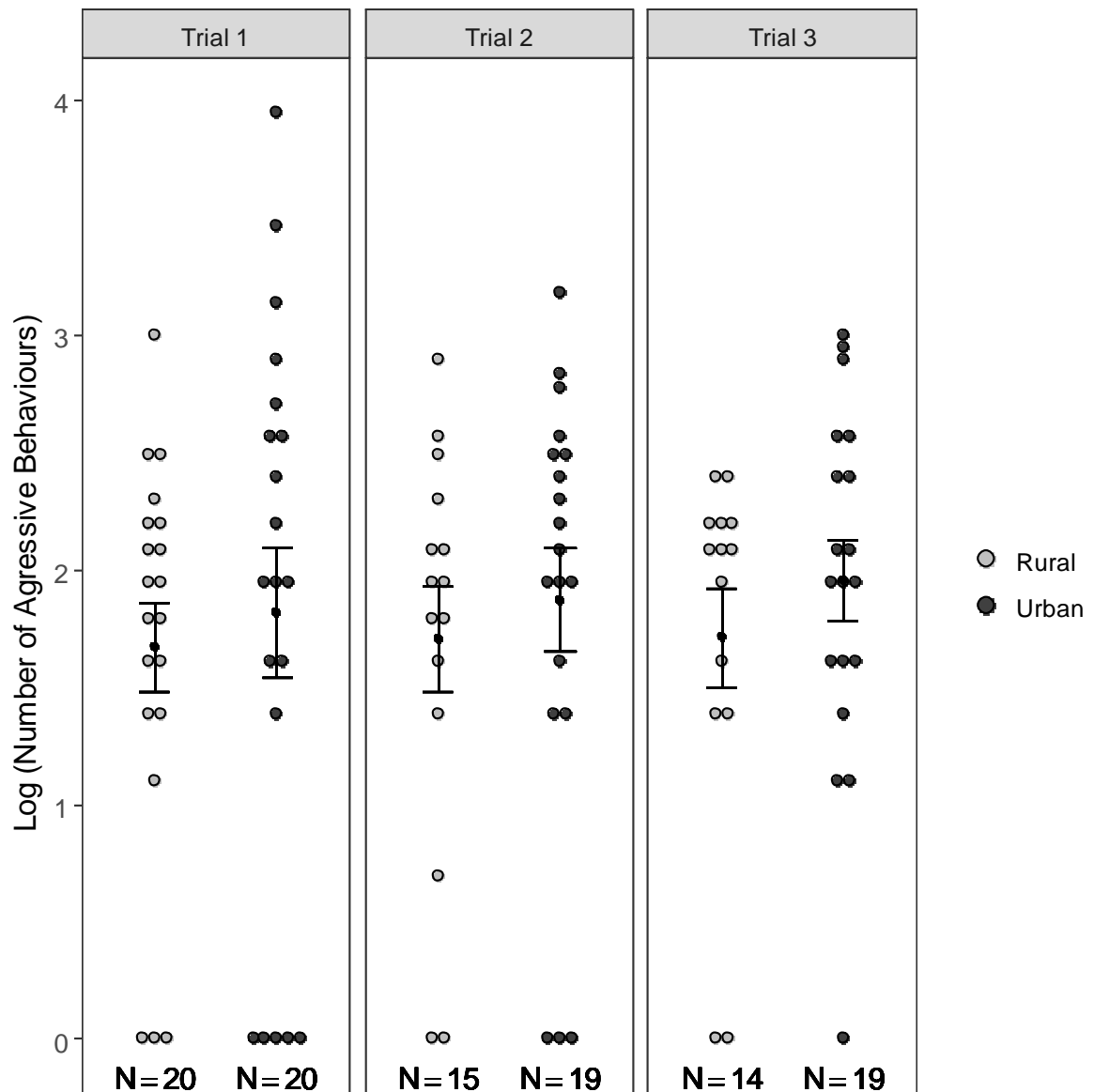


Figure 3: Aggressiveness during Simulated Territorial Intrusion for rural (light grey) and urban (dark grey) *T. hispidus* in each trial. Points represent aggressiveness for each individual. Means \pm standard errors are shown. Number of aggressive behaviors was log-transformed.

Tables

Table 1: For all the studied individuals, for the rural individuals, and for the urban individuals, this table shows for each trial the Pearson correlation coefficients (ρ) between tonic immobility, flight initiation distance and aggression and their respective standard errors (se) and p -values.

		Tonic Immobility vs FID			Tonic Immobility VS Aggression			FID vs Aggression		
		ρ	95% CI	p	ρ	95% CI	p	ρ	95% CI	p
All	Trial 1	0.046	[-0.129, 0.473]	0.84	0.226	[0.091, 0.502]	0.159	0.062	[0.366, 0.254]	0.703
	Trial 2	0.189	[0.129, 0.473]	0.2403	-0.161	[-0.326 0.296]	0.912	-0.061	[0.317, 0.305]	0.97
	Trial 3	0.023	[-0.315, 0.360]	0.8869	0.246	[-0.195,0.473]	0.178	-0.236	[-0.531,0.110]	0.178
Rural	Trial 1	0.164	[0.299, 0.565]	0.488	0.246	[0.219, 0.621]	0.294	-0.267	[0.443, 0.441]	0.335
	Trial 2	0.208	[-0.596, 0.257]	0.377	0.09	[-0.367 0.512]	0.705	0.058	[-0.488 0.394]	0.807
	Trial 3	0.02	[-0.513, 0.744]	p=0.993	0.375	[0.596, 0.283]	0.167	-0.267	[-0.685,0.283]	0.335

Urban	Trial 1	0.046	[0.404, 0.478]	0.84	0.229	[-0.236 0.610]	0.329	- 0.27 9	[- 0.509,0.369]	0.246
	Trial 2	0.39	[-0.715,0.052]	0.081	0.033	[-0.469 0.414]	0.887	0.05 8	[0.394,0.48 8]	0.806
	Trial 3	0.029	[-0.430, 0.477]	0.905	0.27	[0.646, 0.207]	0.259	- 0.27 9	[- 0.650,0.200]	0.246

Table 2: Sum of Squares (SS), Mean Squares (MS), and Satterthwaite's P-values for fixed effects in linear mixed-effects models for tonic immobility, flight initiation distance and aggression (log-transformed).

Parameter	Tonic Immobility			Flight Initiation Distance			Aggression		
	SS	MS	P	SS	MS	P	SS	MS	P
Origin	0.906	0.906	0.307	2.070	2.070	0.091	0.291	0.291	0.402
Trial	2.316	1.158	0.261	0.288	0.144	0.811	0.111	0.056	0.872

Supplementary Material



Figure S1: Terraria: a) outside view; b) inside view.

ANEXOS

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Lemelin, P. (1996a). Relationships between hand morphology and feeding strategies in small-bodied prosimians. *Am. J. phys. Anthropol.* (Suppl.) 22, 148.

Lemelin, P. (1996b). *The evolution of manual prehensility in primates: a comparative study of prosimians and didelphid marsupials*. PhD thesis, State University of New York at Stony Brook.

Pianka, E. R. (1978). *Evolutionary ecology*. 2nd edn. New York: Harper & Row.

Whitear, M. (1992). Solitary chemosensory cells. In *Fish chemoreception*: 103-125. Hara, T. J. (Ed.). London: Chapman & Hall.

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