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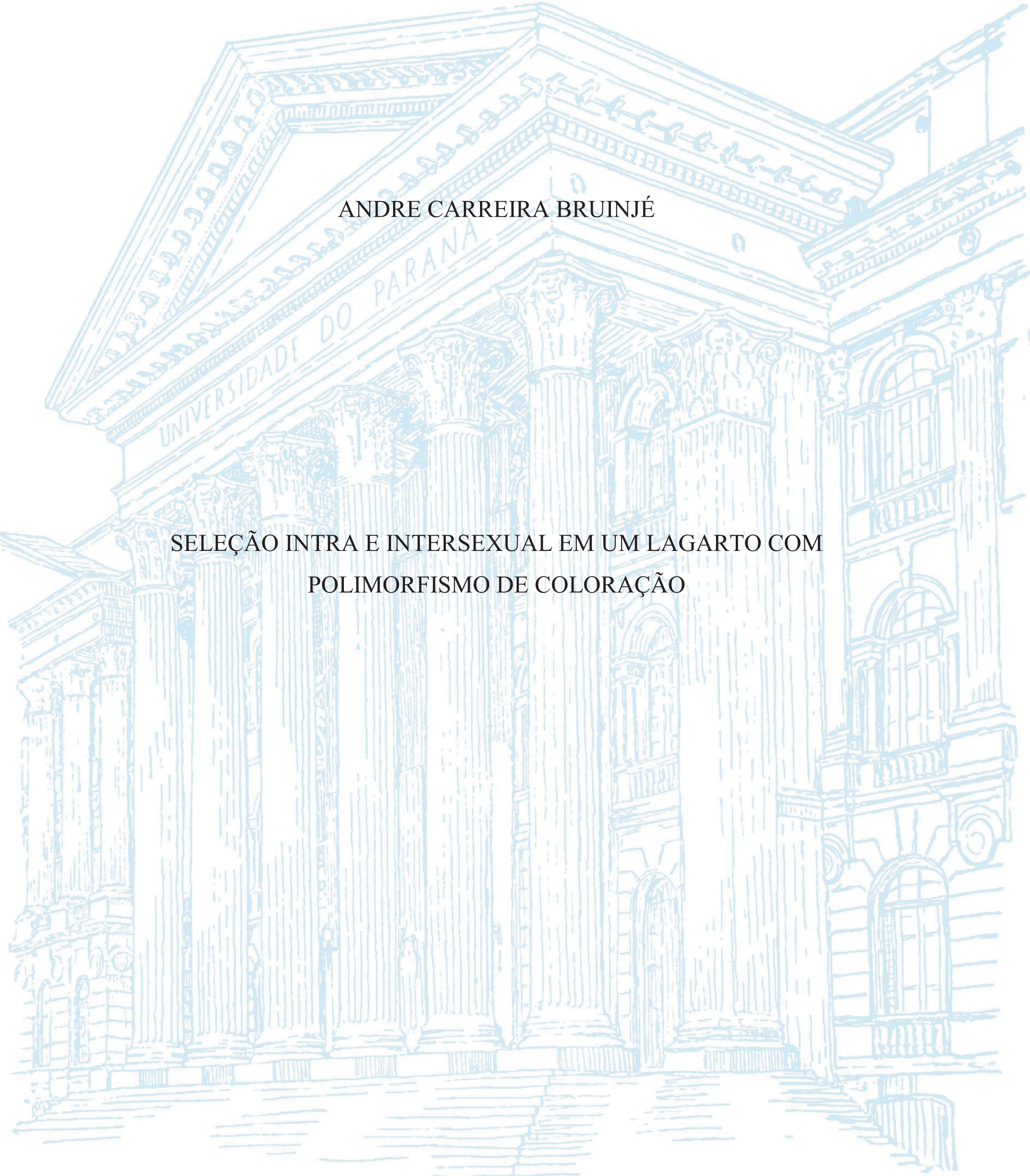

ANDRE CARREIRA BRUINJÉ

SELEÇÃO INTRA E INTERSEXUAL EM UM LAGARTO COM POLIMORFISMO DE COLORAÇÃO

CURITIBA

2018

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Tese apresentada ao curso de Pós-Graduação em Ecologia e Conservação, Setor de Ciências Biológicas, Universidade Federal do Paraná, como requisito parcial à obtenção do título de Doutor em Ecologia e Conservação.

Orientador: Prof. Dr. Mauricio Osvaldo Moura

Coorientador: Prof. Dr. Gabriel Corrêa Costa

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TERMO DE APROVAÇÃO

Os membros da Banca Examinadora designada pelo Colegiado do Programa de Pós-Graduação em ECOLOGIA E CONSERVAÇÃO da Universidade Federal do Paraná foram convocados para realizar a arguição da tese de Doutorado de **ANDRE CARREIRA BRUINJE** intitulada: **Seleção intra e intersexual em um lagarto com polimorfismo de coloração**, após terem inquirido o aluno e realizado a avaliação do trabalho, são de parecer pela sua APROVAÇÃO no rito de defesa.

A outorga do título de doutor está sujeita à homologação pelo colegiado, ao atendimento de todas as indicações e correções solicitadas pela banca e ao pleno atendimento das demandas regimentais do Programa de Pós-Graduação.

Curitiba, 06 de Abril de 2018.

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“Toda generalização é burra”

Algum professor meu do ensino fundamental
(provavelmente inspirado em Nelson Rodrigues)

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RESUMO

Seleção sexual é um dos mais importantes promotores de diversidade morfológica e comportamental. Dentre esta diversidade biológica estão as estratégias reprodutivas alternativas de cada espécie, nas quais variantes de comportamento e de coloração são, muitas vezes, mantidas por reprodução diferencial. Neste contexto, é esperado que machos informem sua “qualidade individual” através de sinalização, fêmeas escolheriam então “melhores” parceiros, e tais machos tenderiam a vencer encontros de competição entre machos. A lagartixa-do-lajedo, *Tropidurus semitaeniatus*, é um lagarto saxícola de pequeno porte endêmico ao bioma da Caatinga na América do Sul que possui dois morfos de cores entre machos adultos. Nesta Tese, exploro os papéis dos morfos dos machos em seleção intra- e inter-sexual considerando comportamento, performance do organismo, e coloração. No Capítulo 1, exploro se os morfos de machos, e fêmeas, diferem em sua coloração ao longo do corpo todo e se eles são capazes de perceber estas diferenças de coloração. Resultados demonstram que não apenas fêmeas, machos pretos e machos amarelos caracterizam três classes distintas nos padrões de cor, mas também que as diferenças entre os grupos são perceptíveis pela visão de conspecíficos tanto em colorações dorsais quanto ventrais. No Capítulo 2, exploro o papel dos morfos em ensaios de competição intra-sexual entre morfos. Os resultados demonstram que os morfos de cor de machos de *T. semitaeniatus* tendem a apresentar comportamentos diferentes. Machos pretos tendem a ser mais agressivos enquanto machos amarelos dentem a se comportar de forma mais evasiva. A performance de velocidade máxima de corrida não teve relação com agressividade nem com a tendência de vencer os embates. No entanto, colorações ventrais mais escuras e amareladas sinalizam a habilidade de luta dos machos. No Capítulo 3, exploro o papel dos morfos em contextos inter-sexuais. Através de experimentos de escolha, testo se as fêmeas possuem preferencia pelos morfos enviesada, através de sinais visuais e/ou químicos. Fêmeas preferem machos do morfo pretos por sinais químicos, mas não por sinais visuais, e também não acessam a performance do macho por nenhum destes. Visualmente, no entanto, fêmeas preferem colorações ventrais mais escuras e esverdeadas (mas não um morfo específico). No Capítulo 4, apresento frequências relativas de morfos e sexos de lagartos coletados em três populações relativamente próximas. Curiosamente, frequências dos morfos apresentam alta variação entre todas as três populações. Machos amarelos representaram de um mínimo de 5% dos machos adultos em uma população para até 85% dos machos em uma segunda população. Em suma, meus resultados sugerem que os machos de cor da lagartixa-do-lajedo têm um papel no acesso à reprodução, e fazem uso de diferentes estratégias comportamentais. Além disso, que a comunicação ocorre através de múltiplas vias de sinalização. Finalmente, uma vasta gama de possibilidades para estudos futuros é aberta por estes resultados tais como redes de interação sociais dos morfos; a associação de estratégias alternativas de reprodução dos morfos ao longo de diferentes estações reprodutivas; a relação da sinalização química e da produção de colorações baseadas em pigmentos; e a variação da performance imunológica e de força de mordida entre os morfos.

Palavras-chave: Seleção sexual, competição entre machos, escolha de parceiro, *Tropidurus semitaeniatus*, comportamento, morfos de coloração

ABSTRACT

Sexual selection is one of the most important drivers of morphological and behavioral diversity. Among this biological diversity there are alternative reproductive tactics within species, of which behavioral and color variants are often maintained by differential reproduction. In these contexts, it is expected that males would inform individual quality through signaling, females would then choose "better quality" males, and such males would win male-male competition encounters. The striped lava lizard, *Tropidurus semitaeniatus*, is a small sized rock-dwelling lizard endemic to the Caatinga biome in South America that has two color morphs among adult males. In this Thesis, I access the role of male color morphs in intra- and inter-sexual selection taking into account behavior, whole-organism performance, and coloration. In chapter 1, I access whether male morphs, and females, differ in their whole body coloration and whether they are able to perceive such differences in coloration. My results show that, not only females, black males, and yellow males show distinct color patterns, but also that such differences among groups are perceivable by conspecifics' vision in both dorsal and ventral coloration. In chapter 2, I access the role of color morphs in staged intra-sexual competition trials between morphs. My results show that male color morphs of *T. semitaeniatus* tend to behave differently. Black males tend to behave more aggressively while yellow males tend to be more evasive. Sprint-speed performance has no relationship to aggressiveness or tendency to win encounters. However, darker and yellowish ventral colors signal fighting ability of males. In chapter 3, I explore the role of male color morphs in inter-sexual contexts. Through multi-modal choice experiments I access whether females have biased preference of color morphs through visual and/or chemical cues. Females prefer black morph males by chemical cues, but not by visual ones, and they do not access male's performance by any. Visually, however, females tend to prefer darker-greenish ventral colorations (but not a specific morph). Finally, in Chapter 4, I present morph and sex relative frequencies of lizards sampled in three relatively close populations. Curiously, color morph frequencies vary greatly among all three populations. Yellow males accounted for as low as 5% of adult males of one population, for up to 85% of adult males of a second population. All together, my results suggest that male color morphs of the striped lava lizard play a role in the assessment of reproduction and make use of different behavioral strategies. Also, that communication occurs through multiple modes of signaling. Lastly, a wide range of possibilities for future studies is opened by these results such as morphs' social network; association of alternative reproductive tactics of morphs throughout breeding seasons; the relationship of chemical signaling and the production of pigment-based colorations; and distinction of immunological and bite-force performances between color morphs.

Keywords: Sexual selection, male-male competition, mate choice, *Tropidurus semitaeniatus*, behavior, color morphs

SUMÁRIO

Introdução geral

Grande parcela da diversidade morfológica e comportamental observada na natureza é criada por processos de seleção sexual. Originalmente, seleção sexual foi proposta para explicar o fenômeno das grandes diferenças morfológicas entre os sexos de uma mesma espécie (Darwin, 1889; Andersson, 1994). No caso de animais por exemplo, é comum serem observadas espécies em que os machos possuem colorações exuberantes e contrastantes com o ambiente, enquanto fêmeas possuem colorações pálidas, muitas vezes crípticas no ambiente. Wallace propôs que esse dimorfismo sexual acentuado seria promovido por processos de *seleção natural* nas características morfológicas das fêmeas (Wilson, 1992). O argumento é de que seria esperado que características exuberantes surgissem naturalmente ao acaso durante a diversificação das espécies. No entanto, esta conspicuidade seria suprimida nas fêmeas por ação da *seleção natural* devido a necessidade de manterem-se crípticas no ambiente por conta de fatores relacionados a reprodução. Por exemplo, pela necessidade de manter-se no ninho por longos períodos de tempo, uma ave fêmea com coloração mais pálida e críptica teria menor risco de predação do que uma fêmea com coloração chamativa (Chapman, Arnqvist, Bangham, & Rowe, 2003; Wilson, 1992).

A proposta de que o dimorfismo sexual acentuado seria dado por *seleção sexual* reorienta a visão do sexo sob seleção, propondo que as características conspícuas (geralmente dos machos) é que estariam sob seleção na competição pelo acesso a reprodução (Darwin, 1889). Isto se daria por meio de dois processos principais: *seleção intrasexual*, em que a competição entre machos promoveria a seleção de armamentos, e portanto os indivíduos mais competitivos teriam maior acesso as fêmeas; E *seleção intersexual*, em que fêmeas escolheriam seus parceiros por meio de um conjunto de características (ornamentos) que sinalizariam uma qualidade intrínseca do macho. Em ambos os casos, o resultado é o equivalente a uma corrida armamentista. A cada geração, melhores armamentos (e.g. chifres, bicos, tamanho de corpo, musculatura mais robusta) são selecionados para competir com os demais indivíduos do mesmo sexo. Da mesma forma, a cada geração ornamentos mais exuberantes (e.g. plumagem mais colorida e perceptível em contraste com o ambiente; comportamentos mais complexos, elaborados e energeticamente dispendiosos; e vocalizações melhor propagadas, nítidas e percebidas) são selecionados por meio da preferência das fêmeas.

A maioria dos modelos de evolução sob seleção sexual consideram um fator de custo vinculado a sinalização. Este custo pode ser tanto em relação a qualidade intrínseca do indivíduo (como condição imunológica, infestação parasitária ou performance fisiológica) quanto associado a um incremento em riscos infringidos ao individuo sinalizador (maior conspicuidade para seu predador, por exemplo) (Zahavi, 1975; Andersson, 1994). A expressão de diferentes tipos de coloração carrega um fator de custo em uma variedade de situações. Em lagartos, por exemplo, a reflexão ultravioleta nos machos é preferida por fêmeas (Bajer *et al.*, 2011; Lisboa *et al.*, 2017) e também informa a habilidade de disputas agonísticas entre machos (Stapley & Whiting, 2006), mas carrega o custo de incrementar conspicuidade a predadores (Zuk & Kolluru, 1998; Whiting *et al.*, 2006). Outro exemplo é a sinalização através da expressão de colorações baseadas em pigmentos (geralmente colorações mais escuras, amareladas, avermelhadas, ou amarronzadas), pois pigmentos são custosos ao indivíduo para produzir (Lozano, 1994; Olson & Owens, 1998).

A sinalização, no entanto, pode ocorrer por diferentes (ou múltiplas) vias. Além da coloração, fêmeas comumente escolhem machos que apresentam *displays* comportamentais custosos (Wikelski *et al.*, 2001). Outro exemplo são feromônios que, muitas vezes, são produzidos com base em compostos precursores de vitamina D. Gerando um custo metabólico diretamente proporcional a sua excreção (Martín & López, 2006). Em todos estes exemplos, sinalização em contextos sexuais (tanto intra- quanto inter-sexuais) são diretamente relacionadas a “qualidade” do indivíduo, conferindo um custo ao emissor. Fêmeas, portanto, escolheriam parceiros em relação a sua qualidade por meio de seus sinais em troca de benefícios diretos e/ou indiretos. Por exemplo, ao escolher um macho menos parasitado, as chances de a própria fêmea ser parasitada é reduzida; escolher um macho mais forte e agressivo que defende um território melhor, permitiria à fêmea se beneficiar de recursos oriundos do território; mas também, ao escolher um macho com a desvantagem de um sinal exuberante e custoso garantiria a sua prole tais características (Trivers, 1972; Zahavi, 1975). De forma análoga, ao utilizar um sinal honesto para medir a qualidade de seu oponente (e.g. tamanho da galhada em ungulados), indivíduos do mesmo sexo evitariam um maior custo da agressão (Smith & Price, 1973). Mesmo que para produzir e manter tal morfologia, eles também tenham um custo (e.g. metabólico) elevado.

Uma situação singular em seleção sexual é a existência de polimorfismos de coloração (PC) (i.e. classes de cor distintas), especialmente se restritos a um dos sexos. A manutenção de PCs têm fascinado biólogos por décadas (Clarke, 1979; Mallet & Joron, 1999; Punzalan, Rodd, & Hughes, 2005; Olendorf *et al.*, 2006; Bond, 2007; McKinnon & Pierotti, 2010; Westerman *et al.*, 2018), pois depende de um equilíbrio seletivo entre os morfos para que sejam mantidos (Smith & Price, 1973). Ambas as seleções intra- e intersexual têm um papel importante na manutenção de PCs (e.g. Eakley & Houde, 2004; Farr, 1977). Comumente relacionadas a PCs são as estratégias reprodutivas alternativas, que conferem sucesso reprodutivo distintos entre morfos. Por exemplo, diversos sistemas biológicos desenvolvem um sistema reprodutivo no qual duas estratégias singulares coexistem entre machos (Moczek & Emlen, 2000; Fraser *et al.*, 2014). Geralmente um sendo o tipo estereotipado de macho da espécie, com sinalização exuberante, morfologias de armamentos desenvolvidas, e agressão (i.e. o macho dominante); e um segundo tipo de macho com colorações pálidas, por vezes semelhante a fêmea, com comportamento evasivo (i.e. o macho satélite, ou sorrateiro) (Shuster & Wade, 2003). Outro exemplo ainda mais intrigante são três os morfos de coloração do lagarto *Uta stansburiana*. Estes, possuem tanto colorações quanto estratégias reprodutivas, comportamentos sociais, e performance fisiológicas, distintas (Sinervo & Lively, 1996; Sinervo *et al.*, 2000). Estes três morfos superam um ao outro ciclicamente ao longo do tempo em termos de estratégias reprodutivas.

Além de intrigantes com relação aos mecanismos que garantem sua manutenção, grupos de espécies que possuem PCs ou estratégias reprodutivas alternativas podem apresentar taxas de diversificação mais elevadas do que grupos de espécies que não os apresentam (Gray & McKinnon, 2007; Forsman *et al.*, 2008; Pizzatto & Dubey, 2012). Portanto, algumas hipóteses para explicar esta manutenção é sua mediação por diferentes estratégias comportamentais, distinção em performances fisiológicas e diferentes estratégias reprodutivas, como no caso de *U. stansburiana*.

O lagarto *Tropidurus semitaeniatus* Spix (1825) é uma espécie de pequeno porte (≤14g), especialista de hábitats rochosos e endêmico da Caatinga. À uma população desta espécie foi descrito um PC em machos adultos com base na visão humana: das manchas ventrais pré-cloacais e femorais comuns em Tropiduridae, dois tipos discretos de morfos de manchas co-ocorrem (amarela ou amarela-e-preta, daqui em diante referidos como morfo amarelo, e morfo preto, respectivamente) (Ribeiro, Kolodiuk, & Freire, 2010). É provável que a expressão destas manchas seja relacionada a reprodução, visto que sua coloração se intensifica durante as estações reprodutivas (Bruinjé, comunicação pessoal). No entanto, até o presente momento não foram exploradas as funções das manchas ventrais em relação a condições fisiológicas ou reprodutivas. Tampouco as diferenças entre os morfos de *T. semitaeniatus* foram exploradas, exceto com relação a medidas morfométricas (Ribeiro *et al.*, 2010).

Esta tese tem como objetivo explorar os papéis dos morfos dos machos de *T. semitaeniatus* em contexto de seleção sexual, vinculando coloração, comportamento, performance individual, e sinalização multimodal. Estruturei-a em quatro capítulos. No Capítulo 1 abordo a relação de ambos os morfos de uma população com a coloração em outras partes do corpo, tanto ventrais como dorsais. Exploro se machos dos dois morfos e fêmeas de fato diferem em sua coloração em diversas partes do corpo através de medidas espectrofotométricas de sua coloração. Posteriormente, avalio se os próprios lagartos têm capacidade de distinguir visualmente estes três grupos. No Capítulo 2, foco na relação dos morfos em contexto intrasexual. Exploro características comportamentais relativas aos morfos em ensaios comportamentais de disputas agonísticas entre eles. Além disso, através de medidas de velocidade máxima de corrida, avalio se a performance individual é relacionada ao resultado das disputas entre machos. Já no Capítulo 3, investigo a relação dos morfos em contexto intersexual. Através de experimentos comportamentais de escolha, testo se as fêmeas têm preferência por algum dos morfos por diferentes vias de sinalização (visual e química). Posteriormente, avalio a relação desta escolha com características de coloração e de performance dos machos. Finalmente, devido aos processos de seleção sexual serem atuantes a nível intrapopulacional e possivelmente sob regimes de seleção distintos entre populações, o Capítulo 4 tem o objetivo de avaliar as frequências relativas dos morfos entre mais de uma população. Assim, a fim de lançar luz sobre a dinâmica dos morfos de *T. semitaeniatus*, exploro as frequências relativas de morfos, razão sexual, e variação morfométrica em três populações distintas, porém relativamente próximas do estado do Rio Grande do Norte.

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Considerações finais

Este estudo traz informações valiosas sobre os aspectos da coloração e comportamento em seleção sexual de *Tropidurus semitaeniatus*. Confirmamos a ocorrência de polimorfismo de coloração entre machos através de análise de espectrofotometria. Também, demonstramos que os próprios lagartos são capazes de diferenciar ambos sexos e morfos através das colorações de partes do corpo antes consideradas homogêneas, como por exemplo no dorso. Este fato sugere a ocorrência de seleção a um canal alternativo de comunicação. Pois, é possível que estas distinções sejam mais contrastantes para a visão dos próprios lagartos do que para possíveis predadores, por exemplo tricromatas. Demonstramos também que os dois morfos de machos possuem perfis comportamentais diferentes, variando nas escalas tanto de tendência a se comportar de forma evasiva quanto de agressividade. Além de que a comunicação interespecífica se dá por canais de sinalização distintos, visual e olfatório/químico.

É importante ressaltar que, até o momento, as bases genéticas por detrás dessas classes de coloração de *Tropidurus semitaeniatus* ainda não foram estudadas. Esta espécie tem ampla distribuição ao longo de toda a Caatinga, com grande variação em sua coloração ao longo desta distribuição. O fato de ter sido descrito um polimorfismo de coloração de uma população gera dúvidas a respeito de se estas classes de cores são, de fato, duas classes distintas de machos, ou se são fases diferentes dependentes da idade do macho. Por exemplo, se a intensidade de coloração escura é dependente da idade – suposição que pode ser levantada pelo fato de machos do morfo amarelo serem, em média, menores em tamanho do corpo do que machos do morfo preto. Até este momento, as evidências – juntamente com as apresentadas neste trabalho – apontam para uma real distinção entre os grupos de machos adultos nestas populações. Primeiramente, ambos os morfos são reprodutivamente maduros, além de possuírem uma performance equivalente inclusive em relação a dominância em embates agonísticos. Segundo, as análises *post hoc* do Capítulo 1 demonstram que há uma alta taxa de distinção dos grupos em sua coloração sem atribuição *a priori* dos indivíduos aos grupos de morfos. Em terceiro, e talvez mais importante, é que esta espécie tem sua estação reprodutiva marcada anualmente. De forma que é esperado que as frequências relativas de idade dos indivíduos de cada população sejam relativamente homogêneas. Portanto, se correspondentes a idade, as frequências relativas dos morfos deveriam igualmente ser homogêneas entre populações quando observadas no mesmo período do ano. O fato observado neste trabalho e apresentado no Capítulo 4 é que estas frequências apresentam grande variação entre populações nestas condições. Assim, é improvável que estas variações reflitam a grupos de idade tão diferentes entre populações, ao invés de caracterizarem duas classes de coloração sob regimes de seleção distintos.

É provável que outros fatores, como diferenças de cripsidade dos morfos em ambientes diferentes, tenham um papel importante na dinâmica de suas frequências em diferentes populações. Estes, e outros aspectos com relação a diferenças ambientais entre populações, são aspectos promissores para investigações futuras. A dinâmica de sistemas polimórficos com relação a seus modos de acasalamento são um tópico quente na ecologia evolutiva e têm importância fundamental para o desenvolvimento das teorias e modelos de evolução sexual. Em particular, os achados deste trabalho trazem para uma espécie de lagarto sul americana a possibilidade de se explorar estas dinâmicas intrapopulacionais de seleção sexual – área majoritariamente ocupada na literatura por trabalhos com espécies norte americanas ou europeias. Ressaltando, portanto, a importância de investir em pesquisas locais, com espécies comuns, que muitas vezes se mostram bons modelos para o estudo de dinâmicas evolutivas mas possivelmente negligenciados, em especial na área de ecologia comportamental.

ANEXO I: CAPÍTULO I*

Conspecifics of the Striped Lava Lizard, *Tropidurus semitaeniatus*, are able to distinguish sex and male color morphs in apparently homogeneous dull dorsal coloration

*Capítulo submetido a *Amphibia-Reptilia*, formatado de acordo com as normas da revista.

Conspecifics of the Striped Lava Lizard, *Tropidurus semitaeniatus*, are able to distinguish sex and male color morphs in apparently homogeneous dull dorsal coloration

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ABSTRACT

Animal coloration plays a key role in intraspecific interactions, especially in mate signaling. Multiple types of coloration within sexes suggest alternate reproductive strategies. In lizards, however, not every coloration studies incorporate the way in which color is perceived by conspecifics. Here, we use unbiased color analysis methods (spectrophotometry and visual modeling) to test for sexual dimorphism and male polymorphism in the lizard *Tropidurus semitaeniatus*. We found that males express two distinct colorations that are both different from females in several dorsal and ventral body regions, confirming the existence of three distinguishable morphs. Our results showed that *T. semitaeniatus* reflect UV at the throat, an important region of the lizard's body for visual signaling. Ventral patches, a colored badge that is present in every species of the genera and that is only present in adult males, have two distinct colors within males (black and yellow). Morphs are best discriminated by blue and yellow chroma, and brightness. Body size had little influence on coloration, suggesting that color may be linked to inheritance rather than growth. Our study clearly shows sexual color dimorphism and the existence of color morphs in this species. Moreover, morphs' differences in coloration are clearly perceptible by conspecifics. This perceptible color differences are not only between ventral patches, but also in other parts of the body such as the dorsum, previously considered as homogeneous and cryptic by human observers. Future studies should explore the relative functions of distinct males color morphs within reproductive tactics for this species.

Keywords: color polymorphism, visual modeling, animal coloration, male morphs, Tropiduridae, alternate reproductive tactics

INTRODUCTION

Sex-restricted polymorphism is an intriguing phenomenon because its maintenance depends on the selective balance among morphs fitness (Gray and McKinnon, 2007). Otherwise, one could expect that the morph with higher fitness would take over within a polymorphic system (Iwasa and Pomiankowski, 1994; Jennions and Petrie, 1997; Neff and Svensson, 2013). However, discrete morphological groups within one sex have been documented in many species, especially in vertebrates such as fishes and lizards (Elmer, Lehtonen, and Meyer, 2009; Calsbeek, Hasselquist, and Clobert, 2010). These kinds of polymorphisms are usually related to different reproductive strategies (Vercken et al., 2007), and one of the most common polymorphic traits in alternative reproductive tactics is coloration (Gray and McKinnon, 2007; Neff and Svensson, 2013). A possibility for the maintenance of these polymorphisms is that the discrete groups might have differential reproductive success. For example, polymorphism is maintained by color morph assortative mating in two cichlid fish species of the genus *Amphilophus* (Elmer, Lehtonen, and Meyer, 2009). In the lizard *Podarcis muralis*, polymorphic ventral coloration reflects differences in body size and parasite loads, which suggests that different selective pressures may favor alternative phenotypes (Calsbeek, Hasselquist, and Clobert, 2010). Color polymorphism is of particular interest in evolutionary ecology since it is one of the most proposed causes of sympatric speciation by sexual selection (van Doorn, Dieckmann, and Weissing, 2004; Gavrilets and Hayashi, 2005; Gray and McKinnon, 2007).

Coloration and color patterns in animals may have multiple functions. For instance, coloration that matches the environment background may increase survival (Stuart-Fox, Moussalli, and Whiting, 2008). Color traits can also function as warning signals (Mcelroy, 2016), allow for the recognition between conspecifics and even sex-specific recognition (Keren-Rotem et al., 2016), inform quality to potential mates (Bajer et al., 2010, 2011), increase thermoregulation efficiency (Smith et al., 2016a), and convey information on behavioral state (e.g. aggression, submissiveness or courtship) (Smith et al., 2016b). In addition, sexual selection often increases both sexual dichromatism and sexual size dimorphism, usually towards the male (Hamilton and Zuk, 1982; Cox, Skelly, and John-Alder, 2003). In lizards, color patches and discrete color variations have been reported in many species (e. g. Lobo and Nenda, 2015; McLean, Stuart-Fox, and Moussalli, 2015; Wang et al., 2016). These variations in coloration are usually related to alternative reproductive tactics (Thompson and Moore, 1991; Sinervo and Lively, 1996; Miles et al., 2007; Lattanzio and Miles, 2016). An example is the common chameleon (*Chamaeleo chamaeleo*), of which males have two distinct mating tactics (dominant and subordinate) associated to different behaviorally displayed color patterns and behavioral displays (Keren-Rotem et al., 2016).

Recent studies are showing that distinct morphs may also have ecological and functional distinctness. Differences in trophic ecology, spatial distribution, behavior, parasite loads, and immunological and physiological differences that affect performance have been reported (Vaclav, Prokop, and Fekiac, 2007; Calsbeek, Hasselquist, and Clobert, 2010; Lattanzio and Miles, 2016). Also, the intensity of the color itself has been directly related to performance (Zajitschek et al., 2012). Ecological distinctiveness is often responsible for promoting persistence of color polymorphisms (Lattanzio and Miles, 2016). Nevertheless, a number of classical and recent articles shows different reproductive outcomes of color morphs, with a special role in females' choice for mates and males' mating behaviors (Hamilton and

Sullivan, 2005; Gray and McKinnon, 2007; Neff and Svensson, 2013). Ultimately, differences among morph traits can result in different relative mating success and/or survival.

There are multiple selection forces acting on animal coloration. Some of them may act antagonistically favoring different color patterns in different body regions. For instance, while predation usually selects for crypsis and homogeneous coloration, sexual selection selects for an improved conspecific communication, which often results in conspicuousness (Endler, 1992; Garcia, Rohr, and Dyer, 2013). Body size dimorphism and dichromatism are also expected under sexual selection (Székely, Freckleton, and Reynolds, 2004). Hence, one could expect that parts of the body that are more visible to a conspecific would be conspicuous, while body parts that are more visible to predators would be cryptic (Marshall and Stevens, 2014). These expectations are stronger in an intra-sexual polychromatic system, in which the prediction would be an increased difference in ventral body regions while homogeneous coloration at the dorsum. More than favoring just conspicuousness, and in contrast to natural selection, sexual selection may increase and maintain multiple discrete morphologies. Moreover, this disruptive selection pressure could foster reproductive isolation (Cox, Skelly, and John-Alder, 2003). However, despite the increasing documentation of color polymorphism in the literature, only few studies have characterized lizard color patterns according to the eye of the beholder (e.g. conspecifics and predators) (Stuart-Fox et al., 2003; Macedonia et al., 2009; Teasdale, Stevens, and Stuart-Fox, 2013; Marshall and Stevens, 2014; Pérez i de Lanuza and Font, 2014). This approach is essential if we want to understand which role color polymorphism might play in mating systems, in reproductive isolation, in recognition and, ultimately, on fitness.

The striped-lava lizard (*Tropidurus semitaeniatus*) is a saxicolous small sized lizard (≤14g). Its dorsoventrally flattened body and dorsal color pattern seem to be adapted to the life in rock outcrops. Similarly to several other Tropiduridae species, reproductive active males exhibit a dark patch in the ventral thighs and pre-cloacal flap (Pinto, Wiederhecker, and Colli, 2005). In males of *T. semitaeniatus*, however, the patches can be yellow or yellow-and-black (hereafter referred solely as 'yellow males' and 'black males') (Ribeiro, Kolodiuk, and Freire, 2010). The patch coloration increases during mating season suggesting a role in reproduction (Bruinjé & Costa. unpublished data). However, the description of male patches was based just on human vision, lacking statistical testing of spectrophotometric variables and interpretations based on conspecific visual system. Modeling the visual system of the studied species, within its ecological context, is essential to capture whether or not the spectra variances can be perceived (Kemp et al., 2015; Renoult, Kelber, and Schaefer, 2017). In addition, it is still unknown whether the male morphs differ in other color traits and other body parts (e.g. dorsum or ventral).

Here, we characterize *T. semitaeniatus'* coloration and its relative visual perceptiveness through comparable and unbiased color analysis methods (spectrophotometry and visual modeling). Our goal is to confirm the existence of three discrete groups within adults: females, yellow males and black males. We hypothesize that females, yellow males, and black males belong to three distinct groups with possible differences in body size, morphology, coloration and ecological traits. Thus, we will hereafter refer to each of the groups as color morph. As such, we expect that color morphs will differ in coloration even when controlling for body size and that differences are going to be greater on ventral than on dorsal regions. As theory predicts that morphs are related to alternative mating strategies, we expect that conspecifics will be able to differentiate between morph colorations in ventral body regions. Therefore, we tested whether the difference in coloration can be perceived by conspecifics. Our aim was to provide unbiased information on this species about the existence of distinct color morphs and contribute to the understanding of coloration and visual system in lizards related to alternative mating strategies.

MATERIAL AND METHODS

Studied system and sampling

The striped-lava lizard, *T. semitaeniatus*, is endemic to Northeastern Brazil. It is widely distributed throughout the Caatinga but restricted to rock-outcrop habitats (Carvalho, 2013). It has a dorsoventral flattened body adapted to hide in rocky crevices, and a cryptic dorsal coloration (according to human vision). There are also light brown to dark spots and a marked longitudinal bright stripe ranging from its head to the middle of the dorsum that might eventually reach the base of the tail. From a human perspective, its coloration pattern seems to function as anti-predatory coloration because it closely resembles the rocky background in which they inhabit (supplementary figure S_1). Also, longitudinal stripes are inferred to be a defense strategy as it confuses potential predators when the animal is moving (Halperin, Carmel, and Hawlena, 2017). Ventrally, *T. semitaeniatus* has a pale light grey color along the whole body. Cloacal and ventral thigh regions express colored patches in adult males only. The strength of the color in the patches increases during mating season suggesting a role in reproduction. Males can express two distinct types of color patches (yellow or black) while females and juveniles maintain the same light grey color ventrally throughout the whole body (Ribeiro, Kolodiuk, and Freire, 2010).

We collected 240 lizards from a single population located in João Câmara-RN, Brazil (5.4431° S, 35.8716° W). We collected live specimens by noose or hand on four expeditions (four days each) during mating season (January 2015). We measured morphometric and color of the lizards and identified sexes manually by gently pressing the cloaca exposing males' hemipenis. We used only individuals larger than the minimum size for reproduction (59.0 mm and 68.5 mm SVL for females and males, respectively) (Ribeiro, Silva, and Freire, 2012). Also, we discarded individuals with any visible injuries or in an apparent malnourished state. Thus, our final sample size was 107 individuals (61 males, 46 females). After we obtained all measurements we released the lizards at the sampled location.

Morphometrics, color measures and visual modeling

To test for color differences among morphs we obtained reflectance spectra using an optic fiber (QR450-7-XSR, Ocean Optics, Dunedin, FL) attached to a spectrophotometer (USB4000-UV-VIS). Before measures, we calibrated white with standard white (WS-1-SL). We calibrated black turning off the lamp and obstructing the optic fiber with a completely opaque dark cloth. Measures were registered with illumination of a DH-2000-BAL. We took three measures of 8 body regions. We measured five body regions in the ventral portion of the body (Fig 1A): throat (V_{Throat}), chest (V_{Chest}), ventral patch (V_{Patch}, measured within the patch area at the cloacal region), femoral patch ($V_{FemoralPatch}$, measured within the patch area) and ventral tail base ($V_{TailBase}$). We also measured three body regions in the dorsal portion of the body (Fig 1B): head stripe ($D_{HeadStripe}$, measured within the dorsal bright stripe in between the lizard's orbicular cavities), dorsum stripe (D_{Stripe}, measured within the dorsal bright stripe approximately 10 mm below the collarbones), and side stripe ($D_{SideStripe}$, measured at the dark stripes directly at the side of D_{Stripe}). We derived different coloration variables from the spectral reflectance curves in the R package *pavo* (Maia et al., 2013). First, we restricted spectra curves between 300 nm and 700 nm because this is the wavelength range perceivable by lizards' visual system (Loew et al., 2002). Next, we averaged the three measures taken at each body region. Finally, we derived 8 color variables that represent the different aspects of colorations: hue (*Hue*), brightness (*Bri*) and saturation (*S*). *Hue* is calculated as the wavelength of peak reflectance. *Bri* is the mean brightness, the average reflectance over all wavelengths. *S* is a segment-specific chroma calculated by dividing the sum of the reflectance by the total reflectance within each reflectance segment, resulting in the calculated chroma for 6 segments (*S.UV*, *S.violet*, *S.blue*, *S.green*, *S.yellow*, *S.red*). A detailed description of these variables is shown in table S_1. In order to account for the effect of body size on lizards coloration we calculated a single variable *size* (see below) from the linear morphometric measures: snout-vent length, body width, body height, head width, head height, head length, forelimb, hindlimb length (measured to the nearest 0.01mm with a digital caliper) and weight (measured to the nearest 0.01g with a digital scale). We did not use tail length due to possible previously autotomized and regenerated tails. To meet requirements of normality, we log-transformed (base 10) all morphometric variables. We composed *size* as an isometric size variable following the protocol proposed by Somers (1986). We calculated an isometric eigenvector of *p* variables with all coefficients equal to $p^{-0.5}$ (Jolicoeur, 1963). We obtained the isometric size-adjusted variables by multiplying the *n* X *p* matrix of log-transformed morphometric data by the isometric eigenvector.

Figure 1 here

We calculated visual contrasts (ΔS for chromatic and ΔL for achromatic) among morphs (black males against yellow males, females against black males, and females against yellow males), considering a diurnal lizard's visual perception (Vorobyev and Osorio, 1998). In order to assess the perceptual differences between two patches we applied the receptor noise model, which estimates the distance between two spectra in the chromatic and achromatic spaces in 'just noticeable difference' (JND), a physiological threshold unit (Vorobyev and Osorio, 1998; Osorio et al., 2004). This method has been shown to be very accurate to predict visual perception in lizards (Fleishman et al., 2016). Based on the spectral sensitivity of a given animal eye this model calculates relative quantum catch by each photoreceptor type according to data on light entering the eye. Because there is still no data available specifically for the visual system of *T. semitaeniatus* we used photoreceptor data from *Podarcis muralis* (Martin et al., 2015). *P. muralis* is the diurnal lizard species most closely related to *T. semitaeniatus* with available photoreceptor data. The visual system of diurnal lizards is known to be phylogeneticaly conserved with four types of cones in the retina (sensitive to UV, short, medium and long wavelengths) (Martin et al., 2015). Irradiance data used in the model was measured in the natural habitat of *T. semitaeniatus,* at 1100h under blue sky with an optic fiber (QP450-2-XSR) connected to a cosine corrector (CC-3-UV-S). We considered that differences between two patches yielding JND values smaller than one were indistinguishable by the visual system modeled, while differences between one and three JND are noticeable under optimal light conditions (Osorio et al., 2004). Patches that differed in more than three JND units were considered highly distinguishable. Visual modeling was conducted with the R package *pavo* (Maia et al., 2013).

Statistical analysis

To test for differences in body size among color morphs we performed a One-way Analysis of Variance (ANOVA) on the composed variable *size* with color morph (female, black male, yellow male) as fixed factor. We performed Tukey's multiple comparison of means following the ANOVA to determine the significant pairwise differences between morphs.

Because different body regions may be exposed to different selective pressures, we test for differences in color variables among color morphs separately for each body region. Spectra variables and the composed variable *size* were centered and scaled in order to fit normality and homoscedasticity. To avoid co-linearity we first excluded color variables with a coefficient of correlation (r_{pearson}) greater than 0.85. The color variable *S.violet* was highly correlated with several color variables in all body regions and was, therefore, removed from all analysis (Table 2). We then performed a multivariate analysis of covariance (MANCOVA) on the color variables with color morph as fixed factor to test for color differences among these morphs. To account for the effect of body size on color we included *size* as a covariate in the model. We applied a Linear Discriminant Analysis (LDA) in the cases in which the MANCOVA showed a significant difference ($p < 0.05$). We performed LDA in order to identify which color variables better discriminate among the color morphs. At last, we used a stepwise classification function (stepclass) (Weihs et al., 2005) to determine the correctness rate of prediction of each individual to the morphs based on its color variables. Function stepclass uses the posterior probabilities derived from the LDA to perform a stepwise variable selection. The models are ranked based on the rate of prediction estimated by cross-validation (1000 runs), including or excluding the variables until it reaches the fittest model. We ran all statistical analysis in R software (R Core Team, 2015).

RESULTS

Color morph characterization

In our full sample (240), 16 were juveniles, 49 subadult males (males that did not reach the reproductive size nor presented ventral colored patches), 106 adult females, and 69 adult males. Among adult males, 40 were black males and 29 were yellow males. After removing juveniles, and individuals that seemed to have been inflicted by any disproportional energetic cost (injured or recent tail autotomized, for instance), we got a subset of 107 lizards from the full sample (see methods), out of which 46 were females, 36 black males and 25 yellow males.

Total *size* of color morphs, composed from the linear morphometric variables, differed significantly (One-way ANOVA: $F_{2,\,104} = 97.38$, $p < 0.001$). Post-hoc Tukey test showed that all morphs differed significantly from each other ($p < 0.001$). Females are smaller, with mean *size* of -0.85 (±0.5), black males are bigger in average with mean *size* of 0.99 (±0.54). Yellow males are intermediate in body size, being smaller than black males but bigger than females in average, with mean *size* of 0.13 (±0.79).

Color of morphs differed significantly in almost every body regions with the exception of one ventral variable ($V_{TailBase}$) (Table 1, see supplementary figures S_2 and S_3 for reflectance curves of each body region). Both ventral patches (V_{Patch} and $V_{FemoralPatch}$), as well as the dorsal variable $D_{Stripe,}$ had a significant effect of *size* on coloration within morphs. All other body regions did not have effect of body size (Table 1). As expected, the body parts with most marked differences in reflectance curves are the ventral patches (V_{Patch} and $V_{FemoralPatch}$), (Fig 2A-B). Females V_{Patch} spectrum is characterized by overall greater brightness, with a steeper slope between 400 and 500 nm, a peak around 600 nm, and an offset from 650 to 700 nm. This slope between 400 and 500 nm is the most distinctive pattern between females and males patches spectra (Fig 2A-B). Black males V_{Patch} spectrum is characterized by an overall lower brightness, with the steeper slope beginning at 500 nm and the higher reflectance at 700 nm (Fig 2A). Yellow males V_{Patch} spectrum has an intermediate shape in relation to females and black males with a steeper increasing slope at 500 nm, which differentiate them from black males (Fig 2A). Dorsal regions tended to be similar, regarding their spectra curves, among color morphs (Fig 2C-D). Throat (V_{Throat}) spectra of all color morphs have a marked UV reflection (from 325 to 400 nm) (Fig 2D).

Table 1 here

Figure 2 here

Color morph discrimination

The discriminant function showed a striking segregation among morphs by their ventral patches (V_{Patch} and $V_{FemoralPatch}$) (Table 2, Fig 3A-B). LD1 axis segregates between sexes whereas LD2 segregates male color morphs (see Fig 3A-B where centroids of distribution are segregated by sex in LD1, and by morphs in LD2 axis). Overall, brightness (*Bri*), blue chroma (*S.blue*) and hue (*Hue*) were the variables that best discriminated among morphs (Table 2). However, there was also a marked influence in UV chroma (*S.UV*) at the throat (V_{Throat}) and yellow chroma (*S.yellow*) at the femoral patch (V_{Patch}). In general, the stepwise classification function had a better correctness rate on ventral (56 to 83%) than on dorsal (44 and 46%) body regions (Table 2).

Table 2 here

Figure 3 here

Visual modeling

The spectral differences we found among color morphs are perceptible to lizard's visual system through both chromatic and achromatic cues (Fig 4). Two ventral (V_{Patch} and $V_{FemoralPatch}$) and two dorsal ($D_{HeadStripe}$ and $D_{SideStripe}$) body regions are highly contrasting in chromatic distance (Fig 4) in all pairwise comparisons between morphs, with a median JND value greater than 3. The greater chromatic contrasts among all body regions were found in V_{Patch}, especially between females and yellow males. The remaining body regions (V_{Throat}, V_{Chest} and D_{Stripe}) had a partially perceivable chromatic difference between color morphs, with median JND values ranging from 1 to 2.99. Achromatic contrasts, on the other hand, had a median

JND value greater than 3 in every comparison among all body regions with the higher contrast for V_{Patch} when comparing between sexes (females against yellow or black males).

Figure 4 here

DISCUSSION

We have provided corroboration for the hypothesis that the striped-lava lizard exhibits color polymorphism among males and that this species is sexually dichromatic. Both male color morphs occur sympatrically within this single population, even though not every population of *T. semitaeniatus* has both male color morphs (Bruinjé & Costa. unpublished data). In addition, we show that conspecifics can distinguish color morphs both in ventral and dorsal colorations. More importantly, both sexual dichromatism and color polymorphism described within males are not just artifacts derived by human visual perception on ventral patches but are effectively perceptible by the lizards even in dorsal body regions. This novel information suggests a possible role of color signal in the sexual selection of a dull colored lizard.

Among all body parts, color differences were more perceivable in the ventral patches ($V_{FemoralPatch}$ and V_{Patch}). This result is congruent with our expectations as these patches are common traits present in several species of this clade and also because patches are expressed only in adult males (Pinto, Wiederhecker, and Colli, 2005; Ribeiro, Kolodiuk, and Freire, 2010). The biological function of both ventral patches is, however, still unclear. Animal signaling is complex and is commonly multi-modal with different signals conveying complementary information (Johnstone, 1996). Behavioral experiments could address this issue specifically and test whether the patches function as a trait that signals true quality of the bearer (Whiting, Nagy, and Bateman, 2003; Allard-Duchêne et al., 2014). It is possible that yellow is a carotenoid-based color, which is a high cost trait and considered an honest signal of male quality (Svensson and Wong, 2011). Thus, the ventral patches could play a role signaling individual's quality in interactions between conspecifics. Under intraspecific interactions, individuals display the behavior of showing up the ventral tail base and cloacal region. Also, this display seems to occur as a submissive signaling to conspecifics (Coelho, Bruinjé & Costa, in Review) in the same way as observed in females of other species of *Tropidurus* while rejecting males (Carpenter, 1977). *Size* had also a significant effect on patches' coloration. Therefore, coloration on patches differs between morphs and also in relation to body size within morphs. Body size affected coloration only on the patches and D_{Stripe}. This reinforces the fact that coloration differs among morphs but not because morphs differ in body size. Further experimental studies with the multiple signals of *T. semitaeniatus*' color morphs may address the function of ventral patches in relation to intrasexual competition and mate choice.

Another important color trait we found was the marked UV reflection at the throat (V_{Throat}) region (Fig 2D). UV in lizards is known to play a role in intraspecific communication in several contexts. For instance, in the color polymorphic lizard *Podarcis muralis,* the hue and UV chroma of outer ventral scales are good predictors of bite force and body condition, respectively (Pérez i De Lanuza, Carazo, and Font, 2014). High UV chroma also predicts female choice (Bajer et al., 2010) and male fight success (Bajer et al., 2011) in the lizard *Lacerta vivipara*. We found that UV reflection is present mostly at the throat (V_{Throat}), and femoral patch ($V_{FemoralPatch}$). A possibility is that *T. semitaeniatus* uses structural conspicuous coloration as a signal in interspecific interactions. The throat is often showed during headbob and push-up behavior, which is very common in all species of the genera. In *T. semitaeniatus*, the rate of headbob display increases during intraspecific interactions and differs between male color morphs, sexes and social status among competing males (Bruinjé, Coelho, Paiva & Costa. unpublished data).

At the dorsal region, the greater contrasts we found among color morphs were both within the bright longitudinal stripe ($D_{HeadStripe}$ and D_{Stripe}), but also interestingly at the darker side stripe ($D_{SideStripe}$), especially in the achromatic space (Fig 4). This difference is counterintuitive as it is expected that coloration at the dorsum would be selected to be homogeneous (e.g. by predation pressure) and, thus, not show sexual color polymorphism. This is because color morphs inhabit the same outcrop patches, likely with the same background. However, it is possible that conspicuousness or color morph differences were selected to be enhanced to a conspecific visual system but to be less perceptible under heterospecific visual system (e.g. mammal or avian predators). Some adaptations can decrease the potential cost of conspicuousness by tuning the communication to specific channels. For instance, the natural predator (*Astyanax mexicanus*) of swordtails fishes (*Xiphophorus* spp) is less sensitive to UV. On the other hand, UV is a trait that is highly conspicuous and increases attractiveness to female swordtails (Cummings, Rosenthal, and Ryan, 2003). Thus, despite being considered conspicuous and costly, the swordtail's trait that attracts females (UV reflection) is tuned to decrease the cost of signaling in relation to its predator while enhancing intraspecific signaling. An analysis taking into account differences in visual systems and contrast against natural background inhabited by *T. semitaeniatus* could address this issue further (specific channels of communication in relation to heterospecifics). Another possible explanation for the color polymorphism at the dorsum and its perceptiveness is that the visual angle that these lizards have towards a conspecific from a middle distance (not in direct physical interaction) usually shows the dorsum. This is due to the rock-dwelling behavior that maintains lizards in surfaces at different angles than that of the interactive individual. Nonetheless, the significant difference among morphs in $D_{SideStripe}$ (Table 1), which is a very dark set of patches in the dorsum, together with a high identification of morphs by the visual model (Fig 4) reinforce the fact that color morphs are wholly identified by conspecifics.

Although contrast differences were high among all color morphs, no specific pairwise comparison (e.g. female against yellow male or female against black male) contrasted more, nor less, to each other (Fig 4). The discrimination among color morphs is marked and distinguishable independently of the pair contrasted (between males or between male morphs and females). A common alternative reproductive tactic among animals, including polymorphic lizards, is the sneaker male strategy. For instance, some males of the flat lizard *Platysaurus broadleyi* mimic females' characteristics by delaying the development of male coloration while already sexually mature. These 'she-males' guarantee their offspring, and prevent injury, by visually deceiving dominant males while approaching mate candidates (Whiting, Webb, and Keogh, 2009). One could expect that the average smaller size and lighter colors of ventral patches of the yellow male color morph of *T. semitaeniatus* are due to a sneaker strategy resembling the coloration of a female. However, the patterns showed by the visual contrasts (Fig 4), with no significant differences in contrasts between pairings suggest that yellow males may not resemble females and therefore do not use a female-like coloration as a mating strategy.

Our results show that the apparently discrete coloration described in previous studies using non-statistical methods is corroborated by spectrophotometric measures in this species. And that differences among color morphs are perceivable by lizard conspecifics, not solely in ventral patches but even in dorsal body regions. Colors in lizards are structural or produced by pigments (Pérez i De Lanuza, Carazo, and Font, 2014), which can both be costly and reflect individual quality (Bajer et al., 2011). The discrete coloration on ventral patches described here for the striped-lava lizard strongly suggests that it is pigment based, which is costly. It is also likely that the color in both ventral patches plays a role in reproductive interactions because it increases both in saturation and patch area (according to human perception) during mating season. Our results highlight the importance of taking into account the visual modeling in analysis of colorations. Species that are dull in appearance might actually display polychromatic, and even conspicuous, color patterns, to conspecifics. These patterns could be under intense selection and, thus, playing a role in intra and interspecific interactions. Our results also stimulate different questions that can be addressed in future studies. Particularly, experimental studies designed to test whether color polymorphism is linked to dominance behavior, aggressiveness and social status.

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Tables

Table 1. Color differences among morphs.

Body region		**Color morph**		**Size**	
		Wilks' □λ	**P**	**Wilks' λ□**	**P**
Tail Base	$\mathbf{V}_{\mathrm{TailBase}}$	0.859	0.121	0.985	0.913
Femoral Patch	$\mathbf{V}_{\mathrm{FemoralPatch}}$	0.329	**<0.001**	0.867	**<0.05**
Ventral Patch	$\mathbf{V}_{\mathrm{Patch}}$	0.114	**<0.001**	0.869	**<0.05**
Throat	$\mathbf{V}_{\mathrm{Throat}}$	0.776	**<0.01**	0.987	0.935
Chest	$\mathbf{V}_{\mathrm{Chest}}$	0.702	**<0.001**	0.970	0.882
Head Stripe	$\mathbf{D}_{\mathrm{HeadStripe}}$	0.783	**<0.01**	0.976	0.799
Dorsum Stripe	$\mathbf{D}_{\mathrm{Stripe}}$	0.775	**<0.05**	0.857	**<0.05**

Side Stripe	$\mathbf{D}_{\text{SideStripe}}$	0.803	**<0.01**	0.986	0.928

Results of MANCOVA to test for differences in color variables among color morph groups. Bold indicates significant values.

Table 2. Linear Discriminants (LD1 and LD2) of color morphs by body region.

Variable	$V_{FemoralPatch}$		V_{Patch}		V_{Throat}		V_{Chest}		$D_{HeadStripe}$		D_{Stripe}		$D_{SideStripe}$	
	LD1	LD2	LD1	LD2	LD1	LD2	LD1	LD2	LD1	LD2	LD1	LD2	LD1	LD2
Bri	**-0.66**	**0.70**	**-0.80**	**0.55**	-0.21	0.04	**-0.99**	**-0.32**	**-0.86**	**-0.30**	-0.44	-0.60	-0.88	-0.37
S.UV	-1.04	-5.52	-3.74	-5.92	**-0.29**	**-2.85**	2.52	271.10	0.24	-0.70	7.57	-7.19	-	-
S.blue	-1.73	-7.26	-4.03	-4.98	**-0.99**	**-2.06**	0.67	154.93	1.33	-1.44	**3.15**	**-3.35**	-0.69	0.16
S.green	-	-	-	-	-	-	2.47	140.29	-	-	-	-	1.61	1.42
S.yellow	**-1.07**	**-3.78**	-2.05	-2.72	-	-	-0.58	-1.83	-	-	5.63	-4.29	-	-
S.red	-0.83	-3.68	-3.08	-3.75	0.09	-3.24	1.56	267.77	1.95	-1.18	5.22	-5.22	-1.69	0.09
Hue	-0.66	0.70	**-0.80**	**0.55**	-0.21	0.04	-0.99	-0.32	-0.86	-0.30	-0.44	-0.60	**-0.14**	**-0.43**
Correctness rate	0.75		0.83		0.56		0.56		0.46		0.45		0.44	

Loadings of spectra variables on the Linear Discriminants (LD1 and LD2) of color morphs by body region. Variables with correlation greater than 0.85 within a body region were removed. Only body regions with significant differences in the MANCOVA are shown. Bold indicates spectra variables of the final model of the stepwise variable selection (Weihs et al., 2005).

Figure legends

Figure 1. Body regions for spectra measures. Scheme of body regions of *T. semitaeniatus* for spectra measures. Dorsal (a) and ventral (b) regions are indicated with acronyms referring to head stripe ($D_{HeadStripe}$), dorsum stripe (D_{Stripe}), side stripe ($D_{SideStripe}$), throat (V_{Throat}), chest (V_{Chest}), ventral patch (V_{Patch}), femoral patch ($V_{FemoralPatch}$) and tail base ($V_{TailBase}$).

Figure 2. Reflectance spectra of color morphs. Reflectance spectra curves by body region. Females (red dotted lines), yellow males (yellow solid lines) and black males (grey dashed lines) are plotted separately. Spectra curves show different body regions: Ventral Patch - V_{Patch} (a); Femoral Patch – $V_{FemoralPatch}$ (b); Head Stripe – $D_{HeadStripe}$ (c) and Throat – V_{Throat} (d).

Figure 3. Linear discriminant functions by body regions. Linear discriminant functions of color morphs. Females (grey triangles), yellow males (yellow squares) and black males (black circles) distributions are plotted separately by body regions: Ventral Patch - V_{Patch} (a); Femoral Patch – $V_{FemoralPatch}$ (b); Head Stripe – $D_{HeadStripe}$ (c) and Throat – V_{Throat} (d). Continuous lines delimit 95% of confidence interval. Centroids are marked by cross signs. Note that LD1 and LD2 axis show the functions that better discriminate sex's and male color morph's centroids, respectively.

Figure 4. Visual modeling. Boxplots of chromatic (ΔS, plots on the left) and achromatic (ΔL, plots on the right) distances, in units of Just Noticeable Difference (JND), between each kind of color morph considering the visual system of a lizard. Boxes are separated by body region and show high (dark grey - greater than 3 JND), medium (light grey - between 1 and 3 JND) and unperceivable (white – lower than 1 JND) chromatic and achromatic contrasts between two color morphs. First row shows chromatic (a) and achromatic (d) contrasts of black males against yellow males.

Second row shows chromatic (b) and achromatic (e) contrasts of females against yellow males. Third row shows chromatic (c) and achromatic (f) contrasts of females against black males. Only body regions with significant difference among color morphs were modeled. Acronyms of body regions refer to femoral patch ($V_{FemoralPatch}$), ventral patch (V_{Patch}), throat (V_{Throat}), chest (V_{Chest}), head stripe ($D_{HeadStripe}$), dorsum stripe (D_{Stripe}) and side stripe ($D_{SideStripe}$).

Figures

Figure 1

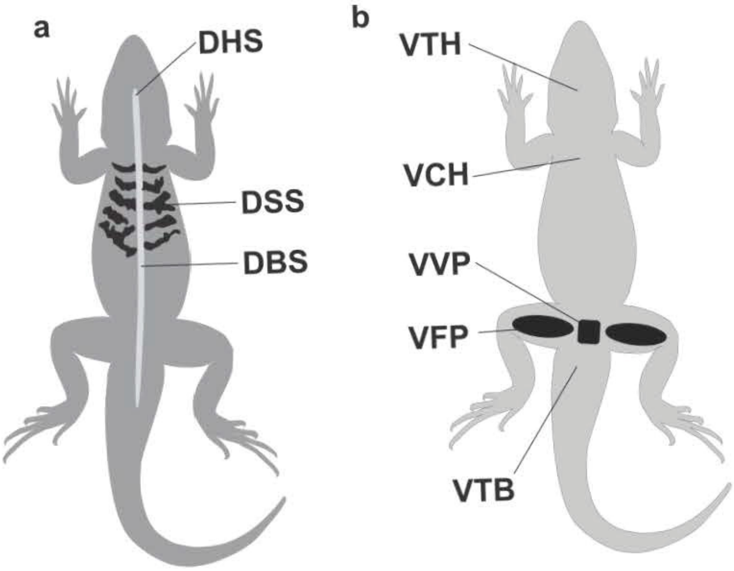


Figure 2

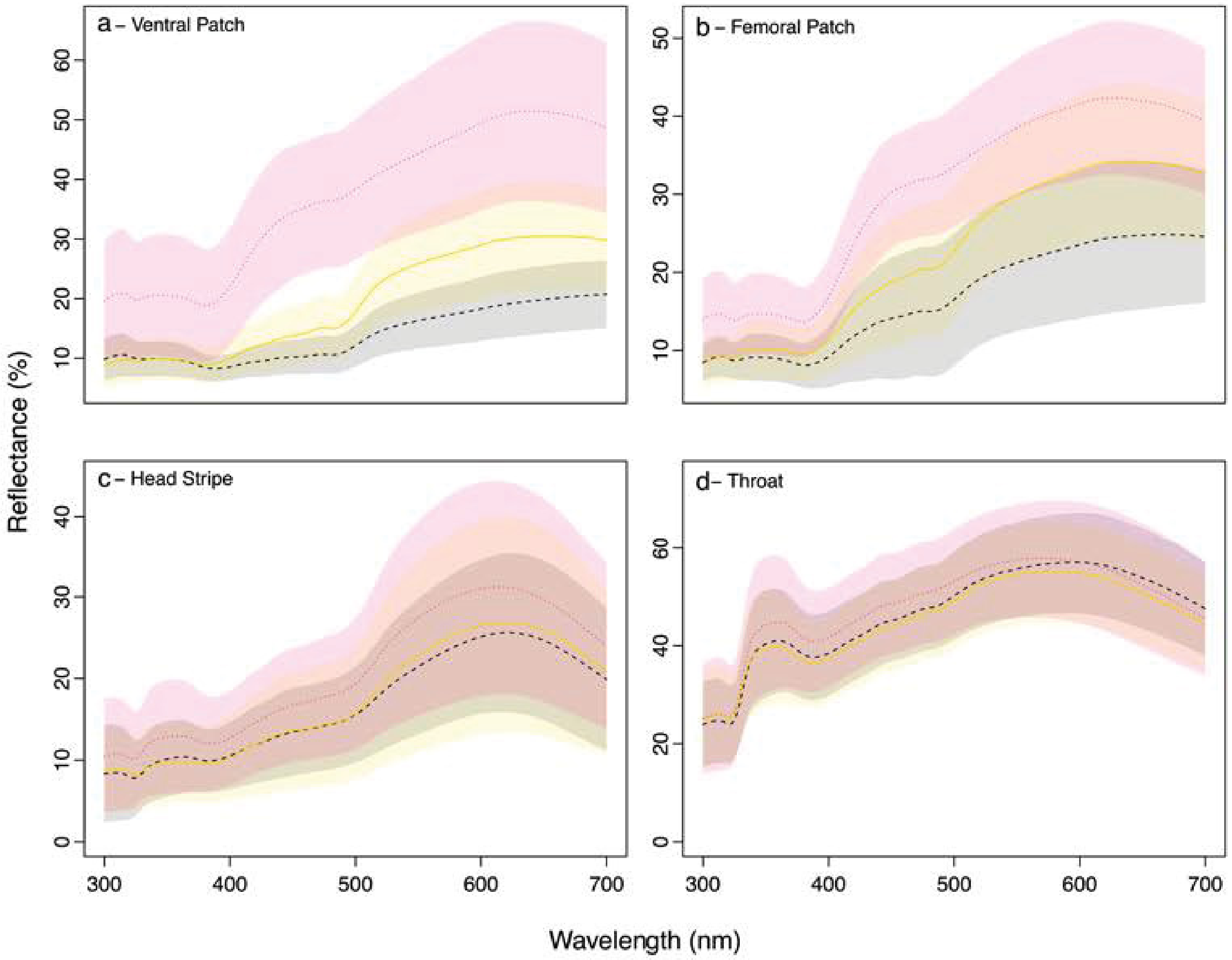

a – Ventral Patch
b – Femoral Patch
c – Head Stripe
d– Throat
Reflectance (%)
Wavelength (nm)
60
50
40
30
20
10
0
300
400
500
600
700

Figure 3

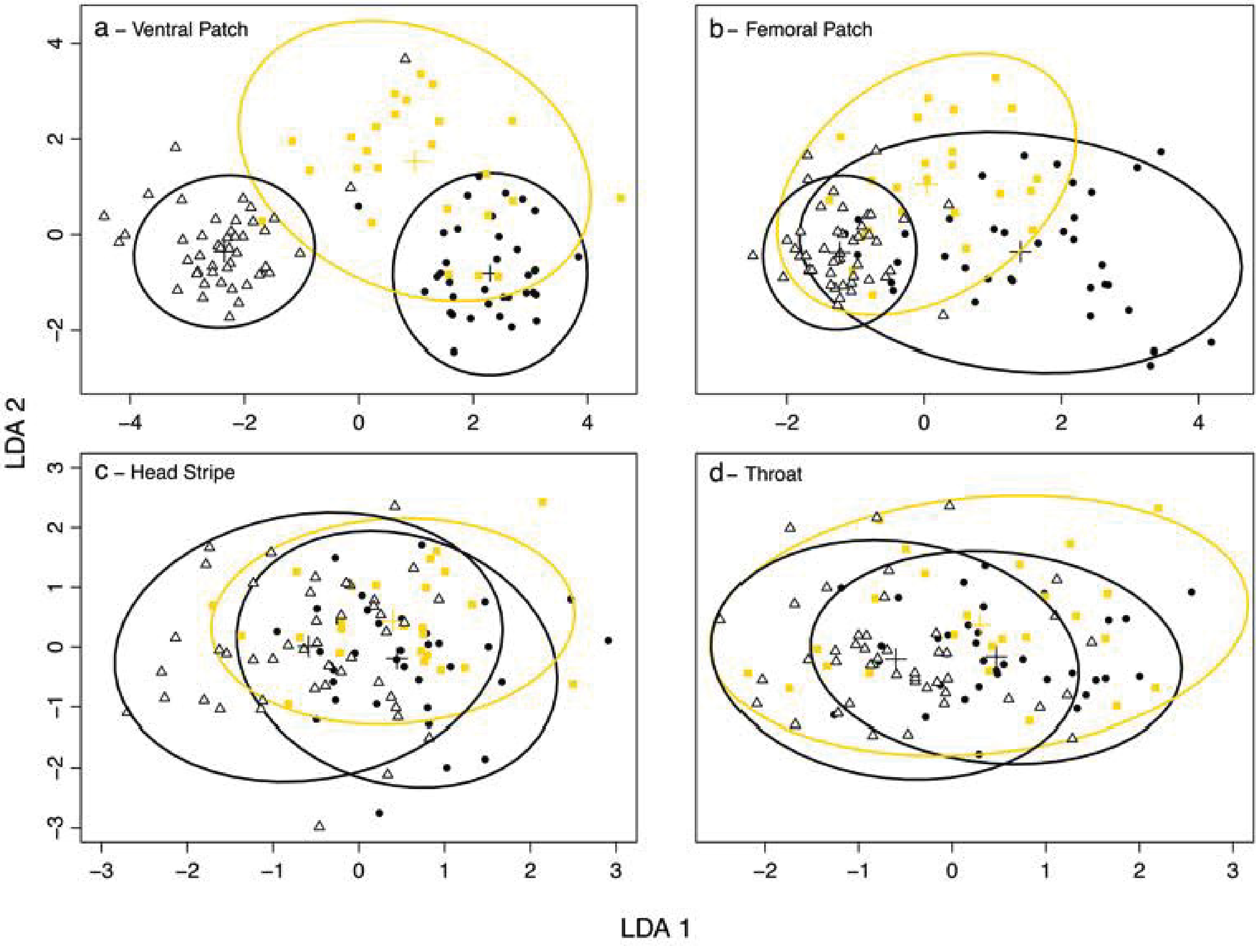
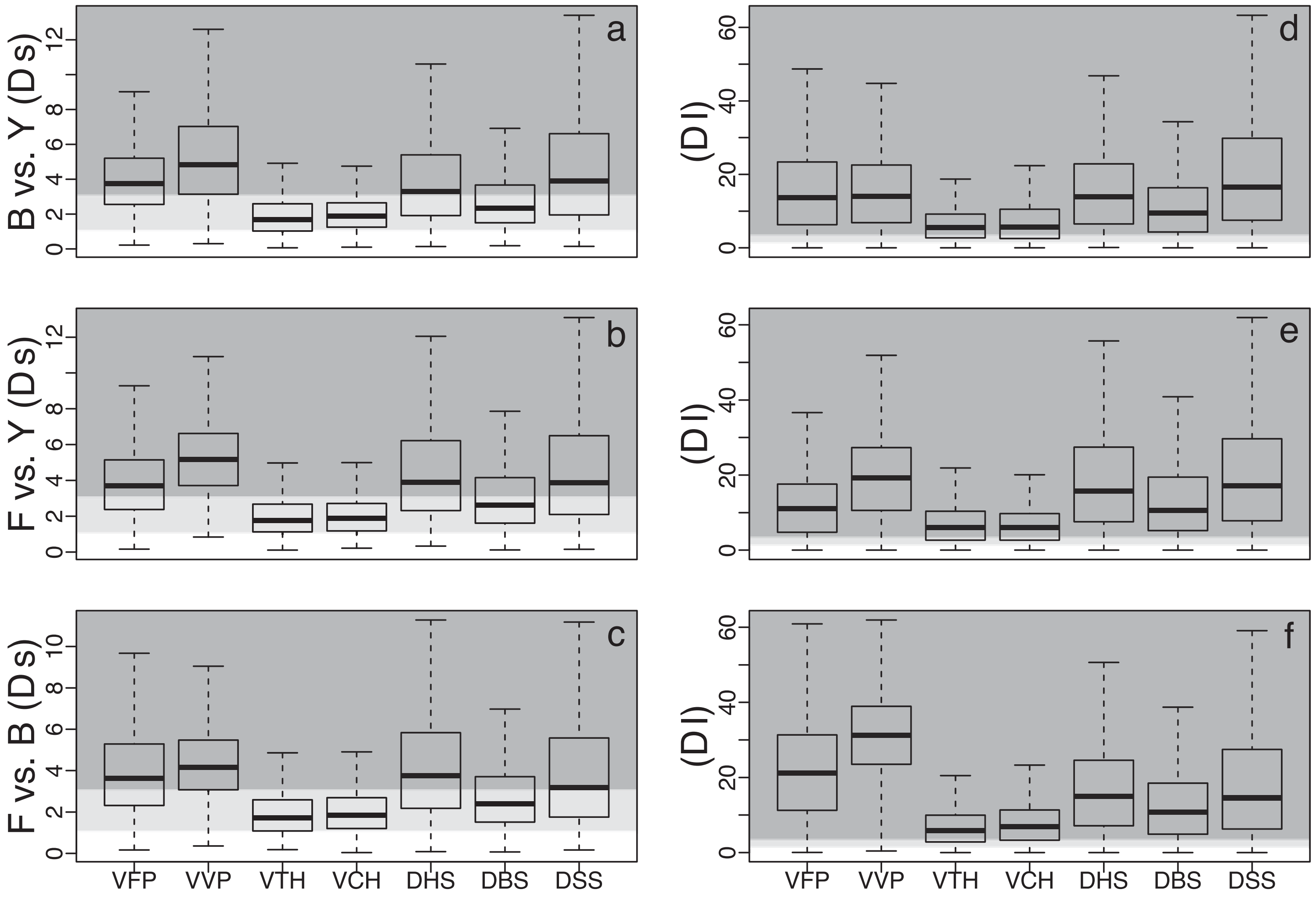

a – Ventral Patch
b – Femoral Patch
c – Head Stripe
d – Throat
LDA 2
LDA 1
4
2
0
−2
−4
3
1
−1
−3

Figure 4


B vs. Y (Ds)
F vs. Y (Ds)
F vs. B (Ds)
(DI)
(DI)
(DI)
a
b
c
d
e
f
0
2
4
6
8
10
12
20
40
60
VFP
VVP
VTH
VCH
DHS
DBS
DSS

MATERIAL SUPLEMENTAR CAPÍTULO I

Amphibia-Reptilia

Conspecifics of the Striped Lava Lizard, *Tropidurus semitaeniatus*, are able to distinguish sex and male color morphs in apparently homogeneous dull dorsal coloration

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Supplementary material

S1 Table. Descriptions of color variables. Adapted from Maia et al. 2013

Color Variable	Description
Hue = λR_{max}	Hue: wavelength of peak reflectance.
$S = \sum_{\lambda a}^{\lambda b} R\lambda / B1$	Chroma: segment-specific chroma calculated by dividing the sum of reflectance values over region of interest (e.g., from λa to λb) by the total reflectance.
Bri = B1/nwl	Mean brightness: average reflectance over all wavelengths.

S1 Figure. Dorsal view of individual of *T. semitaeniatus*. Dorsal view of an adult individual of *T. semitaeniatus* pointing dorsal color patterns and dorsal body regions for spectra measures.

S2 Figure. Reflectance curves of ventral body regions. Plots of reflectance curves of all ventral body regions. Females (red dotted lines), yellow males (yellow solid lines) and black males (grey dashed lines) are plotted separately. Spectra curves show different body regions: Ventral Patch - V_{Patch} (a); Femoral Patch – $V_{FemoralPatch}$ (b); Throat – V_{Throat} (c); Tail Base – $V_{TailBase}$ (d); and Chest – V_{Chest} (e).

S3 Figure. Reflectance curves of dorsal body regions. Plots of reflectance curves of all dorsal body regions. Females (red dotted lines), yellow males (yellow solid lines) and black males (grey dashed lines) are plotted separately. Spectra curves show different body regions: Head Stripe – $D_{HeadStripe}$ (a); Side Stripe – $D_{SideStripe}$ (b); and Dorsum Stripe – D_{Stripe} (c).

S4 Figure. Plots of linear discriminants by body regions. Linear discriminant plots of the remaining body regions with significant difference among morphs: Chest – V_{Chest} (a); and Dorsum Stripe – D_{Stripe} (b). Females (grey triangles), yellow males (yellow squares) and black males (black circles) distributions are plotted separately. Continuous lines delimit 95% of confidence interval. Centroids are marked by cross signs. LD1 and LD2 axis show the functions that better discriminate sex and male color morph, respectively.

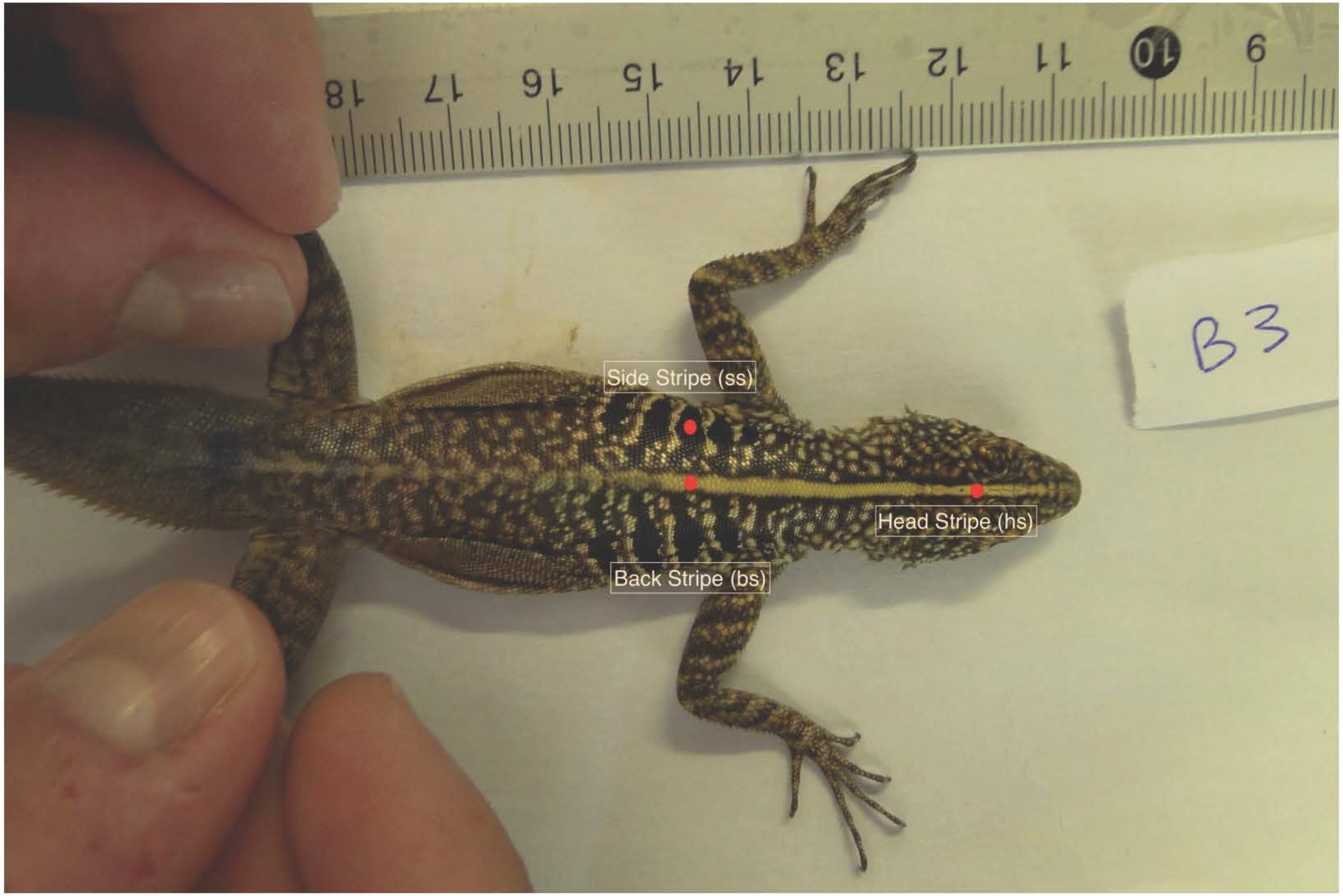

Figure S1

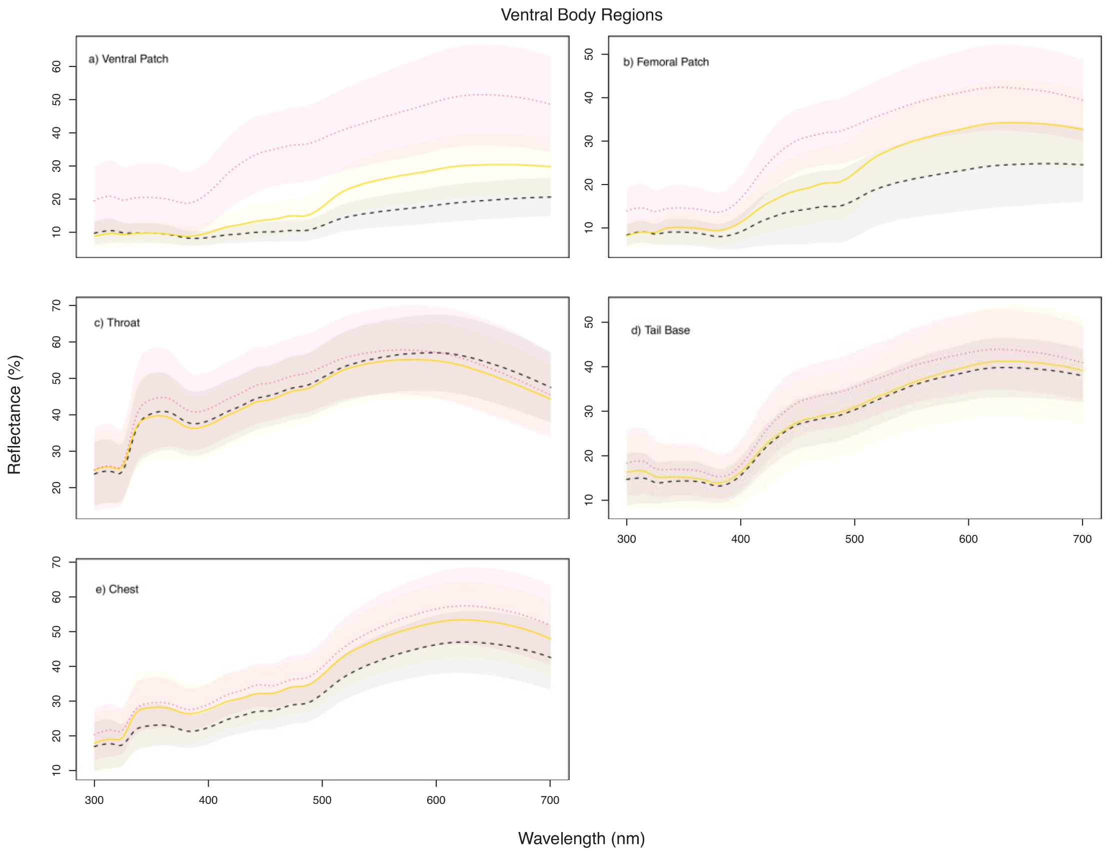
Ventral Body Regions
a) Ventral Patch
b) Femoral Patch
c) Throat
d) Tail Base
e) Chest
Reflectance (%)
Wavelength (nm)
10
20
30
40
50
60
70
300
400
500
600
700

Figure S2

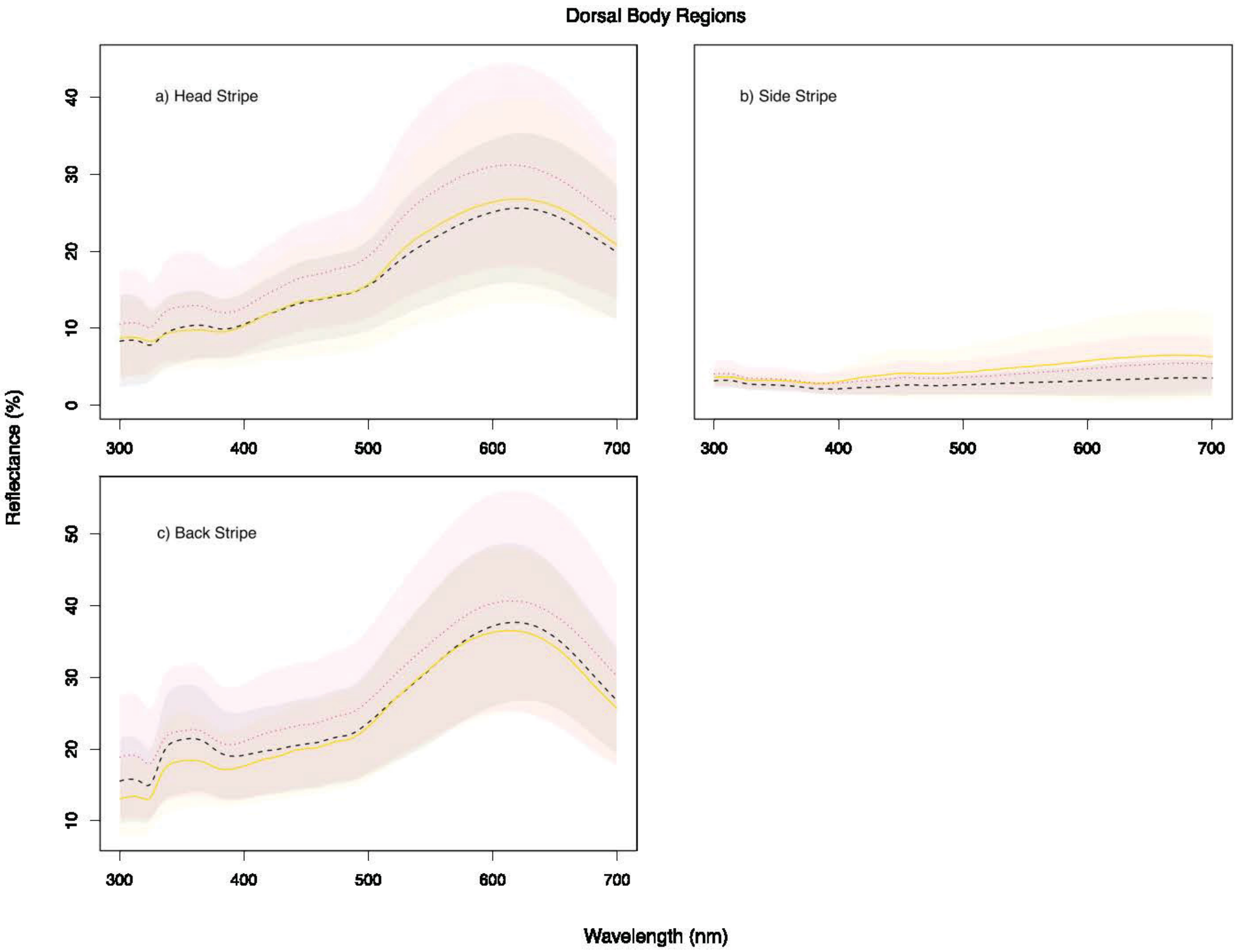
Dorsal Body Regions
a) Head Stripe
b) Side Stripe
c) Back Stripe
Reflectance (%)
Wavelength (nm)
0
10
20
30
40
50
300
400
500
600
700

Figure S3

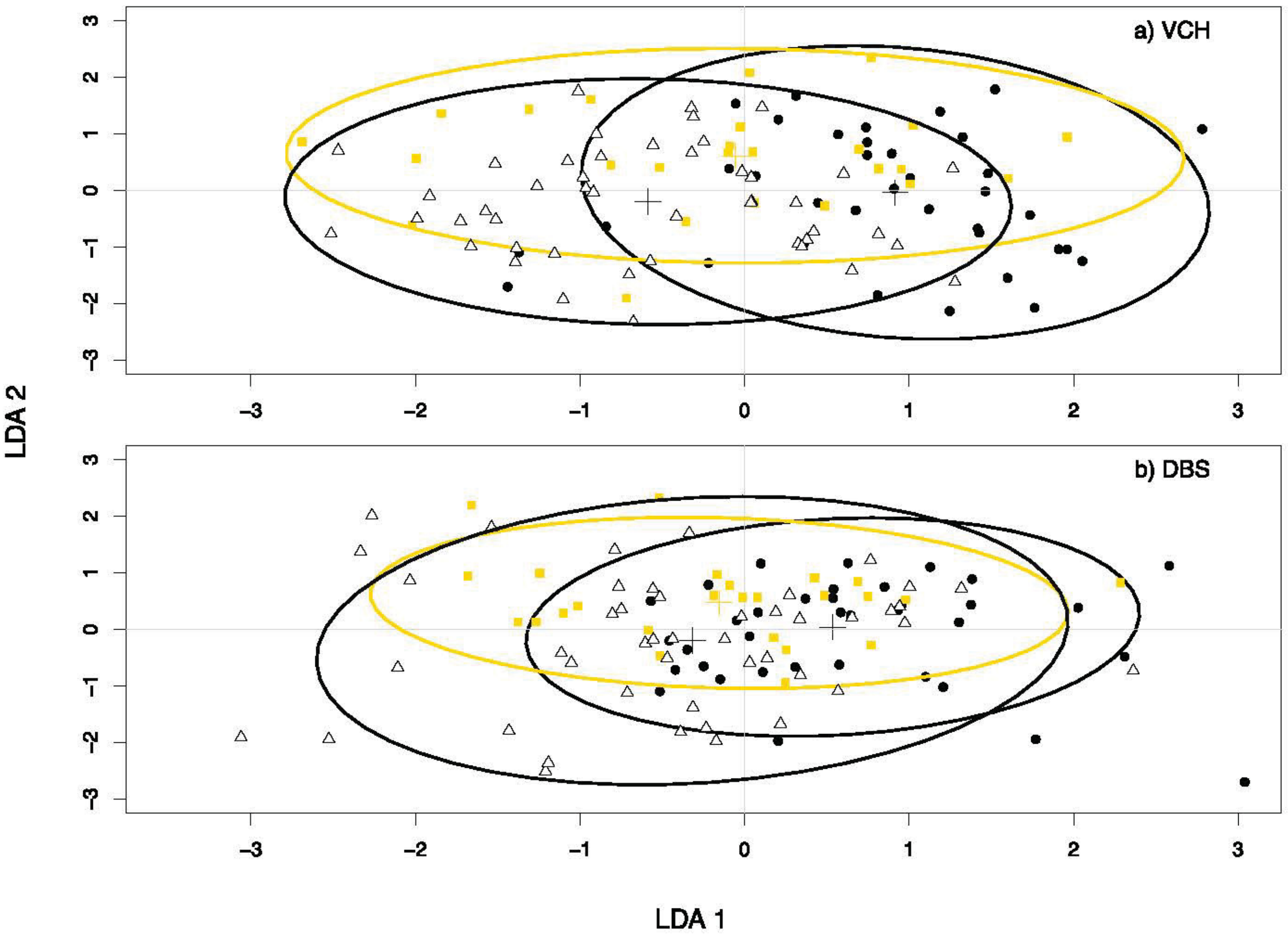

Figure S4

ANEXO II: CAPÍTULO II*

Behavioural syndrome of male colour morphs of the Striped Lava Lizard: aggressiveness and dominance are predicted by yellow colouration, but not performance

*Capítulo formatado de acordo com as normas da revista *Behavioural Processes* para *Short Reports*.

Behavioural syndrome of male colour morphs of the Striped Lava Lizard: aggressiveness and dominance are predicted by yellow colouration, but not performance

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ABSTRACT

Behaviour can be determinant to establish dominance in intrasexual social interactions, preventing higher costs of aggression, and improving access to mates. The saxicolous Striped Lava Lizard, *Tropidurus semitaeniatus* has a colour polymorphism among adult males. It is likely that these morphs play a role in reproduction, however such role is still unknown. Herein, we test whether there is dominance of one morph over the other during intrasexual interactions. We staged pairwise encounters of males of different morphs in *ex situ* behavioural trials. We determined dominance trough the attribution of scores to aggressive and submissive behaviours. Then, we tested whether winning related to individual sprint speed performance, and whether colour traits expressed in other parts of the body predict dominance. Colour morphs showed differences in displays suggesting an aggressive behavioural syndrome but these did not predict the outcome of interactions. Contrary to expectations, winner males do not perform better. Outcome of encounters is highly predicted by the chest coloration, a body region often displayed during encounters. Lightness, ultraviolet reflection, and especially yellow chroma, were highly related to winning outcome. We provide a list of displayed behaviours and their frequencies. Black and yellow colour morphs are not a dominant, and a subordinate, strategies. However, black males are more aggressive and less evasive while yellow males are the opposite. Our results also suggest that lizards might signal their competitive condition through the exposure of the chest. Further studies should address whether or not there is a relationship between colour morphs and female preference, such experiments would reveal the role of colour morphs in intersexual selection.

Keywords: colour polymorphism, behavioural display, animal colouration, intrasexual competition, alternate reproductive tactics, *Tropidurus semitaeniatus*

HIGHLIGHTS

- Lizard males of different colour morphs were stimulated to compete for a resource.
- Male morphs differed in frequency of displayed behaviours, but not in the results of the interactions. Dominant males did not have faster performance. Chest's UV-chroma coloration was less intense while yellow chroma was higher in dominant males.
- Our results suggest the existence of a behavioural syndrome in terms of aggressiveness between male colour morphs and a role of yellow colouration on dominance.

INTRODUCTION

Much of biological diversity is produced by sexual selection processes. An example is the selective pressure for conspicuous traits that increases signalling in the competition for the access of mates (Endler, 1980). In addition to these selected signals, competition for females can also select for many different behavioural strategies in males (Hurtado-Gonzales and Uy, 2010). In turn, these multiple tactics are often associated with colour polymorphisms (Taborsky et al., 2008). Hence behaviour (i.e. in terms of both female preference or male behavioural tactics) drives variation in morphology and colouration. Some examples are males' ornaments selected by female choice; males' armaments and behavioural signals selected by male competition; and social hierarchy that is determined by behaviour and directly influences mating success (e.g. Andersson, 1986; Berglund et al., 1996; Hover, 1985).

In male-male competition, behavioural signals are important because they might convey information on individual fighting ability (Arak, 1983), establishing dominance without major costs (Smith and Price, 1973). Animal signalling is expected to be honest (Zahavi, 1975) and dominance is often determined by behavioural signalling. Because dominance influences reproductive success through the differential assessment of mates, hence this influenced fitness will in turn be correlated to signalling (Robson and Miles, 2000). In addition to behaviour, colouration can also signal individual quality. For instance, ultraviolet reflection, a highly conspicuous colouration signal, might inform individual's fighting ability and aggression (Stapley and Whiting, 2006). Also, pigment-based colouration such as yellow chroma has been shown to signal quality and predict fitness (Grether, 2000). Nonetheless, morphs differing in hue are often related to different behavioural strategies (i.e. colour morphs) (e.g. Moore et al., 1998; Seaver and Hurd, 2017; Sinervo and Lively, 1996). For instance several systems, from arthropods to lizards, develop a mating system in which two singular mating tactics coexist: commonly one being the stereotyped male of the species, with either conspicuous or colourful signalling, developed armament morphologies, and aggression (i.e. the dominant); and one pale and dull, often female-like and evasive, type of male (i.e. the sneaker) (Shuster and Wade, 2003). Even more interestingly are the systems in which distinct classes of hue depict distinct classes of behaviour such as the yellow, blue, or orange morphs of the side-blotched lizard that behaviourally outcompete one another cyclically (Sinervo and Lively, 1996).

In the particular situation of polymorphic species, one hypothesis to explain the coexistence of multiple morphotypes is its mediation by different behavioural strategies and physiological performance. For example, among three morphs of the lizard *Podarcis melisellensis*, males with orange gular and ventral regions are more territorial and win more agonistic encounters (Huyghe et al., 2007). Therefore, increasing evidences point to a close link between behaviour, colouration, and performance playing a role in individual fitness (e.g. Herrel et al., 2009; Seaver and Hurd, 2017; Sinervo et al., 2000; Zajitschek et al., 2012).

Subsets of individuals from a group might tend to behave consistently throughout a continuous axis of a particular set of behaviours (for instance, a continuous axis from evasiveness to aggression). In these situations, it is arguable that such group exhibit a behavioural syndrome (Sih et al., 2004). In the aforementioned context, multiple subsets of individuals could behave consistently in relation to an aggression axis. Hence individuals fit in two types of behavioural response (evasive vs. aggressive behavioural types) within a *single behavioural syndrome* of aggression axis. The identification of a behavioural syndrome is important because it can explain individual behaviours that do not seem to be proper for a particular context (e.g. engaging in aggression in the presence of predators). A behavioural syndrome can also explain different behaviours that tend to correlate across situations (e.g. aggression and boldness), and it has being often related to sex-restricted colour polymorphisms (Seaver and Hurd, 2017). One of the main responsible factors for aggressiveness is testosterone levels, which in turn influences muscle development (Regnier and Herrera, 1993). So it is expected that more aggressive behavioural types would also have a better physiological performance.

The striped lava lizard (*Tropidurus semitaeniatus*) is a flat rock dwelling specialist endemic to the Caatinga biome in South America that has a distribution restricted to rocky habitats. Adult males can be either black, or yellow coloured morph (Ribeiro et al., 2010). Besides body size and colouration, differences of *T. semitaeniatus*' colour morphs have not yet being investigated. Herein, we use pairwise male competition trials to test whether the male colour morphs are unevenly distributed on an intrinsic behavioural syndrome of evasiveness to aggressiveness. Thus, whether colour morphs characterize two behavioural types (i.e. *more aggressive and less evasive* vs. *less aggressive and more evasive* behavioural types) within a behavioural syndrome (Sih et al., 2004). Then, scoring displayed behaviours, we test whether one of the two types of male colour morphs tend to win more encounters (dominant). Colour morphs have different body sizes and are not evenly distributed among males in the population, so we expect that they would be socially distinct, presenting different outcomes in between-morph encounters. Because aggression levels and muscular performance are influenced by the same mechanism (testosterone levels) (Regnier and Herrera, 1993), we expect that winner individuals would also have a better performance. Lastly, through several spectrophotometric measures of body colouration, we explore whether individual colour predicts the outcome of encounters. We expect that colour traits likely to be costly (i.e. conspicuous and pigment-based colourations) would predict the winning outcomes.

MATERIAL AND METHODS

Sampling and housing

Tropidurus semitaeniatus is a polymorphic lizard that inhabits rocky outcrops and has two coloured morphotypes among adult males. Its thighs and pre-cloacal flaps may have yellow or black-and-yellow ventral patches (Ribeiro et al., 2010), hereafter yellow males and black males. We conducted male-male interaction trials in March and April of 2015 (within breeding season, see Ribeiro et al., 2012). We collected 42 lizards from a single population (João Câmara, RN 05º32’15”S, 35º49’11”W) using a noose. We kept lizards in individual plastic terrariums (35 x 24 x 12 cm; width x length x height) in the laboratory and feed them every other day with three larvae of

Tenebrio molitor. Terrariums had shelter, *ad libitum* clean water, and 60-Watt lamps as heat source timed to natural photoperiod 12:12 h.

Male-male competition between colour morphs

To access whether colour morphs of *T. semitaeniatus* have a social structure in relation to dominance/submissiveness, we staged pairwise encounters between colour morphs. We obtained behavioural data from trials in which we analysed and quantified displayed agonistic behaviours. In order to form pairs with similar body size, we measured snout-vent length (SVL) to the nearest 0.01mm and paired unrepeated lizards (17 pairs) of different morphs by size (mean ± SD male size difference: SVL, 1.65±1.31 mm). We conducted the trials in a terrarium (70 x 33 x 33 cm) divided into three compartments (Fig 1a). We deprived lizards from heating and kept them in room temperature (26ºC) for a period of 24 h prior to the trials. Individuals had 15 minutes to adjust, each in one side of the terrarium and both separated from each other and from the central area by removable opaque cardboard walls (Fig 1b). Then, we encouraged interactions by heating a natural rock (39ºC±2.3SD) with a heat lamp and positioning both rock and heat lamp in the central compartment. There was no visual contact, access to the rock, or lamplight, before the beginning of the 30 minutes long trial (adapted from: Schall & Dearing, 1987). In order to eliminate chemical traces we thoroughly cleaned the terrarium and replaced sand substrate at the end of each trial. We recorded all trials (120 fps) and used the software *VC Griffin* for display quantification. We analysed each video twice, once for each focal male, and considered only behaviours displayed in the range of 30 min. We defined encounter's winner of intrasexual competitions attributing scores to the behaviours. Each aggressive behaviour displayed counted 1 score and each submissive/evasive behaviour displayed deducted 1 score for each individual. Behaviours were categorized based on the agonistic ethogram of the species (Coelho et al., 2018). We considered as winner of the encounter the individual that had the higher score at the end of each trial (adapted from Garland Jr., Hankins, & Huey, 1990).

Performance and male dominance

Aggressiveness is directly influenced by testosterone levels which, in turn, affects muscle development (Regnier and Herrera, 1993). Therefore, we expect that more aggressive and dominant individuals would also perform better. To test the hypothesis that males with better performance tend to win more agonistic encounters, we compared the outcome of encounters (“winner” or “looser”) with individual’s maximum sprint-speed. To gather this measure, we ran each individual in a 2 m long racetrack with sandpaper as substrate for a proper traction (Brandt et al., 2015), scaled every 1 cm. Because body-temperature (T_b) is known to influence performance in lizards, we allowed individuals to thermoregulate for a period of 90 min prior to the trials distanced 45 cm from a heat lamp. We measured T_b right before the sprint trials with a cloacal thermometer in order to assure that lizards had reached T_b around their preferred temperature (37±2ºC, Paiva et al., unpublished data). Lizards ran 3 times with a minimum resting period of 24 h between trials. We stimulated the lizards to run with soft touches at the tip of the tail with a feather. The value of maximum sprint was the fastest 25 cm interval of all runs of each individual analysed from 120 fps recordings. Performance measures were made 10 days after behavioural trials.

Colour as predictor of male dominance

In order to access whether colour traits are related to outcome of encounters (winning/loosing) we measured colouration in several parts of the body of each lizard. For that, we obtained reflectance spectra with an optic fibre (R400-7-UV-VIS, Ocean Optics, Dunedin, FL) attached to a spectrophotometer (USB4000-UV-VIS). We took three measures of 8 body regions that might be displayed during encounters: throat ($\mathrm{V}_{\mathrm{Throat}}$), chest ($\mathrm{V}_{\mathrm{Chest}}$), ventral patch ($\mathrm{V}_{\mathrm{Patch}}$, the patch cloacal region), femoral patch ($\mathrm{V}_{\mathrm{FemoralPatch}}$), ventral tail base ($\mathrm{V}_{\mathrm{TailBase}}$), head stripe ($\mathrm{D}_{\mathrm{HeadStripe}}$, measured within the head's dorsal bright stripe), dorsum stripe ($\mathrm{D}_{\mathrm{Stripe}}$, measured within the dorsal bright stripe), and side stripe ($\mathrm{D}_{\mathrm{SideStripe}}$, measured at the dark stripes directly at the side of $\mathrm{D}_{\mathrm{Stripe}}$) (Fig 2). We derived different colour variables from the spectral reflectance curves using the R package *pavo* (Table S2, Maia et al., 2013). First, we restricted spectra curves between 300 nm and 700 nm (the wavelength range perceivable by lizards' visual system, Loew et al., 2002) and averaged all three measures taken at each region. Ultraviolet reflection and carotenoid-based colouration are known to relate with several individual qualities and signalling (Martín and López, 2009; Stapley and Whiting, 2006). Also, yellow colouration was found to be produced both by pigment-based and structural reflectors in lizards (e.g. Saenko et al., 2013). So, we derived colour variables that represent the different aspects of colouration: segment-specific ultraviolet and yellow saturations (S_{UV} and S_{Yellow}, respectively), hue (*Hue*), and mean lightness ($M_{Lightness}$).

Statistical Analysis

To access whether male colour morphs of *T. semitaeniatus* characterize different behavioural types of a behavioural syndrome of aggressiveness (Sih et al., 2004) we compared the frequencies of aggressive and evasive behaviours displayed by morphs with chi-squared tests. Also, to explore whether male colour morphs differ in the amount of displays of each behaviour, we performed Wilcoxon tests with colour morph as fixed factor and each behaviour (Table S1, adapted from Coelho et al., 2018) as response variables. Next, to determine whether there is a relationship between colour morphs and the outcome of encounters we performed a paired Wilcoxon signed rank test with the total score of individuals as response variable and colour morph as fixed factor. We used the same test in order to explore whether colour morphs differ in performance with colour morph as fixed factor and maximum sprint speed as response variable. Then, we attributed to each individual a final status of winner (1) or looser (0) as *outcome* and tested the association of performance on dominance. For that, we used *outcome* as factorial predictor and maximum sprint speed as response variable of a Wilcoxon signed rank test. Finally, to access whether colouration predicts outcome of encounters we performed a binomial logistic regression analysis with the colour variables as predictors of *outcome*. Due to sample size of trials (n = 17 pairs), we performed 32 separate binomial generalized linear model functions with logit model using individually 4 colour variables (*Hue*, $M_{Lightness}$, S_{UV} and S_{Yellow}) of each body region (V_{Throat}, V_{Chest}, V_{Patch}, $V_{\text{FemoralPatch}}$, V_{TailBase}, $D_{\text{HeadStripe}}$, D_{Stripe} and $D_{\text{SideStripe}}$). We ran all statistical analysis in R software (R Core Team, 2015).

RESULTS AND DISCUSSION

Colour morphs did not differ in dominance (V = 95, $p = 0.394$), neither in performance (W = 141, $p = 0.917$). In relation to their behaviour however, yellow morphs performed less aggressive behaviours, X^2 (1, $N = 267$) = 5.69, $p < 0.05$ (*approach*, *intimidation posture*, *bite* and *dorsum show*, Table 1) and more submissive behaviours, X^2 (1, $N = 195$) = 14.4, $p < 0.001$ (e.g. *retreat*). Yellow males also displayed significantly more *tail wave* (W = 169, p = 0.049). Tail displays are usually described as anti-predatory behaviours, but it is also observed in subordinate individuals within social interactions (e.g. Alonso, Cotrina, Pardo, Font, & Molina-Borja, 2010; Machado, Galdino, & Sousa, 2007; Sánchez-Hernández, Ramírez-Pinilla, & Molina-Borja, 2012). Different behavioural types (Sih et al., 2004) are known to occur in some polymorphic species, enabling morph coexistence (Dijkstra et al., 2009). An example is the well described morphs of *Uta stansburiana* that, among other traits, differ in their defence of territory and of females (Sinervo, Miles, Frankino, Klukowski, & DeNardo, 2000). In *T. semitaeniatus*, the prevalence of *tail wave* displays among yellow males, together with fewer displays of aggressive behaviours and higher displays of evasive behaviours suggests that the species has a behavioural syndrome of aggressiveness, with yellow males showing a more evasive behavioural type. Further studies should explore whether male colour morphs of *T. semitaeniatus* also differ in behaviours in other contexts such as boldness, which could characterize male morphs within a proactive-reactive axis (Sih et al., 2004).

Dominant males do not have better performance than submissive ones (V = 89, p = 0.5791) Interestingly, this result goes against our expectations and findings in literature for other species of lizard where performance was found to influence dominance. For instance, dominance was found to be highly associated with sprint-speed and stamina performances in *Urosaurus ornatus* (Robson and Miles, 2000). Likewise, sprint-speed is significantly higher in winner males of *Sceloporus occidentalis.* However stamina is not (Garland Jr. et al., 1990).

Although maximum sprint-speed is a common proxy for performance in lizards in literature, it is possible that it does not capture whole organism performance depending on ecological habits of the species. *T. semitaeniatus* is a sit-and-wait lizard that tend to remain in the same rock outcrops for long periods of time during the day, moving short distances eventually to capture prey, thermoregulate, and hide in rock crevices. Sprint-speed might play a role in retreating from threats, but may not capture a performance measure related to dominance in this species. A possibility would be to explore the relationship between bite force performance and dominance, as *Bite* had a significant portion of displayed behaviours during encounters (Table 1).

Chest colouration had strong relation to dominance (Table 2, Figure 1a-c). Logistic regression showed that low values of lightness in V_{Chest} are related to a higher probability of winning encounters (Figure 1a). Also, that higher S_{Yellow} values increase the probability of winning (Figure 1c). In other words, lizards with darker and more intense yellow saturation in their chests have a better chance of winning the encounters. This is an interesting finding, since the expression of both dark and yellow colours are often related to pigment-based colouration (e.g. carotenoid and melanin) (Steffen and McGraw, 2009), being both costly and indicative of individual quality (Grether, 2000; Martín and López, 2009). However, the underlying mechanisms of the expression of yellow colouration in *T. semitaeniatus* were not yet studied. Thus, although our results are not a proof of a costly signal of chest colouration in this species, it suggests a possible role of costly colouration in conspecific communication in ventral parts of the body. Therefore, future studies might explore physiological mechanisms of the production of pigment-based colouration in these lizards. In addition, S_{UV}, likewise $M_{Lightness}$, had a negative effect on the probability of winning (Table 2, Figures 1a-b). That is, individuals with lower ultraviolet reflectance in chest tend to win encounters (Figure 1b). This finding is contrary to our expectations based in the literature. Intrasexually, UV-reflection is known to correlate with fighting skills (*Lacerta viridis*, Bajer, Molnár, Török, & Herczeg, 2011), and inform fighting capacity in lizards (*Platysaurus broadleyi*, Stapley & Whiting, 2006). Whereas intersexually, males choose females with high ventral UV (*Ctenophorus ornatus*, LeBas & Marshall, 2000) and UV-deprived males are also less likely to be chosen by females (Lisboa, Bajer, Pessoa, Huber, & Costa, 2017). Therefore, although there is evidence that *T. semitaeniatus* reflects UV at ventral parts of the body (e.g. throat area, Bruinjé et al., Capítulo 1 in review), UV signalling does not appear to determine male social dominance. Nonetheless, *Hue* at V_{Patch} highly predicts the outcome of agonistic encounters (Table 2, Figure 1d). Although behaviours that exhibit the patches are not displayed very often, it appears that colouration at the patches plays a role in the probability of winning, as darker yellow/greenish colour is expressed at the patch (results not shown).

We did not find a strict social status relationship of dominance/subordinate between *T. semitaeniatus*' colour morphs. However, we found a higher proportion of aggressive against evasive displays in black males, while the opposite was found in yellow males. These results suggest the existence of a behavioural syndrome of aggressiveness to evasiveness in this species. In addition, we found that chest colouration plays a significant role on dominance in intrasexual context. Moreover, we found strong association with low lightness and yellow colouration to dominance, which suggests the signalling of the quality of individuals. Future steps would be to explore the physiological mechanisms responsible for the production of colour of chest and ventral patch to access whether it is pigment-based or structural colouration. This information would allow inferences on the costs of this signal and its function in social interactions. Also, manipulating colouration at the chest in female choice experiments would allow the assessment of whether this trait is also a male ornament used for females to choose for mates.

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Tables

Table 1

Behaviour	Displayed by	
	Black morph (%)	Yellow morph (%)
Approach	24% (n = 53)	19% (n = 46)
Intimidation Posture	17% (n = 38)	9% (n = 22)
Chase	6% (n = 14)	5% (n = 13)
Bite	14% (n = 31)	12% (n = 28)
Dorsum Show	8% (n = 17)	2% (n = 5)
Tail Wave	2% (n = 4)	10% (n = 23)
Retreat	30% (n = 67)	42% (n = 101)

Percentage and total number of aggressive and submissive behaviours displayed by both male colour morphs of *Tropidurus semitaeniatus* during male-male competition encounters.

Table 2

Variable	*p*
Chest Lightness	**0.022**
Chest UV Saturation	**0.034**
Chest Yellow Saturation	**0.036**
Ventral Patch Hue	**0.017**

Results of logistic regression of variables on outcome of male-male competition encounters.

Figure legends

Figure 1. Scheme of tank used in male-male agonistic trials between colour morphs. a) Tank in the beginning of the trial, with opaque walls (in grey) visually and physically separating subject compartments (left and right compartments) from each other and from natural heated rock (at the centre). b) Scheme shows trial after 15 min of acclimatization of subjects with opaque walls being removed allowing subjects to get in contact with each other. Illustrated rock at centre is a natural rock heated with heat lamp prior to trials. Subjects were prevented from thermoregulating for 24 h prior to trials and kept in room temperature (26ºC). The rock is positioned at the centre of the tank in order to promote competition between subjects.

Figure 2. Dorsal (a) and ventral (b) views of male *Tropidurus semitaeniatus* showing body regions in which colour measurements were taken. Dorsal numbering refers to locations of dorsal head stripe (a-I), dorsal stripe (a-II) and dorsal side stripe (a-III). Ventral numbering refers to locations of throat (b-I), chest (b-II), ventral patch (b-III), femoral patch (b-IV), and ventral tail base (b-V). White checkerboarded areas cover researcher holding subject.

Figure 3. Plots of logistic regression models of colour variables on the outcome of encounters. Red continuous lines show logistic model of the probability of winning encounters (Y left axis) in relation to trait value (X axis). Barplots show the frequency (Y right axis) of individuals that won (upper bars) and loose encounters (lower bars) distributed on trait value (X axis). Significant (that yielded *p*-values <.05) models are plotted by colour variables in body regions: a) Mean lightness at the chest; b) ultraviolet chroma at the chest; c) yellow chroma at the chest; d) hue at ventral patch.

Figures

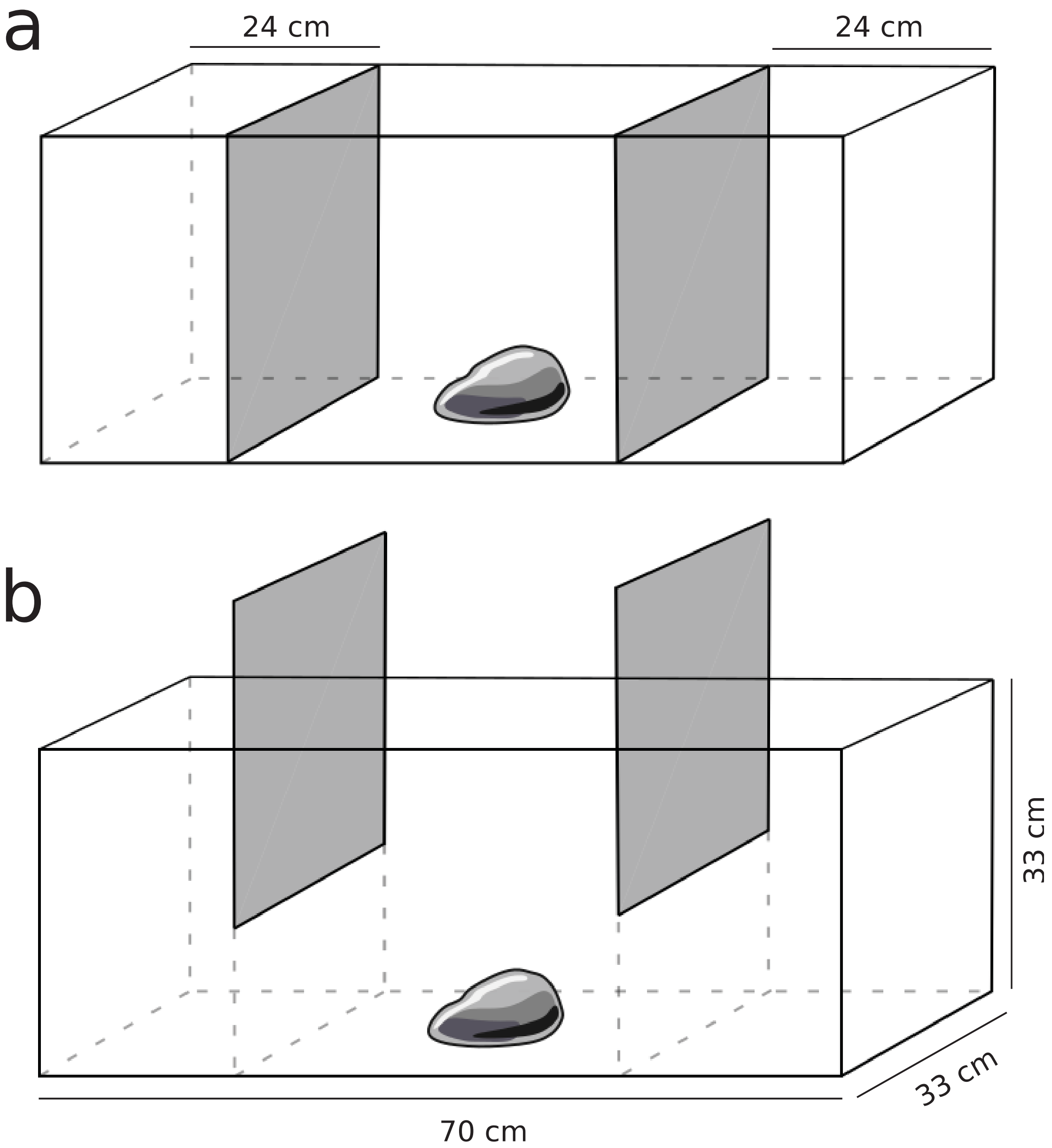

Figure 1

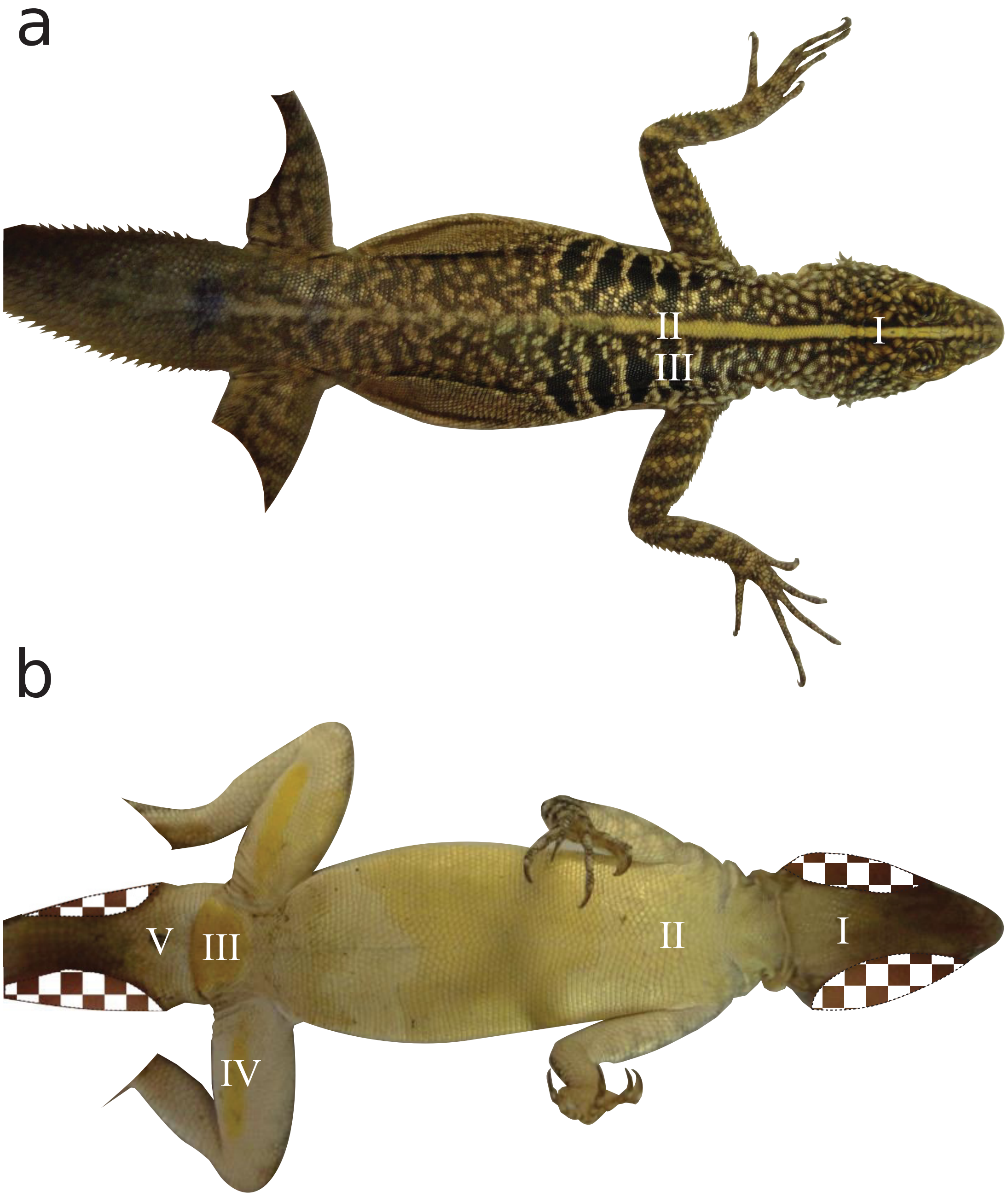

Figure 2

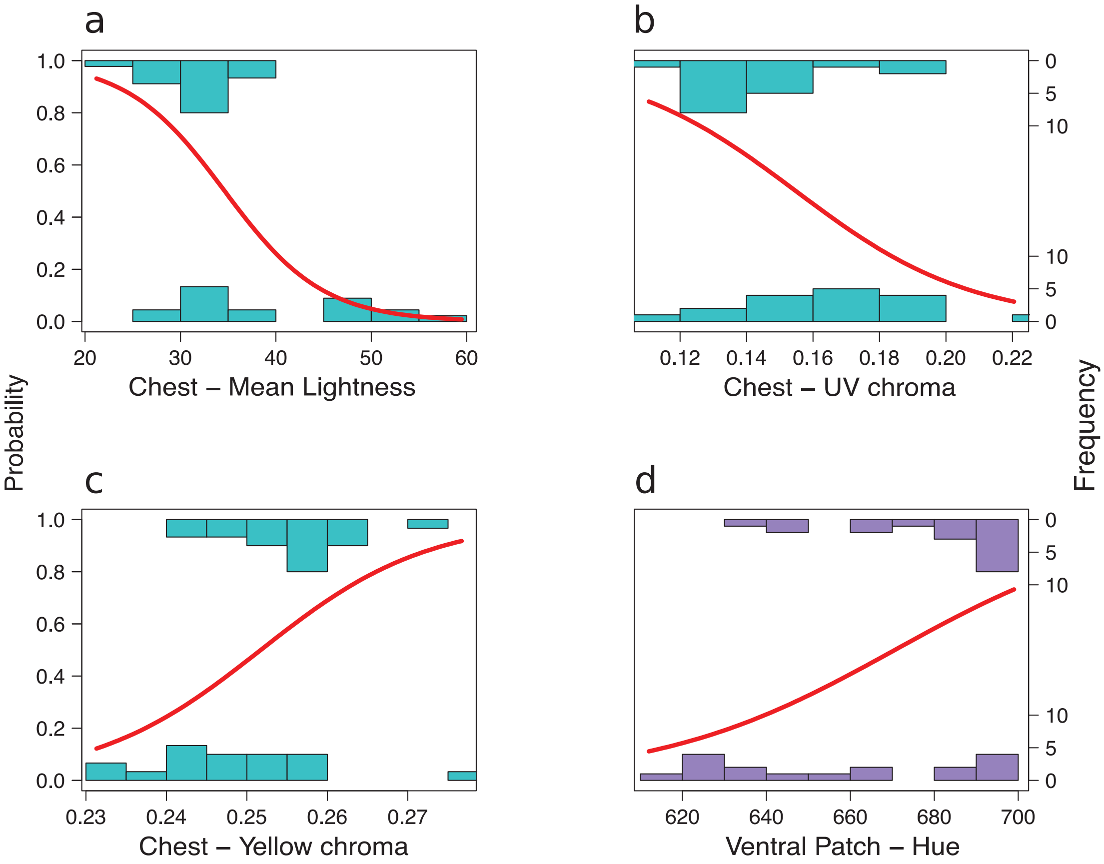
a
b
c
d
Probability
Frequency
1.0
0.8
0.6
0.4
0.2
0.0
0
5
10
10
5
0
20
30
40
50
60
Chest – Mean Lightness
0.12
0.14
0.16
0.18
0.20
0.22
Chest – UV chroma
0.23
0.24
0.25
0.26
0.27
Chest – Yellow chroma
620
640
660
680
700
Ventral Patch – Hue

Figure 3

MATERIAL SUPLEMENTAR CAPÍTULO II

Supporting information

S1 Table. Ethogram of *T. semitaeniatus* based on the agonistic interactions between male colour morphs (adapted from Coelho et al. 2018).

Behaviour	Description
Approach	Movement straight towards the opponent, in a fast or slow speed.
Intimidation Posture	Rise of the anterior part of the body or the whole body, curving its head towards the ground, curving its dorsum. Sometimes it inflates its gular region.
Chase	Quick move towards retreating opponent, bites may or may not occur.
Bite	Bites the opponent, mainly in the regions of the neck or tail base, releasing it afterwards. The approach towards a bite is either laterally or dorsally.
Dorsum Show	Lift of the anterior part of the body exposing the gular region and inclines laterally the upper body. Changes the angle of the scapular waist, expanding the thoracic region and showing the full dorsum towards the opponent.
Tail Wave	All ventral parts of the body are in contact with the substrate, while waving only the final portion of tail laterally in rapid movements.
Retreat	Moves rapidly towards the opposite direction of the opponent.

S2 Table. Descriptions of colour variables.

Colour variable	Description
$H_{ue} = \lambda_{Rmax}$	Hue: wavelength of peak reflectance.
$S = \sum_{\lambda a}^{\lambda b} R\lambda / B1$	Chroma: segment-specific chroma calculated by dividing the sum of reflectance values over region of interest (e.g., from λ_a to λ_b) by the total reflectance.

$B_{ri} = B_1/n_{wl}$	Mean lightness: average reflectance over all wavelengths.

Description of colour variables according to Maia et al. 2013

ANEXO III: CAPÍTULO III*

Performance, coloration, and multi-modal female mate preference for male color morph in the Striped Lava Lizard

*Capítulo formatado de acordo com as normas da revista *Behavioral Ecology and Sociobiology* para *Featured Student Research Paper*.

Performance, coloration, and multi-modal female mate preference for male color morph in the Striped Lava Lizard

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ABSTRACT

Intersexual selection is one of the most important drivers of morphological and behavioral diversity. Among this diversity there are the alternative reproductive tactics, of witch behavioral and color variants are often maintained by differential reproduction. In these contexts, it is expected that males would inform individual quality through signaling, and females would choose “better quality” males. Here, through behavioral choice experiments using two different signal paths (visual and chemical), we test whether females of the Striped Lava Lizard have differential preference between the two color morphs present in males of the species. We access whether a better sprint speed performance and the expression of conspicuous and costly colorations would influence the probability of being chosen by females. Black morph males tend to be more aggressive and were preferred by females based on chemical cues, but not on visual ones. Individual performance had no effect on the probability of being chosen. However, an increase in darker and greener colorations at ventral-posterior parts of the body of the lizards had a significant effect on the probability of being visually chosen. These results suggest that females of *T. semitaeniatus* make use of chemical cues, even though males do not have femoral pores. Also, that pigment-based coloration might play a role in female choice, as it is costly and may be informing male quality. Our results open possibilities for future research to explore chemical signaling in *Tropiduridae* lizards. Likewise, to explore the role of alternate reproductive tactics in this species, as it is likely that differential reproduction occurs due to differential mating outcomes between male morphs.

Keywords: color polymorphism, sexual selection, mate choice, alternative reproductive tactics, multi-modal signaling

INTRODUCTION

Mate choice is often responsible for the evolution and maintenance of conspicuous and exuberant traits, promoting sexual dimorphism (Endler 1980). The most common phenomenon is conspicuousness of males and dullness of females, a pattern that has been intriguing biologists ever since Darwin (Darwin 1889). A more specific situation occurs when mate choice plays a role in species with color polymorphisms (CP). Within-sex CP depends on a selective balance between morphs in order to be maintained (Smith and Price 1973), and female mating preferences can play a role in explaining the maintenance of the CP (e.g. Farr 1977; Eakley and Houde 2004).

Discrete types of colorations in one sex are often related to alternative reproductive strategies, conveying distinct mating success between morphs. For example, males of the common chameleon (*Chamaeleo chamaeleo*) have two types of color patterns and behavioral displays. Each one is related to a distinct mating tactic (dominant and subordinate) (Keren-Rotem et al. 2016). Thus differences in coloration can convey different information on behavior for reproduction through visual signaling. Moreover, animal signaling can function through multiple paths, such as acoustic (for example in anurans, e.g. Sullivan and Kwiatkowski 2007), or chemical (for example in felids, e.g. Gorman and Trowbridge 1989).

The majority of models of the evolution of mate choice consider a cost factor, being those in terms of individual quality (such as immunological condition, parasite load, or physiological performance) or associated costs related to male signaling (reviewed in Andersson 1994). The expression of colors is known to carry a cost parameter in a variety of situations. Structural ultraviolet reflectance was found to be chosen by females (Bajer et al. 2011; Lisboa et al. 2017) and inform fighting capacity in males (Stapley and Whiting 2006), but carries a cost of increased conspicuousness to predators (Zuk and Kolluru 1998; Whiting et al. 2006). Another example is the female preference for pigment-based colorations (often dark, yellow and red colors), a different type of color expression that is known to be costly to produce (Lozano 1994; Olson and Owens 1998). Indeed, darker-yellowish coloration at the chest, and also darker-greenish coloration at the ventral portion of the body (at the cloaca), were found to signal fighting ability of males of *Tropidurus semitaeniatus* (Bruinjé et al. Capítulo 2). In addition, besides color signals, females often choose males that display energetic costlier behaviors (Wikelski et al. 2001). In all those examples, signals in sexual contexts (both intra- and inter-sexual) are directly related to the "quality" of the individual, conveying a cost to the signaler. Females would therefore choose mates in relation to its individual quality in exchange of direct or indirect benefits. For instance, choosing a less parasitized male would decrease the chances of the female to be parasitized as well; choosing a stronger and more aggressive male that defends a better territory would allow the female to benefit from territory resources; but also, choosing a male handicapped by costly signals would confer such qualities (i.e. showy traits) to the female's offspring (Trivers 1972; Zahavi 1975).

Sprint speed is commonly used as proxy of individual quality in lizards (e.g. Miles 2004; Irschick et al. 2008; Zajitschek et al. 2012). The development of muscle structures needed for sexual behavior is much influenced by testosterone levels (Regnier and Herrera 1993) that in turn correlate with both performance and aggressiveness. Better performance and higher levels of aggressiveness would therefore increase fitness since it would confer to the bearer better territories, resources and, much likely, access to mates. This has been found in *Uta stamburiana* lizards relating their behavioral morphs to performance (endurance) to home range control which influences mating success (Sinervo et al. 2000). Bite force performance was also found to correlate with aggressiveness and less escape reaction in *Tupinambis merianae* (Herrel et al. 2009). Besides, individual performance was found to correlate with size of territory (Peterson and Husak 2006) and thus mating success through sexual selection, increasing fitness (Husak and Fox 2008). Also, a direct link between performance and reproductive success was found in *Crotaphytus collaris* (Husak et al. 2006).

The Striped Lava Lizard (*T. semitaeniatus*), a flat shaped lizard that inhabits rocky outcrops within the Caatinga biome in South America, was recently found to express two classes of color morphs within males (Ribeiro et al. 2010). To a human observer, the coloration differs mainly in two sets of ventral color patches (see Material and Methods section). These regions of the body are similar to several other lizard species that contain femoral pores (e.g. *Sceloporus*), which are known to play a role in chemical signaling (e.g. *Podarcis hispanica*, Lopez and Martin 2005). *T. semitaeniatus* does not have femoral pores, but it was suggested that these color patches are due to glandular scales, and that its coloration is simply a byproduct of chemical differences in such secretions (Harvey and Gutberlet 1998). However, up to this date, both visual and chemical signaling functions of ventral patches of Tropiduridae have not yet being investigated.

Herein, using two sets of choice experiments with different signal paths (visual and chemical) we access whether females of the Striped Lava Lizard (*Tropidurus semitaeniatus*) have differential preference in relation to male color morphs. Male morphs are known to have distinct mean body sizes (Ribeiro et al. 2010), ventral and dorsal colorations (Bruinjé et al. in Review, Capítulo 1) and behaviors (Bruinjé et al. Capítulo 2), so we expect that females will differ in preference between morphs. In order to account for cost factors, we proceed with two separate approaches: First, we access whether males of *T. semitaeniatus* with higher sprint speed performance (i.e. "better" males) have a higher probability of being chosen by females. Second, we access whether different aspects of lizards' coloration (i.e. conspicuous and color traits that are often related to pigment-based expression) increase the probability of being chosen by females. We expect that males with higher expression of colorations that are likely to be costly will have a better chance of being chosen by females.

MATERIAL AND METHODS

Studied system, sampling and husbandry

T. semitaeniatus, is a small sized rock dwelling lizard (≤14g) endemic to northeastern Brazil. It is distributed along the whole Caatinga, and eventually in the Cerrado biomes. Even though it is widely distributed, it is restricted to rock-outcrop patches. It has a flattered dorsal-ventral body shape adapted to hide in rocky crevices. Also, it has a cryptic dorsal coloration (to a human observer), with light brown to dark spots and a longitudinal light stripe ranging from its head to at least the middle of the dorsum, often reaching the base of the tail. Ventrally, *T. semitaeniatus* has a bright color along the whole body. Cloacal and ventral thighs regions express colored patches solely in adult and reproductive males (Ribeiro et al. 2010). Males can express two distinct types of color patches (yellow or black) while females, sub adults and juveniles maintain the same bright color ventrally (Ribeiro et al. 2010; Bruinjé et al. in Review, Capítulo 1). Although the lizards seem cryptic and unidentifiable at the dorsum, male morphs are identifiable both dorsally and ventrally by conspecifics

(Bruinjé et al. in Review, Capítulo 1).

We sampled 240 lizards from a population in João Câmara, RN, Brazil (5.4431° S, 35.8716° W) by noose or hand on four expeditions of four days each during their mating season (January 2015). We developed sampling and experiments during the most active period of the breeding season that lasts until early April (Ribeiro et al. 2012). We kept the lizards in the laboratory individually in plastic terraria (35 x 24 x 12 cm), provided with a plastic shelter, *ad lib* water and three mealworms every second day with no visual contact to other lizards before behavioral trials. Room temperature ranged from 25° to 31° C with fixed natural photoperiod (12:12 h). We identified sexes through presence of ventral patch and confirmed it manually pressing gently the cloaca, exposing the hemipenis. We used only mature individuals (following maturity size threshold according to Ribeiro, Silva, & Freire, 2012) that did not appear malnourished or recently tail autotomized.

Visual mate choice experiments

We paired males by morph (one yellow, one black) minimizing differences in body size measuring snout-to-vent length (SVL) to the nearest 0.01 mm (mean ± SD male size difference: SVL, 1.65±0.99 mm). We thus obtained a subsample of 32 females and 32 male pairs from 53 male individuals. Because black and yellow morphs have different average body sizes (yellow males are smaller in average, Bruinjé et al. in Review, Capítulo 1) we used some of the males twice in order maximize the number of pairs. As the males do not have any direct contact with females during the experiment, and because the individual under behavioral experimenting is the female (by choosing), we consider that repeating a male individual has no influence on the results of the experiment. We assigned females randomly to a pair, assuring that the female did not exceed the males in size. Size pairing is important because females tend to prefer males with greater body sizes in lizards (Cooper and Vitt 1993). Females were not repeated in experiments in any form.

We developed the experiments in five identical large terraria measuring 80 x 60 x 50 cm (length, width, and height respectively) divided onto three compartments (Fig. 1). The tanks had two UV lamps for reptiles Repti Glo 5.0 Tropical Full Spectrum (Exo Terra, Rolf C. Hagen Inc., Holm, Germany) and two heat lamps for thermoregulation each. Tank's temperature ranged between 29.5ºC and 31ºC. Males' and females' compartment areas had sand substrate, a plastic shelter, *ad lib* water and 3 mealworms (*Tenebrio molitor*) all placed symmetrically. We randomly assigned males into one of two compartments. The female compartment is partially divided by an opaque wall that divides the compartment in three areas: left, neutral, and right. Left and right areas enable the female to get in visual contact solely with its respective male, whereas the neutral area allows the female to visualize both males. This is a commonly used set-up in mate choice experiments with lizards (e.g. Bajer et al. 2010; Lisboa et al. 2017). Males had no visual contact with each other while they were separated from females by a transparent plexiglass wall. Plexiglass enables full visual contact and perceptiveness, including UV (allows the full spectrum of interest: 300 – 700 nm). We let lizards acclimatize for 15 min and then started to record the female's position every 10 min for a total of 6 hours. We only started counting visits once the female had been in visual contact with both males (i.e. visited both sides or visited neutral area). We discarded trials if the female spent more time (i.e. more observed positions) at neutral than the sum of visiting positions. We recorded the experiments with digital camcorders set to 120 fps placed in a blind spot and counted visits from the recordings. After each trial, we replaced the sand of all compartments and cleaned tanks with neutral detergent and ethanol in order to remove any chemical traces from the previous trial.

Chemical mate choice experiments

For the chemical mate choice experiments we randomly paired males by morph restricted by size. We attempted to reduce body size differences in pairs (N=18 pairs, 36 male lizards, mean ± SD male size difference: SVL, 2.01±1.04 mm). No lizard, male or female, was used in previous experiments nor was repeated. *T. semitaeniatus* do not have femoral pores. However, tongue flicking at the substrate and at other lizards' body is often common in this species (Coelho et al. 2018) and it is a strong indicative that the animals collect chemical cues from its environment. For a period of 10 days prior to the experiments, we placed one high-absorbent paper (30 x 30 cm) as substrate in each individual husbandry box in order to collect chemical compounds secreted by the lizards. We used 18 plastic tanks (50 x 30 x 20 cm) for the behavioral experiments. Each tank had three plastic shelters (one at each side and one at the middle of the tank), *ad lib* water and three mealworms, all placed symmetrically. We placed paper slices (30 x 6 cm) from the males of a pair in each side of the tanks in a way that 50% of the slice was positioned below the plastic shelter and the other 50% outside the shelter. Sides of the tank for each paper slice were determined randomly. Animals, paper-slices, and tanks were manipulated with fresh disposable gloves in order to avoid contamination with human odor (addapted from Kopena et al. 2011). We assigned females to a male pair randomly but in a way that the females had a smaller body size than the males. Light source, heat source, temperature (30ºC ± 0.5) and time were homogeneous among tanks. At 0815 h we placed females at the center of each tank and let them acclimatize for 15 min. After acclimatization, we monitored females' position (left, right and neutral) every 10 min from 0830 to 1330 h from a blind. We started counting visits once the female had visited both males' scents (i.e. visited both sides or visited neutral area). We excluded trials if the female spent more time (i.e. number of observed positions) at neutral than the sum of visiting positions. We also excluded trials in which females did not visit both male scents. After the experiments, we released individuals at the very same sample location.

Is male sprint speed performance assessed by visual and chemical cues, increasing female choice?

To test the hypothesis that a higher individual performance increases the chance of a male of being chosen by a female through visual or chemical cues we used males' maximum sprint speed and the outcome of both choice experiments. First, we classified individuals according to the outcome of the visual experiment as being *chosen* vs. *not chosen* by the female. We did the same procedure to obtain the outcome of the chemical experiment also following the methodology described in both choice experiments methods. So, for each male we obtained two sets of outcome binary variables of the choice experiments, hereafter referred as *visual outcome* and *chemical outcome*. For these analyses we excluded repetitions and considered only the outcome of the first trial of males in the visual experiments. Then, to obtain a measure of performance we proceeded with individual maximum sprint speed experiments. We ran each individual in a 2 m long racetrack, scaled every 1 cm, with sandpaper substrate (Brandt et al. 2015). Body-temperature is known to influence performance in lizards, so we allowed individuals to thermoregulate for a period of 90 min before the trials placing a heat lamp 45 cm to pre-experiment housing boxes. We allowed a minimum resting period of 24 h between all 3 trials that each lizard ran. We stimulated the lizards to run with soft touches at the tip of the tail with a feather. The value of maximum sprint was the fastest 25 cm interval of all runs of each individual. Performance measures were made after behavioral trials.

Are any aspects of male's coloration influential on female choice?

To test our predictions that the expression of costly colorations would increase the probability of males to be chosen by females we used spectrophotometric measures of the coloration of different parts of the body. For that, we used the visual outcome of each individual obtained as described previously. We obtained reflectance spectra with an optic fiber (R400-7-UV-VIS, Ocean Optics, Dunedin, FL) attached to a spectrophotometer (USB4000-UV-VIS). We took three measures of 8 body regions that might be displayed during intraspecific interactions: throat (V_{Throat}), chest (V_{Chest}), ventral patch (V_{Patch}, the patch cloacal region), femoral patch ($V_{FemoralPatch}$), ventral tail base ($V_{TailBase}$) (Fig. 2a), head stripe ($D_{HeadStripe}$, the head's dorsal bright stripe), dorsum stripe (D_{Stripe}, the dorsal bright stripe), and side stripe ($D_{SideStripe}$, measured at the dark stripes beside D_{Stripe}) (Fig. 2b). Then, we restricted spectra curves between 300 nm and 700 nm (the wavelength range perceivable by lizards' visual system, Loew et al. 2002) and averaged all three measures taken at each body region. Ultraviolet reflectance is known to be costly and correlate to different measures of individual quality (Zuk and Kolluru 1998; Stapley and Whiting 2006; Whiting et al. 2006). So, the first color variable we calculated was segment-specific UV-chroma

(S_{UV}) of each body region. Darker-yellowish coloration at the chest, and darker-greenish coloration at the cloaca, inform fighting ability of *T. semitaeniatus* in male-male competitions (Bruinjé et al. Capítulo 2). Also, pigment-based coloration is one possible costly mechanism for the production of yellow and darker colorations (e.g. Olson and Owens 1998; Saenko et al. 2013). Therefore, we calculated segment-specific yellow and green chroma, and mean lightness (S_{Yellow}, S_{Green}, and $M_{Lightness}$, respectively) to access the influence of such colorations in female choice. We derived color variables from the spectral reflectance curves using the R package *pavo* (Table S1, Maia et al. 2013).

Statistical analysis

To test whether females choose male morphs based on visual and chemical cues we performed Wilcoxon's signed rank paired tests separately by experiment. We used color morph as fixed factor, the number of times a female was observed at the black vs. yellow male side as response variable for the visual analysis, and the number of observations of the chemical experiment as response variable for the chemical analysis. To minimize observer bias, we used blinded methods re-labeling animals before the experiments and the assignment of pairs and sides of experiment terrariums. Morph type of lizards was not possible to identify during counting. Lizards were then identified only after number of observations was recorded. Next, to access whether males with better performance have a higher chance of being chosen by females through visual and chemical cues, we used the binary variables *visual outcome* and *chemical outcome*. Then, we performed two separate binomial generalized linear model (GLM) functions with logit model. In the visual model, we used sprint speed as predictor variable and *visual outcome* as response factor. Similarly, for the chemical model we performed a GLM with sprint speed as predictor variable and *chemical outcome* as response binary factor. Finally, to access whether the expression of ultraviolet, yellow, green and darker colorations increase the chances of a male to be chosen by a female we used the binary variable *visual outcome*. Due to sample size restrictions, we performed separate GLM functions with *visual outcome* as response factor. The predictor variables of the 32 logistic regression models were the four color variables (S_{UV}, S_{Yellow}, S_{Green}, and $M_{Lightness}$) measured at each body region (V_{Throat}, V_{Chest}, V_{Patch}, $V_{\mathrm{FemoralPatch}}$, V_{TailBase}, $D_{\mathrm{HeadStripe}}$, D_{Stripe}, and $D_{\mathrm{SideStripe}}$). We performed all statistical analysis in R software (R Core Team 2015).

RESULTS

Chemical choice experiments showed that females choose more black males than expected by chance ($V = 119$, $p < 0.05$). However, logistic regression of chemical outcome on sprint speed showed that performance does not influence female choice by chemical cues ($p = 0.098$).

Of the visual experiments, due to the methodology criteria (in which a trial would be excluded if neutral observations achieved more than 50% of all observations), we dismissed 7 out of the 32 trials. From the remaining 25 trials, one was a tie and 24 were valid trials. Wilcoxon's paired test showed that females did not visually choose males based on color morph ($V = 196.5$, $p = 0.316$). Also, a better performance does not increase the chances of a male to be chosen visually by females ($p = 0.858$). In relation to color, logistic regression models showed that among all body regions analyzed, only color traits expressed at V_{TailBase} had a significant effect on the probability of being chosen (Table 1). Specifically, green chroma at $V_{TailBase}$ had a positive relationship on the probability of being chosen (Fig. 3).

DISCUSSION

Our experiments show that females of the Striped Lava Lizard have a preference for black morph males through male scents. Black males of *T. semitaeniatus* display more aggressive behaviors than yellow males (Bruinjé et al. Capítulo 2). However, the reason why these females would prefer more aggressive males is still not studied. Presumably, aggressive males may have ecological and social advantages. Even though the latter was not confirmed in encounters between male color morphs (Bruinjé et al. Capítulo 2). One could expect that individuals that tend to engage in aggression more easily would benefit from better territories, access to better refugees and resources, but would also have increased costs of aggression from competitive interactions. Thereafter, choosing such individual as mate could benefit the female direct and indirectly, as its offspring is likely to inherit some of the male's traits while the female could benefit from territory resources.

Females did not choose males with better sprint performance neither from chemical nor visual cues. Research on female choice based on chemical signals in lizards has shown mixed results (reviewed in Font et al. 2012). In some occasions, scent was found to be an important source of information on individual's quality. Through scent compounds, *Lacerta monticola* females tend to choose males with lower levels of asymmetry and higher levels of immune response (i.e. "better quality" males) (Martín and López 2006a). Similarly, females of *Podarcis hispanica* prefer femoral gland secretions that correlate with male's immune response (López and Martín 2005), and *Psammodromus alginus* females identify male's parasite loads and immune response through scents (Martín et al. 2007). Chemical signaling is also influential on female mimicry as an alternate reproductive strategy of flat lizard males (*Platysaurus broadleyi*). In this system, males are visually fooled by other males mimicking females but are able to identify those fake females through their scents (Whiting et al. 2009). On the other hand, females of *Podarcis melisellensis* do not choose dominant males by scent, and prefer males with lower bite forces (although they choose males with larger body sizes) (Huyghe et al. 2012). Rarely however, it is explored the role of chemical signaling in femoral-poreless lizards, which is the case of *T. semitaeniatus*.

Whether or not sexual selection favors increased sprint performance in lizards has been reported also with mixed results in literature. In some occasions (as in chemical signaling) females' selection for costly signals might decrease specific measures of performance. For instance, chemical ornaments itself (i.e. pheromones) are costly to produce for lizards because some of the compounds secreted for chemical signaling are precursors of vitamin D. Thus, with this secretion, enhancing signaling confers an increase in costs to metabolism (Martín and López 2006b). In the same way that the trade-off between sexual ornaments and immune performance would decrease sexual ornamentation due to costs on immune reaction to parasite infection (Wedekind and Folstad 1994).

Through visual cues, females of *T. semitaeniatus* do not appear to choose males based on color morphs. Even though male color morphs are distinguishable to conspecifics in several parts of the body, including some dorsal ones (Bruinjé et al. in Review, Capítulo 1). Interesting enough, males of *P. broadleyi* (also a flat species of lizard that inhabits rocky outcrops, Branch and Whiting 1997) that mimics females deceive its competitors by visual cues. However, the scent of such males is still a male's, and not a female's, scent (Whiting et al. 2009).

A few aspects of coloration appear to play a role in *T. semitaeniatus*' female choice, especially ventral colors (Fig 3). Recently it was found that darker-yellowish colors at the chests and darker-greenish colors at the ventral patch of *T. semitaeniatus*' males are related to an increase in the chance of winning male-male encounters (Bruinjé et al. Capítulo 2). We did not find any relationship of female choice and ventral yellow coloration of males. However, darker-greener coloration appears to also play a role in intrasexual selection, as its expression at posterior-ventral parts of the body ($V_{TailBase}$) increases the chance of being chosen by females (Fig 3c). Ventral patches are common in *Tropiduridae* lizards, and it is a trait present in adult males of at least 26 species of the genus *Tropidurus* (e.g. Rodrigues 1987; Harvey and Gutberlet 1998; Carvalho 2016). Whether such color patches have an adaptive function, is a trait important in reproduction context, or a trait present simply due to phylogenetic inertia, is still unexplored. It is likely that it has much to do with reproduction since it increases its intensity on coloration during reproductive season in *Tropidurus hispidus* and *T. semitaeniatus* lizards (Bruinjé et al., personal communication): it is clearly pigment-based, but functional and comparative research on this subject are negligible. So far, the evidences point to a role in mating establishment, being an important trait in intrasexual interactions (Bruinjé et al. Capítulo 2). We show that a similar coloration at $V_{TailBase}$ has an influence in intersexual interactions. In fact, in some males, the coloration common in the ventral patches is expressed also in part of their tail bases (which is right after the ventral patch's area, Bruinjé et al. personal communication), but this fact has not yet being investigated. Nonetheless, the means in which these dark-patches interact or influence such results (e.g. whether it is a costly signal displayed in conspecific interactions or whether it has a physiological function on reproduction) has yet to be explored.

It is important to mention the remaining results of $V_{TailBase}$ and $D_{HeadStripe}$ color variables on female choice (Fig 3a-f). Despite the fact that analyses did not yield significant results, further studies could explore ultraviolet, green, and low mean lightness in these body regions in relation to female choice with increased sample sizes and manipulating color expression. Particularly, it is possible that both ultraviolet and mean lightness would have a negative effect on probability of being chosen by females. Which means that darker hues would be beneficial in such contexts as it was shown in intrasexual interactions (Bruinjé et al. Capítulo 2). The results of female preference by chemical cues presented here provide new opportunities for future studies on multi-modal signaling and polymorphism maintenance in lizards. Especially because we show that chemical communication occurs in this species of lizard without femoral pores. Moreover, more importance must be given to apparently (to a human observer) dull species, as intersexual selection occurs through female choice of male's scents, and can be determinant of population dynamics of species of disconnected distributions such as the Striped Lava Lizard. Nonetheless, it is important to mention that this is the first behavioral assessment of a South American lizard species exploring its sex-restricted CP. Further studies should address whether the signals under selection remain constant among different populations. This could provide an understanding of the mechanisms under which this CP is maintained.

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Tables

Table 1 Results of binomial logistic regression models of color variables measured at 8 body regions of male lizards as predictors of female choice. Color acronyms $M_{Lightness}$, S_{UV}, S_{Green} and S_{Yellow} correspond to mean lightness, and segment-specific ultraviolet, green and yellow chroma, respectively. Body regions acronyms refer to throat ($\mathrm{V_{Throat}}$), chest ($\mathrm{V_{Chest}}$), ventral patch ($\mathrm{V_{Patch}}$), femoral patch ($\mathrm{V_{FemoralPatch}}$), ventral tail base ($\mathrm{V_{TailBase}}$), dorsal head stripe ($\mathrm{D_{HeadStripe}}$), dorsal stripe ($\mathrm{D_{Stripe}}$), and dorsal side stripe ($\mathrm{D_{SideStripe}}$). Asterisk denotes significance with *p*-values yielding <.05. Values of *p* yielding <.1 are denoted in bold.

Color variables	$\mathrm{V_{Throat}}$	$\mathrm{V_{Chest}}$	$\mathrm{V_{Patch}}$	$\mathrm{V_{FemoralPatch}}$	$\mathrm{V_{TailBase}}$	$\mathrm{D_{HeadStripe}}$	$\mathrm{D_{Stripe}}$	$\mathrm{D_{SideStripe}}$
$M_{Lightness}$	0.2633	0.2993	0.7775	0.8945	**0.0522**	0.6075	0.6472	0.8965
S_{UV}	0.3213	0.4076	0.9671	0.3206	**0.0580**	**0.0942**	0.4330	0.7432
S_{Green}	0.2237	0.9182	0.9927	0.2862	**0.0458***	**0.0536**	0.3762	0.8416
S_{Yellow}	0.1504	0.8013	0.7471	0.5957	0.1558	**0.0884**	0.4669	0.9744

Figure captions

Fig. 1 Scheme of visual choice experiment tanks seen from above. Males' compartments (above in blue, *A* and *B*) are separated from the female's compartment (below, in pink and white colors) by a transparent plexiglass (dashed-lines). A solid opaque wall separates the males' compartments (*A* from *B*) and female's *Left* and *Right* counting areas (in pink). A female positioned at the *Left* area (pink) is able to visualize uniquely the male in compartment *A*. A female positioned in the *Right* area can only visually access the male in compartment *B*. Whereas a female located in *Neutral* area (in white) is able to visually access both males.

Fig. 2 Dorsal (a) and ventral (b) views of male *Tropidurus semitaeniatus* showing body regions in which colour measurements were taken. Dorsal numbering refers to locations of dorsal head stripe (a-I), dorsal stripe (a-II) and dorsal side stripe (a-III). Ventral numbering refers to locations of throat (b-I), chest (b-II), ventral patch (b-III), femoral patch (b-IV), and ventral tail base (b-V). White checkerboarded areas cover pictured objects other than the subject.

Figures

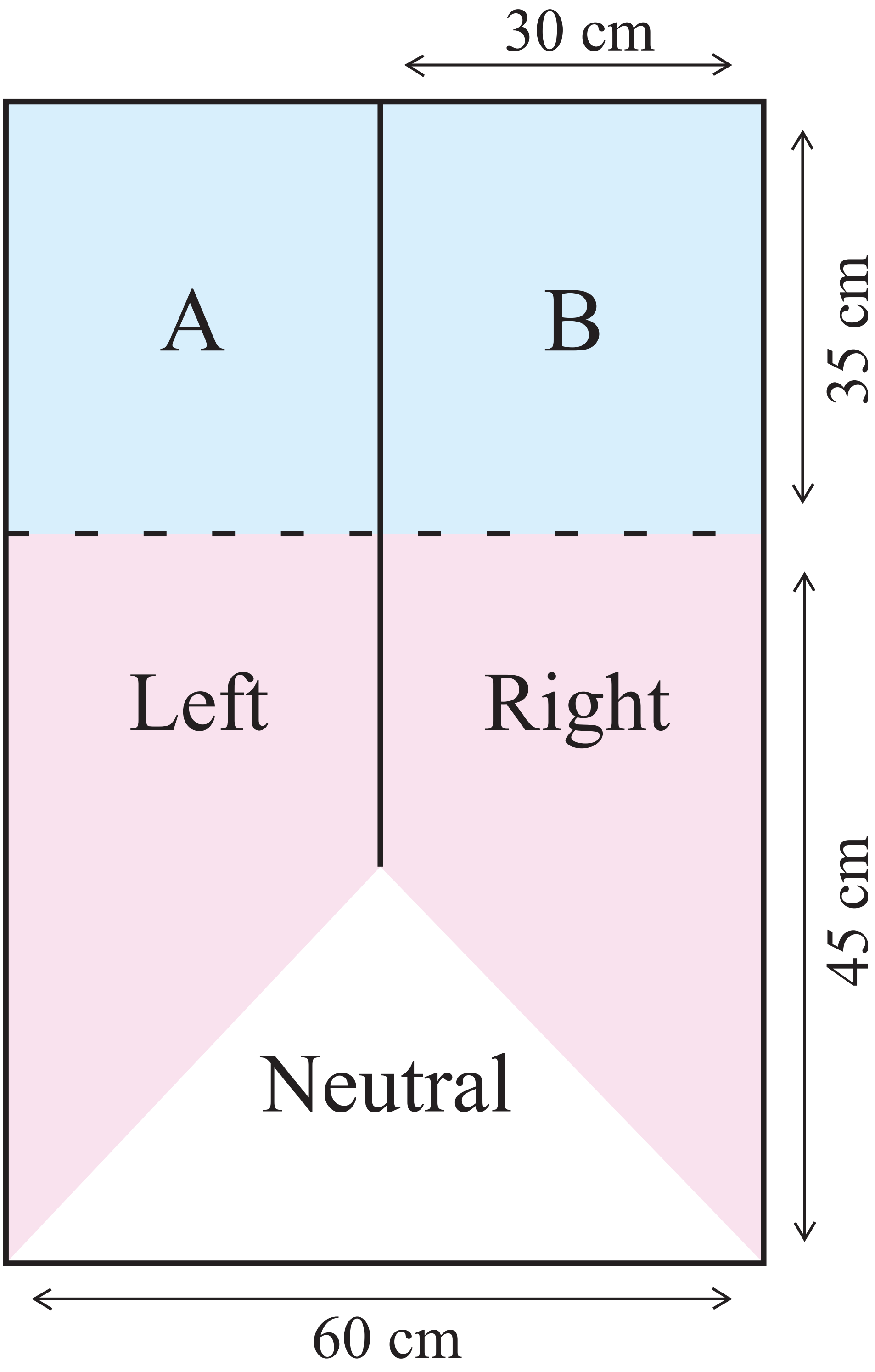

Fig. 1

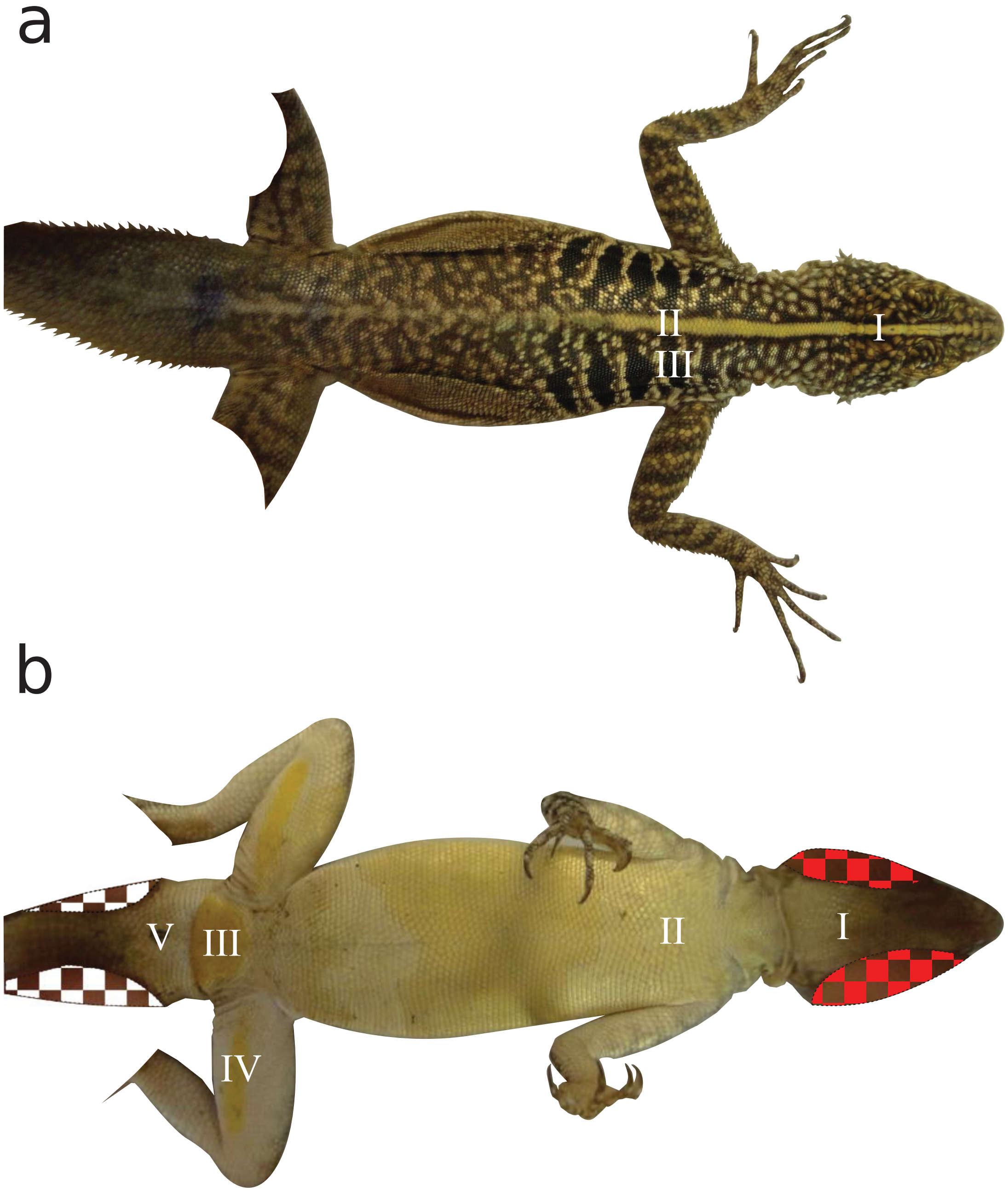

Fig. 2

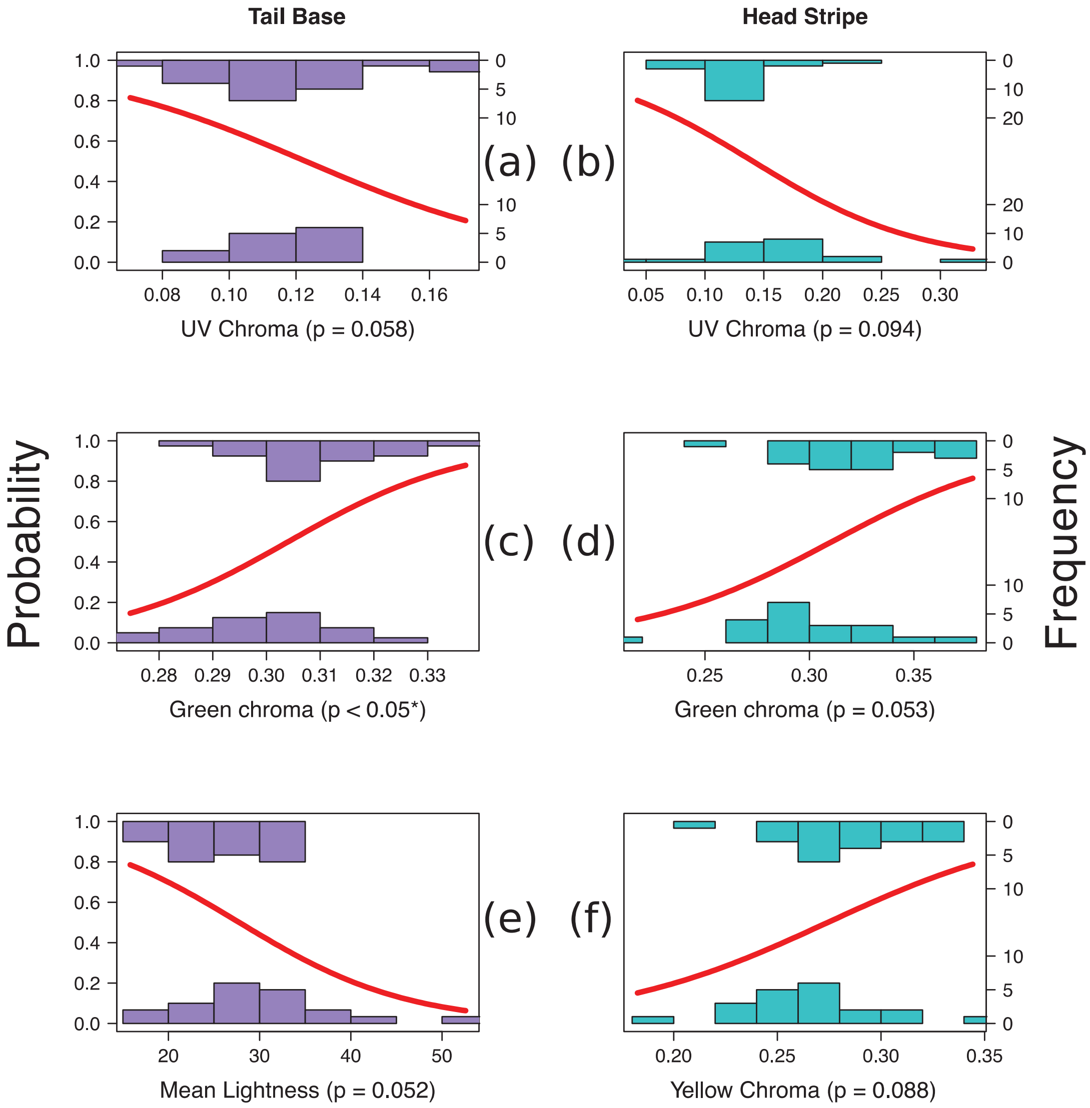
Tail Base
Head Stripe
Probability
Frequency
(a)
(b)
(c)
(d)
(e)
(f)
1.0
0.8
0.6
0.4
0.2
0.0
0
5
10
20
0.08
0.10
0.12
0.14
0.16
UV Chroma (p = 0.058)
0.05
0.10
0.15
0.20
0.25
0.30
UV Chroma (p = 0.094)
0.28
0.29
0.30
0.31
0.32
0.33
Green chroma (p < 0.05*)
0.25
0.30
0.35
Green chroma (p = 0.053)
20
30
40
50
Mean Lightness (p = 0.052)
0.20
0.25
0.30
0.35
Yellow Chroma (p = 0.088)

Fig. 3

ANEXO IV: CAPÍTULO IV*

Characterization of sexual dimorphism and male colour polymorphism of *Tropidurus semitaeniatus* (Spix, 1825) in three populations from northeast of Brazil

*Capítulo submetido a *Herpetology Notes*, formatado de acordo com as normas da revista para *Short Notes*.

Characterization of sexual dimorphism and male colour polymorphism of *Tropidurus semitaeniatus* (Spix, 1825) in three populations from northeast of Brazil

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INTRODUCTION

Sexual dimorphism, different phenotypes between sexes of a species, is described in several groups of animals (e.g., Cullum, 1998; Isaac, 2005; Pinto et al., 2005). There are many different hypotheses to explain it, including mechanism that relates sexual dimorphism to gametic investment or anisogamy (Wells, 2007), resource partitioning or availability (Schoener, 1967), sexual selection (Olsson et al., 2002), species' life history (Andersson, 1994; Isaac, 2005), and phylogeny (Isaac, 2005).

Among the examples of sexual dimorphism known in mammals, birds, amphibians and reptiles, differences in body size, morphology, behaviour, and coloration are described (e.g., Fairbairn et al., 2007). In Squamate reptiles, most reports of sexual dimorphism are in body size and coloration (Vitt and Cooper, 1985; Pinto et al., 2005). Within the genus *Tropidurus*, in addition to sexual dimorphism in body size, colour differences are reported for several species (Vitt, 1993; Van Sluys, 1998; Pinto et al., 2005). Also, colour polymorphism within adult males is known for *Tropidurus semitaeniatus* (Spix, 1825) (Ribeiro et al., 2010).

Tropidurus semitaeniatus has two male colour morphotypes occurring often in sympatry: the coloured patches in the pre-cloacal flap and ventral thighs common in Tropiduridae males can be either yellow, or black (Ribeiro et al., 2010). Adult males dorsal coloration is apparently (according to human vision) homogeneous. However, there are evidences suggesting that lizards are able to distinguish sexes and male colour morphs even on dorsal coloration (Bruinjé et al. in review). Despite these interesting patterns, colour variation polymorphism in *T. semitaeniatus* is reported only from a single population (Ribeiro et al., 2010). Therefore, issues of variations among different populations are still unknown. Both composition and relative frequencies of different morphs of a polymorphic system are fundamental information to understand whether polymorphism is widely distributed or a particular pattern of a single population. In addition, morphological differences (such as body size and other morphometric measures) between colour morphs are also of a particular interest for behavioural ecology studies. For instance, body size is known to influence female choice in lizards (Van Sluys et al., 2002). Also, differences in lizards' limb length are known to vary according to microhabitat use (Losos et al., 1998).

Information of occurrence, composition, frequency, and variation of multiple morphotypes among populations are important for studies on several areas, ranging from behavioural ecology to evolutionary dynamics on alternative reproductive strategies (Sinervo et al., 2007). Our goal was to characterize the composition and identify whether there are differences in morphometry and relative frequencies of sexes and male colour morphs among three populations of *T. semitaeniatus*.

MATERIAL AND METHODS

We collected lizards from three populations within the Caatinga biome, located in Rio Grande do Norte state's at municipality of João Câmara (JC) (S -5.535209, W -35.815176), Lagoa de Velhos (LV) (S -6.007682, W -35.871824) and Jucurutú (JU) (6.035178, W -37.018430). Regional climate is characterized as BsWh according to Koeppen (Alvares et al., 2013) and vegetation is characterized as hyperxerophytic (Andrade-Lima, 1981).

We sampled the lizards actively by noose or hand between 08:00 and 17:00h, between January and February of 2015, and between December of 2015 and January of 2016. Total sampling time in the localities of JC, JU and LV were 144, 120 and 90 hours respectively (9h per day per researcher).

We classified lizards as juveniles or adults based on their morphological traits (coloration and body size, see Ribeiro et al., 2010). We sexed adults through the manual exposure of the hemipenis. We then measured the following morphometric variables: snout-to-vent length (SVL), body width (BW), body height (BH), head width (HW), head height (HH), head length (HL), foreleg (F), hindleg (H) and tail length (TL). We used a digital calliper with precision of 0.01 mm in our length measurements. We classified males according to their colour morph (two morphs: yellow-black or black) that are expressed in their pre-cloacal flap and ventral thighs (Ribeiro et al., 2010), hereafter referred as yellow males and black males, respectively. After the measurements, we released the lizards at each sampling location.

For the morphometric characterization of each population of the species we calculated mean and standard deviation of the linear morphometric variables (SVL, BW, BH, HW, HH, HL, F, H, TL) of juveniles, males and females. We also characterized both colour morphs' (black and yellow) mean and standard deviation of morphometric variables for each population.

To test whether there are differences in body size between sexes and among populations we performed an ANOVA with SVL as dependent variable, and sex and population as factors. Similarly, to test for differences in body size of males among populations and between male colour morphs we performed an ANOVA with SVL as dependent variable, and colour morph and population as factors. We considered as significant the analysis yielding a p value below 0.05. Further, we performed Tukey-tests to access pair wise comparisons. To characterize occurrence of male colour morphs among populations we determined frequency of occurrence of male colour morphs of each population.

RESULTS

From our total sample size (n = 324 lizards), 61 were juveniles and 263 adults. Among sexed adult individuals, 148 were females and 115 males. The population with most individuals was JC with 227 (61 juveniles, 68 males and 98 females), followed by JU with 49 individuals (26 males and 23 females) and LV with 48 individuals (21 males and 27 females) (Table 1; Figure 1).

SVL of juveniles varied between 44.32 and 71.1 mm (mean 62.29 ± 5.53). SVL of females varied between 54.64 and 76.3 mm (mean 67.07 ± 0.36) and of males varied between 59.00 and 88.2 mm (mean 76.34 ± 0.49). Black males' SVL varied between 68.00 and 88.2 mm (mean 78.41 ± 4.13), while yellow males varied between 59.00 and 87.7 mm (mean 73.65 ± 5.46). Body size of colour morphs of all males differed (F = 29.83, df = 1, $p < 0.0001$) and within populations (F = 5.04, df = 2, $p < 0.01$). Post hoc Tukey test showed that SVL of male morphs differed within JC ($p < 0.0001$) and LV ($p < 0.05$) populations, but not within JU ($p = 0.99$).

SVL of females differed among populations (F = 20.89, df = 2, $p < 0.0001$). A Tukey HSD further indicated that JU´s females differed in body size from JC ($p < 0.01$) and from LV ($p < 0.01$). Females from JC and LV did not differ in SVL ($p = 0.71$). Males' SVL did not differ among populations (F = 2.47, df = 2, $p = 0.08$). In relation to male colour morphs, SVL of black males did not differ among populations (F = 2.10, df = 2, $p = 0.13$); neither did SVL of yellow males between JC and JU populations ($p = 0.43$). The remaining morphometric variables also showed differences among groups (sexes and male morphs within and among populations, Table 1).

Among all sampled males, 56% (n = 65) were black morph and 43% (n = 50) were yellow morph. Among populations, JC had 60% of black males (n = 41) and 40% of yellow males (n = 27), LV had 95% of black males (n = 20) and 5% of yellow males (n = 1), and JU had 15% of black males (n = 4) and 85% of yellow males (n = 22) (Figure 1).

DISCUSSION

Squamate reptiles usually show sexual dimorphism of body size and often of coloration (Pinto et al., 2005). Many species of the genus *Tropidurus* show dimorphism in these traits and one species show colour polymorphism within males (Ribeiro et al., 2010). Our results show that, among the analysed populations, the polymorphic species *T. semitaeniatus* differs in SVL of both males and females, and that black male colour morph tends to have a larger body size than yellow males. Moreover, besides differences in body size, the two male colour morphs have distinct frequencies of occurrence depending on the population. Interestingly, these relative frequencies might be from as low as 5% of males of one colour morph in one population (e.g. yellow males in LV), to 85% of the occurrences of this same colour morph in another population (e.g. yellow males in JU). In other words, relative frequencies of colour morphs among populations are not uniform. In JC, relative frequencies of morphs are very similar, even though black males presented a slightly higher proportion. However, morph frequencies of LV are highly imbalanced, as only one individual with yellow morph was found. In contrast, the majority of males from JU population were yellow morph males. This pattern might be due to ecological differences among populations, such as microhabitat or exposure from differences in vegetation (Shine, 1989). Further studies taking into account the contrast of colour morphs in relation to background of different populations might address the adaptive function of this polymorphism.

In our study, body size of lizards from both sexes was similar or larger than registered for the species in other studies (Ribeiro et al., 2010, Ribeiro et al., 2011).

Specifically, mean and maximum SVL of females was larger than previously reported. For adult males, regardless of colour morph, mean SVL was similar to previously registered whereas maximum SVL was superior. Minimum and mean SVL of juveniles were larger than the values found by Ribeiro et al. 2010. When analysing males of different colour morphs between studies, both colour morphs had higher minimum and maximum SVL than already registered, whereas mean SVL showed similar, or lower, values than already registered. This result suggests that variance in body size of the populations analysed in the present study tends to be wider, while samples from previous studies showed more homogeneous values (Ribeiro et al., 2010, Ribeiro et al., 2011).

The body size variations among populations reported here might be related to sample size (number of individuals) analysed in each study (e.g. 324 in this study compared to 83 reported in Ribeiro et al. 2010). This is because the greater the sample size, the greater the representation of each class within samples. However, biotic interactions (e.g. predation, reproductive behaviour, or resource availability) and abiotic interactions (e.g. environmental temperature, precipitation, and luminosity) might also be affecting differences in body size among populations (Anderson and Vitt, 1990; Pinto et al., 2005).

The difference of body size between colour morphs appears to be a pattern of the species in polymorphic populations, with black males presenting greater mean SVL than yellow ones (Ribeiro et al., 2010). This pattern might influence the propagation of this phenotype; as females tend to prefer larger males (Van Sluys et al., 2002; Pinto et al., 2005). Reproductive behaviour and the relation of it to male colour morphs of *T. semitaeniatus* is, however, still unclear. Further studies, especially *in situ* observations, could address this issue in order to clarify whether reproduction in this species is affected mainly by female mate choice or intrasexual competition within males. In addition, larger males also have advantages in disputes over territory, food, and agonistic encounters (Cooper and Vitt, 1988; Anderson and Vitt, 1990; Watkins, 1998).

Furthermore, our results indicate that individuals from different populations of *T. semitaeniatus* may vary in average body size. We found interpopulational variation in the SVL of females, but not males. Within males however, and in accordance to previous studies, colour morphs tend to differ in mean SVL, with black males usually being larger. Nonetheless, we show that male colour morphs have distinct relative frequencies among populations. Also, that *T. semitaeniatus* does not appear to have a pattern of relative abundance or frequency of a determined colour morph. Both male colour morphs had higher (e.g. black males in LV) and lower (e.g. black males in JU) relative frequencies in different populations. Thus, frequencies of colour morphs appear to be influenced by ecological factors, some of which could be addressed in further studies accessing crypsis against background, vegetation covery, and thermophysiological differences between colour morphs.

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Tables

Table 1: Linear morphometric measures (minimum, maximum, mean, and standard deviation) of *T. semitaeniatus* lizards sampled in three populations of Rio Grande do Norte, Brazil. Measures are presented by rows referring to the populations of João Câmara (JC), Jucurutú (JU) and Lagoa de Velhos (LV). Values presented by columns refer to number of individuals sampled by group (N), snout-to-vent length (SVL), body width (BW), body height (BH), head width (HW), head height (HH), head length (HL), foreleg (F), hindleg (H), and tail length (TL).

Population	N	SVL	BW	BH	HW	HH	HL	F	H	TL
Female (n=148)										
JC	98									
Values		57.9-76.3	12.5-25.3	3-11.5	8.9-12.8	3.9-8.6	12.4-16.6	29.8-41.2	37.9-60	30-128
Mean		67.72 (SD±4.30)	18.35 (SD±2.55)	5.7 (SD±1.19)	11.04 (SD±0.75)	5.56 (SD±0.58)	14.63 (SD±0.92)	34.21 (SD±2.05)	48.87 (SD±3.02)	108.39 (SD±13.75)
JU	23									
Values		54.64-67.59	12.31-20.32	5.49-8.9	8.89-10.65	4.79-6.4	12.21-14.84	27.38-34.43	40.62-50.49	59-117
Mean		62.26	16.20	7.09	9.87	5.44	14.00	31.25	45.60	97.13

		(SD±3.48)	(SD±1.82)	(SD±1.03)	(SD±0.43)	(SD±0.7)	(SD±0.62)	(SD±1.78)	(SD±2.50)	(SD±14.40)
LV	27									
Values		61.3-72.7	14.7-22.2	4.6-9.4	9.5-12.2	4.7-6.5	13.2-15.7	29.78-36.5	45.5-54.7	29-151
Mean		68.83 (SD±2.88)	18.83 (SD±1.78)	7.12 (SD±1.16)	10.82 (SD±0.61)	5.78 (SD±0.41)	14.75 SD±0.58)	33.91 (SD±1.50)	50.90 (SD±2.27)	107.44 (SD±27.60)
Male (n=115)										
JC	68									
Values		64-87.7	14.7-28.9	4.2-73	10.8-15.5	4.8-8.4	14.2	32.4-39.5	43.4-62	75-221
Mean		76.1 (SD±5.60)	21.03 (SD±0.43)	7.81 (SD±8.13)	13.07 (SD±1.13)	6.55 (SD±0.74)	17.15 (SD±1.63)	43.73 (SD±43.29)	56.12 (SD±3.91)	126.33 (SD±21.41)
JU	26									
Values		59-81.8	13.47-22.81	5.5-10.2	9.36-13.95	5.82-7.5	13.28-17.8	29.89	46.21-41.6	31-140
Mean		75.22 (SD±4.33)	19.36 (SD±2.22)	7.57 (SD±1.21)	12.44 (SD±0.93)	6.94 (SD±0.37)	16.95 (SD±0.89)	37.78 (SD±2.48)	56.58 (SD±3.38)	109.73 (SD±28.74)

LV	21									
Values		63.4-88.2	15.4-27.4	6.1-11.2	11.1-14.9	5.9-8.3	15.1-19.9	34.5-43.7	52.7-65.9	86-164
Mean		78.50 (SD±4.93)	22.11 (SD±2.82)	8.20 (SD±1.10)	13.51 (SD±0.93)	7.23 (SD±0.61)	17.62 (SD±1.08)	39.60 (SD±2.53)	59.83 (SD±3.31)	133.57 (SD±20.61)
Male Morph: Black (n=65) and Yellow (n=50)										
JC										
Black	41									
Values		68-87.1	17.7-28.9	4.7-73	10.8-15.2	5.2-8.4	14.2-19.3	35.7-39.5	47.3-61.9	75-221
Mean		78.35 (SD±19.03)	22.46 (SD±10.17)	8.52 (SD±1.70)	13.5 (SD±0.98)	6.77 (SD±0.50)	17.49 (SD±0.91)	47.89 (SD±30.90)	57.04 (SD±12.18)	131.58 (SD±44.30)
Yellow	27									
Values		64-87.7	14.7-27	4.2-11.4	10.8-15.5	4.8-7.5	14.3-25.4	32.4-42.2	43.4-62	77-160
Mean		72.68 (SD±5.60)	18.86 (SD±2.56)	6.72 (SD±1.67)	12.42 (SD±1.04)	6.22 (SD±0.66)	16.64 (SD±2.25)	37.41 (SD±2.55)	54.73 (SD±4.18)	118.37 (SD±19.74)
JU										

Black	4									
Values		71.8-76.9	17.65-22.6	6.11-8.64	11.63-12.99	6.67-7.33	16.87-17.64	34.17-38.57	52.85-56.78	103-124
Mean		74.70 (SD±2.25)	19.1 (SD±2.34)	7.61 (SD±1.13)	12.4 (SD±0.60)	7.02 (SD±0.27)	17.13 (SD±0.36)	37.02 (SD±1.95)	55.53 (SD±1.81)	114.5 (SD±9.39)
Yellow	22									
Values		59-81.8	13.47-22.81	5.5-10.2	9.36-13.95	5.82-7.5	13.28-17.8	29.89-41.6	46.21-62.8	31-140
Mean		75.31 (SD±4.64)	19.41 (SD±2.25)	7.56 (SD±1.25)	12.44 (SD±0.88)	6.92 (SD±0.39)	16.92 (SD±0.96)	37.92 (SD±2.58)	56.77 (SD±3.60)	108.86 (SD±31.08)
LV										
Black	20									
Values		69.3-88.2	18.9-27.4	6.1-11.2	11.86-14.9	6.3-8.3	15.3-19.9	35.3-43.7	55.7-65.9	86-164
Mean		79.26 (SD±3.60)	22.45 (SD±2.43)	8.17 (SD±1.12)	13.63 (SD±0.77)	7.29 (SD±0.55)	17.75 (SD±0.93)	39.85 (SD±2.30)	60.19 (SD±2.95)	135.15 (SD±19.80)

Yellow	1									
Values		63.4	15.4	8.8	11.1	5.9	15.1	34.5	52.7	102

Figures

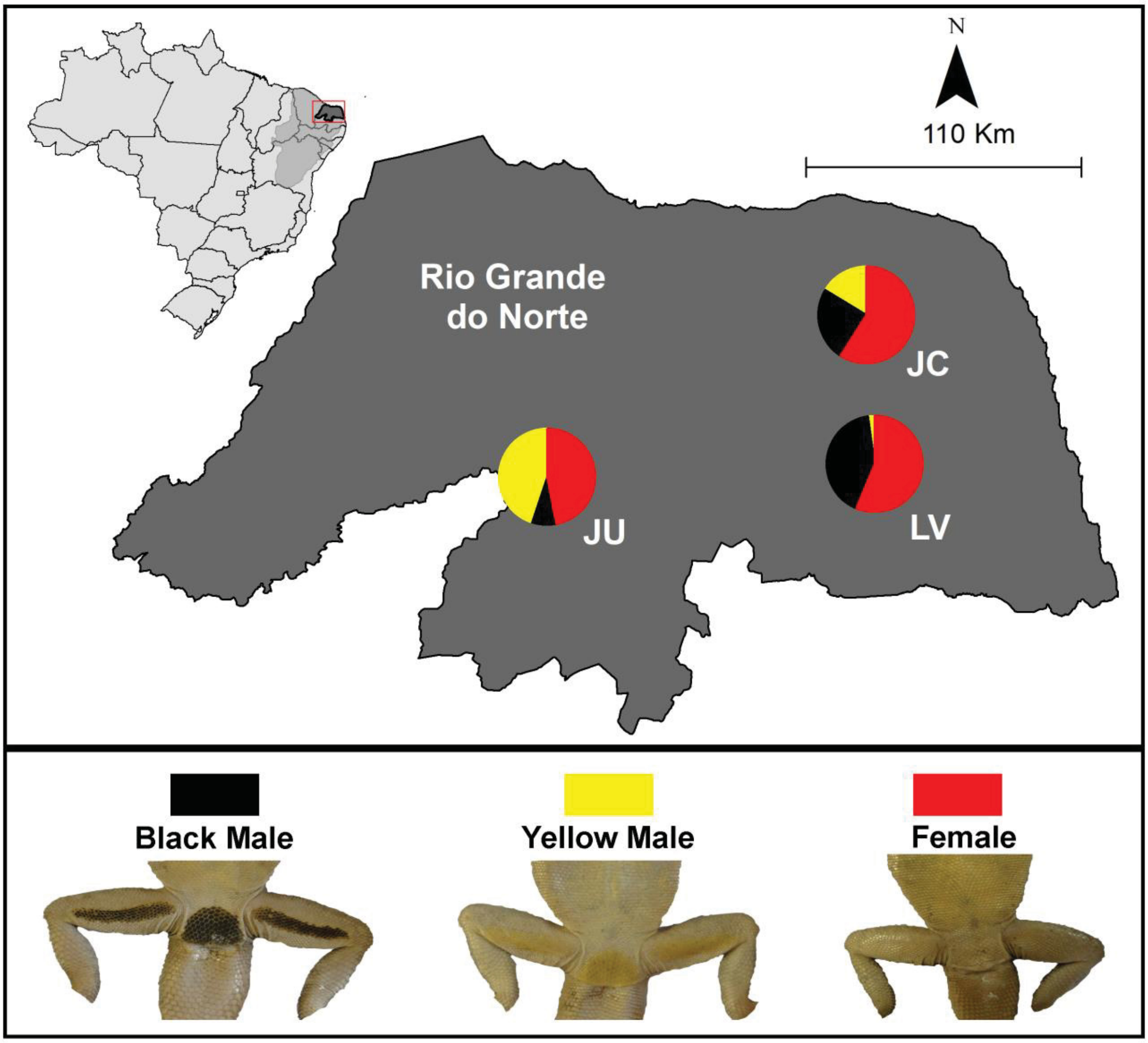

Figure 1. Study sites in the municipalities of Jucurutú (JU), João Câmara (JC) and Lagoa de Velhos (LV), in the state of Rio Grande do Norte, Brazil, with the relative proportions of individuals per population (above). Ventral view of the lizards (below) showing femoral and pre cloacal flap of black male colour morph (left, in black), yellow male colour morph (centre, in yellow), and female (right, in red). Adult females do not express any ventral coloured patch. Distribution of the Caatinga biome is shown in medium grey in northeast region of Brazil (top-left).