UNIVERSIDADE FEDERAL DE MINAS GERAIS

INSTITUTO DE CIÊNCIAS BIOLÓGICAS

PROGRAMA DE PÓS-GRADUAÇÃO EM ECOLOGIA, CONSERVAÇÃO E MANEJO DA VIDA SILVESTRE

Stefânia Pereira Ventura dos Reis

CUSTOS SOCIAIS NA ECONOMIA DA FUGA DE PREDADORES DO LAGARTO *EUROLOPHOSAURUS NANUZAE*

Belo Horizonte

2022

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CUSTOS SOCIAIS NA ECONOMIA DA FUGA DE PREDADORES DO LAGARTO *EUROLOPHOSAURUS NANUZAE*

Tese apresentada ao Instituto de Ciências Biológicas, para a obtenção de Título de Doutor em Ecologia Conservação e Manejo da Vida Silvestre pela Universidade Federal de Minas Gerais.

Orientador: Dr. Paulo Enrique Cardoso Peixoto

Co-orientadores: Dr. Conrado Alexsander Barbosa Galdino

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ECMVS

Ata da Defesa de Tese

N° 212
Entrada: 2018/1

Stefania Pereira Ventura dos Reis

No dia 30 de agosto de 2022, às 11:00 horas, por vídeo conferência, teve lugar a defesa de tese de doutorado no Programa de Pós-Graduação em Ecologia, Conservação e Manejo da Vida Silvestre, de autoria do(a) doutorando(a) Stefania Pereira Ventura dos Reis, orientando do Professor Paulo Enrique Cardoso Peixoto, intitulada: "**Custos sociais na economia da fuga de predadores do lagarto Eurolophosaurus nanuzae**". Abrindo a sessão, o(a) Presidente(a) da Comissão, Doutor(a) Paulo Enrique Cardoso Peixoto, após dar a conhecer aos presentes o teor das normas regulamentares do trabalho final, passou a palavra para o(a) candidato(a) para apresentação de seu trabalho. Estiveram presentes a Banca Examinadora composta pelos Doutores: Paula Cabral Eterovick (Technische Universität Braunschweig), Marcos Costa Vieira (University of Chicago), Igor Luis Kaefer (UFAM), Paulo De Marco Junior (UFG) e demais convidados. Seguiu-se a arguição pelos examinadores, com a respectiva defesa do(a) candidato(a). Após a arguição, apenas os senhores examinadores permaneceram no recinto para avaliação e deliberação acerca do resultado final, sendo a decisão da banca pela:

(X) Aprovação da tese, com eventuais correções mínimas e entrega de versão final pelo orientador diretamente à Secretaria do Programa, no prazo máximo de 30 dias;
( ) Reavaliação da tese com avaliação pelos membros da banca do documento revisado, sem nova defesa, no prazo máximo de 30 dias, sob possibilidade de reprovação;
( ) Reformulação da tese com indicação de nova defesa em data estabelecida a critério do Colegiado em observância às Normas Gerais da Pós-graduação na UFMG a ao Regimento do PPG-ECMVS;
( ) Reprovação

A banca indica esta tese aos Prêmios CAPES e UFMG de teses? (X) SIM ( ) NÃO

Nada mais havendo a tratar, o Presidente da Comissão encerrou a reunião e lavrou a presente ata, que será assinada por todos os membros participantes da Comissão Examinadora.

Belo Horizonte, 30 de agosto de 2022.

Assinaturas dos Membros da Banca Examinadora

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sei! assinatura eletrônica

Documento assinado eletronicamente por **Paulo de Marco Junior**, **Usuário Externo**, em 01/09/2022, às 11:24, conforme horário oficial de Brasília, com fundamento no art. 5º do Decreto nº 10.543, de 13 de novembro de 2020.

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PROGRAMA DE PÓS-GRADUAÇÃO EM ECOLOGIA, CONSERVAÇÃO E MANEJO DA VIDA SILVESTRE

FOLHA DE APROVAÇÃO

"Custos sociais na economia da fuga de predadores do lagarto Eurolophosaurus nanuzae"

STEFANIA PEREIRA VENTURA DOS REIS

Tese de Doutorado defendida e aprovada, no dia **30 de agosto de 2022**, pela Banca Examinadora designada pelo Colegiado do Programa de Pós-Graduação em Ecologia, Conservação e Manejo da Vida Silvestre da Universidade Federal de Minas Gerais constituída pelos seguintes professores:

Doutor(a) Paula Cabral Eterovick
(Technische Universität Braunschweig)

Doutor(a) Marcos Costa Vieira
(University of Chicago)

Doutor(a) Igor Luis Kaefer
(UFAM)

Doutor(a) Paulo De Marco Junior
(UFG)

Doutor(a) Paulo Enrique Cardoso Peixoto
(Presidente da Banca)

Belo Horizonte, 30 de agosto de 2022.

Assinaturas dos Membros da Banca

Documento assinado eletronicamente por **Paulo de Marco Junior**, **Usuário Externo**, em 01/09/2022, às 11:24, conforme horário oficial de Brasília, com fundamento no art. 5º do Decreto nº 10.543, de 13 de novembro de 2020.

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Dedico esse trabalho ao meu irmão, Douglas.

Sei que onde você estiver, estará olhando por mim,

vibrando com as minhas conquistas e me dando muita força.

Eu vou te amar pra sempre.

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RESUMO

Comportamentos anti-predatórios são comportamentos presentes em basicamente todas as espécies de animais do planeta. Um dos comportamentos anti-predatórios mais comuns é a fuga do predador. Entretanto, abandonar o habitat para escapar do predador não envolve apenas os riscos de ser predado, mas também os custos que podem ser gerados quando a presa abandona as atividades que estava realizando. Em espécies territoriais as presas podem sofrer maiores custos, como a perda de territórios de acasalamento ou até mesmo uma oportunidade reprodutiva, por isso tendem a ser mais resistentes à fuga que presas que não correm tais riscos. Mas os poucos estudos que avaliaram a influência desses custos no comportamento de fuga geralmente se limitam a simplesmente avaliar o efeito da presença de co-específicos nos comportamentos anti-predatórios adotados pelas presas. Como em muitas espécies esse ambiente social pode variar de acordo com a época do ano ou com a disponibilidade de recursos, avaliar apenas a presença de co-especificos pode fornecer informações limitadas acerca da influência do contexto social na modulação do comportamento de fuga. Nesta tese, nós avaliamos como o contexto social, mais especificamente a influência da presença das fêmeas e da sua receptividade sexual e também a identidade do intruso (vizinho familiar ou intruso não familiar), pode influenciar nas estratégias anti-predatórias adotadas pelos machos. Nós observamos que apesar dos machos responderem a presença das fêmeas, eles respondem mais fortemente a fêmeas férteis quando comparado a presença de fêmeas não férteis. Adicionalmente, os machos assumem maior risco predatório na presença de intrusos não familiares do que na presença de indivíduos familiares localizados em territórios vizinhos. Esse resultado indica que o histórico prévio de interações sociais do macho também é um fator importante modulando as decisões de fuga dos machos territoriais. Por fim, usando um modelo de simulação baseado em individuo, nós observamos a presença das fêmeas parece ser o fator mais importante na evolução dos comportamentos anti-predatórios dos machos.

Palavras-chave: comportamento anti-predatório, fêmeas sexualmente receptivas, territorialidade, distância de iniciação de fuga e teoria do escape ótimo.

ABSTRACT

Anti-predatory behaviours are behaviours present in basically every species of animal on the planet. One of the most common anti-predatory behaviour is predator escape. But one thing that many people do not know abandoning the habitat to escape the predator does not only involve the risks of being preyed, but also the costs that can be generated when the prey abandons the activities it was doing. In territorial species, prey can suffer greater costs, such as the loss of mating territories or even a reproductive opportunity, so they tend to be more resistant to flight than prey that are not at risk. But the few studies that have evaluated the influence of these costs on escape behaviour are generally limited to simply evaluating the effect of the presence of conspecifics on the anti-predatory behaviours adopted by prey. As in many species this social environment can vary according to the time of year or the availability of resources, evaluating only the presence of conspecifics can provide limited information about the influence of the social context on the modulation of escape behaviour. In this thesis, we evaluated how the social context, more specifically the influence of the presence of females and their sexual receptivity and also the identity of the intruder (familiar neighbour or unfamiliar intruder), can influence the anti-predatory strategies adopted by males. We observed that males assume greater predatory risk in the presence of fertile females when compared to the presence of non-fertile females. Additionally, males assume greater predatory risk in the presence of unfamiliar intruders than in the presence of familiar individuals located in neighbouring territories. This result indicates that the male's previous history of social interactions is also an important factor modulating territorial males' escape decisions. Finally, using an individual-based simulation model, we observed that the presence of females appears to be the most important factor in the evolution of male anti-predatory behaviour.

Key words: anti-predatory behaviour, sexually receptive females, territoriality, flight initiation distance and optimal escape theory.

SUMÁRIO

APRESENTAÇÃO

Acho que todo mundo já deve ter visto alguma cena de um predador correndo atrás de uma presa, né? Seja no quintal da sua casa ou assistindo ao globo repórter ou até mesmo na novela pantanal. Agora, vou pedir para você relembrar esse evento predatório para eu te fazer uma pergunta, ok! Vamos lá, quando o predador se aproximou da presa, o que a presa fez? Acho que será quase uma unanimidade que a presa fugiu do predador, certo?! Por mais que possa parecer um pouco obvio que a presa deva fugir do predador imediatamente após detectá-lo, essa tomada de decisão não é tão simples assim. Se a presa foge muito rápido ela pode ter alguns custos. Primeiro, ao fugir do predador a presa pode ter um alto gasto energético, caso fuja muito rápido ou por longas distâncias. Pensando nisso, imagina se a presa encontra com muitos predadores ao longo do dia? Se toda vez ela investir uma alta energia na fuga, pode ser que em algum momento o combustível acabe. Segundo, quando a presa foge muito cedo do predador e abandona seu habitat isso pode gerar alguns custos para ela, pois ao se ausentar do seu habitat ela pode acabar deixando de realizar outras atividades que também são importantes para ela. Por exemplo, ela diminui o tempo disponível para forrageamento ou para cortejar parceiros sexuais. Bom, dito isso, você poderia me perguntar: quando então seria o melhor momento para a presa fugir do predador? Existe uma teoria chamada “teoria do escape ótimo” que prevê justamente que durante um evento predatório, as presas devem balancear os riscos de ser predada e os custos da fuga e então, fugir apenas quando os riscos igualarem ou excederem os custos. Essa teoria foi proposta por dois pesquisadores americanos chamados Ronald Ydenberg e Lawrence Dill em 1986.

Mais de 35 anos após a publicação da “teoria do escape ótimo”, centenas de estudos parecem corroborar suas predições. A grande maioria dos estudos sobre a teoria do escape ótimo se utiliza da distância do início da fuga (em inglês *flight initiation distance*-FID) para testar suas predições. Uma das predições da teoria do escape ótimo é a de que os riscos da presa ser capturada aumentam, proporcionalmente, à medida em que o predador se aproxima. Por este motivo o FID tem sido utilizado como uma importante medida do risco tolerado pelas presas. Deste modo, quanto menor o FID, maior será a aproximação entre predador e presa e com isso, maiores os riscos predatórios. Estudos empíricos têm demonstrado que o risco predatório tolerado pelas presas (medido pelo FID), dependem de múltiplos fatores, tais como o tamanho corporal da presa e do predador, a velocidade do ataque, a presença e distância do refúgio. Mas uma coisa que observei durante a leitura desses estudos é que eles raramente avaliam a influência do contexto social na modulação do FID. O contexto social está relacionado com o ambiente social do indivíduo, por exemplo, se um animal vive em grupo ou vive solitário, se ele defende ou não territórios e se tem muitos parceiros disponíveis para acasalar. Com isso, o contexto social é potencialmente importante porque ao abandonar uma área para fugir do predador, a presa pode deixar de realizar um determinado número de interações sociais com seus co-específicos. Essa perda de interações sociais pode gerar custos como perder a chance de copular com uma fêmea e perder a chance de comunicar a outros machos que o território está sendo ocupado. Vamos nos referir a esses custos ao longo dos capítulos como custos sociais.

Os poucos estudos que avaliaram a influência dos custos sociais no comportamento de fuga das presas são usualmente limitados a avaliar o efeito da presença de co-específicos no comportamento anti-predatório. No entanto, em muitas espécies esse contexto social pode variar de acordo com a época do ano, por exemplo em espécies que se reproduzem apenas em uma estação do ano. Nessas espécies, avaliar apenas a presença de co-específicos pode fornecer informações limitadas sobre a influência do contexto social na modulação do comportamento de fuga. Além disso, considerar só a presença do co-específico pode trazer um efeito de confusão porque muitas vezes não é possível saber se as alterações no comportamento de fuga são causadas porque a presença do co-específico indica para a presa que ela vai pagar um custo muito alto se ela fugir ou porque a presença de outro individuo próximo desvia a atenção da presa e assim, ela demora mais tempo para detectar que tem um predador se aproximando. Daí surgiu a motivação da minha tese. Meu objetivo geral foi adquirir uma compreensão mais profunda sobre como o contexto social pode modular o comportamento anti-predatório. Para isso, eu dividi a tese em três capítulos que compreendem dois estudos empíricos e um modelo de simulação. Nos capítulos empíricos, eu estudei a espécie de lagarto *Eurolophosaurus nanuzae* (A seguir tem um tópico contando mais sobre a minha história com esse lagartinho e porque escolhi ele como modelo de estudo) e investiguei se a presença e o período reprodutivo das fêmeas podem influenciar o comportamento anti-predatório dos machos (Capítulo I), e avaliei se o grau de familiaridade com o co-específico poderia influenciar o comportamento anti-predatório adotado pelos machos residentes (Capítulo II). Já no Capítulo III, inicialmente eu tinha como objetivo avaliar como as alterações hormonais devido as interações agonísticas entre os machos, poderiam afetar o comportamento anti-predatório dos machos. Mas no meio do meu doutorado aconteceu uma pandemia mundial que impossibilitou a minha ida para o campo, e consequentemente, a realização desse capítulo. Então, eu e o Paulo, meu orientador, tivemos que pensar em um novo capítulo. A ideia desse novo capítulo surgiu após a gente ver os resultados do nosso Capítulo I (quem não gosta de spoiler, sugiro não continuar lendo essa frase e pular para a última frase desse parágrafo), que mostravam que, apesar de os machos postergarem mais a fuga na presença de fêmeas férteis, eles também o fizeram mesmo quando havia fêmeas não-férteis em seu território. Então começamos a pensar que esse comportamento de postergar a fuga, mesmo na presença de fêmeas não férteis, poderia trazer um benefício reprodutivo futuro para os machos, e daí surgiu a ideia do nosso Capítulo III. Nele, nós fizemos um modelo de simulação baseado em indivíduos para avaliar como variações no sucesso reprodutivo atual e futuro associado com uma variação sazonal na receptividade sexual das fêmeas pode afetar a evolução das decisões de fuga dos machos.

1.1 Modelo de estudo

Bom, já falei um pouco para vocês sobre a motivação e o tema da minha tese. Mas vocês têm ideia do porquê eu escolhi trabalhar com um lagarto? Por que não escolhi trabalhar com beija-flor ou golfinhos? Eu poderia falar com vocês que escolhi o lagartinho da montanha (*Eurolophosaurus nanuzae)* por achar esse lagarto lindo (Fig. 1), mas acho que muita gente não iria concordar, né?! Por mais que achar um animal bonito possa ser uma explicação, a gente precisa ter um argumento mais convincente para justificar o uso de um modelo de estudo. E para conseguir ser convincente, é essencial a gente conhecer um pouco sobre a história natural daquele animal, pois só assim vamos conseguir explicar por que o animal x é melhor que o animal y para responder uma pergunta e/ou testar uma hipótese. Sendo assim, escolhi trabalhar com o lagarto *Eurolophosaurus nanuzae*, pois desde a minha graduação faço parte de um grupo (NeoLibe) que estuda diversos aspectos da história natural, do comportamento e da ecologia dessa e de outras espécies de lagartos. Todos esses anos de estudo, nos permitiu conhecer muita coisa sobre essa espécie e a manipular esses animais em campo.

Fig. 1 Macho adulto de *Eurolophosaurus nanuzae* (Tropiduridae) em uma lage de pedra em área de campo rupestre na Serra do Cipó, Minas Gerais, Brasil.

O lagarto *E. nanuzae* é uma espécie que vive em rochas e que ocorre apenas na Cadeia do Espinhaço em locais com altitudes próximas ou acima de 900 metros. Essa espécie tem um pequeno porte, que raramente alcança tamanhos superiores a 6 cm de comprimento rostro-cloacal (Galdino et al. 2003), o que facilita a captura e a manipulação desses animais sem oferecer riscos aos pesquisadores. São diurnos e forrageadores de “espreita” (senta-e-espera), na qual esperam a presa se aproximar para capturá-la, e consomem preferencialmente formigas e cupins ao longo do ano. Os machos desses lagartinhos defendem áreas de uso exclusivo e recentemente, foi observado que os machos são capazes de reconhecer os seus vizinhos e que eles tendem a ser menos agressivos com os vizinhos quando comparado a indivíduos desconhecidos (Fenômeno conhecido como “inimigo querido”). A reprodução dessa espécie é bem conhecida, tendo seu início no fim da estação seca estendendo-se até o fim da estação chuvosa. O pico do período reprodutivo das fêmeas, quando 100% das fêmeas estão férteis, ocorre de novembro a janeiro. Durante a corte os machos exibem diversos comportamentos para tentar atrair as fêmeas, mas é muito comum observar machos tentando forçar copulas com as fêmeas. As fêmeas geralmente produzem ninhadas com dois ovos, sendo que algumas podem reproduzir-se mais de uma vez a cada estação reprodutiva. Além disso, esse lagarto apresenta um comportamento anti-predatório bem comum, quando percebem a presença de predadores eles costumam correr e se esconder na vegetação.

Referências

Chan AAYH, Giraldo-Perez P, Smith S & Blumstein D T (2010) Anthropogenic noise affects risk assessment and attention: the distracted prey hypothesis. Biology Letters 6: 458-461.

Cooper WEJr (1999) Tradeoffs between courtship, fighting, and antipredatory behavior by a lizard, *Eumeces laticeps*. Behavioral Ecology and Sociobiology 47: 54-59.

Cooper WEJr & Frederick WG (2007) Optimal flight initiation distance. Journal of Theoretical Biology 244: 59–67.

Cooper WEJr & Pérez-Mellado V (2004) Tradeoffs between escape behavior and foraging opportunity by the Balearic lizard (*Podarcis lilfordi*). Herpetologica 60: 321–4**.**

Cooper WEJr (2009) Flight initiation distance decreases during social activity in lizards (*Sceloporus virgatus*). Behavioral Ecology and Sociobiology 63: 1765-1771.

Cooper WEJr & Wilson DS (2007) Sex and social costs of escaping in the striped plateau lizard *Sceloporus virgatus*. Behavioral Ecology 18: 764–768.

Díaz-Uriarte R (1999) Anti-predator behaviour changes following an aggressive encounter in the lizard *Tropidurus hispidus*. Proc R Soc Lond B Biol Sci. 266: 2457–2464.

Filogonio R., Del Lama F.S., Machado L. L., Drumond M., Zanon I., Mezzetti N.A., and Galdino C.A.B. 2010. Daily activity and microhabitat use of sympatric lizards from Serra do Cipó, southeastern Brazil. Iheringia, 100: 336–340.

Galdino CAB, Assis VB, Kiefer M & Van Sluys M (2003) Reproduction and fat body cycle of *Eurolophosaurus nanuza*e (Sauria, Tropiduridae) from a seasonal montane habitat of southeastern Brazil. Journal of Herpetology 37: 6876-6894.

Galdino, C.A., Pereira, E.G., Fontes, A.F. & Van Sluys, M. (2006) Defense behavior and tail loss in the endemic lizard *Eurolophosaurus nanuzae* (Squamata, Tropiduridae) from southeastern Brazil. *Phyllomedusa: Journal of Herpetology,* **5,** 25-30.

Jordão JM & Oliveira RF (2001) Sex differences in predator evasion in the fiddler crab *Uca tangeri* (Decapoda: *Ocypodidae*). Journal of Crustacean Biology 21: 948–953.

Kiefer M.C. 1998. Dieta, modo de forrageamento e uso de microhabitat em duas espécies simpátricas de Tropidurus (Sauria, Tropiduridae) na Serra do Cipó, Minas Gerais. Dissertacion, Universidade Estadual Paulista, Rio Claro, Brasil.

Quintana, E.C. & Galdino, C.A. (2017) Aggression towards unfamiliar intruders by male lizards *Eurolophosaurus nanuzae* depends on contestant’s body traits: a test of the dear enemy effect. *Behaviour,* **154,** 693-708.

Rodríguez-Prieto I & Fernández-Juricic E (2005) Effects of direct human disturbance on the endemic Iberian frog at individual and population levels. Biological Conservation 123: 1–9.

Samia DSM, Blumstein DT, Stankowich T & Cooper WEJr (2016) Fifty years of chasing lizards: new insights advance optimal escape theory. Biological Reviews 91: 349–366.

Stankowich T & Blumstein DT (2005) Fear in animals: a meta-analysis and review of risk assessment. Proceedings of the Royal Society of London, series B: Biological Sciences 272: 2627-2634.

Ventura SPR, Galdino CAB & Young RJ (2013) *Eurolophosaurus nanuzae* (calango): courtship and copulation. Herpetol. Bull. 124: 25.

Ventura SPR, Galdino C A & Peixoto PEC (2021) Fatal attraction: territorial males of a neotropical lizard increase predation risk when females are sexually receptive. Behavioral Ecology and Sociobiology 75: 1-11.

Ydenberg RC & Dill LM (1986) The economics of fleeing from predators. Advances in the Study of Behavior 16: 229–249.

Weston MA, McLeod EM, Blumstein DT & Guay PJ (2012) A review of flight-initiation distances and their application to managing disturbance to Australian birds. Emu 112: 269–286.

Capítulo I

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Fatal attraction: territorial males of a neotropical lizard increase predation risk when females are sexually receptive

Abstract: Studies that test the optimal escape theory often show that males base their escape strategies on the costs and benefits of escaping. Consequently, some studies have shown that males exhibit riskier anti-predatory strategies when they are near females, probably to avoid losing reproductive opportunities. However, since in some species females have a limited reproductive season, this reduction in mating opportunities should be more pronounced during the female reproductive season**.** Therefore, males should express reduced anti-predatory behaviours when females are fertile. In this study, we used the lizard *Eurolophosaurus nanuzae* as study subject to evaluate the hypothesis that during the female reproductive season, males will express riskier anti-predatory behaviours than in the non-reproductive season. To accomplish this, we recorded the flight initiation distance (FID) and the time spent in the refuge of males with and without previous exposure to a female, during both the female reproductive and non-reproductive seasons. We found that after exposure to females, males decreased their FID. Although this effect occurred in both seasons, it was stronger during the female reproductive season. Males also spent less time in refuges when females were sexually receptive. Our results indicated that the presence of females induces males to adopt riskier escape decisions, and that the assumed risks are even greater when females represent an immediate chance to mate.

Keywords: anti-predatory strategies, social cost, flight initiation distance, optimal escape theory.

Introduction

When a potential prey detects a predator, it should immediately escape because postponing escape increases its chances of being predated (Blumstein 2010; Williams et al. 2014). However, in many species of prey, individuals avoid escaping promptly as they perceive a predator (e.g. Holley 1993; Cooper and Sherbrooke 2016), indicating that escaping as soon as they detect a predator may not always be the best strategy. Therefore, it is probable that by escaping too early, prey pays other costs that make them avoid such a decision. For example, when the prey flees from the predator and temporarily abandons its previously occupied area, the prey may pay social costs if conspecific individuals are able to explore the temporarily abandoned site or use local resources (Lima and Dill 1990; Lima 1998). Escaping too early can also impair courting, mating, or mate-guarding behaviours (Cooper 1999a, b; Martín and López 1999). Therefore, although escaping from predators can increase fitness by prolonging survival – increasing an individual’s residual reproductive value – it can otherwise negatively impact current reproductive output.

Optimal escape theory (Ydenberg and Dill 1989) presumes that prey should adjust their escaping behaviours according to the costs and benefits among a set of behavioural responses in order to maximize fitness (Cooper and Frederick 2007a). Such cost-benefit relationships may be particularly important for species in which males defend mating territories. For example, when a male runs to a shelter or to a distant area to escape from a predator, it may reduce its mating opportunities by missing previously guarded females or females that may pass through the territory when the male is absent (Cooper 1999a, b; Martín and López 1999). In addition, a territory has higher chances of being invaded by rivals when a resident male is absent after fleeing from a predator (Díaz-Uriarte 1999; Cooper and Wilson 2007). Therefore, males that postpone their fleeing and/or spend less time hiding in shelters increase their available time for important social relations, thereby reducing the social costs of the flight. At the same time, individuals that postpone flight allow predators to get closer (i.e.

the prey exhibit a shorter flight initiation distance or FID - Ydenberg and Dill 1986), increasing their risk of being preyed upon. Additionally, if the prey spends only a short time hidden in a shelter after fleeing, it can also increase the risk of being caught because the predator may ambush it when it leaves the shelter.

Since the costs of leaving a territory or the gains of postponing fleeing can change dynamically over time and space, animals should not always adopt the same escape strategies (Cooper and Blumstein 2015). For example, males of the crab species *Austruca mjoebergi* spend less time hiding from predators in the presence of females compared with those in absence of females (Reaney 2007). This probably occurs because when females are present, males might lose reproductive opportunities if they immediately flee from a predator. In fact, the few studies that have evaluated whether the presence of a female influences male anti-predatory behaviours have indicated that males adjust their escaping behaviours in response to the female presence (Cooper 1999a, b, 2009; Martín and López 1999; Martín et al. 2003). However, such studies often do not consider two factors. The first is that males may delay their escaping behaviours because the presence of another individual may distract the male and increase the time needed to detect a predator (Dukas 2004). The second, and more important point, is that some studies do not consider other factors that may affect male reproductive output, such as male or female condition or reproductive status (Cooper 1999a, b, 2009; Martín and López 1999; but see Martín et al. 2003; Reaney 2007; Kopena et al. 2015). In particular, the female reproductive status may be an important factor affecting male escaping decisions because, in many species, females reproduce cyclically, being fertile and/or sexually receptive during a short period of the year (Ziegler et al. 2000; Vitt and Caldwell 2014). This seasonality in female reproductive status restricts males' reproductive opportunities to short periods of time. Thus, among species that have these restricted reproductive seasons, losing a mating opportunity could be very costly for each individual

(Vitt and Caldwell 2014). In these species, it may be that males preferentially adopt riskier anti-predatory behaviours in response to female presence during breeding season.

Lizards have been used as models for studies related to anti-predatory behaviours since 1964 (Rand 1964; Samia et al. 2016). Studies on escaping behaviors in lizards have shown that, like other taxa, they are sensitive to the costs of flight (Samia et al. 2016). The small neotropical tropidurid lizard *Eurolophosaurus nanuzae* (Squamata, Tropiduridae) uses crypsis as a primary defense strategy to avoid predators (Galdino et al. 2006). However, if the predator detects the prey and performs a capture attempt, individuals of this species escape by running into vegetation and hiding there (Galdino et al. 2006). Females have a discrete reproductive season. They start gonadal maturation from July to September. From November through January all adult females are reproductive (Galdino et al. 2003; Melo et al. 2019). Female fecundity varies from one to three eggs, with most females producing a clutch of two eggs. In addition, females are able to store sperm, and this might promote sperm competition (Melo et al. 2019). Males of *E. nanuzae* defend territories where most mating takes place. These males are known to act aggressively against conspecific males, chasing and fighting rivals that try to take over their territory (Quintana and Galdino 2017). Given that females of *E. nanuzae* have a restricted reproductive period and that males of this species defend mating territories, one can expect that males modulate their escape behaviours in response to variations in the potential reproductive outputs. Therefore, we used the lizard *E. nanuzae* as a model to evaluate the hypothesis that males will adopt riskier escape behaviours during the female reproductive season due to increased immediate social costs of fleeing. According to this hypothesis, we predicted that during the peak reproductive season when all females are sexually fertile, males will (i) exhibit a smaller FID and (ii) spend less time in refuges after fleeing from predators than they would during the non-reproductive season.

Methods

Study site

We conducted a manipulative field study in the Brazilian old, climatically buffered, infertile landscapes (OCBIL) of the Campos Rupestres (Silveira et al. 2016). This type of habitat constitutes ‘a montane, grassy-shrubby, fire-prone vegetation mosaic with rocky outcrops of quartzite, sandstone or ironstone’ from south-eastern Brazil (Conceição et al. 2016) occurring mostly above 900 m (a.s.l.). In this type of habitat, lizards can be easily observed in activity, captured, and handled (Galdino et al. 2006) on the patches of rock outcrops embedded in a habitat matrix of grass vegetation. Experiments were conducted at Serra do Cipó locality, Santana do Riacho Municipality, Minas Gerais State, Brazil.

Field experiments

To evaluate the influence of an imminent reproductive opportunity on the escape behaviours of males, we submitted 30 adult males to two treatments (15 males subjected to two treatments each during the non-reproductive season of the females and 15 additional males subjected to the same two treatments during the reproductive season of the females, resulting in a total of 60 trials), following a within-subject design: (i) a simulation of a predatory attack after the exhibition and removal of a female (female exposure treatment - see below for a detailed description of how we handled and presented females to males) and (ii) a simulation of a predatory attack without the exhibition of a female (negative control treatment). For these trials, we used only adult (reproductive) individuals with body sizes above the threshold of sexual maturity (as defined by Galdino et al. 2003). The sequence in which individuals were submitted to each treatment was random. In addition, no lizard was exposed to more than one treatment on the same day to avoid the interference of a prior trial on a subsequent one. We waited between three and 10 days to perform a second trial on the same male (this variation in the number of days between trials occurred because we did not conduct any trial during days with rainy or cloudy conditions). We performed all experiments only on sunny days without the prevalence of winds during the activity period of the species (09:00 h and 15:30 h - Filogonio et al. 2010). Only lizards performing normal activities, such as thermoregulation and foraging were used in trials. We first submitted males to both treatments during the non-reproductive season of females (May to June in 2019), and then during the peak of the reproductive season of females (November to December in 2019). We chose these two seasons to perform our experiments because a prior study with this species in the same study location showed that no female had vitellogenic follicles between April and June, while all females are fertile between November and December (Galdino et al. 2003; Melo et al. 2019).

To be able to apply both treatments to the same individual on different days, we captured all males after applying the first treatment to mark them. For this, we performed a permanent marking that consisted in a unique combination of coloured beads, strung by surgical nylon monofilament at the base of the tail (Galdino et al. 2014). This allowed visual identification of the lizards at distance, without the necessity to perform new captures, enabling us to use the same individuals for the second treatment. During the marking, we also measured individual body size (in the form of snout-vent length -SVL), and weight (using a spring scales Pesola, with precision of 0.2 g). We recorded these two measures because they may also affect male escaping decisions and must be controlled for in our analyses.

To perform the treatments, we approached the males with care to avoid disturbing them. In fact, in all trials (control and female exposure treatments), when we arrived at a rocky outcrop, no male escaped to a shelter or exhibited behaviours that indicated that they were affected by our presence (we always stayed approximately 3 m distant from the males, including the period when we were performing the trials). Thus, even with the observers present, the males continued to show normal activities such as resting, feeding or patrolling behaviours. Nevertheless, we waited 3 min to habituate males before starting the trials (following Quintana and Galdino 2017). During this period, we continuously observed the males to ensure that they were not adopting anti-predatory behaviours or interacting with a female (if we detected one of these two situations, we aborted the trial on that day). For the control treatment, we simulated a predatory attack after the 3 min habituation period.

For the female exposure treatment, after the 3 min habituation period, we placed a female 50 cm apart from the males, a distance permitting the visual detection of females by males (see Martín et al. 2003; Quintana and Galdino 2017). We collected females in rock outcrops that were apart from those where we were conducting the experiments, ensuring that the females were not neighbours to the experimental males. During the experiments, we used two females per day, one in the morning and one in the afternoon. We also used each female for a maximum of two trials per day to avoid over stressing them. To place the female near the male, we tethered the female around the chest on a 1 m nylon filament loop attached to a 2.5 m pole (similar to a fishing rod). No tension was applied to the nylon filament, permitting lizards to freely behave (following the same procedure of Quintana and Galdino 2017). We kept females presented to males for a maximum period of 3 min. We chose this presentation period because it was enough for males to detect the female and exhibit typical courtship behaviours (see results for a detailed description of these behaviours). However, if a male tried to bite the female or to make a forced copulation before reaching 3 min, we removed the female to avoid it being injured or forcefully fertilized. After the female exposure period, we carefully removed the female from the territory by pulling the pole with the nylon filament that was attached to the female. We opted to remove the female in this way to avoid stressing the male (in fact, no male tried to escape or to hide when we were removing the female). After removing the female, we waited for 50 s to simulate predatory attacks. We chose to wait a short period to start the simulation of the predatory attack to prevent the focal male from interacting with other individuals that might appear. In addition, we opted to remove the female before simulating the predatory attack because male flight behaviour can be affected by the attention disruption caused by the presence of other individuals (Chan et al. 2010). Therefore, by removing the females before beginning the simulation of the predatory attack, we minimized the possibility that males would postpone their responses because another individual was distracting them. On the other hand, it could be that males do not adjust their escaping behaviours when females are absent because they do not have a reliable cue that they may lose a potential mate if they flee. For this reason, we did a pilot study to ensure that males adjusted their anti-predatory behaviours even after we removed the females. In this test, we simulated predatory attacks on five males after the exhibition and removal of a female and on five other males who had experienced no previous contact with a female (following the same procedure as described in the previous paragraph). At the end of the pilot test, we observed that males modulated the anti-predatory behaviour even after the females' removal (our results also showed this pattern).

As a predator model, we used a taxidermied roadside hawk, *Rupornis magnirostris* (Accipitriformes: Accipitridae). Roadside hawks are known to prey upon lizards, and they also appear in the rocky fields of Serra do Cipó (Sick 1997, Willis and Oniki 2002) in sympatry with *E. nanuzae*. We opted to use a natural predator model because the use of this type of model elicits more cautious escape responses from the prey (Ventura et al. 2017). The use of different taxidermied individuals would be preferable to avoid that similar lizard responses could be attributed to the same individual hawk used in our simulations (Milinski 1997). However, we used the same model due to logistic constraints in obtaining more than one individual with the specified requirements to be used in our experiments (such as adopting a flight posture). In addition, to minimize possible biases in our results, we adopted some specific procedures. First, we certified that the model had no evident morphological difference from a typical roadside hawk. Second, we repeated the control and treatment trials using the same lizard. Therefore, variations in the male responses between the control and treatment trials cannot be attributed to the model predator used. Third, by using the same individual hawk, we have the advantage that the changes observed in male responses between reproductive seasons (see results) were not related to any change in the individual hawk used in the predation simulations.

To simulate each predator attack event, the hawk model was prepared in a typical flight posture of the species and attached to the end of a pole (c.a. 3.0 m). The pole had a distance sensor attached above the hawk and connected to an electronic system that showed distance information on a display located at the base of the pole (Fig. S1- supplementary material). The distance sensor was functioning since the beginning of the simulation attack. When we detected that the prey started to flee, we triggered the electronic system that recorded the distance estimated by the distance sensor. We used this distance as the FID exhibited by the lizard (we also performed pilot tests in which we stopped the hawk movement at known distances from the ground to assure that the distance sensor was correctly measuring the distance between the hawk and the point in which the lizard was located). In all predatory simulations, the person responsible for the simulation oriented the axis of the hawk's body forming an angle of approximately 60° in relation to the longest lizard’s body axis. This person initiated the attack at a height of approximately 3 m from the initial lizard’s position and then moved the hawk to execute a ‘V’ trajectory with a vertex (angle = c.a. 60°) that corresponded to the point c.a. 50 cm above the lizard’s position. We always focused the sensor on the central body region of males. However, any variation in the sensor position on males would hardly affect our results because males of *E. nanuzae* stayed with their body in contact with the rock surface during all predatory attack simulations. Therefore, if the sensor was not focused exactly on the male, it would reach the rock surface around the male, which would provide a variation of less than 1 cm in our FID estimations. Such variation would not affect our conclusions since it represents only 1% of the observed FID variation between treatments. To ensure uniformity of risk levels experienced by lizards across experiments, the same person performed the attacks, always wearing the same clothes, following Ventura et al. (2017).

Whenever a male ran to a refuge (n = 13 for the control treatment during the reproductive season, n = 12 for the control treatment during the non-reproductive season, n = 10 for the female exposure treatment during the reproductive season, n = 6 for the female exposure treatment during the non-reproductive season), we recorded the time spent hidden up to a limit of 3 min (we opted to wait up to 3 min because, during our pilot experiments mentioned above, we observed that most lizards emerged from the refuge before this period. This also occurred in our results). We considered that animals chose a refuge when they did not remain exposed on rocks after fleeing. As our study involved observing focal animals in the field, it was not possible to record data blind.

Statistical analysis

To evaluate the effect of treatments on male FID, we made a generalized mixed model (GLMM) with a gamma error distribution. In this model, we considered the treatments (female exposure and control treatments) and reproductive season to be fixed predictor variables and the FID to be the response variable. In addition, we included the interaction between the treatment and the reproductive season as a fixed predictor variable. Since body weight (which was highly correlated with SVL) and ambient temperature can influence the locomotive performance of lizards, we inserted these variables in our model as covariates (Samia et al. 2016). We also inserted the male identities, date, and hour of observation as random predictor variables. We used ‘male identity’ as a random factor because each male received two treatments (with and without the female presence); and date and hour due to environmental variations across different days. We initiated the model with all covariates and random predictor variables inserted, but when the variables were unimportant for the model (i.e., a covariate was non-significant, or a random variable explained no variance in the model), we removed them. To calculate *p* values, we used maximum likelihood ratio tests (Zuur et al. 2009), comparing a null model without the fixed explanatory variables with a model with the same variables inserted (full model). When we found a significant effect in the comparison between the full and the null models, we made new comparisons between the full model and a reduced model without the interaction term between the fixed predictor variables (Table 1).

During the experiments, we had animals that did not hide after the simulation of the predatory attack and other males that did not return to their territories after the observation period ended. Therefore, to evaluate whether the time spent in the refuge changed according to treatment and reproductive season, we used the Cox proportional hazard regression model. This regression was suitable for our data because it estimated the proportion of hidden males that remained in the refuge at each unit of time. The proportional hazards assumption was checked using statistical tests and graphical diagnostics based on the scaled Schoenfeld residuals. In this model, we used the proportion of males that remained in the refuge each time (i.e., the survival object) as the response variable (we considered only the males that ran to a refuge after the simulation of the predatory attack). We used as predictor variables the treatment, the reproductive season, and the interaction between the two. We used the temperature and weight of the animals as covariates and also controlled for male identity. To calculate *p* values, we also used maximum likelihood ratio tests (Zuur et al. 2009), comparing a full model with the fixed explanatory variables and their interaction term with the null model. Again, when we found a significant effect in this comparison, we made a new comparison between the full model and a reduced model without the interaction. We performed all statistical procedures using the R environment (R Core Team 2019). For GLMM analysis, we used the package lme4 (Bates et al. 2015). For Cox proportional hazard regression, we used the package survminer (Kassambara et al. 2017) and survival (Therneau 2021). To assess the proportional risk assumptions, we used the cox.zph function in the survival package. We used the frailty function to add male identity as a random effect term. We evaluated all model predictions (for both the GLMM and the Cox proportional hazard regression) by visual inspections of the residual plots (residuals vs fitted values - Zuur et al. 2009).

Results

Males *E. nanuzae* responded to female presence by exhibiting rapid up-and-down movements of their hind limbs; up-and-down head movements (head bob); flexion and extension of the front legs raising the head and body region (push-up) and also by approaching the female. In relation to attempts to bite females, during the female non-reproductive season, 47% of males (n = 7 of 15) tried to bite the females, whereas, during the female reproductive season, all males exhibited this behaviour (n = 15). Females never initiated any behaviour after being presented to males. But they usually responded to male exhibitions with head bobs, dorsally raising their backs (producing an arch effect), exhibition of tail-waiving movements, and/or push-ups. Some females tried to flee when the male approached. But none exhibited any unusual behaviour during the experiments and no apparent behavioural change between the reproductive and no-reproductive seasons. After female removal, three males during the reproductive season and one male during the non-reproductive season continued to perform the same displays exhibited at the female presence until we initiated the predator attack simulation, showing that animals might remain stimulated even after female removal.

Neither temperature (b= - 0.0007 ± 0.04 (slope ±standard error), χ^2=0.0004, df =1, p =0.98, n=60) nor body weight covariates (b=0.04 ± 0.03, χ^2=1.091, df =1, p =0.29, n=60) explained the variance in the model testing the effects of treatments on FID. Thus, our final full model only contained the fixed predictor variables (treatments and reproductive season) and the identity of the focal male (σ2= 0.012), date (σ2= 0.008) and hour (σ2= 0.009) as random variables. The interaction term between previous exposure to females and the reproductive season of females affected the FID exhibited by males (Table 1). In the female exposure treatment, the FID was lower in the reproductive season compared to that of the non-reproductive season, while in the control treatment there was no difference in FID across reproductive seasons (Fig. 1). Although in both seasons, the FID exhibited by males in the female exposure treatment was lower than that of the control treatment, the FID difference between female exposure and control treatments was larger during the female reproductive season (Fig. 1).

Table 1 Final GLMM models with their respective response variables, explanatory fixed variables, and random variables. Test results refer to comparisons between the (i) full and null models and (ii) the model without the interaction term between the fixed predictor variables and the full model. Our goal was to test whether the exhibition and removal of a female or no exhibition of a female, female reproductive season, and interaction term between these two factors affected the flight initiation distance (FID) exhibited by males of the lizard species *Eurolophosaurus nanuzae*

Response variable	**Explanatory fixed variables**	**Explanatory random variable**	**Comparisons between models**	**N**	**χ^2(df)**	**P**
FID	Treatment + Reproductive season + Treatment: Reproductive season	Male identity, date and hour	Full model x Null model	60	$92.61_{(3)}$	<0.001
			Full model x Model without the interaction between treatment and reproductive season	60	$22.44_{(1)}$	<0.001

Regarding the model testing how the time spent in the refuge by males changed in response to the treatments and reproductive season, both covariates, temperature (χ^2=7.11, df =2.70, p= 0.054) and weight (χ^2=0.66, df =1.42, p= 0.56, n=41), did not explain variance in the model. Thus, our final full model only contained the fixed predictor variables and the identity of the focal male as a random variable. The comparison between the model containing all predictor variables and their interaction (full model) and the null model indicated that the time spent in the refuge changed according to the predictor variables (χ^2=26.02, df =7.51, p < 0.001, n=41; Fig. 2). The subsequent comparison between the full model and the model without the interaction term indicated that the time spent in the refuge by the males after escaping changed according to the interaction between female reproductive season and treatment (χ^2=15.86, df =5.41, p <0.01, n=41). However, this occurred in a slightly different way than when compared with the FID responses. Males of the female exposure treatment during the reproductive season spent less time in the refuge compared with the other treatments (Fig. 2), followed by males of the control treatment during the reproductive season (Fig. 2). The males of the female exposure treatment during the reproductive season were the only treatment from which all the lizards emerged from the refuge before the end of the observation period (3 min - Fig. 2). During the female non-reproductive season, there was an inversion between the responses observed for female exposure and control treatments: males of the control treatment remained less time in the refuge than males in the treatment (Fig. 2).

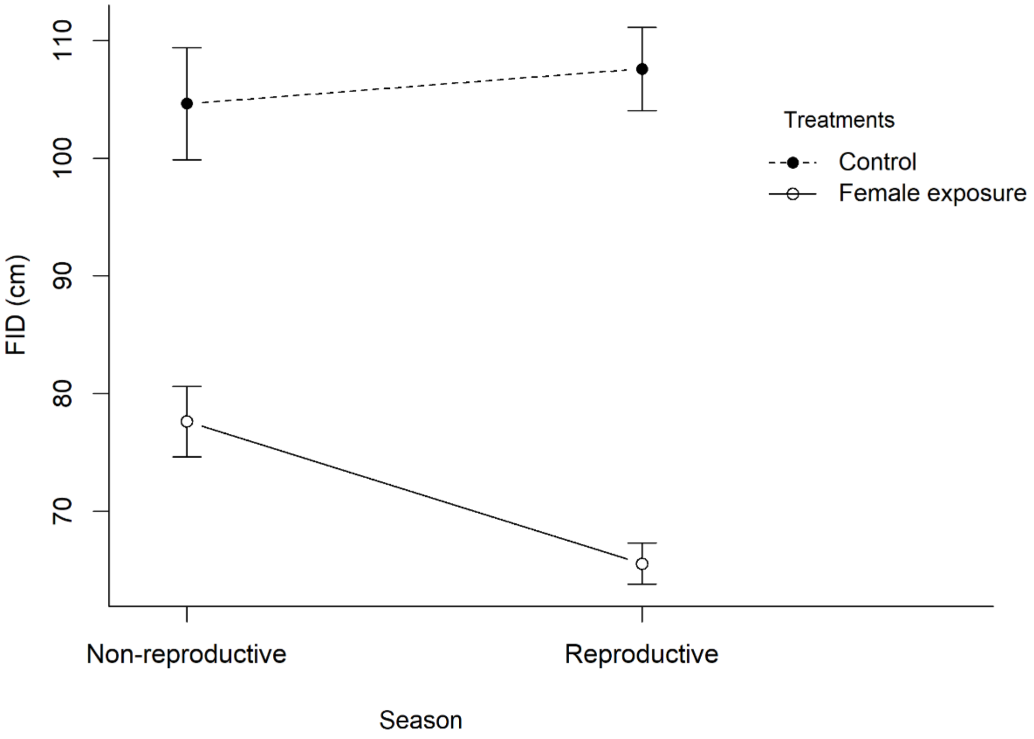

Fig. 1 Effect of exhibition and removal of a female (female exposure treatment) or no exhibition of a female (control treatment) and female reproductive season in flight initiation distance (FID) of males of the lizard species *Eurolophosaurus nanuzae*. Error bars represent the standard deviation

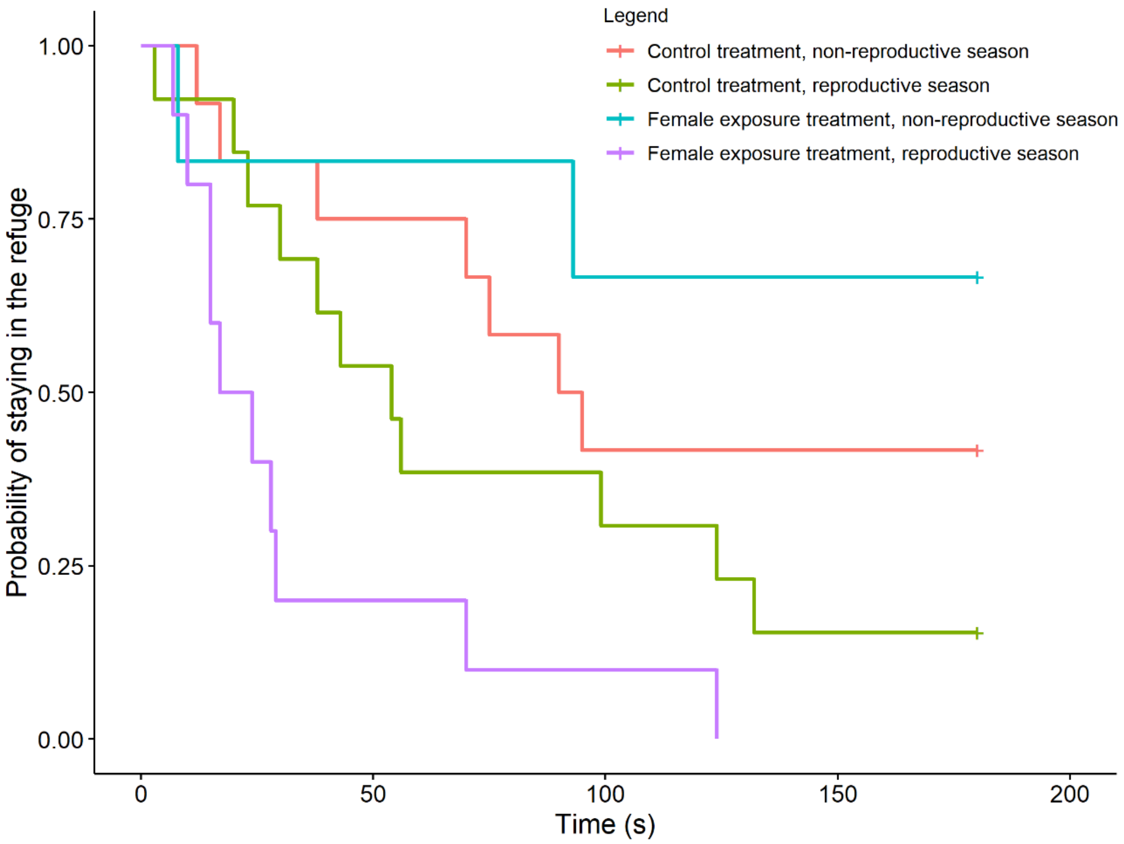

Fig. 2 Probability of males of the lizard species *Eurolophosaurus nanuzae* staying in the refuge in relation to the time they spent hidden after fleeing from a predatory attack simulation. The lines depict males submitted to different treatment combinations between exhibition and removal of a female (female exposure treatment) or no exhibition of a female (control treatment) and female reproductive seasons

Discussion

Our results indicated that males of *E. nanuzae* adjusted their FID and the time spent in the refuge depending on the combination between the reproductive season of the female and whether they had contact with females in their territories before the attacks. In relation to FID, males that had the previous contact with the females accepted greater predation risks after a predatory attack when compared to the trials in which they were not previously exposed to a female. The risk accepted by males exposed to females increased during the female reproductive season, indicating that males under current mating opportunities employ riskier flight tactics. To our knowledge, this is the first study demonstrating that, in addition to female presence, the social cost of losing a current reproductive opportunity, through the presence of a reproductive female affects males' FID. In relation to time spent in the refuge, our results showed that males in both the female exposure and control treatments were more likely to leave the refuge soon after fleeing from predators during the reproductive season of females, with the males exposed to the females leaving even faster. Together, these results indicated that males adjust their anti-predatory strategies when they have reliable cues that they will lose an opportunity to mate if they flee from a predator. It is still unclear how the physiological process that leads to behavioural variation in males works. Males may change their flight behaviours because they are able to recognize female cues that indicate that they are reproductive (allowing males to differentially adjust their behaviours in response to the sexual status of each female they encounter) or may predictably adopt riskier anti-predatory behaviours irrespective of female sexual status during the months in which most females are fertile. Although females did not show any apparent behavioural change during the reproductive season, it is still possible that males recognize the female reproductive status by other pathways, such as chemical ones (e.g. Cooper and Perez-Mellado 2002; Head et al 2005). However, in any case (a predictable change in male escaping decisions during the year or a fine adjustment according to female cues), it seems that the adoption of riskier anti-predatory behaviour during periods with higher chances of fertilization are favored by selection in this species.

Our predictions that males exposed to females should exhibit lower FID and spend less time in the refuges during the reproductive season in comparison to the non-reproductive season were confirmed. For the FID, although the major differences occurred between the female exposure/control treatments, the reproductive season intensified the response exhibited by males that were exposed to females. Therefore, our results indicated that males exhibit riskier anti-predatory behaviours in periods when the chance to mate with fertile females is higher. Such riskier behaviours occur both in relation to their resistance to abandon their territories and their proneness to resume territorial defense. An important consequence of the behavioural adjustments we observed is that the chance of males to be killed should increase during the reproductive season (Smith and Blumstein 2008; Jablonszky et al. 2018). In addition to reducing FID and the time spent hiding, all males in the reproductive season of females exhibited courtship displays and tried to bite the females. In some species the displays performed by males during courtship can also attract the attention of predators (Lima and Dill 1990; Magnhagen 1991). Therefore, the prevalence of reproductive displays in males of *E. nanuzae* during the reproductive season may represent an additional predatory cost paid by males facing females.

When we compared the variation of the FID between the female exposure and control treatments and between the reproductive and non-reproductive seasons, the variation in FID was much greater between the treatments than between the seasons. This result indicated that, for males of *E. nanuzae*, previous contact with the female was more important in modulating the FID compared with the reproductive season of the females. Additionally, in both seasons males exhibited different behaviours to females. Our suggestion is that males may be trying to attract females into their territory, even when females are not fertile. In some species, males that make more displays are those that attract a greater number of females and consequently have greater reproductive success (Kotiaho et al. 1996; Alonso et al. 2010). Perhaps males respond to female presence during the non-reproductive season to keep females near the territory until they become fertile in the reproductive season. In addition, by taking longer to escape the predator, males can spend more time courting females, increasing their chances of remaining in the territory. There is also the possibility that males copulate with females during the non-reproductive season because females may store sperm (Melo et al. 2019). However, very few females have stored sperm at the beginning of the reproductive season (Melo et al. 2019). Therefore, this decreases the chances that males are copulating with females in the non-reproductive season for sperm to be used in the reproductive season (Melo et al. 2019). However, regardless of the reasons that may explain why males adopt riskier anti-predatory behaviours when females are nearby in the non-reproductive season, both explanations suggest that males are investing in strategies that could maximize future fitness increments.

Another intriguing result was that, during the non-reproductive season, the males submitted to the control treatment spent less time in the refuge when compared to the female exposure treatment. Males in the female exposure treatment also reduced their FIDs when compared to the control treatment. Perhaps when exposed to females, males increased the time spent in the refuge to compensate for the greater risk expressed when they were deciding when to start fleeing. Predators may take some time to leave a place after trying to capture a prey. Since males in the female exposure treatment allowed a greater approximation of the predator, a longer time in the refuge could increase the chances that the predator leaves the territory and, therefore, decrease the chance that they would encounter the predator again when leaving the refuge (Cooper and Frederick 2007b). On the other hand, this compensation does not seem to happen in the reproductive season, as the males in the female exposure treatment had both smaller FID and spent less time hiding in the refuges when compared to the control treatment. As previously discussed, during the female reproductive season, males seem to invest in their current reproductive opportunities, so they maximize these opportunities while increasing the risk of being predated when a predator approaches or when encountering a predator that may still be in the area when the male leaves a shelter.

Our results showed that the seasonality in female reproductive status affects the anti-predatory decisions made by territorial males. However, although males expressed higher predatory risk when females are fertile, female reproductive status and female presence had different effects on the fleeing and hiding responses. While the FID was more strongly modulated by female exposure, the time that the males spent in the refuge were more strongly affected by the female reproductive season. Therefore, the evaluation of the influence of female presence and reproductive status on different male responses could provide a better understanding of the strategies adopted by males in response to the trade-off between the chances of being predated and the current or future social costs of fleeing. Seasonality in female reproductive status is common in many species (e.g. King and Duvall 1990; Scott and Mayden 2008; Pinot et al. 2014). Therefore, the effects we detected here may be pervasive in animals.

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References

Alonso JC, Magaña M, Palacín C & Martín CA (2010) Correlates of male mating success in great bustard leks: the effects of age, weight, and display effort. Behavioral Ecology and Sociobiology 64: 1589-1600.

Bates D, Maechler M, Bolker B & Walker S (2015) Fitting linear mixed-effects models using lme4. J Stat Softw 67: 1-48.

Blumstein DT (2010) Flush early and avoid the rush: a general rule of antipredator behavior? Behavioral Ecology 21: 440-442.

Chan AAYH, Giraldo-Perez P, Smith S & Blumstein DT (2010) Anthropogenic noise affects risk assessment and attention: the distracted prey hypothesis. Biology Letters 6: 458-461.

Conceição AA, Rapini A, Carmo FF, Brito JC, Silva GA, Neves SPS & Jacobi CM (2016) Rupestrian grassland vegetation, diversity, and origin. In: Fernandes G (ed) *Ecology and Conservation of Mountaintop Grasslands in Brazil*. Springer, Cham, pp 105-127

Cooper WEJr (1999a) Tradeoffs between courtship, fighting, and antipredatory behavior by a lizard, *Eumeces laticeps*. Behavioral Ecology and Sociobiology 47: 54-59.

Cooper WEJr (2009b) Flight initiation distance decreases during social activity in lizards (*Sceloporus virgatus*). Behavioral Ecology and Sociobiology 63: 1765-1771.

Cooper WEJr, Blumstein DT (eds) (2015) *Escaping from predators: an integrative view of escape decisions*. Cambridge University Press, Cambridge

Cooper WEJr & Frederick WG (2007a) Optimal flight initiation distance. Journal of Theoretical Biology 244: 59-67.

Cooper WEJr & Frederick WG (2007b) Optimal time to emerge from refuge. Biol J Linn Soc Lond 91: 375-382.

Cooper WEJr & Sherbrooke WC (2016) Strategic escape direction: orientation, turning, and escape trajectories of zebra-tailed lizards (*Callisaurus draconoides*). Ethology 122: 542-551.

Cooper WEJr & Perez-Mellado V (2002) Pheromonal discriminations of sex, reproductive condition, and species by the lacertid lizard *Podarcis hispanica*. J Exp Zool 292: 523–527.

Cooper WEJr & Wilson DS (2007) Sex and social costs of escaping in the striped plateau lizard *Sceloporus virgatus*. Behavioral Ecology 18: 764-768.

Díaz-Uriarte R (1999) Anti-predator behaviour changes following an aggressive encounter in the lizard *Tropidurus hispidus*. Proc R Soc Lond B 266:2457-2464.

Dukas R (2004) Causes and consequences of limited attention. Brain Behav Evol 63: 197-210.

Filogonio R, Del Lama FS, Machado LL, Drumond M, Zanon I, Mezzetti NA & Galdino CAB (2010) Daily activity and microhabitat use of sympatric lizards from Serra do Cipó, southeastern Brazil. Iheringia 100: 336-340.

Galdino CAB (2004) Dinâmica populacional, dimorfismo sexual e uso do hábitat por *Eurolophosaurus nanuzae* (Rodrigues 1981) (Tropiduridae) em uma área de campo rupestre em Minas Gerais. PhD thesis, Universidade do Estado do Rio de Janeiro, Rio de Janeiro

Galdino CAB, Assis VB, Kiefer M & Van Sluys M (2003) Reproduction and fat body cycle of *Eurolophosaurus nanuza*e (Sauria, Tropiduridae) from a seasonal montane habitat of southeastern Brazil. Journal of Herpetology 37: 6876-6894.

Galdino CAB, Horta GCMM & Young RJ (2014) An update to a bead-tagging method for marking lizards. Herpetol Rev 45: 587-589

Galdino CAB, Pereira EG, Fontes AF & Van Sluys M (2006) Defense behavior and tail loss in the endemic lizard *Eurolophosaurus nanuzae* (Squamata, Tropiduridae) from southeastern Brazil. Phyllomedusa 5: 25-30.

Giese AC (1959) Comparative physiology: annual reproductive cycles of marine invertebrates. Annu Rev Physiol 21: 547-576

Haenel GJ, Smith LC & John-Alder HB (2003). Home-range analysis in *Sceloporus undulatus*. II. A test of spatial relationships and reproductive success. Copeia 2003: 113-123.

Head ML, Keogh JS & Doughty P (2005) Male southern water skinks (*Eulamprus heatwolei*) use both visual and chemical cues to detect female sexual receptivity. Acta Ethol 8: 79-85.

Holley AJF (1993) Do brown hares signal to foxes? Ethology 94: 21-30.

Jablonszky M, Szász E, Krenhardt K et al (2018) Unravelling the relationships between life history, behaviour and condition under the pace-of-life syndromes hypothesis using long-term data from a wild bird. Behavioral Ecology and Sociobiology 72: 52.

Kassambara A, Kosinski M, Biecek P & Fabian S (2017) Package ‘survminer’. Drawing Survival Curves using ‘ggplot2’,

King MB & Duvall D (1990) Prairie rattlesnake seasonal migrations: episodes of movement, vernal foraging and sex differences. Animal Behaviour 39: 924-935.

Kopena R, Herczeg G, López P & Martín J (2015) Escape strategy of Schreiber's green lizards (*Lacerta schreiberi*) is determined by environment but not season or sex. Behaviour 152: 1527-1542.

Kotiaho J, Alatalo RV, Mappes J & Parri S (1996) Sexual selection in a wolf spider: male drumming activity, body size, and viability. Evolution 50: 1977-1981.

Lima SL (1998) Nonlethal effects in the ecology of predator–prey interactions. What are the ecological effects of anti-predator decision-making? BioScience 48: 25-34.

Lima SL & Dill LM (1990) Behavioral decisions made under the risk of predation: a review and prospectus. Can J Zool 68: 619-640.

Magnhagen C (1991) Predation risk as a cost of reproduction. Trends Ecol Evol 6: 183-186.

Martín J & López P (1999) Nuptial coloration and mate-guarding affect escape decisions of male lizards, *Psammodromus algirus*. Ethology 105: 439-447.

Martín J, López P & Cooper WEJr (2003) Loss of mating opportunities influences refuge use in the Iberian rock lizard, *Lacerta monticola*. Behavioral Ecology and Sociobiology 54: 505–510.

Melo GC, Nascimento LB & Galdino CA (2019) Lizard reproductive biology beyond the gonads: an investigation of sperm storage structures and renal sexual segments. Zoology 135: 125690.

Milinski M (1997) How to avoid seven deadly sins in the study. Advances in the Study of Behavior 26: 159-180.

Pinot A, Gauffre B & Bretagnolle V (2014) The interplay between seasonality and density: consequences for female breeding decisions in a small cyclic herbivore. BMC Ecol 14: 17.

Quintana EC & Galdino CAB (2017) Aggression towards unfamiliar intruders by male lizards *Eurolophosaurus nanuzae* depends on contestant's body traits: a test of the dear enemy effect. Behaviour 154: 693-708.

R Core Team (2018) R: A language and environment for statistical computing. R foundation for Statistical Computing, Vienna, Austria, https://www.R-project.org/

Rand AS (1964) Inverse relationship between temperature and shyness in the lizard *Anolis lineatopus*. Ecology 45: 863-864.

Reaney LT (2007) Foraging and mating opportunities influence refuge use in the fiddler crab, *Uca mjoebergi*. Animal Behaviour 73: 711-716.

Samia DSM, Blumstein DT, Stankowich T & Cooper WEJr (2016) Fifty years of chasing lizards: new insights advance optimal escape theory. Biol Rev 91: 349-366.

Scott JH & Mayden RL (2008) Life history of the tricolor shiner, *Cyprinella trichroistia* (Teleostei: Cyprinidae), in Alabama. Southeast Nat 7: 69-80.

Sick H (1997) *Ornitologia brasileira: uma introdução*. Editora Nova Fronteira, Rio de Janeiro

Silveira FA, Negreiros D, Barbosa NP, Buisson E, Carmo FF, Carstensen DW & Garcia QS (2016) Ecology and evolution of plant diversity in the endangered campo rupestre: a neglected conservation priority. Plant Soil 403: 129-152.

Smith BR & Blumstein DT (2008) Fitness consequences of personality: a meta-analysis. Behavioral Ecology 19: 448-455.

Therneau TM & Lumley T (2014) Package 'survival'.

Ventura SPR, Passos DC, Machado LL, Horta G & Galdino CAB (2017) Escape tactics by a neotropical montane lizard: a comparison of flight responses against natural and nonnatural predators. Acta Ethol 20: 9-15.

Vitt LJ & Caldwell JP (2014) *Herpetology: an introductory biology of amphibians and reptiles*. Academic Press, San Diego

Williams DM, Samia DSM, Cooper WEJr & Blumstein DT (2014) The flush early and avoid the rush hypothesis holds after accounting for spontaneous behavior. Behavioral Ecology 25: 1136-1147.

Willis EO & Oniki Y (2002) Birds of Santa Teresa, Espirito Santo, Brazil: Do humans add or subtract species? Pap Avulsos Zool 42: 193-264.

Ydenberg RC & Dill LM (1986) The economics of fleeing from predators. Advances in the Study of Behavior 16: 229-249.

Ziegler T, Hodges K, Winkler P & Heistermann M (2000) Hormonal correlates of reproductive seasonality in wild female Hanuman langurs (*Presbytis entellus*). Am J Primatol 51: 119-134.

Zuur AF, Ieno EN, Walker NJ, Saveliev AA & Smith GM (2009) *Mixed effects models and extensions in ecology with R*. Springer, New York

Supplementary material

Fig.S1: Pole used during the simulation of a predatory attack on the lizard *Eurolophosaurus nanuzae* at Serra do Cipó locality, Minas Gerais State, Brazil. A) Taxidermized predator model (hawk *Rupornis magnirostris*) attached in typical flight posture at the end of the pole and above the hawk we connected distance sensor to measure the flight initiation distance (FID); B) Display showing the FID estimated by the distance sensor and C) Full view of the pole with the predator model and the electronic system used during the field experiments.

Capítulo II

O artigo referente a este capítulo está sob revisão na Revista Animal Behaviour.

I love to hate my neighbour: how the recognition of dear enemies affects male anti-predatory behaviours in a lizard species

Abstract

In species in which individuals defend territories for long periods, it is common that rivals in neighbouring territories learn to recognise each other or the territory boundaries and reduce their mutual aggressiveness to decrease the costs of territorial defence ("dear enemy" phenomenon). Although the dear enemy phenomenon is generally evaluated in terms of aggressive behaviours between rivals, the ability to recognise neighbours ("dear enemy recognition") may affect other behaviours. In particular, anti-predatory behaviours may be mediated by the status of rivals (familiar neighbours or unfamiliar intruders) because individuals may be more resistant to escape from predators if the nearby rivals are unfamiliar intruders than familiar neighbours that have not historically infringed on their territory. In this scenario, the ability to recognise familiar neighbours would affect an individual's escape decisions. Here, we evaluated the hypothesis that resident males of the lizard *Eurolophosaurus nanuzae* would adopt lower-risk anti-predatory behaviours after encountering a familiar neighbour as compared to an unfamiliar intruder. For this, we measured the flight initiation distance (FID) and time spent in the refuge of lizards under three conditions: without recent contact with other males, previous exposure to a familiar neighbour or to an unfamiliar intruder. We observed lower FIDs for males who had encountered an unfamiliar intruder compared to a familiar neighbour and greatest FIDs when the same lizards did not have any recent contact with other individuals (familiar neighbours or unfamiliar intruders). As expected, lizards without contact with rivals spent more time hidden in comparison to the other treatments, but the time spent hidden was similar when the lizard was exposed to a familiar neighbour or an unfamiliar intruder. These results indicate the existence of an important cognitive mechanism that allows individuals to recognise a rival along with its interaction history and modulate their initial escape strategy accordingly.

Keywords: escape behaviour, social cost, flight initiation distance, territoriality and intruders.

Introduction

Species in which individuals aggressively defend a fixed area against conspecifics, ensuring exclusive use of space, are common in many animal groups, including insects (Benelli 2014), arachnids (Porto and Peixoto 2013), fishes (Spence and Smith 2005), amphibians (Valenzuela-Sánchez et al. 2014), squamates (Bandara 2012), birds (Tobias et al. 2016) and mammals (Lacey and Wieczorek 2001). Territorial defence can ensure the major use of resources by the territory owner, directly increasing their fitness (Maher and Lott 2000). However, holding a territory comes at a cost, including increased energy expenditure (Marler et al. 1995), predation risk (Jakobsson, Brick and Kullberg 1995) and injuries from fighting (Candaten et al. 2020). Consequently, behavioural traits that reduce the cost of maintaining a territory without increasing the chance of losing it are expected to be favoured by selection (Arnott and Elwood 2008; Pinto et al. 2019).

An important strategy to reduce the costs of territorial maintenance involves the constant defence of the same area over extended periods (i.e. being faithful to a territory - Koronkiewicz et al. 2006). Maintaining stable territories decreases the costs of searching for new areas and fighting against residents in other territories (Hinsch and Komdeur 2010). This strategy reduces fighting costs, as expelling a resident from its territory generally expends greater energy than defending a territory against an intruder (Hinsch and Komdeur 2010). However, territorial fidelity can lead to the formation of stable neighbourhoods between adjacent rivals, with neighbours often incurring unnecessary costs from fighting at their territorial borders, even if neither wants to steal the territory from the other. This scenario favours the evolution of the ‘dear enemy’ phenomenon, in which territory owners often respond with reduced aggression to neighbouring individuals (Fisher 1954). The dear enemy phenomenon may occur both because individuals respect territory boundaries or because they are able to recongnize their neighbours. In this second case, the resident individual may reduce aggressiveness when recognising a neighbour because it represents less of a threat than unfamiliar individuals that may be seeking to acquire territory (e.g. Husak and Fox 2003; Kohn et al. 2013). This "dear enemy recognition" ability allows residents in the associated territories to adjust their behaviour to avoid unnecessary costs with familiar neighbours while maintaining aggression towards unfamiliar intruders (Temeles 1994).

Because the dear enemy recognition ability requires that individuals recognise each other during fights, it may be that this ability also affects other individual behaviours. In particular, the ability to recognise familiar neighbours may affect individuals' anti-predatory strategies. In territorial species, anti-predatory strategies often involve escaping to a shelter or to another area (Cooper and Sherbrooke 2016). Therefore, decisions related to the distance that the prey allows a predator to approximate before starting fleeing (known as flight initiation distance - FID) and how much time the prey should spend hidden are important determinants of the predation risk (Ydenberg and Dill 1986). At the same time, such decisions may affect the costs of abandoning the territory paid by the prey. Fleeing too early (i.e. showing a larger FID) increases the chances of territorial invasion or loss of mates to rivals, as well as the costs of expelling the invader from the territory (Samia et al. 2016). Alternatively, delaying escape (i.e. showing a smaller FID) increases the chances of being predated (Cooper and Sherbrooke 2016). Therefore, individuals of territorial species that counterbalance the risks and costs of fleeing from predators may be favoured by selection (Optimal Escape Theory - Ydenberg and Dill 1986; Cooper and Frederick 2007).

A consequence of the balance between the risks and costs of fleeing is that when there is another rival close to the territory, residents tend to become more resistant to fleeing and return more quickly to the territory after fleeing because they have a cue that there is a competitor male nearby (Díaz-Uriarte 1999; Cooper 2009). However, if that rival is a familiar neighbour, it may be possible that residents increase their willingness to escape from a predator. This is expected because neighbours with territories rarely try to occupy another territory and consequently represent a lower threat to the resident male (e.g. Booksmythe et al. 2010). Unfamiliar intruders, on the other hand, may represent individuals searching for territories. In this situation, if a resident male temporarily abandons his territory when an unfamiliar individual is nearby, it may risk the intruder establishing his own territory in the unoccupied site. When intruders stay more time in an undefended territory, they may increase their willingness to defend the place (e.g. Leuk 1995; O'Connor et al. 2015). Therefore, an early escape by the resident male could elicit a greater fighting investment to expel an unfamiliar intruder upon returning. This investment may represent important costs since fighting is costly in terms of energy expenditure and risk of injury (Neat et al. 1998; Rovero et al. 2000). Nevertheless, it is unknown whether the status of the conspecific (familiar neighbours or unfamiliar intruders) influences the anti-predatory behaviours of residents. Given that territorial systems with stable neighbourhoods are common in many prey species, assessing whether the status of rivals influences the anti-predatory behaviours of residents may be important in showing the extent to which the evolution of escape strategies can be conditioned by the social context in which individuals are embedded. This would also demonstrate the existence of an important cognitive mechanism mediating the expression and evolution of anti-predatory strategies.

A species in which males form stable territories and was reported to show the dear enemy recognition ability (Quintana and Galdino 2017) is the lizard *Eurolophosaurus nanuzae*. Males of this species are known to act aggressively against conspecific males, chasing and fighting with intruders (Galdino et al. 2006). Both males and females of *E. nanuzae* occupy rocky outcrops, with multiple males defending distinct territories within the same outcrop patch. Resident males defending adjacent territories may remain on the same outcrop throughout the year (SPV unpublished data) and this may explain why they show the dear enemy recognition (Quintana and Galdino 2017). Males spend most of the day exposed in their territories but flee to nearby vegetation or cracks in the rocks when they detect an approaching predator (Galdino et al. 2006). Males of *E. nanuzae* are known to alter their resistance to escape from predators according to the social costs of leaving the territory, such as the risk of losing potential mates (Ventura et al. 2021). Because males are able to adjust their escaping strategies according to the social costs and because males are able to recognise rivals in neighbouring territories, it may be that males also change their escaping strategies when nearby rivals are familiar neighbours or unfamiliar individuals that may represent potential intruders. For this reason, in this study, we evaluated whether the dear enemy recognition influences the anti-predatory strategies of *E. nanuzae* males. We hypothesised that resident males would adopt lower-risk anti-predatory strategies in the presence of a familiar neighbour than an unfamiliar intruder. Specifically, we expected that after being exposed to familiar neighbouring territorial males, focal resident males would: (i) exhibit a greater flight initiation distance (FID) and (ii) spend more time in a refuge after fleeing from a predator as compared to responses after being exposed to unfamiliar intruders.

Methods

Study site

We performed this study from October to November 2019 in a rocky field habitat 1100 m above sea level in Serra do Cipó, Santana do Riacho, Minas Gerais, Brazil (19°17'S, 43°35'W). The habitat, 'Campos Rupestres', consisted of a mosaic of herbaceous and shrubby vegetation on quartzite or ironstone (Conceição et al. 2016). Lizards occupied the rocky patches within the grassy vegetation. *E. nanuzae* individuals were easily observed, captured, and handled in this open habitat (Galdino et al. 2006).

Identification of males' territorial neighbourhoods

To select individuals for use in experiments, we identified territorial males of *E. nanuzae* in the field and determined their neighbourhood relationships by mapping the areas typically occupied by each lizard (Quintana and Galdino 2017). Distinguishing familiar neighbours and unfamiliar individuals was essential to simulating encounters with a potential intruder in the focal male territory (see encounter experiments in the *Experimental protocol* section).

To find males that had neighbouring territories, we captured and marked 42 males. We captured each male by lasso and measured each of them for its body size (snout-vent length), weight (using a spring scale; precision = 0.2 g) and tail condition (intact/autotomised). After this, we assigned an identity to individuals by painting a unique combination of coloured dots on the lizard's back using a non-toxic ink (Ferner 2007). After this, for 20 consecutive days, we recorded the locations of each marked male during their active period (9:00 h and 15:30 h) (Filogonio et al. 2010). We considered as resident males, males re-sighted near the same location in which they were first captured (approximately 12 m radius) for a minimum of five days (Quintana and Galdino 2017). As males typically maintain a home range of 170.01 ±

198.86 m² in a single outcrop (Portela 2017), the ~12 m radius from the capture point used for identifying resident male areas is biologically relevant. We considered two resident males to be familiar neighbours when they used adjacent areas in the same outcrop. To determine which males were used as a familiar neighbour to be experimentally introduced in another territory or a focal resident male that was exposed to the introduced rival, we chose individuals that allowed us to increase our sample size. For example, in a group of three males with adjacent territories, we chose the individual sharing territorial boundaries with the other two males to be used as the familiar neighbour and the remaining two as focal resident males. After defining neighbourhood relationships, 14 resident males were selected as focal residents.

To determine the individuals used as unfamiliar intruders for the focal resident males, we captured males at a minimum distance of 1 km from the rocky outcrop in which the focal resident male was present. This minimum distance for capturing unfamiliar intruders has been established by previous research on the dear enemy recognition in this species that identified that individuals located 1 km apart have no history of prior contact (Quintana and Galdino 2017). We size-matched intruders (both familiar neighbours and unfamiliar intruders) to be within ± 5% of the focal resident male body size (Quintana and Galdino 2017). We used 10 unfamiliar intruders during the experiments.

Experimental protocol

To assess whether the anti-predatory behaviour of focal resident males is affected by intruder status, we performed staged territorial encounters in which each focal resident male was subjected to three experimental trials: territorial intrusion by a familiar neighbouring male, intrusion by an unfamiliar male and negative control (no intruder exposure).

We randomly determined the order in which the focal resident males would be used each day. After this, we also randomly determined which treatment would be applied (control, intrusion by an unfamiliar rival or intrusion by a familiar neighbour), by simultaneously sampling the three options for each male. We performed all experiments on sunny days during the species' active period. For each focal resident male, we waited for a minimum of 24 h between trials to avoid long-term effects on lizard responses and overstressing the animal. Each intruder (familiar neighbour or unfamiliar intruder) was used in a maximum of two trials/day.

To start each trial, we first located focal resident males. After locating the focal resident male, we captured the intruding individual (except in the case of the negative control) and transported him to be exposed to the focal resident male in an aerated plastic container. Intruders were kept in plastic boxes for a maximum of 2 h to minimise stress and were released at their site of capture following the experiments. The experiment was initiated 3 min after arriving at the outcrop, as this time interval has been demonstrated to allow this species to habituate to the human presence (Quintana and Galdino 2017). During this period, we continuously monitored the focal resident males, at a distance of approximately 3 m, to ensure that our presence was not disrupting their behaviour. While we waited for the habituation period, the researcher responsible for making the intrusion, tethered the intruder around the chest on a 1 m nylon filament loop attached to a 2.5 m pole. The pole was similar to a fishing rod, with a 2 cm diameter at the base, and for this reason, lizards were unable to detect the tip of the pole even when we were capturing them. No tension was applied to the nylon filament, allowing lizards to move freely (Quintana and Galdino 2017; Ventura et al., 2021). We placed the intruder approximately 50 cm from the focal resident male (Quintana and Galdino 2017; Ventura et al. 2021) and recorded the behaviour of the focal resident male for 5 min before removing the intruder. This intrusion simulated the invasion of territory defended by the focal resident males by both the unfamiliar intruder and familiar neighbour. During the intrusion experiment, the researcher responsible for holding the pole remained motionless. However, to avoid injuring the individuals introduced in the territories, the researcher removed the intruder before the 5 min period if he was bitten by the focal resident male. This generated two different contexts of focal resident males: one involving a 5 min interaction with the intruder and another with an interaction time shorter than 5 min. However, despite this difference in the time of exposure to intruders, it did not influence the FID exhibited by focal males (Supplementary Material 1). We simulated the predatory attack 50 s after removing the intruder (see below). In the negative control treatment, we simulated the predatory attack after the 3 min habituation period to evaluate the focal resident male's behaviour without recent encounters with rival males.

To simulate predatory attacks, we used a taxidermied roadside hawk *Rupornis magnirostris* (Aves: Accipitridae) as a model of a natural predator of *E. nanuzae*. This model has been shown to efficiently induce anti-predatory behaviours in this lizard species (Ventura et al. 2021). The hawk was prepared in its typical flight posture and attached to the end of a 3 m long pole fitted with a distance sensor to measure the linear distance between the hawk and lizards (Ventura et al. 2021). The researcher responsible for simulating the predatory attack (SPV) recorded FID measurements at the onset of the lizards' flight. To initiate attack simulations, we placed the hawk at a height of approximately 3 m and 2 m laterally distant from the lizard and moved it at a constant speed in a 'V' trajectory with a vertex (angle = c.a. 60°) c.a. 50 cm above the lizard's position (Ventura et al. 2017). It is important to note that, all experiments were done in open areas, to prevent the predator model from colliding with the vegetation or causing any bias in the FID measurement. In addition, due to the movement of the focal resident male during the simulation of a predatory attack, the sensor may sometimes have measured the distance of the hawk to the ground. However, this would increase our FID measurement by ≤ 2 cm (due to the small size of the males). Such difference in the FID estimation is negligible compared to the FID variation observed between treatments (see results). Therefore, although we always focused on maintaining the distance sensor aimed at the focal resident male, an eventual error in this task would not compromise our results.

For trials in which the focal male ran to a refuge, we recorded the time (up to 3 min) that it spent hidden (negative control: n = 10, familiar neighbour: n = 9 and unfamiliar intruder: n = 10). We considered that animals chose a refuge when they did not remain in an exposed rock after fleeing. Each focal resident male participated in each treatment for a total of 42 trials, 14 per treatment. Due to logistic constraints in the field, we did not use blind experiments. However, we reduced potential bias by standardizing the speed and the trajectory of the predatory attack during our simulations.

Statistical analyses

We used a general linear mixed model (LMM) to evaluate the effects of the treatments on FID. We considered the treatments (familiar neighbour, unfamiliar intruder, and negative control) as fixed predictor variables and FID as the response variable. Body weight and environmental temperature were used as covariates as they can influence the locomotory performance of lizards (Samia et al. 2016). We also considered identities of individuals (focal resident males), date of the observation, order of treatments applied to each individual and number of each treatment (first, second or third) as random predictor variables. We used the focal resident male identity as a random factor because the same male was used in three treatments; date due to environmental variations across the different days and order and the number of treatments to ensure that the results were not due to repeated exposure to predatory risk or the lizards having already been stimulated by the predator. We excluded the identities of intruders from the model because we had a little repetition of intruders in the experiments (only two intruders, each repeated twice) and because the FID of focal resident males with the same intruders did not differ from the overall FID. To perform the test, we first built a general model with all covariates and the fixed and random predictor variables included, then we performed a likelihood ratio test that compared this model with a null model without the fixed explanatory variables. In case of significant results, we made a subsequent comparison between the general model and a new model without the treatment variable. In case of a significant effect of the treatment variable, we also employed planned comparisons between treatments with familiar neighbours and unfamiliar intruders to determine whether the FID exhibited in the familiar neighbour treatment was less than that in the unfamiliar intruder treatment.

We also evaluated whether the treatments affected the time lizards spent hiding in the refuges using the Cox proportional hazard regression model (Harrell 2015). This regression was suitable for our data because it estimates the proportion of males that left the refuge at each unit of time. The proportional hazards assumption was checked using statistical tests and graphical diagnostics based on scaled Schoenfeld residuals (Hess 1995). In this model, we used the proportion of males that remained in the refuge each time (i.e. the survival object) as the response variable and the treatment as the predictor variable. We used the temperature and weight of the animals as covariates and also controlled for focal resident male identity. To calculate *p* values, we used likelihood ratio tests comparing the models with all predictor variables included with a null model without predictor variables. We performed all statistical procedures using the R environment (Team 2019). For LMM analysis, we used the package lme4 (Bates et al. 2014). For the Cox proportional hazard regression, we used the packages survminer (Kassambara et al. 2017) and survivel (Therneau and Lumley 2014). To assess the proportional risk assumptions and estimate the hazard ratio, we used the cox.zph function in the survival package and ggforest, respectively. We used the frailty function to add male identity as a random effect term in Cox proportional hazard regression. We evaluated all model assumptions (for both the LMM and the Cox proportional hazard regression) by visual inspections of the residual plots (residuals vs fitted values - Zuur et al. 2009). For the planned comparisons we used the multcomp package (Hothorn et al. 2016).

Results

Focal resident males of *E. nanuzae* typically responded to encounters with familiar neighbours with rapid up-and-down movements of their hind limbs (leg flip), raising the head and body region by flexion and extension of the front legs (push-up) and consecutive sideways movements of the tail (tail flick). Most males (71%) approached their familiar neighbours, with 57% attempting to bite them and 14% moving away after approaching without abandoning the territory (see Table S2). Some males responded to unfamiliar intruders by arching their backs along with leg flips, push-ups and tail flicks. All males approached the unfamiliar intruders, and 78% tried to bite them. No male moved away from the unfamiliar intruders (see Table S2).

The FID values exhibited by males showed an outlier individual with extremely high values for all treatments. Although we opted to present the results with this individual included, its exclusion did not change the conclusions (see Figure S3 and Table S4 for the results without the outlier data included). The comparison between the model containing all explanatory variables with a null model indicated that there is an effect on the FID (χ^2 = 46.62, df = 4, n = 42, $p < 0.001$). When we created a new model without the treatment and compared it with the general model, we observed that the FID exhibited by focal resident males changed as a result of the treatments ($\chi^2 = 46.14$, df = 2, n = 42, $p < 0.001$; Fig. 1). FID was greatest for the control treatment, intermediate when the intruder was a familiar neighbour and smallest with unfamiliar intruders (planned comparison for familiar neighbour against unfamiliar intruders: t = 18.97, $p < 0.001$; Fig. 1).

The model testing the proportion of males that remained hidden indicated that the proportion of individuals leaving the shelter did not differ between treatments ($\chi^2 = 7.34$, df = 4, n = 29, $p = 0.10$; Fig. 2). However, there was an outlier individual in the treatment in which males were exposed to familiar neighbours. While eight individuals in this treatment showed hiding times that varied between 5 and 45 s, one individual did not leave the refuge during the 3 min period of observation (and therefore, was considered to stay hidden for 180 s). After removing the hiding time of this individual from the analysis, we found that the proportion of individuals remaining in the shelter during the observation time did not differ between the familiar neighbour or unfamiliar intruder treatments but decreased more abruptly in these two treatments when compared to the control ($\chi^2 = 13.7$, df = 4, n = 28, $p = 0.008$, Fig. 2).

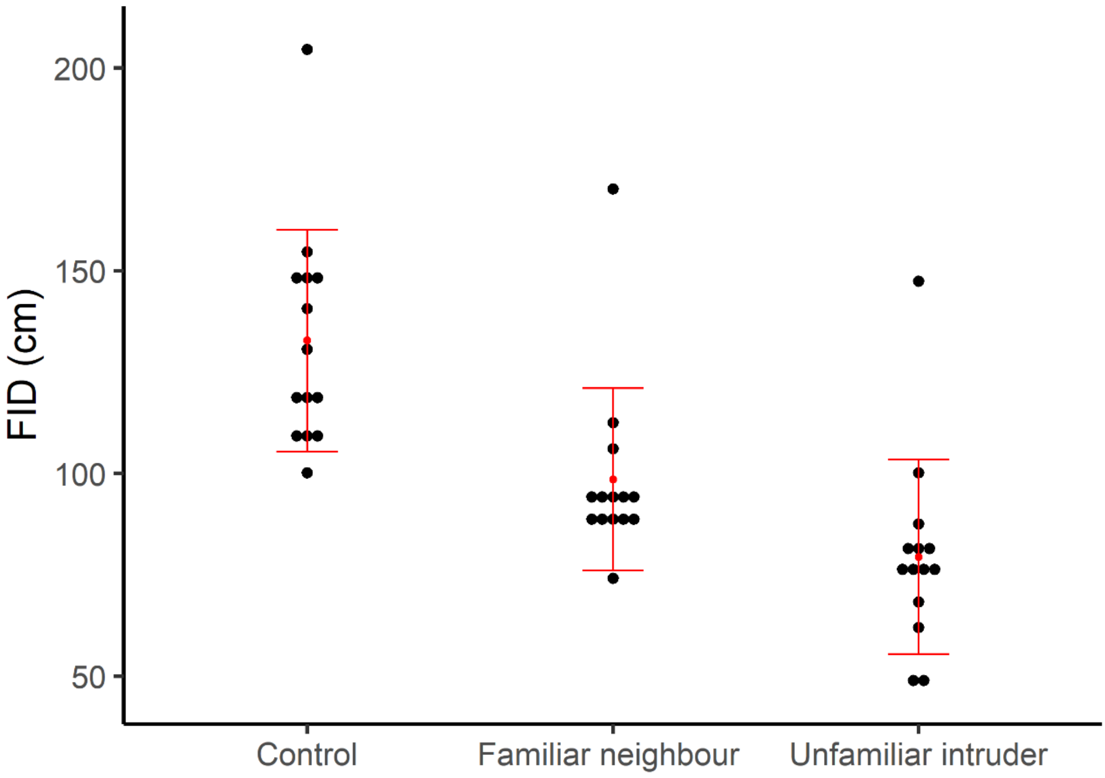

Fig. 1 Effect of exhibition and removal of an intruder (familiar neighbour or unfamiliar intruder) or no exhibition of another male (control group) on the flight initiation distance of focal resident males of the lizard *Eurolophosaurus nanuzae* located in their territories. Control: no encounter with another male. Bars represent standard deviation. Mean and standard deviations: control =132.77 ± 27.40; familiar neighbour =98.55 ± 13.30 and unfamiliar intruder =79.41 ± 23.98.

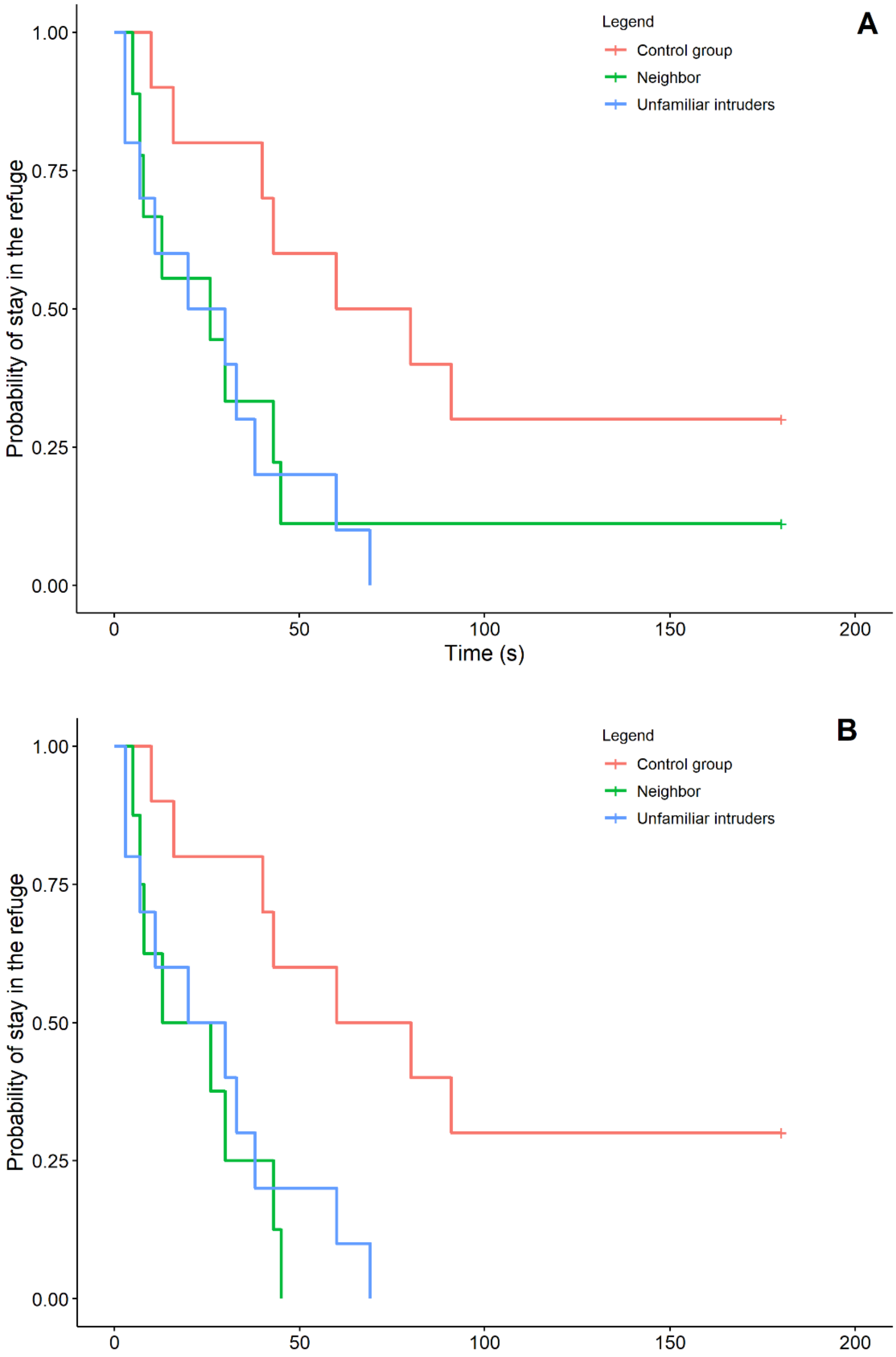

Fig. 2 Probability of *Eurolophosaurus nanuzae* males remaining in refuge over time after fleeing from a simulated predatory attack without the outlier data. The lines depict males submitted to exhibition and removal of an unfamiliar intruder or a familiar neighbour.

Control: no encounter with another male. Mean and standard deviation of time spent in refuge: control =88 ± 68.18; familiar neighbour =39.66 ± 54.76 and unfamiliar intruder =27.4 ± 23.27. (A) data considering all samples males and (B) data after the removal of an outlier in the familiar neighbour treatment.

Discussion

Here we used a field experimental approach to show that, a neglected factor under the optimal escape theory, the dear enemy recognition, may play an important role in male escaping decisions. It is important to note that the focal resident males showed distinct responses to unfamiliar intruders and familiar neighbours after our simulation of an invasion of the territory by them. If the focal resident males use territory boundaries as cues to exhibit the dear enemy response, they would react to both the unfamiliar intruder and familiar neighbour in a similar way in our experiments. The distinct responses, in this case, indicate that males, in fact, are able to recognise other individuals and respond accordingly. Therefore, the fact that focal resident males postponed the escape from the predators after facing an unfamiliar intruder in relation to a familiar neighbour indicates that these males recognize the rival’s status and its previous interaction history with it when deciding how to deal with an imminent predatory attack. To the best of our knowledge, this is the first study demonstrating an effect of the dear enemy recognition on a component of male escape behaviours, specifically FID. As this response requires recognition of a familiar neighbour, this work indicates the existence of an important cognitive mechanism for the evolution of escape strategies.

The observed resistance to initiate the escape from the potential predator following an encounter with an unfamiliar intruder compared to a familiar neighbour is consistent with optimal escape theory (Ydenberg and Dill 1986; Cooper and Frederick 2007). This indicates that, in fact, unfamiliar intruders may impose higher costs to focal resident males that temporarily abandon the territory. However, it is important to note that although focal resident males showed a greater FID after encountering a familiar neighbour as compared to an unfamiliar intruder, the FID after encountering a familiar neighbour was lower as compared to the control treatment. This indicates that, contrary to our initial expectations, the familiar neighbour may still pose a threat to the focal resident male, albeit to a lesser extent than an unfamiliar intruder (Temeles 1994). This intermediate response may reflect the risk of familiar neighbours stealing females or expanding their borders rather than usurping the territory (Hinsch and Komdeur 2010).

In contrast to the FID responses, the time spent hidden after fleeing a predator did not follow our expectations that males should exhibit different responses to the familiar neighbour and unfamiliar intruders. However, since we had one outlier male in the familiar neighbour treatment, our result must be interpreted with caution. If our results without the outlier individual are representative of the population pattern, the main indication would be that prior contact with rivals reduces the time that males spend hidden after a predator attack, but this time is unaffected by the history of prior interactions between the focal resident male and the intruder male. Therefore, focal resident males were more prone to return to their territories whenever they had a cue that a potential rival is nearby. Theoretical models on predator behaviour indicate that predators would not wait long in a given area if their prey was successful in their escape (Hugie 2003). Notably, prey rarely re-encounters predators after leaving the refuge (Johansson and Englund 1995; Hugie 2004; but see Katz et al. 2010). Thus, it may be that the time the focal resident males spent in the refuge following either familiar or unfamiliar rival encounters represent the minimum time needed to avoid encountering the predator after leaving the refuge. This may indicate that while the cost-benefit relationship associated with the decision to start fleeing may be affected by the status of nearby rival males, this is not the case for the decision involving a returning to the territory. It would be interesting to investigate the physiological mechanisms associated with the individual recognition process and the associated escaping responses to be able to understand the differential responses regarding the time to start fleeing and the time spent hiding. Although there is no study specifically for lizards, there are indications in fishes and birds that the amount of androgen hormones released differs when a focal individual encounters an unfamiliar or a familiar conspecific (Aires et al. 2015; Moser-Purdy et al. 2017). Such hormones may increase individual aggressiveness (Oliveira and Oliveira 2014) or induce an "emergency life history stage" that may impact their flight responses (Wingfield et al. 1998). However, it remains to be investigated if and how such differences affect both the decision to start fleeing and to return to the territory after escaping from a predator.

Most studies related to escape strategies have focused on understanding how such anti-predatory behaviours are influenced by predators, habitat or prey characteristics (Stankowich and Blumstein 2005; Stankowich 2008; Samia et al. 2019), whereas the role of social interactions has received attention more recently (Samia et al. 2016). The few investigations about the effect of social interactions on escape decisions have focused on understanding how the presence of a conspecific can modulate an individual decision (Reaney 2007; Cooper 2009). As non-optimal decisions may come at extremely high costs (e.g. losing mating opportunities with an early escape or suffering predation with a late escape), subtle behavioural adjustments should be highly favoured (Ydenberg and Dill 1986; Cooper and Frederick 2007). Therefore, along with an individual's presence, its status, interaction history with the focal resident male and many other social variations may have profound implications on male escape decisions. The ability to recognize rival males and the interaction history with them also indicate that the evolution of a cognitive mechanism able to retain information about the dynamics of agonistic interactions with rival males was favoured. The dynamics of male-male interactions, including behaviours related to the dear enemy phenomenon, observed in *E. nanuzae* are common to many territorial species (Hardy and Briffa 2013). Therefore, the effect of a rival's status on escape decisions could be pervasive in many species, representing an important factor in the evolution of territorial animals' escape behaviours. Understanding how this cognitive process and its associated physiological pathways occur is essential for improving our descriptions of the underlying mechanisms modulating the evolution of anti-predatory behaviours.

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Data Availability Statement

Data available from the OSF https://osf.io/xfupy/ (Ventura 2021)."

References

Aires, R.F., Oliveira, G.A., Oliveira, T.F., Ros, A.F. & Oliveira, R.F. (2015) Dear enemies elicit lower androgen responses to territorial challenges than unfamiliar intruders in a Cichlid fish. *PLoS One,* **10,** e0137705.

Arnott, G. & Elwood, R.W. (2008) Information gathering and decision making about resource value in animal contests. *Animal Behaviour,* **76,** 529-542.

Bandara, I.N. (2012) Territorial and site fidelity behavior of *Lyriocephalus scutatus* (Agamidae: Draconinae) in Sri Lanka. *Amphibian & Reptile Conservation,* **5,** 101-113.

Bates, D., Mächler, M., Bolker, B. & Walker, S. (2014) Fitting linear mixed-effects models using lme4. *arXiv preprint arXiv:1406.5823*.

Benelli, G. (2014) Aggressive behavior and territoriality in the olive fruit fly, *Bactrocera oleae* (Rossi) (Diptera: Tephritidae): role of residence and time of day. *Journal of Insect Behavior,* **27,** 145-161.

Booksmythe, I., Jennions, M. D. & Backwell, P.R. (2010) Investigating the ‘dear enemy’phenomenon in the territory defence of the fiddler crab, *Uca mjoebergi*. *Animal Behaviour,* **79,** 419-423.

Candaten, A., Possenti, A.G., Mainardi, Á.A., da Rocha, M.C. & Palaoro, A.V. (2020) Fighting scars: heavier Gladiator frogs bear more injuries than lighter frogs. *Acta Ethologica,* **23,** 39-44.

Conceição, A.A., Rapini, A., do Carmo, F.F., Brito, J.C., Silva, G.A., Neves, S.P. & Jacobi, C.M. (2016) Rupestrian grassland vegetation, diversity, and origin. In: Fernandes G. (eds). *Ecology and Conservation of Mountaintop Grasslands in Brazil,* pp. 105-127. Springer.

Cooper Jr, W.E. (2009) Flight initiation distance decreases during social activity in lizards (*Sceloporus virgatus*). *Behavioral Ecology and Sociobiology,* **63,** 1765-1771.

Cooper Jr, W.E. & Frederick, W.G. (2007) Optimal flight initiation distance. *Journal of Theoretical Biology,* **244,** 59-67.

Cooper Jr, W.E. & Sherbrooke, W.C. (2016) Strategic escape direction: orientation, turning, and escape trajectories of zebra-tailed lizards (*Callisaurus draconoides*). *Ethology,* **122,** 542-551.

Dalton, B., Settle, R., Medley, K. & Mathis, A. (2020) When neighbors cheat: a test of the dear enemy phenomenon in southern red-backed salamanders. *Behavioral Ecology and Sociobiology,* **74,** 56.

Díaz-Uriarte, R. (1999) Anti–predator behaviour changes following an aggressive encounter in the lizard *Tropidurus hispidus*. *Proceedings of the Royal Society of London, Series B: Biological Sciences,* **266,** 2457-2464.

Ferner, J.W. (2007) *A review of marking and individual recognition techniques for amphibians and reptiles*. Society for the Study of Amphibians and Reptiles.

Filogonio, R., Del Lama, F.S., Machado, L.L., Drumond, M., Zanon, I., Mezzetti, N.A. & Galdino, C.A. (2010) Daily activity and microhabitat use of sympatric lizards from Serra do Cipó, southeastern Brazil. *Iheringia. Série Zoologia,* **100,** 336-340.

Fisher, J. (1954) *Evolution and bird sociality.* London.

Galdino, C.A., Pereira, E.G., Fontes, A.F. & Van Sluys, M. (2006) Defense behavior and tail loss in the endemic lizard *Eurolophosaurus nanuzae* (Squamata, Tropiduridae) from southeastern Brazil. *Phyllomedusa: Journal of Herpetology,* **5,** 25-30.

Hardy, I.C. & Briffa, M. (2013) *Animal contests*. Cambridge University Press.

Harrell Jr, F.E. (2015) *Regression modeling strategies: with applications to linear models, logistic and ordinal regression, and survival analysis*. Springer.

Hess, K.R. (1995) Graphical methods for assessing violations of the proportional hazards assumption in Cox regression. *Statistics in Medicine,* **14,** 1707-1723.

Hinsch, M. & Komdeur, J. (2010) Defence, intrusion and the evolutionary stability of territoriality. *Journal of Theoretical Biology,* **266,** 606-613.

Hothorn, T., Bretz, F., Westfall, P., Heiberger, R.M., Schuetzenmeister, A., Scheibe, S. & Hothorn, M.T. (2016) Package 'multcomp'. *Simultaneous inference in general parametric models. Project for Statistical Computing, Vienna, Austria*.

Hugie, D.M. (2003) The waiting game: a "battle of waits" between predator and prey. *Behavioral Ecology,* **14,** 807-817.

Hugie, D.M. (2004) A waiting game between the black-bellied plover and its fiddler crab prey. *Animal Behaviour,* **67,** 823-831.

Husak, J.F. & Fox, S.F. (2003) Adult male collared lizards, *Crotaphytus collaris*, increase aggression towards displaced neighbours. *Animal Behaviour,* **65,** 391-396.

Jakobsson, S., Brick, O. & Kullberg, C. (1995) Escalated fighting behaviour incurs increased predation risk. *Animal Behaviour,* **49,** 235-239.

Johansson, A. & Englund, G. (1995) A predator-prey game between bullheads and case-making caddis larvae. *Animal Behaviour,* **50,** 785-792.

Kassambara, A., Kosinski, M., Biecek, P. & Fabian, S. (2017) Package 'survminer'. *Drawing Survival Curves using 'ggplot2'(R package version 03 1)*.

Katz, M.W., Abramsky, Z., Kotler, B., Altstein, O. & Rosenzweig, M.L. (2010) Playing the waiting game: predator and prey in a test environment. *Evolutionary Ecology Research,* **12,** 793-801.

Kohn, N.R., Deitloff, J.M., Dartez, S.F., Wilcox, M.M. & Jaeger, R.G. (2013) Memory of conspecifics in male salamanders *Plethodon cinereus*: Implications for territorial defense. *Current Zoology,* **59,** 326-334.

Koronkiewicz, T.J., Sogge, M.K., Van Riper III, C. & Paxton, E.H. (2006) Territoriality, site fidelity, and survivorship of Willow Flycatchers wintering in Costa Rica. *The Condor,* **108,** 558-570.

Lacey, E.A. & Wieczorek, J.R. (2001) Territoriality and male reproductive success in arctic ground squirrels. *Behavioral Ecology,* **12,** 626-632.

Leuk, B.E. (1995) Territorial defense by male green anoles: an experimental test of the roles of residency and resource quality. *Herpetological Monographs,* **9,** 63-74.

Maher, C.R. & Lott, D.F. (2000) A review of ecological determinants of territoriality within vertebrate species. *The American Midland Naturalist,* **143,** 1-29.

Marler, C.A., Walsberg, G., White, M.L., Moore, M. & Marler, C. (1995) Increased energy expenditure due to increased territorial defense in male lizards after phenotypic manipulation. *Behavioral Ecology and Sociobiology,* **37,** 225-231.

Moser-Purdy, C., MacDougall-Shackleton, S.A., Bonier, F., Graham, B.A., Boyer, A.C. & Mennill, D.J. (2017) Male song sparrows have elevated testosterone in response to neighbors versus strangers. *Hormones Behavior,* **93,** 47-52.

Neat, F.C., Taylor, A.C. & Huntingford, F.A. (1998) Proximate costs of fighting in male cichlid fish: the role of injuries and energy metabolism. *Animal Behaviour,* **55,** 875-882.

O'Connor, C.M., Reddon, A.R., Ligocki, I.Y., Hellman, J.K., Garvy, K.A., Marsh-Rollo, S.E., Hamilton, I.M. & Balshine, S. (2015) Motivation but not body size influences territorial contest dynamics in a wild cichlid fish. Animal Behaviour, 107, 19-29.

Oliveira, G.A. & Oliveira, R.F. (2014) Androgen modulation of social decision- making mechanisms in the brain: an integrative and embodied perspective. *Frontiers in Neuroscience,* **8,** 209.

Pinto, N.S., Palaoro, A.V. & Peixoto, P.E. (2019) All by myself? Meta-analysis of animal contests shows stronger support for self than for mutual assessment models. *Biological Reviews,* **94,** 1430-1442.

Portela, A.V.B.H. (2017) Avaliação da adequabilidade de habitat para o lagarto *Eurolophosaurus nanuzae*. Master's degree, Pontifícia Universidade Federal de Minas Gerais.

Porto, T.J. & Peixoto, P.E.C. (2013) Experimental evidence of habitat selection and territoriality in the Amazonian whip spider *Heterophrynus longicornis* (Arachnida, Amblypygi). *Journal of Ethology,* **31,** 299-304.

Quintana, E.C. & Galdino, C.A. (2017) Aggression towards unfamiliar intruders by male lizards *Eurolophosaurus nanuzae* depends on contestant's body traits: a test of the dear enemy effect. *Behaviour,* **154,** 693-708.

Reaney, L.T. (2007) Foraging and mating opportunities influence refuge use in the fiddler crab, *Uca mjoebergi*. *Animal Behaviour,* **73,** 711-716.

Rovero, F., Hughes, R.N., Whiteley, N.M. & Chelazzi, G. (2000) Estimating the energetic cost of fighting in shore crabs by noninvasive monitoring of heartbeat rate. *Animal Behaviour,* **59,** 705-713.

Samia, D.S., Bessa, E., Blumstein, D.T., Nunes, J.A., Azzurro, E., Morroni, L., Sbragaglia, V., Januchowski-Hartley, F.A. & Geffroy, B. (2019) A meta-analysis of fish behavioural reaction to underwater human presence. *Fish and Fisheries,* **20,** 817-829.

Samia, D.S., Blumstein, D.T., Stankowich, T. & Cooper Jr, W.E. (2016) Fifty years of chasing lizards: new insights advance optimal escape theory. *Biological Reviews,* **91,** 349-366.

Spence, R. & Smith, C. (2005) Male territoriality mediates density and sex ratio effects on oviposition in the zebrafish, *Danio rerio*. *Animal Behaviour,* **69,** 1317-1323.

Stankowich, T. (2008) Ungulate flight responses to human disturbance: a review and meta-analysis. *Biological Conservation,* **141,** 2159-2173.

Stankowich, T. & Blumstein, D.T. (2005) Fear in animals: a meta-analysis and review of risk assessment. *Proceedings of the Royal Society of London, series B: Biological Sciences,* **272,** 2627-2634.

Team, R.C. (2019) R: A language and environment for statistical computing. *R Foundation for Statistical Computing*. Viena, Austria.

Temeles, E.J. (1994) The role of neighbours in territorial systems: when are they'dear enemies'? *Animal Behaviour,* **47,** 339-350.

Therneau, T.M. & Lumley, T. (2014) Package ‘survival’. *Survival analysis Published on CRAN,* **2,** 119.

Tobias, J.A., Sheard, C., Seddon, N., Meade, A., Cotton, A.J. & Nakagawa, S. (2016) Territoriality, social bonds, and the evolution of communal signaling in birds. *Frontiers in Ecology and Evolution,* **4,** 74.

Valenzuela-Sánchez, A., Harding, G., Cunningham, A., Chirgwin, C. & Soto-Azat, C. (2014) Home range and social analyses in a mouth brooding frog: testing the coexistence of paternal care and male territoriality. *Journal of Zoology,* **294,** 215-223.

Ventura, S.P., Passos, D.C., Machado, L.L., Horta, G. & Galdino, C.A. (2017) Escape tactics by a neotropical montane lizard: a comparison of flight responses against natural and nonnatural predators. *Acta Ethologica,* **20,** 9-15.

Ventura, S.P., Galdino, C.A. & Peixoto, P.E.C. (2021) Fatal attraction: territorial males of a neotropical lizard increase predation risk when females are sexually receptive. *Behavioral Ecology and Sociobiology,* **75,** 1-11.

Ydenberg, R.C. & Dill, L.M. (1986) The economics of fleeing from predators. *Advances in the Study of Behavior*, **16,** 229-249.

Wingfield, J.C., Maney, D.L., Breuner, C.W., Jacobs, J.D., Lynn, S., Ramenofsky, M. & Richardson, R.D. (1998) Ecological bases of hormone—behavior interactions: the "emergency life history stage". *American Zoologist,* **38,** 191-206.

Zuur, A., Ieno, E.N., Walker, N., Saveliev, A.A. & Smith, G.M. (2009) *Mixed effects models and extensions in ecology with R*. Springer Science & Business Media.

Supplementary material

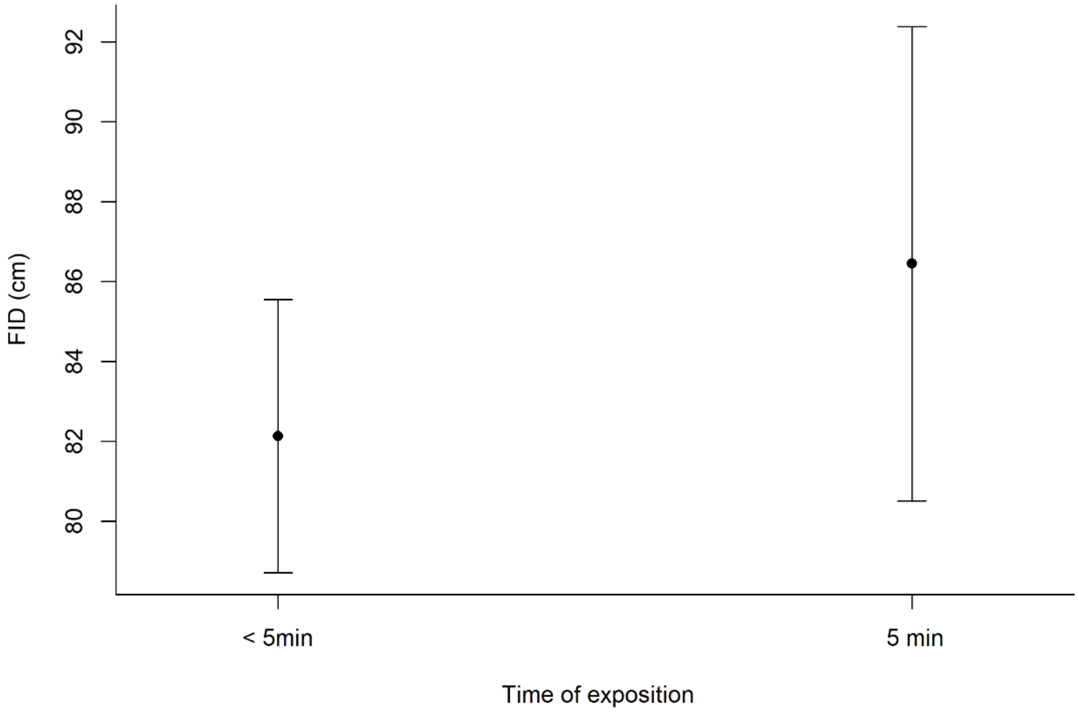

Figure S1 Effect of time of exposition of known and unfamiliar intruders (less or equal to 5 minutes) on the flight initiation distance exhibited by focal resident males of the lizard *Eurolophosaurus nanuzae*. Bars represent standard deviation (N=39).

Table S2 Behaviours exhibited by the lizard *Eurolophosaurus nanuzae* during the exposure of a familiar neighbour and an unfamiliar intruder.

Behaviours	**Percentage**	
	Familiar neighbour	Unfamiliar intruder
Approached their intruder	71%	100%
Arched their backs	0 %	7 %
Attempted to bite	57%	78%
Leg flip	29	29
Moved away from the intruders	14%	0%
Push-up	86%	71%
Tail flick	21 %	43%

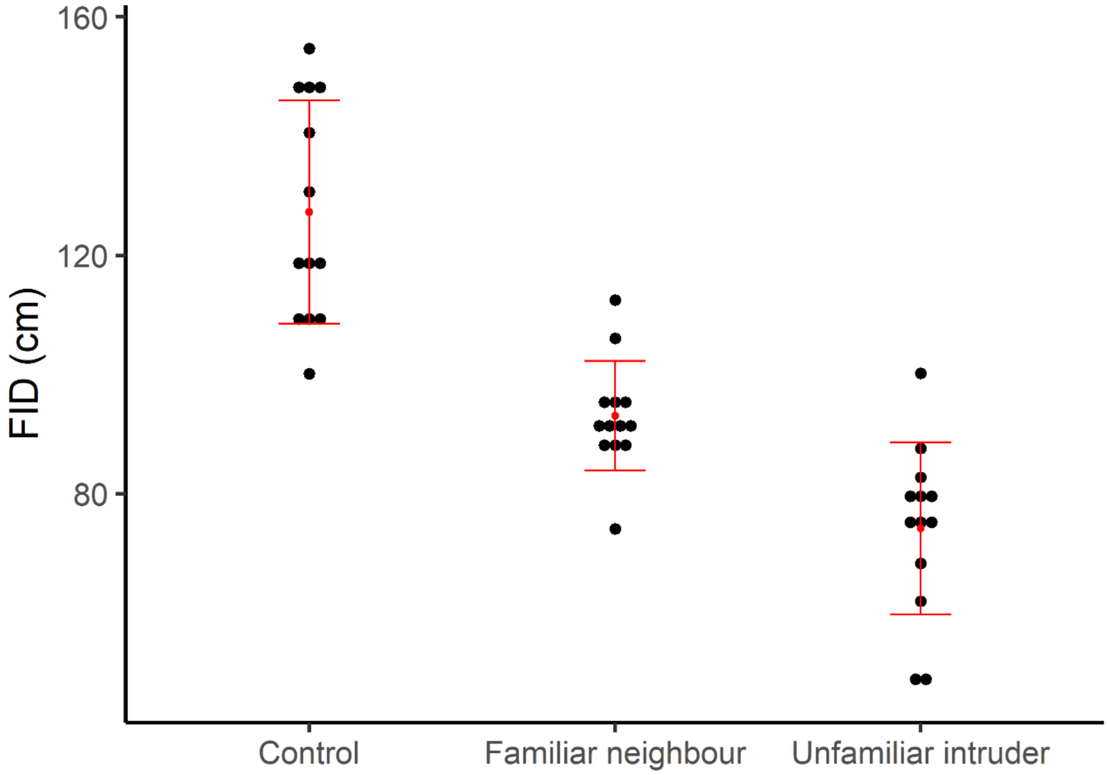

Figure S3 Effect of exhibition and removal of an intruder (familiar neighbour or unfamiliar intruder) or no exhibition of another male (control group) on the flight initiation distance of focal resident males of the lizard *Eurolophosaurus nanuzae* located in their territories without an outlier. Control: no encounter with another male. Bars represent standard deviation (N=39). Mean and standard deviations: control =125.25 ± 18.74; familiar neighbour =93.04 ± 9.19 and unfamiliar intruder =74.18 ± 14.44.

Table S4 Final LMM models without the outlier data with their respective responses, explanatory fixed, covariates and explanatory random variables. First, we built a general model with all covariates and the fixed and random predictor variables included. Then performed a log-likelihood ratio test by comparing this model with a null model without the fixed explanatory variables. Second, we made a new comparison between the general model and a new model without the treatment variable.

Response variable	**Explanatory fixed variables**	**Covariates**	**Explanatory random variable**	**Comparisons between models**	**N**	**χ^2(df)**	**P**
FID	Treatment	Body weight	Male identity, date, number and order of treatment,	Full model x Null model	39	$51.18_{(4)}$	<0.001
		Temperature		Full model x Model without treatment	39	$50.47_{(2)}$	<0.001

Capítulo III

Pretendemos submeter o artigo referente a esse capítulo a revista Behavioral Ecology.

Evolving under varying conditions: how female presence and reproductive period may affect the evolution of male escaping decisions

Abstract: In many species, males often suffer predatory attacks while trying to copulate with females. The decision to escape from the predator may depend on the costs and benefits obtained with the escape. In fact, males postpone the decision to escape when a female is present in the territory. However, it is not known how temporal differences in the availability of females and in the chance of retaining them can affect the evolution of escape behaviour. In this work, we used an individual-based simulation model to investigate how variations in current and future reproductive success associated with seasonal variation in female sexual receptivity can affect the evolution of escape decisions of males. We observed that the modulation of the male escape decision is favored if there is little chance of female retention for males postpone escape (in contrast to scenarios in which the chances of retaining females are high). But once the chance of retention is low, variations in female abundance between the reproductive and non-reproductive periods appear to have a secondary effect on the evolution of escaping decisions. When the chance of retaining females by postponing escape was high, males that never escape from the predator are favored, and this was independent of seasonal variations in female abundance. Thus, we suggest that the evolution of male escaping decisions is strongly affected by the chances of retaining females by postponing escaping when females are nearby, even when females are sexually unreceptive.

Keywords: anti-predatory strategies, escape behaviour, flight initiation distance, reproductive value and theoretical models

Introduction

Prey decisions about when and how to escape during a predatory attack involve several factors beyond simply detecting the predator (Cooper and Sherbrooke 2016, Samia et al. 2016). On the one hand, prey that escape too early, despite increasing the chance of survival, may pay other costs such as losing of reproductive opportunities or having less available for foraging and territorial defense (Cooper 1999; Martín and López 1999; Cooper and Pérez-Mellado 2004; Pérez-Cembranos 2013). On the other hand, postponing escape increases the risk of being killed (Blumstein 2010; Williams et al. 2014). Therefore, when they detect a potential predator, prey adjust their decision a series of cues that indicate how the costs of escaping compare with the risk of predation (Hemmi 2005; Moller et al. 2011).

For species in which males defend mating territories, adjusting in the decision to escape can be especially. On the one hand, actively defending a mating site can make those animals more exposed to predators (Komdeur and Kats 1999; Cooper and Vitt 2002; Abbey-Lee et al. 2016). On the other hand, if the male flees too soon upon detecting a potential predator and/or is absent too long from the territory, he may lose a reproductive opportunity if a female passes by the territory when he is absent (Martín and López 1999; Martín et al. 2003). Thus, escaping too early when a female is present can be very costly for males of territorial species. In fact, some studies have shown that, in agreement with the optimal escape theory (Ydenberg and Dill 1986) males take longer to escape an approaching predator or spend less time hiding after fleeing when a female is present, possibly to avoid losing a reproductive opportunity (Cooper 1999, 2009; Martín and López 1999; Martín et al. 2003; Reaney 2007). However, tolerating higher predation risks when females are presents may be non-adaptive if the females present in the territory are not sexually receptive. Only two study, to our knowledge, evaluated the effect of female reproductive state on male escaping decisions. The first found no difference in male risk-taking behavior between the reproductive and non-reproductive periods but showed that males assume greater risk in the presence of females (Gruber et al 2019). The second, showed that males respond to both female presence and female reproductive period when deciding when to flee from a predator. However, males tolerate higher predation risks in the presence of females even when the female are not fertile (Ventura et al. 2021). These results is unexpected under the optimal escape theory because taking a higher predatory risk when an unfertile increases the chances of being preyed without increasing the immediate chance of breeding.

The fact that males tolerate higher predation risks in the presence of females, even during periods of the year in which the females are infertile, might be due to males trying to keep females in the territory for future mating opportunities (Weiss 2002; Hayes et al. 2004). Additionally, the number of females available may vary between seasons (Altmann 1990; Cappozzo et al. 2008). But trying to keep the females in the non-reproductive season should have a small effect on male future reproduction, unless the courted females remain with males until they become fertile. Thus, males may postpone their escape whenever there are females nearby if this increases the male reproductive output during the reproductive season. Thus, the evolution of male escape decisions may depend on how much male current investment in females affects his future reproductive success. But to our knowledge, studies evaluating the evolution of this type of adjustment are lacking. Perhaps this occurs because the empirical evaluation of the evolutionary patterns of escape behaviour is impractical for many species due to their long generation time, which makes an experimental approach challenging. An alternative approach involves the use of simulation models that allow assessing the extent to which relative differences in current and future reproductive benefit can predict variation in male escape decisions.

Most theoretical models that attempt to assess the evolution of escape decisions assess the impact of decisions on either current reproductive success or future reproductive success, but not both (Clark 1994; Jablonszky 2018). However, there are numerous species in which female fertility may vary throughout the year (Ziegler et al. 2000; Vitt and Caldwell 2014). This temporal variation in female fertility can also influence the current and future reproductive success of males because only during the female reproductive period do males have a real chance of reproducing.

In this work, we used an individual-based simulation model to investigate how variations in current and future reproductive opportunities associated with seasonal variation in female fertility can affect the evolution of escape decisions of males. We hypothesized when male investment in females have a low impact on future reproductive success, the evolution of male escaping decisions will be strongly affected by temporal variations in female fertility. In contrast when male investment in females has a high impact on future reproductive success, temporal variation in female fertility will have a minor effect on the evolution of male escaping decisions.

Methods

General description and model purpose.

To evaluate the relative importance of the presence of the female and her reproductive period in the evolution of escape behaviour of males, we built an individual-based evolutionary model. We used the distance between the predator and prey when the prey begins to escape (Flight Initiation Distance - FID) as a measure of the risk tolerance of males. We opted to use the FID because it allows estimating the predatory risk tolerated by the prey based on the distance the prey allows the predator to approach and also the capacity of prey animals to avoid predators (Samia et al. 2016). The key feature of the model is to allow males to reduce their FID if a female is nearby). We simulated two seasons during the year: a non-reproductive period followed by reproductive period of females. In each season, males had some chance of surviving a predatory attack and to retain a visiting female in the territory until she becomes fertile. The survival chance was positively related to the FID exhibited by the male, while the chance of retaining a female that visited the territory was inversely related to the FID. At the end of the reproductive season, the surviving males that retained females in their territory reproduced and the offspring inherited a FID value similar to the father. To obtain scenarios that represented variations in the importance of male investment in females during the non-reproductive and reproductive seasons and in female availability during the year, we varied the correlation between the FID and the chances of retaining a female in the territory and the number of females available to males in each season.

Model description

We structured the model as follows: first we created 100 males, with each individual having its own FID value. The FID values were randomly drawn from a normal distribution with a mean of 70 cm and a standard deviation of 20 cm. After this, we created a group of females and distributed them randomly among males. The number of females distributed varied between scenarios. For males that had any females in their territory, we subtracted a value from their FID. This new value represented the actual FID that each male will exhibit when attacked by a predator. The value used to subtract from the FID for each male was randomly drawn from a normal distribution with mean of 10 cm and standard deviation of 3 cm. After determining the actual FID of each male, we stablished a survival probability associated with the actual FID. This probability followed a binomial distribution and was inversely related to the FID (r= -0.1). After that, we simulated a predatory attack on all males in the population and determined which ones survived based on the survival probability. We chose to simulate a predatory attack on all males in the population to assess which males survived this attack. Additionally, we determined which males kept females in their territories based on a probability of retaining females that was inversely associated with FID. At the end of the non-reproductive period, we excluded from the model all males that did not survive the predatory attack and redistributed the females that were eventually in the territory of a dead male among the surviving males. We also redistributed the females that were not retained in the territories of the males who survived the predatory attack.

We simulated the reproductive period of the females after the non-reproductive one. For the reproductive period, we repeated the same steps we described earlier but added a new group of females in the territories of the males. The number of females added in each season varied across scenarios (Table 1). This simulation started with the females present in the non-reproductive period and the males that survived the predatory attack. During the reproductive period, we maintained the base FIDs of males with the same value as the one used in the non-reproductive period. However, we increased the reduction in FID because we expected that males should invest more in females due to immediate chances of reproduction.

After simulating the reproductive season, we created a new generation of males by simulating the reproduction of the females that the males kept in their territories. Each female generated four males. The FID of each newly generated individual was randomly drawn from a normal distribution with mean value equal to the FID of the father and standard deviation of 2 cm. When the breeding females collectively generated more than 100 individuals, we randomly selected 100 of them to compose the next generation of males.Therfore, males that had more offspring because they retained more females were better represented in the next generation. After this, we replicated the entire model considering the offspring as a new set of adult males and determining a new set of females arriving at the beginning of each season.

We ran these simulations over 1000 generations, and, in each replicate, we measured the average actual FID exhibited by males in the population in the presence and absence of females. When we were in doubt about the observed FID pattern over time, we extend the simulation to 2000 generations. Using this model structure, we created 16 scenarios that had different combinations of the proportion of available females in each season (high or low) and the probability of males retaining the female (Table 1). To assess the logical consistency of the model, we also created scenarios that should generate predictable results. In the first scenario, we assumed FID had no impact on the chances of retaining a female in the territory but still affect the survival probability. In the second scenario, we assumed FID had no effect on the survival probability but affect the female retention. If our model shows logical consistency, we expected FID to gradually increase across generations in the first scenario and to approach zero in the second scenario.

Table 1 Scenarios created by changing the proportion of females in habitat and the chance to retain the female in both reproductive and non-reproductive periods of females. H(high), L(low), NR (Non-reproductive period of females) and R (Reproductive period of females). The values related to the proportion of females in the environment were 0.45 when the proportion was low and 0.80 when it was high and the probability of males retaining females in the territory was 0.4 when was low and 0.8 when was high.

PROPORTION OF FEMALES IN HABITAT / CHANCE TO KEEP THE FEMALE	$\mathbf{H_{NR}H_R}$	$\mathbf{L_{NR}L_R}$	$\mathbf{H_{NR}L_R}$	$\mathbf{L_{NR}H_R}$
$\mathbf{H_{NR}H_R}$	$H_{NR}H_R/H_{NR}H_R$	$L_{NR}L_R/H_{NR}H_R$	$H_{NR}L_R/H_{NR}H_R$	$L_{NR}H_R/H_{NR}H_R$
$\mathbf{L_{NR}L_R}$	$H_{NR}H_R/L_{NR}L_R$	$L_{NR}L_R$ / $L_{NR}L_R$	$H_{NR}L_R$ /$L_{NR}L_R$	$L_{NR}H_R$/ $L_{NR}L_R$
$\mathbf{H_{NR}L_R}$	$H_{NR}H_R/H_{NR}L_R$	$L_{NR}L_R$ /$H_{NR}L_R$	$H_{NR}L_R$ /$H_{NR}L_R$	$L_{NR}H_R$/ $H_{NR}L_R$
$\mathbf{L_{NR}H_R}$	$H_{NR}H_R/L_{NR}H_R$	$L_{NR}L_R$ /$L_{NR}H_R$	$H_{NR}L_R$ /$L_{NR}H_R$	$L_{NR}H_R$/ $L_{NR}H_R$

Results

Regarding the scenarios we created to evaluate the logical consistency of our model, we observed that in the first scenario males FID increased over time, while in the second scenario the average FID reached zero (Fig. 1). Regarding the 16 scenarios, we observed two evolutionary patterns. In one of them, the FID decreases over the generations until reaching zero (11 out of the 16 scenarios) and in the other, the FID presented a small increase or decrease, followed by a dynamic equilibrium of small oscillations around a constant mean FID value across generations (5 out of 16 scenarios - Table 2).

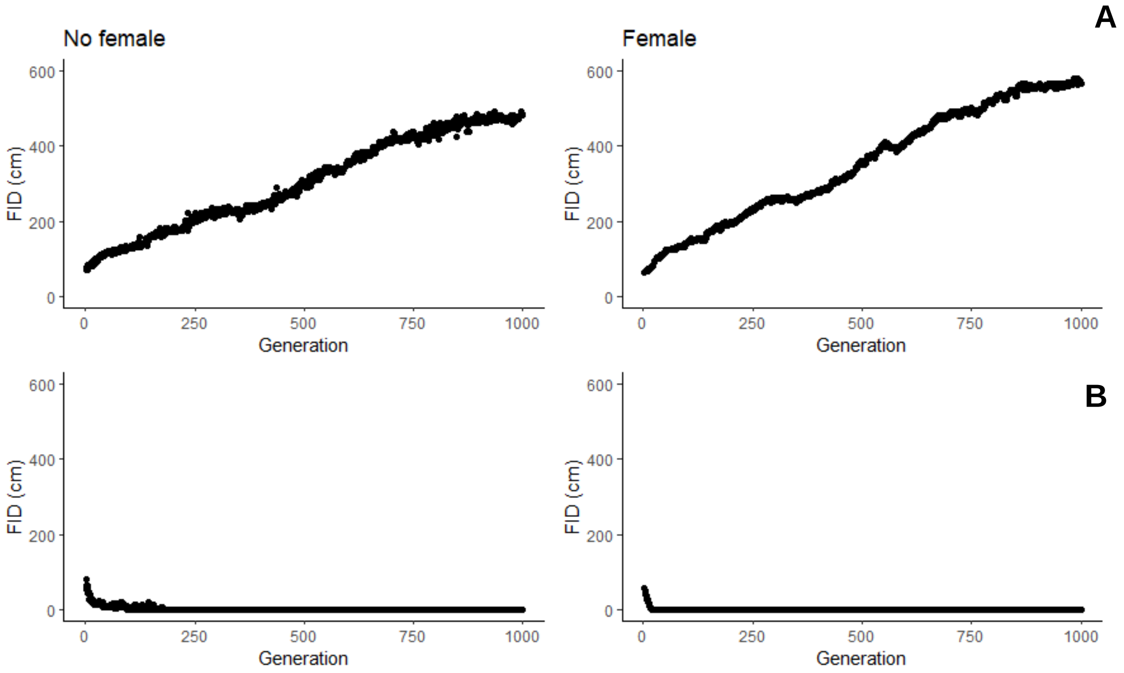

Fig. 1 Scenarios created to evaluate the logical consistency of our model. In the A scenario, we determined the correlation between the FID and the chances of retaining a female in the territory to be zero. In the B scenario, we determined an absence of correlation between the FID and the survival probability.

When males that postponed escaping had high chances of retaining females in both periods or only in the reproductive period, selection favored males that never escaped from the predator, regardless of the proportion of females available (Table 2; Figs. 2 and 3). On the other hand, if the chance of retaining the feale after postponing escaping is low, males that modulated their FID when females were present were selected (Fig. 4). The only exception occurred in the scenario with a high proportion of females in the non-reproductive period and low proportion in the reproductive period (Fig 3c). The other scenarios that also favored the evolution of a FID greater than zero occurred when the chance of retaining the female by postponing escaping was high in the non-reproductive period and low in the reproductive period combined with a low proportion of females in the environment in both periods or with a low proportion of females only in the non-reproductive period (Fig. 5). The average FID exhibited by males was similar among the scenarios with a non-zero FID.

Table 2 Scenarios created by changing the proportion of females in habitat and the chance to retain the female in both reproductive and non-reproductive periods of females.

PROPORTION OF FEMALES IN HABITAT / CHANCE TO KEEP THE FEMALE	**HNRHR**	**LNRLR**	**HNRLR**	**LNRHR**
HNRHR	FID zero	FID zero	FID zero	FID zero
LNRLR	FID greater than zero	FID greater than zero	FID zero	FID greater than zero
HNRLR	FID zero	FID greater than zero	FID zero	FID greater than zero
LNRHR	FID zero	FID zero	FID zero	FID zero

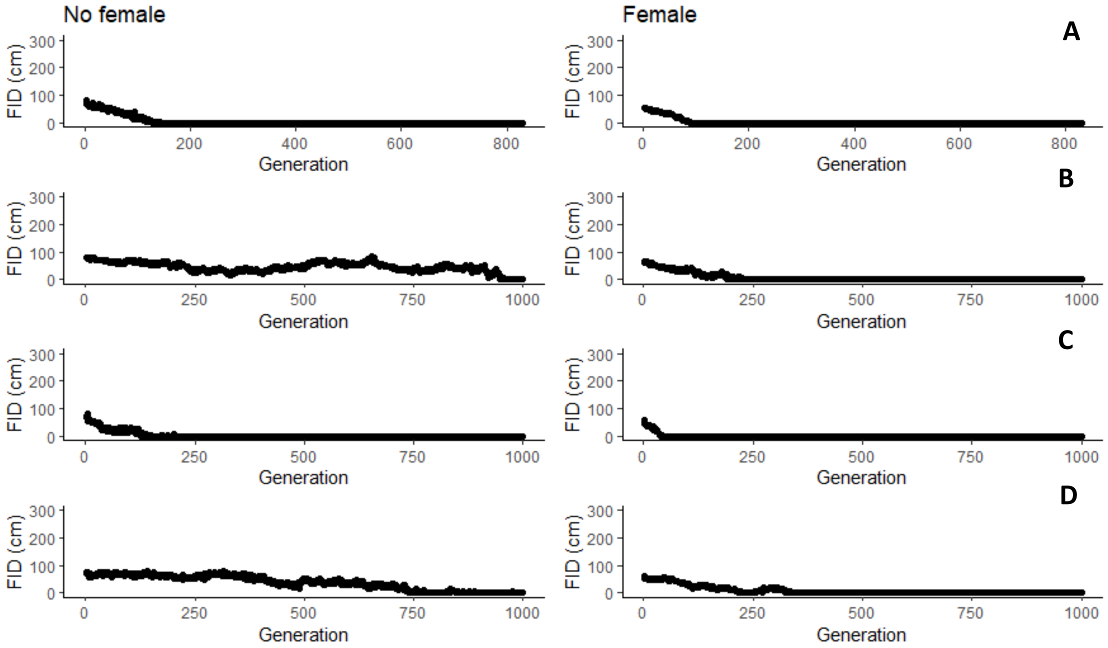

Fig. 2 Evolution of FID throughout 1000 generations in a scenario that: a) the total number of females represents 80% of the males that survived and a negative correlation of 0.8 between the chance of retaining females in the territory during the reproductive e non-reproductive periods; b) the total number of females represents 40% of the males that survived and a negative correlation of 0.8 between the chance of retaining females in the territory during the reproductive e non-reproductive periods; c) the total number of females represents 80% during non-reproductive and 45% in reproductive periods of the males that survived and a negative correlation of 0.8 between the chance of retaining females in the territory during the reproductive e non-reproductive period and d) the total number of females represents 45% during non-reproductive and 80% in reproductive periods of the males that survived and a negative correlation of 0.8 between the chance of retaining females in the territory during the reproductive e non-reproductive period.

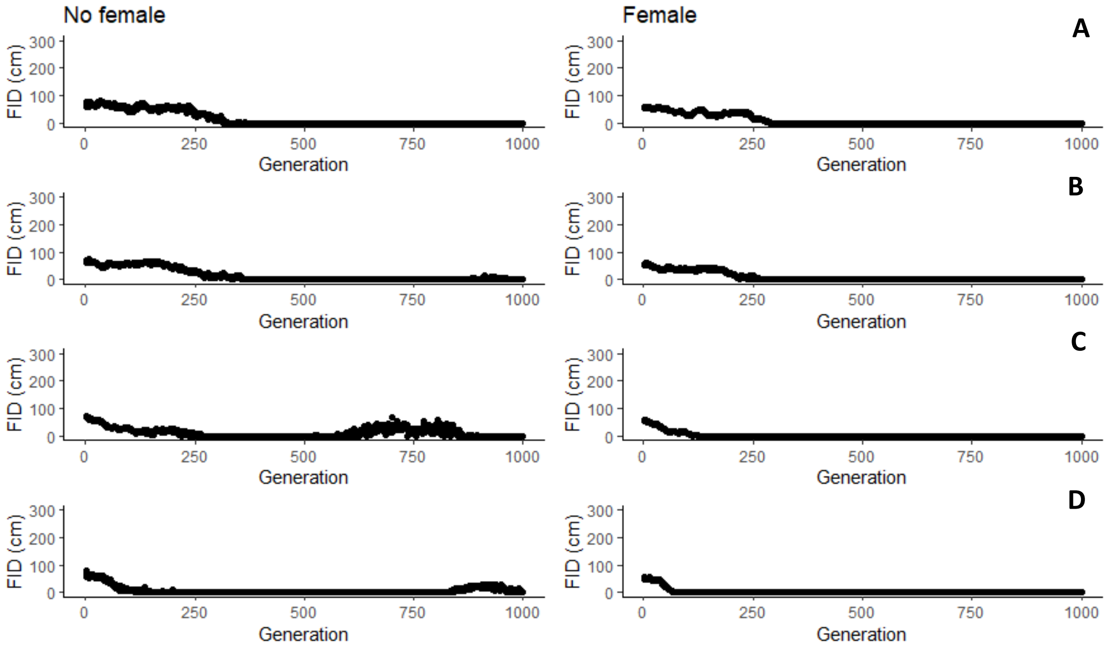

Fig. 3 Evolution of FID throughout 1000 generations in a scenario with: a) the total number of females representing 80% of the males that survived and a negative correlation of 0.4 between the chance of retaining females in the territory during the non-reproductive periods and 0.8 in reproductive period; b) the total number of females representing 45% of the males that survived and a negative correlation of 0.4 between the chance of retaining females in the territory during the non-reproductive periods and 0.8 in reproductive period; c) the total number of females representing 80% during non-reproductive and 45% in reproductive periods of the males that survived and a negative correlation of 0.4 between the chance of retaining females in the territory during the non-reproductive periods and 0.8 in reproductive period and d) the total number of females representing 45% during non-reproductive and 80% in reproductive periods of the males that survived and a negative correlation of 0.4 between the chance of retaining females in the territory during the non-reproductive periods and 0.8 in reproductive period.

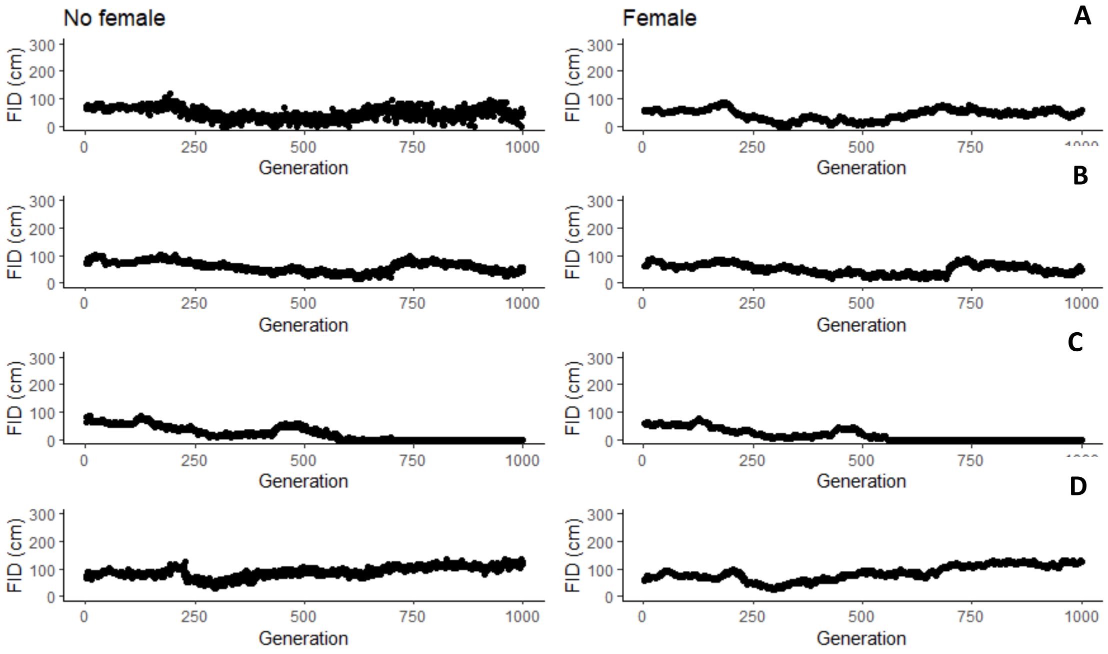

Fig. 4 Evolution of FID throughout 1000 generations in a scenario with: a) the total number of females representing 80% of the males that survived and a negative correlation of 0.4 between the chance of retaining females in the territory during the reproductive e non-reproductive periods; b) the total number of females representing 45% of the males that survived and a negative correlation of 0.4 between the chance of retaining females in the territory during the reproductive e non-reproductive periods; c) the total number of females representing 80% during non-reproductive and 45% in reproductive periods of the males that survived and a negative correlation of 0.4 between the chance of retaining females in the territory during the reproductive e non-reproductive period and d) the total number of females representing 45% during non-reproductive and 80% in reproductive periods of the males that survived and a negative correlation of 0.4 between the chance of retaining females in the territory during the reproductive e non-reproductive period.

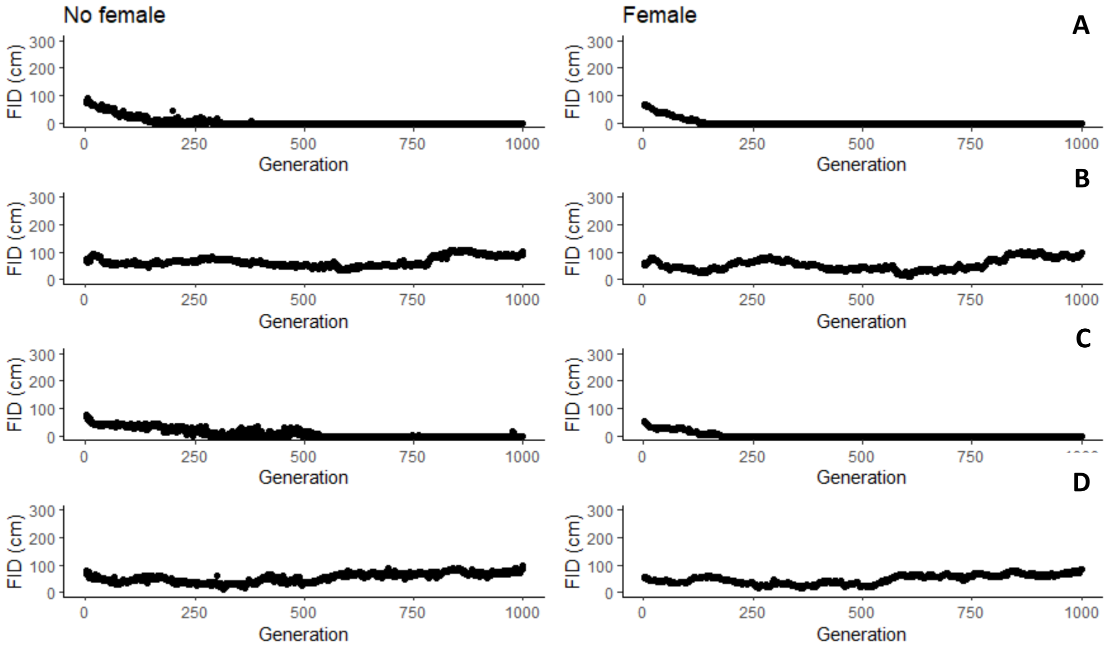

Fig. 5 Evolution of FID throughout 1000 generations in a scenario with: a) the total number of females representing 80% of the males that survived and a negative correlation of 0.8 between the chance of retaining females in the territory during the non-reproductive periods and 0.4 in reproductive period; b) the total number of females representing 45% of the males that survived and a negative correlation of 0.8 between the chance of retaining females in the territory during the non-reproductive periods and 0.4 in reproductive period; c) the total number of females representing 80% during non-reproductive and 45% in reproductive periods of the males that survived and a negative correlation of 0.8 between the chance of retaining females in the territory during the non-reproductive periods and 0.4 in reproductive period and d) the total number of females representing 45% during non-reproductive and 80% in reproductive periods of the males that survived and a negative correlation of 0.8 between the chance of retaining females in the territory during the non-reproductive periods and 0.4 in reproductive period.

Discussion

In this study we built an individual-based model to investigate possible evolutionary routes of the escaping decision rules of males in scenarios that provided different combinations of the chances of retaining females when postponing escaping and the proportion of females available in the reproductive and non-reproductive seasons. An interesting result is that for most scenarios, the FID exhibited by males in the presence of females was predicted to go to zero. Our model indicates that FID modulation in response to the presence of females seems to be favored under very specific conditions that occur when males have a low chance of retaining the female in the territory in both periods or in the reproductive period. Thus, our model shows that an initial condition for the modulation of the

FID is the low chance of retention of the females. However, it is important to highlight that when the correlation between FID and chance of retaining females was zero, the FID increased over generations. Thus, although low, it is necessary that males have same chance of retaining females for the FID modulation becomes evolutionarily stable.

Specifically for the scenario in which the chance of retaining females is high in the non-reproductive period and low in the reproductive period, the evolution of an FID greater than zero is favored if it is combined with a low proportion of females in both periods or a low proportion of females in the non-reproductive period. Although these scenarios represent the smallest proportion of the possible scenarios in our model, they are common in nature. In numerous species that the operational sex ratio is biased towards males. (Gonzalez-Soriano and Cordoba-Aguilar 2003; Reading and Backwell 2007; Suzuki et al. 2010; York and Baird 2015), indicating that proportion of females available to mate is low throughout year. In addition, species in which the number of females is lower in the non-reproductive period than in the reproductive period are also reported (Hissmann 1990; Kingma et al. 2008). The scenario where females are scarce in the non-reproductive period is interesting, especially in species in which males court or copulate with females when they are not reproductive. Our result indicated that such behaviours is favored if males have a smaller chance to retain the females in to became fertile. Thus, males may be making a high current investment, that may generate the future return. However, studies evaluating the influence of female fertility on male escaping decisions, or even, on male aggressiveness are very rare (see Moller et al. 2010). To our knowledge, there two study that investigated the influence of female fertility in male escaping decisions (Gruber et al. 2019; Ventura et al. 2021), but only one showed that in fact, males showed a greater FID variation in response to female presence than female reproductive period (Ventugra et al. 2021).

Regarding the scenarios that favored the evolution of a zero-FID, it is important to note that they consisted of a high proportion of females during both season or only in the reproductive season. Such scenarios led to a zero-FID pattern even with a low chance of retaining females in both periods. The high proportion of females in such scenarios is probably inducing a major proportion of males to reduce their FID during predatory attacks. This leaded to the death of a greater portion of males in the non-reproductive season. Consequently, the sex ratio during the reproductive season becomes closer to equality or biased for females, as females that were available or that were with a male who died in the non-reproductive season are redistributed to males present in the reproductive season. With this sex ratio close to equality or biased for females, males can monopolize many females by postpone the escape. Therefore, these males have created a strong selective pressure that favored FID reduction. Since the predation pressure is low in our model, the gain with the increasing the number of females and consequently, the reproduction, compensates for the greater risk of predation by postponing escape.

Our results also show an overall pattern of FID equal to zero when males have high chances of keeping females in territories in both periods or only in the reproductive period. This indicates that when the chances of retaining females are high, males should stop escaping from predators, regardless of proportion of females in the environment. However, there are no studies that have evaluated how the chance of female retention influences the anti-predatory strategy. Furthermore, we believe that these high-chance female retention scenarios are often rare in the nature. First because females are usually a limited resource for males and second because keeping females can be energetically costly since courting behaviours preclude other activities important to survival, such as foraging (Willis and Dill 2007) and predator avoidance (Cothran 2004). Although it is widely accepted that animals alter their behaviours due to the presence of predators (Candolin 1997; ter Hofstede 2008), there are species that maintain their courtship or spawning behaviour even with the presence of the predator (e.g. Hazlett and Rittschof 2000; Magnhagen 1990). Despite having evidence that males do not flee when they have opportunities to mate, this is more associated with a low chance of getting a new mating.

In general, FID modulation seems to be favored if there is little, but nonzero chance of female retention in the territory, since the proportion of females in the environment tends to be lower. But once the chance of retention is low, seasonal variations in female abundance appear to have a secondary effect on the evolution of FID. Thus, our study makes it possible to predict that in species in which males exhibit alterations in FID, this alteration is more intense in response to the presence of the female and not to her fertility. It would be interesting if more studies were carried out, especially in species that have a marked breeding season in the year or that have a high availability of females to assess whether in fact males assume high predatory risk, without modulating the FID.

Data Availability Statement

Data available from the OSF https://osf.io/n8s6k/?view_only=3cc571c1b33447a0aa128f8ddcd22326 (Ventura et al. 2022)

References

Abbey-Lee RN, Kaiser A, Mouchet A & Dingemanse NJ (2016) Immediate and carry-over effects of perceived predation risk on communication behavior in wild birds. Behavioral ecology 27: 708-716E

Altmann J (1990) Primate males go where the females are. Animal Behaviour 39: 193-195.

Blumstein DT (2010) Flush early and avoid the rush: a general rule of antipredator behavior? Behavioral Ecology 21: 440-442.

Candolin U (1997) Predation risk affects courtship and attractiveness of competing threespine stickleback males. Behavioral Ecology and Sociobiology 41: 81-87.

Cappozzo HL, Túnez JI & Cassini MH (2008) Sexual harassment and female gregariousness in the South American sea lion, Otaria flavescens. Naturwissenschaften 95: 625–630.

Colin WC (1994) Antipredator behavior and the asset-protection principle. Behavioral Ecology 5: 159-170.

Cooper WEJr (1999) Tradeoffs between courtship, fighting, and antipredatory behavior by a lizard, *Eumeces laticeps*. Behavioral Ecology and Sociobiology 47:54-59.

Cooper WEJr & Sherbrooke WC (2016) Strategic escape direction: orientation, turning, and escape trajectories of zebra-tailed lizards (*Callisaurus draconoides*). Ethology 122:542-551.

Cooper WEJr (2000) Tradeoffs between predation risk and feeding in a lizard, the broad headed skink (Eumeces laticeps). Behaviour 137: 1175-1189.

Cooper WEJr & Pérez-Mellado V (2004) Tradeoffs between escape behavior and foraging opportunity by the Balearic lizard (Podarcis lilfordi). Herpetologica 60: 321-324.

Cooper WEJr (2009) Flight initiation distance decreases during social activity in lizards (*Sceloporus virgatus*). Behavioral Ecology and Sociobiology 63: 1765-1771.

Cothran RD (2004) Precopulatory mate guarding affects predation risk in two freshwater amphipod species. Animal Behaviour 68: 1133-1138.

González-Soriano E & Córdoba-Aguilar A (2003) Sexual behaviour in Paraphlebia quinta Calvert: male dimorphism and a possible example of female control (Zygoptera: Megapodagrionidae). Odonatologica 32: 345-353.

Gruber J, Kahn A & Backwell PR (2019) Risks and rewards: balancing costs and benefits of predator avoidance in a fiddler crab. Animal behaviour 158: 9-13.

Hazlett B A & Rittschof D (2000) Predation–reproduction conflict resolution in the hermit crab, Clibanarius vittatus. Ethology: Research Papers 106: 811-818.

Hemmi JM (2005) Predator avoidance in fiddler crabs: 2. The visual cues. Animal Behaviour 69: 615-625.

Hissmann K (1990) Strategies of mate finding in the European field cricket (Gryllus campestris) at different population densities: a field study. Ecological Entomology 15: 281-291.

Jablonszky M, Szász E, Krenhardt K et al. (2018) Unravelling the relationships between life history, behaviour and condition under the pace-of-life syndromes hypothesis using long-term data from a wild bird. Behavioral Ecology and Sociobiology 72: 52.

Kingma SA, Szentirmai I, Székely T. et al. (2008) Sexual selection and the function of a melanin-based plumage ornament in polygamous penduline tits Remiz pendulinus. Behavioral Ecology and Sociobiology 62: 1277–1288.

Komdeur J & Kats RK (1999) Predation risk affects trade-off between nest guarding and foraging in Seychelles warblers. Behavioral Ecology10: 648-658.

Magnhagen, C (1990) Reproduction under predation risk in the sand goby, Pomatoschistus minutes, and the black goby, Gobius niger: the effect of age and longevity. Behavioral Ecology and Sociobiology 26: 331-335.

Martín J & López P (1999) Nuptial coloration and mate-guarding affect escape decisions of male lizards, *Psammodromus algirus*. Ethology 105: 439-447.

Martín J, López P & Cooper WEJr (2003) Loss of mating opportunities influences refuge use in the Iberian rock lizard, *Lacerta monticola*. Behavioral Ecology and Sociobiology 54: 505–510.

Moller AP, Christiansen SS & Mousseau TA (2011). Sexual signals, risk of predation and escape behavior. Behavioral Ecology 22: 800-807.

Pérez-Cembranos A, Pérez-Mellado V & Cooper WEJr (2013) Predation risk and opportunity cost of fleeing while foraging on plants influence escape decisions of an insular lizard. Ethology 119: 522-530.

Reading K & Backwell P (2007) Can beggars be choosers? Male mate choice in a fiddler crab. Animal Behaviour 74: 867e872.

Reaney LT (2007) Foraging and mating opportunities influence refuge use in the fiddler crab, *Uca mjoebergi*. Animal Behaviour 73: 711-716.

Samia DSM, Blumstein DT, Stankowich T & Cooper WEJr (2016) Fifty years of chasing lizards: new insights advance optimal escape theory. Biol Rev 91: 349-366.

Suzuki S, Kuwamura T, Nakashima, Y. *et al.* (2010) Social factors of group spawning as an alternative mating tactic in the territorial males of the threespot wrasse *Halichoeres trimaculatus*. Environ Biol Fish 89: 71-77.

Ventura SP, Galdino C A & Peixoto PEC (2021) Fatal attraction: territorial males of a neotropical lizard increase predation risk when females are sexually receptive. Behavioral Ecology and Sociobiology 75**:** 1-11.

Vitt LJ & Caldwell JP (2014) *Herpetology: an introductory biology of amphibians and reptiles*. Academic Press, San Diego

Weiss SL (2002) Reproductive signals of female lizards: pattern of trait expression and male response. Ethology 108: 793-813.

Williams DM, Samia DSM, Cooper WEJr & Blumstein DT (2014) The flush early and avoid the rush hypothesis holds after accounting for spontaneous behavior. Behavioral Ecology 25: 1136-1147.

Willis PM & Dill LM (2007) Mate guarding in male Dall's porpoises (*Phocoenoides dalli*). Ethology 113: 587-597.

Ydenberg RC & Dill LM (1986) The economics of fleeing from predators. Advances in the Study of Behavior 16:229-249.

York JR & Baird TA (2015) Testing the adaptive significance of sex-specific mating tactics in collared lizards (*Crotaphytus collaris*). Biological Journal of the Linnean Society 115: 423-436.

Ziegler T, Hodges K, Winkler P & Heistermann M (2000) Hormonal correlates of reproductive seasonality in wild female Hanuman langurs (*Presbytis entellus*). Am J Primatol 51: 119-134.

CONCLUSÕES

A presente tese contribuiu para uma maior compreensão das decisões de fuga feitas pelas presas. Na parte empírica, nós conseguimos preencher duas lacunas na literatura sobre como variações sutis nos custos sociais podem influenciar as decisões de fuga das presas. Nossos resultados mostraram que os animais têm uma resposta anti-predatória bem refinada, a ponto de os machos modularem seu comportamento de acordo com a presença de fêmeas sexualmente receptivas e também de acordo com o grau de familiaridade de potenciais intrusos. Isso mostra que as presas modulam as estratégias de fuga de acordo com o contexto social que estão inseridas. O modelo de simulação que fizemos no capítulo III foi complementar aos resultados que obtivemos sobre como a presença e a receptividade sexual das fêmeas influenciam o comportamento anti-predatório dos machos. Nosso modelo mostra que a presença da fêmea parece ser o fator mais importante na evolução das táticas anti-predatórias dos machos, pelo menos em espécies em que existe uma baixa proporção de fêmeas em relação aos machos na população. Além disso, observamos que, as decisões dos machos podem estar interligadas, com machos escolhendo uma tática que muitas vezes não garante um sucesso reprodutivo atual muito alto, mas que no futuro pode proporcionar um aumento, mesmo que pequeno, no seu sucesso reprodutivo.