



Universidade de Brasília - UnB
Instituto de Ciências Biológicas - IB
Programa de Pós-Graduação em Ecologia

Evolução do Dimorfismo Sexual de Tamanho em Thomisidae (Araneae) e *Trichonephila clavipes* (Araneae: Araneidae)

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Brasília, Brasil
Março/2023

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Dissertação apresentada ao Programa
de Pós-Graduação em Ecologia da
Universidade de Brasília como parte
dos requisitos para a obtenção do título
de Mestre em Ecologia.

Orientador: Felipe M. Gawryszewski

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RESUMO

O dimorfismo sexual de tamanho (*Sexual size dimorphism*; SSD) é um fenômeno que ocorre em quase todos grupos animais. O Dimorfismo com viés para as fêmeas, isto é, fêmeas maiores que machos, é o mais frequente. Aranhas, em particular, possuem o maior SSD entre os animais terrestres. O gigantismo das fêmeas nesse grupo é comumente associado à seleção por fecundidade, hipótese que prediz que fêmeas maiores colocam mais ovos, e conseqüentemente possuem maior aptidão. Porém, para evolução do SSD, além da mudança de tamanho corporal de um sexo, é necessário que o outro não o acompanhe. O modelo do equilíbrio diferencial propõe que pressões evolutivas diferentes agem sobre o tamanho corporal dos sexos, quando essas pressões são antagônicas o SSD evolui. Nós investigamos a evolução de dimorfismo sexual em aranhas, utilizando a família Thomisidae e a espécie *Trichonephila clavipes* (Araneidae) para avaliar como essas pressões evolutivas agem sobre o tamanho de cada sexo. Na família Thomisidae, visamos identificar quais fatores são responsáveis para o aumento de tamanho corporal das fêmeas. Corpos grandes necessitam de mais energia para se sustentar. A família Thomisidae possui uma grande diversidade de estratégias de forrageamento, e algumas, como forragear em flores e mimetismo agressivo, podem fornecer uma quantidade maior de alimento e permitir o aumento de tamanho corporal. Para realizar esse trabalho coletamos medidas de tamanho de espécies de tomisídeos da literatura e as classificamos com base nas estratégias de forrageamento. Nossos resultados indicam que espécies que forrageiam em flores ou adotam mimetismo agressivo possuem fêmeas significativamente maiores e machos significativamente menores que as outras espécies. Esses resultados sugerem que as estratégias de forrageamento possuem um papel central na evolução de SSD. Em *T. clavipes* visamos avaliar quais pressões impedem que os machos aumentem de tamanho com as fêmeas. Duas hipóteses complementares foram propostas como limitantes do tamanho dos machos, a protandria e a hipótese da gravidade. A protandria como forma de limitar o tamanho de machos sugere que machos que se desenvolvem mais rápido possuem vantagens reprodutivas em um contexto de *scrambled competition*: machos que se desenvolvem mais rápido conseguem chegar às fêmeas com pouca ou nenhuma competição. A hipótese da gravidade propõe que existe uma relação positiva entre tamanho e velocidade de escalada, até um limite em que o aumento de tamanho não favorece a velocidade de escalada. Nos hipotetizamos que há um *trade-off* entre protandria e velocidade de escalada em *T. clavipes*. Para testar essa hipótese acompanhamos cinco localidades de *T. clavipes* no Distrito Federal e avaliamos o tamanho dos machos durante o período reprodutivo. Para avaliar o efeito do tamanho na velocidade de escalada, realizamos experimentos de escalada com machos e fêmeas. Nossos resultados indicam que machos protândricos são maiores que machos tardios, e também, que há uma relação positiva entre velocidade de escalada e tamanho para machos, mas não para fêmeas. Esses resultados indicam que machos maiores possuem maior *fitness*, mas que o tamanho

de machos pode ser limitado pelos impactos da gravidade em sua mobilidade, visto que fêmeas, muito maiores, não obtém vantagens em velocidade de escalada.

ABSTRACT

Size sexual dimorphism (SSD) is a phenomenon that occurs in almost all animal groups. Female-biased dimorphism, that is, females larger than males, is the most common, occurring in most species. Spiders, in particular, have the highest female-biased SSD among terrestrial animals. The gigantism of females in this group is commonly associated with fecundity selection, a hypothesis that predicts that larger females lay more eggs, and consequently have greater fitness. However, for the evolution of the SSD, in addition to the change in the body size of one sex, it is necessary that the other does not accompany it. The differential equilibrium model proposes that different evolutionary pressures act on the body size of the sexes, when these pressures are antagonistic, the SSD evolves. We investigated the evolution of sexual dimorphism in spiders, using the family Thomisidae and the species *Trichonephila clavipes* (Araneidae) to assess how these evolutionary pressures act on the size of each sex. In the family Thomisidae, we aimed to identify which factors are responsible for the increase in female body size. Large bodies need more energy to sustain themselves, the Thomisidae family has a wide range of foraging strategies, some, such as foraging on flowers and aggressive mimicry, can provide higher energy intake and allow for an increased body size. To carry out this work, we extracted tomisids measurements of the size from the literature, and classified them into foraging strategies. Our results indicate that species that forage on flowers or adopt aggressive mimicry have significantly larger females and significantly smaller males than other species. These results suggest that foraging strategies play a central role in the evolution of SSD. In *T. clavipes* we aim to evaluate which pressures prevent males from increasing in size with females. Two complementary hypotheses have been proposed as limiting male size, protandry and the gravity hypothesis. Protandry as a way to limit male size suggests that males that develop faster have reproductive advantages in a context of scrambled competition, males with shorter development can reach females with little or no competition. The gravity hypothesis proposes that there is a positive relationship between size and climbing speed, up to a limit where increasing size does not favor climbing speed. We hypothesize that there is a trade-off between protandry and climbing speed in *T. clavipes*. To test this hypothesis, we accompanied *T. clavipes* from five localities at Distro Federal in Brazil and evaluated the size of males during the reproductive period. To evaluate the effect of size on climbing speed, we performed climbing experiments with males and females. Our results indicate that protandrous males are larger than late males, and also, that there is a positive relationship between climbing speed and size for males, but not for females. These results indicate that larger males have higher fitness, but that the size of males might be limited by the impacts of gravity on their mobility, as females, much larger than males, do not gain climbing advantages due to their increased size.

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1. INTRODUÇÃO

O Dimorfismo Sexual de Tamanho (*Sexual size dimorphism*; SSD) é a diferença de tamanho entre machos e fêmeas. Há muito este fenômeno é estudado (Darwin, 1871), mas ainda está longe de ser esclarecido. A origem do SSD é variada, surgindo devido às pressões da seleção sexual ou por machos e fêmeas ocuparem nichos distintos que selecionam diferentes tamanhos corporais (Hedrick & Temeles, 1989). Darwin (1871) propôs que forte competição entre machos tende a resultar em SSD com machos maiores. Na maioria dos grupos de aves, quando presente, o SSD possui um viés para os machos e de fato está associado com competição intrasexual e *displays* de agilidade (Szekely et al., 2007). Em mamíferos, os machos podem ser até 45% maiores do que fêmeas, e da mesma forma que em aves, o nível do SSD está associado a sistemas de acasalamento com maior competição intrasexual (Lindenfors et al., 2007).

Por outro lado, o SSD com viés para as fêmeas ocorre em um maior número de grupos animais (anfíbios (Kupfer, 2007); cobras e tartarugas (Cox et al., 2007); peixes (Horne et al., 2020); insetos (Blanckenhorn et al., 2007) e aranhas (Foellmer & Moya-Larano, 2007; Hormiga et al., 2000; Huber, 2005b; Kuntner et al., 2019; Kuntner & Coddington, 2020; Vollrath & Parker, 1992). Seleção por fecundidade é, na maior parte dos casos, a principal explicação para a origem de SSD com fêmeas maiores. Sugere-se que estas conseguem produzir uma prole maior ou de melhor qualidade (Darwin, 1871; Honěk, 1993; Prenter et al., 1999). Assim, o aumento evolutivo do tamanho das fêmeas não se dá por seleção sexual, mas sim, seleção natural.

Contudo, para que o SSD ocorra, a alteração de tamanho de um sexo deve ser despareada da alteração de outro sexo. Isto é, o SSD surge a partir da diferença de tamanho entre os sexos e não apenas da alteração evolutiva de um deles. Dessa forma, o SSD pode resultar em relações antagonísticas intraloco onde alteração de tamanho que beneficiaria um sexo não necessariamente é proveitosa para o outro (Fairbairn, 2007). As relações antagônicas intraloco são, em sua maioria, devido ao fato de que a maior parte do material genético responsável pela alteração de

tamanho corporal é autossomal e compartilhada por ambos os sexos. Dessa forma, existem limitações genéticas na variação de tamanho de um dos sexos sem influenciar o outro (Rice, 1984). O modelo do equilíbrio diferencial sugere que machos e fêmeas sofrem pressões evolutivas diferentes em seu tamanho ótimo, o resultado desses vetores antagônicos é a perda de correlação genética entre os sexos e a evolução de SSD (Andersson, 1994; Blanckenhorn, 2005).

Aranhas, na grande maioria dos grupos, possuem um marcante SSD com viés para as fêmeas (Coddington et al., 1997; Head, 1995; Hormiga et al., 2000; Kuntner & Coddington, 2020; Prenter et al., 1999; Vollrath & Parker, 1992) e este pode chegar a casos extremos. Em *Arachnura logio* (Araneae, Araneidae), por exemplo, a média do tamanho das fêmeas pode ser até 14,8 vezes maior que o macho (Hormiga et al., 2000), enquanto em *Trichonephila plumipes* (Araneae, Araneidae) os machos são em média 40 vezes menores que as fêmeas (Elgar & Fahey, 1996). Na maioria dos casos assume-se um passado monomórfico para aranhas e se sugere que o aumento evolutivo das fêmeas resulta em SSD (Head, 1995; Prenter et al., 1999; Hormiga et al., 2000). O principal motivo do aumento evolutivo das fêmeas aparenta ser Seleção por Fecundidade, já que o aumento de tamanho no corpo da fêmea está correlacionado com o tamanho e qualidade da prole (Higgins, 2002; Legrand & Morse, 2000; Prenter et al., 1999; Uhl et al., 2004), muito embora alterações no tamanho corporal não afetem igualmente o tamanho de prole entre espécies (Head, 1995). Nephilinae, uma subfamília de Araneidae com SSD extremo, é uma exceção ao padrão de passado monomórfico (Kuntner et al., 2019). A reconstrução do ancestral de Nephilinae indica que esta subfamília já se encontrava em um estado dimórfico. Machos aumentaram significativamente no passado recente e fêmeas não sofreram alteração significativa de tamanho, apesar disso, machos ainda são em média 5 vezes menores que fêmeas (Kuntner et al., 2019).

Um aumento de tamanho corporal advindo da seleção por fecundidade requer uma grande quantidade de alimento para sustentar um corpo maior. Em *Trichonephila clavipes* (Araneae, Araneidae) uma dieta pobre resulta em mais tempo até a maturação (Higgins & Goodnight, 2011), maior mortalidade durante o desenvolvimento (Higgins, 1992) e em proles menores devido a maturação

prolongada (Higgins, 2000). Dessa forma, um corpo maior só pode evoluir caso uma grande quantidade de alimento possa ser adquirida.

Enders (1976) observou proles maiores em aranhas com estratégia de senta-e-espera quando comparadas com caçadoras ativas. Isto sugere que aranhas com estratégia de forrageamento senta-e-espera devem possuir um maior dimorfismo sexual devido ao custo energético de forrageamento ativo. Por exemplo, Araneidae é uma família altamente dimórfica e possui estratégia de forrageamento de senta-e-espera. Lycosidae, por outro lado, é caçadora ativa e possui pouco ou nenhum SSD. Contudo, essa hipótese não parece explicar a evolução no tamanho das fêmeas, já que estudos comparativos e experimentais não encontraram diferença no tamanho do SSD entre grupos de caçadores ativos ou sedentários (Prenter et al., 1997, 1998; Walker & Rypstra, 2003).

Uma derivação da observação de Enders (1976) sugere que não é o baixo gasto energético que está associado ao SSD, mas sim estratégias que permitam adquirir mais alimento (Head, 1995). Foi observado, em Nephilinae, que o SSD extremo está associado a teias maiores (Kuntner et al., 2019). Existem registros de Nephilinae se alimentando de aves ou morcegos (Brooks, 2012; Nyffeler & Knörnschild, 2013) e especula-se que, em grandes teias, presas maiores possam ser capturadas, fornecendo o alimento necessário para o aumento evolutivo do tamanho da fêmea (Kuntner et al., 2019).

Na família de aranhas-caranguejo (Thomisidae) o nível de dimorfismo sexual é bastante variado, e os gêneros possuem uma grande diversidade de estratégias de forrageamento, desde forrageamento em flores e mimetismo agressivo à estratégias tradicionais de senta-e-espera. Gêneros como *Misumena*, que se alimentam em flores, possuem um grande dimorfismo sexual com viés para as fêmeas, enquanto outro como *Tmarus*, que possuem estratégias convencionais de forrageamento, possuem pouco dimorfismo e em alguns casos até com viés para os machos (observação pessoal).

Em algumas espécies de aranhas, os machos são o maior sexo. Este padrão tende a aparecer quando há seleção intrasexual por acesso as fêmeas. O abdome de machos de *Mecolaesthus longissimus* (Araneae, Pholcidae) pode ser até o dobro do

tamanho do de fêmeas. Dados sugerem que os machos dessa espécie utilizam o abdome em competições intrasexuais (Huber, 2005a). Em *T. clavipes*, apesar do maior tamanho das fêmeas, machos maiores tendem a ganhar competições intrasexuais (Christenson & Goist Jr, 1979; Constant et al., 2011; Rittschof, 2010), fornecendo assim, uma pressão evolutiva para o aumento de seu tamanho. Contudo, machos maiores está longe de ser o padrão em aranhas.

Se a maioria dos casos de SSD em aranhas surgem a partir do aumento de tamanho das fêmeas, por que os machos não acompanharam este padrão dada a correlação genética entre os sexos? Uma das primeiras explicações para a manutenção dos machos pequenos é a hipótese do canibalismo sexual (Darwin, 1871). Esta prediz que machos menores são mais ágeis e melhores em escapar dos ataques de fêmeas, ou ainda, estão abaixo do tamanho de interesse como presas, desta forma, machos menores conseguem copular antes que sejam confundidos (Darwin, 1871; Prenter et al., 2006). Em concordância com essa hipótese, existe uma correlação filogenética entre SSD e frequência de canibalismo sexual (Wilder & Rypstra, 2008).

Em uma espécie de *Argiope*, a fêmea parece retardar o canibalismo em machos menores e conseqüentemente aumentam a taxa de fertilização e transferência de esperma (Elgar et al., 2000). Já em *T. plumipes* existem duas estratégias, machos maiores são favorecidos em interações antagonísticas, porém machos menores são menos detectados e canibalizados (Elgar & Fahey, 1996). Além disso, existem espécies em que os machos se oferecem para a fêmea ao posicionar o abdome próximo às quelíceras durante a cópula (Segoli et al., 2008). Em *Latrodectus hasselti* (Araneae, Theridiidae) existe baixa probabilidade de o macho encontrar duas fêmeas (Andrade, 2003), além da fêmea aumentar a chance de recusar futuros machos após canibalizar o primeiro (Andrade, 1996), dessa forma, é mais vantajoso ser canibalizado. Em *Argiope bruennichi* (Araneae, Araneidae) fêmeas que canibalizam os machos produzem ootecas com mais ovos, de maior tamanho e uma prole mais longeva (Welke & Schneider, 2012), apesar dos machos serem canibalizados antes da inserção do segundo pedipalpo (Schneider et al., 2006), resultando em um alto custo reprodutivo para o macho.

Porém, alguns estudos indicam que o canibalismo sexual não é uma das causas da manutenção do SSD. Foellmer e Fairbairn (2004), por exemplo, observaram que em *Argiope aurantia* (Araneae, Araneidae) o canibalismo sexual não explica o alto grau de dimorfismo sexual. Além disso, se o macho canibalizado fornece nutrientes a sua prole, a seleção deveria favorecer a machos maiores e mais nutritivos. Dessa forma, as evidências da efetividade do canibalismo sexual para a manutenção do SSD são conflitantes, e provavelmente variam inter-especificamente.

Vollrath e Parker (1992) propuseram a hipótese da mortalidade diferencial para explicar a evolução de machos menores. Esta hipótese propõe que em espécies sedentárias, os machos teriam de se locomover mais para encontrar fêmeas resultando em maior mortalidade. Esta alteraria a razão sexual e diminuiria a competição intrasexual que deveria selecionar o aumento do tamanho corporal em machos. Porém, a previsão de que haveria um maior dimorfismo em espécies sedentárias não foi corroborada (Prenter et al., 1997, 1998; Walker & Rypstra, 2003) e, na maioria dos casos, o SSD advém do aumento evolutivo do tamanho das fêmeas (Coddington et al., 1997; Head, 1995; Hormiga et al., 2000; Prenter et al., 1999).

Existem outras hipóteses para a evolução despareada de tamanho corporal entre machos e fêmeas. Uma destas é a hipótese da protandria que prediz que, na ausência de seleção sexual, o sucesso das cópulas em aranhas se dá por *scrambled competition*: machos que conseguem chegar antes às fêmeas possuem vantagem na reprodução (i. e. *mate opportunity hypothesis*; Morbey & Ydenberg, 2001). Dessa forma, a vantagem não é ser um macho pequeno, mas sim a curta ontogenia que permita uma rápida maturação sexual. De fato, existem evidências de que machos possuem menos instares que fêmeas (Danielson-François et al., 2012; Higgins, 2002; Legrand & Morse, 2000; Vollrath, 1980), podendo chegar a casos extremos com apenas um ou dois instares (Eberhard, 1980) ou ainda eclodindo adultos da ooteca (Gertsch, 1955).

Chelini e Hebets (2017), porém, observaram em *Mecaphesa celler* (Araneae, Thomisidae) que machos protândricos são maiores quando comparados aos machos tardios, com o mesmo padrão para as fêmeas. Sugerindo duas estratégias: machos

maiores copulam com as fêmeas maiores do início da estação reprodutiva e machos menores com fêmeas menores no fim da estação. Em *T. clavipes* a duração do instar tende a variar mais do que o crescimento por ecdise (Higgins, 1992; Higgins & Goodnight, 2011). Assim, aranhas que se desenvolvem antes são maiores que aquelas que têm de retardar o desenvolvimento até acumular a energia necessária para a ecdise (Higgins & Goodnight, 2011). Neste caso a maturação acelerada resulta em maior tamanho corporal.

Uma hipótese, complementar a protandria, é a de hipótese da gravidade (Moya-Laraño et al., 2002). Machos menores conseguiriam escalar e se locomover mais rapidamente (Moya-Laraño et al., 2002, 2007) o que forneceria uma vantagem adaptativa em um cenário de *scrambled competition*. Estudos também mostram que indivíduos menores são mais propensos a realizar *bridging*, comportamento em que uma aranha solta um fio de seda entre duas árvores para formar uma ponte para sua locomoção (Corcobado et al., 2010), o que pode aumentar a dispersão de machos e os favorecer na procura de parceiros.

Um aperfeiçoamento da hipótese da gravidade sugere que a relação entre tamanho corporal e velocidade de escalada é curvilíneo (Moya-Laraño et al., 2009). Este modelo sugere que para aranhas muito pequenas a velocidade de escalada é proporcional ao tamanho da perna e frequência de passadas. Portanto, a velocidade deve aumentar proporcionalmente ao comprimento da perna. Este padrão deve permanecer até que o tamanho da aranha atinja o limite de operação muscular (tamanho ótimo de escalada), em que o aumento de peso diminui a frequência de passadas contrabalanceando o aumento de comprimento de perna.

Quando é feito um gráfico da relação do tamanho de machos contra o tamanho de fêmeas, aparece um padrão curvilíneo em espécies que escalam. Em espécies pequenas, a relação entre o tamanho dos machos e fêmeas se apresenta linearmente. Porém, quando o limite de tamanho ótimo é ultrapassado, o tamanho das fêmeas continua a aumentar (provavelmente por seleção de fecundidade) e os machos não acompanham a alteração de tamanho (provavelmente por seleção da gravidade). Dessa forma, a relação entre o tamanho dos machos e fêmeas é linear quando as espécies são pequenas, mas se torna curvilíneo quando o tamanho ótimo é ultrapassado. Este padrão, por outro lado, não aparece para espécies que não

escalam, o que indica que a gravidade tem um papel nesse padrão (Moya-Laraño et al., 2009).

A hipótese da gravidade possui evidências empíricas contrastantes, a maioria dos trabalhos indica que não necessariamente machos menores são mais rápidos em escalar, refutando a hipótese inicial (Moya-Laraño et al., 2002). Na verdade, a velocidade de escalada tende a aumentar com o tamanho corporal dentro do previsto pelo padrão curvilíneo (Foellmer & Fairbairn, 2005; Quiñones-Lebrón et al., 2019) ou não ser afetado (Brandt & Andrade, 2007; Prenter et al., 2010). Porém, até o momento nenhum trabalho observou o ponto em que o aumento de tamanho deixa de favorecer a velocidade de escalada, apenas a relação positiva entre tamanho e velocidade foi observado. Assim, a gravidade possivelmente exerce uma pressão limitada na evolução do SSD (Kuntner & Coddington, 2020; Quiñones-Lebrón et al., 2019).

Em vista da grande quantidade de pressões evolutivas que influenciam separadamente no tamanho corporal de machos e fêmeas, é improvável que uma única hipótese ou teoria unificadora seja capaz de explicar a evolução do SSD em aranhas. O modelo de equilíbrio diferencial na evolução do SSD propõe que diferentes forças ajam em conjunto ou antagonicamente sobre o tamanho corporal dos sexos, de forma que a soma dessas pressões resulta nos padrões que observamos (Andersson, 1994; Blanckenhorn, 2005; revisado em Kuntner e Coddington, 2020).

Trichonephila clavipes (Araneidae) é uma espécie de aranha com alto nível de dimorfismo sexual de tamanho, fêmeas são em média 14 vezes mais pesadas que os machos (Capítulo 2; Figura 1B). *Trichonephila clavipes* (Figura 1A) tem uma ampla distribuição geográfica, ocorre da Argentina aos Estados Unidos (World Spider Catalog, 2023), e é bastante comum em áreas urbanas (Motta, 2014). Quando jovens, machos e fêmeas possuem teias separadas; quando os machos estão a um instar de se tornarem adultos abandonam suas próprias teias e vivem na teia de fêmeas jovens (Hill & Christenson, 1988), se alimentando de pequenos artrópodes ou dividindo presas com a fêmea. É comum diversos machos co-habitarem uma mesma teia de fêmea, e possuírem grande variação de tamanho (Vollrath, 1980; Figura 1C). Os machos competem por acesso à fêmea em combates vibratórios ou físicos,

machos maiores costumam vencer estes combates e monopolizar as fêmeas, enquanto os menores permanecem na periferia da teia ou procuram outras fêmeas (Christenson & Goist Jr, 1979).



Figure 1. A) Indivíduo de fêmea jovem de *Trichonephila clavipes*. B) Macho e fêmea adultos de *T. clavipes*, seta indica macho na teia da fêmea. C) Machos de *T. clavipes* coletados na teia de uma mesma fêmea.

Objetivos da Dissertação

Este trabalho visa contribuir com a elucidação de possíveis pressões evolutivas sob o tamanho corporal dos sexos, e, dessa forma, acrescentar informações ao modelo de equilíbrio diferencial. Mais especificamente este trabalho tem o intuito de explorar algumas dessas pressões sob a evolução do tamanho corporal em aranhas-caranguejo (Thomisidae) e em machos de *T. clavipes* (Araneidae).

No primeiro capítulo utilizamos a família Thomisidae para verificar a hipótese de que estratégias alimentares que fornecem uma abundância de alimento favorecem a evolução do SSD com viés para as fêmeas (Head, 1995; Kuntner e Coddington, 2020). Dessa forma, aranhas-caranguejo que forrageiam em flores e possuem mimetismo agressivo devem possuir fêmeas maiores que tomisídeos com outras estratégias alimentares. Devido ao grande movimento de visitantes florais, a aranha conseguiria um fluxo constante e maior de alimento para sustentar maiores tamanhos corporais.

Em *Trichonephila clavipes* (Araneae, Araneidae) estudos indicam que machos maiores são melhores em retornar para teias de fêmeas (Meraz et al., 2012) e vencem mais competições intrasexuais (Christenson & Goist Jr, 1979). Em *T. plumipes* machos maiores escalam mais rápido (Prenter et al., 2010), porém machos pequenos ainda são presentes nas populações. Dessa forma, no segundo capítulo investigar se há um *trade-off* entre rápido desenvolvimento em machos de *T. clavipes* e maior tamanho. Machos menores devem ser os primeiros a maturarem e chegarem às fêmeas, enquanto machos maiores escalariam mais rápido e seriam mais efetivos em guardar a teia da fêmea.

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Chapter I

Foraging strategy as a route for sexual size dimorphism evolution

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2.1 ABSTRACT

Sexual size dimorphism (SSD) is a widespread evolutionary phenomenon, with female-biased SSD being the most common form. The main explanation for larger females is fecundity selection, as larger females produce more offspring. However, larger bodies require higher food intake; therefore, strategies that facilitate food acquisition might allow fecundity selection to increase female body size. Coupled with selection against larger males, fecundity selection should result in larger SSD in species with more lucrative foraging strategies. Crab spiders are sit-and-wait predators that forage in several plant substrata. Species that forage on flowers, or employ prey-luring strategies, likely have access to a higher food intake than other species. Here we extracted size measurements of 1360 crab spider species and classified them based on their foraging strategy. Our findings show that foraging strategies that provide higher energy inputs are indeed associated with larger cephalothorax width on females, and, contrary to our hypothesis, to smaller body length on males. The effects on male size might result from scramble competition, whereas the increase in female size is likely due to fecundity selection. These results suggest that shifts towards more lucrative foraging strategies were a key event in body size and SSD evolution in crab spiders.

Keywords: sexual size dimorphism; foraging strategies; fecundity selection; scrambled competition

2.2 INTRODUCTION

Sexual size dimorphism (SSD) is the difference in size between the sexes of a given species. The differential equilibrium model suggests that contrasting evolutionary pressures are operating on male and female sizes (Andersson, 1994; Blanckenhorn, 2005). In general, a genetic correlation between females and males is expected so that selection favouring a larger body size in one sex would also lead to the evolution of a larger body size in the other sex. However, when antagonistic pressures occur, the correlation between the male and female size may be lessened, resulting in SSD.

It is commonly accepted that the evolution of male-biased SSD (larger males than females) is a product of sexual selection through male-male competition or female choice, as larger males are better competitors for female access or other resources (Andersson, 1994). This pattern is readily observed in endothermic animals such as mammals and birds (Andersson, 1994; Fairbairn et al., 2007). In ectothermic animals, however, female-biased SSD (larger females than males) is the rule.

In *The Descent of Man and Selection in Relation to Sex*, Darwin proposed fecundity selection as why female-biased SSD evolves in so many animal groups (Darwin, 1871). Fecundity selection assumes that the larger the female, the larger their clutch. This phenomenon has been observed in several animal taxa, such as insects (Honěk, 1993), reptiles (Cox et al., 2003; Shine, 1994), mammals (Fokidis et al., 2007), and spiders (Prenter et al., 1999), and is still considered the primary explanation for female-biased SSD evolution (but see Pincheira-Donoso & Hunt, 2017). On insects, for instance, a 1% increase in dry body weight is estimated to result in a 0.95% increase in fecundity (Honěk, 1993). However, there is no clear answer to why female-biased SSD has evolved in some species rather than others.

Spiders have been a long-studied group for the evolution of female-biased SSD. Most spider species are sexually dimorphic, and extreme cases of SSD have evolved; some species with a mean female weight 40 times heavier than the male (Elgar & Fahey, 1996). Overall, the evolution of SSD in spiders appears to have occurred through increases in female size rather than male size reduction (Coddington et al., 1997; Head, 1995; Prenter et al., 1999; Hormiga et al., 2000). Moreover, female-biased SSD has evolved multiple times within the group (Hormiga et al., 2000). The reasons why

are not yet clear, but fecundity selection is the prime candidate (Foellmer & Moya-Larano, 2007).

A higher dietary intake is needed to sustain larger body sizes. In the orb-web spider *Trichonephila clavipes*, for instance, females cannot reach sexual maturity with the same diet as the smaller males (Higgins & Goodnight, 2010). On Nephilinae spiders, extreme SSD is correlated with larger aerial webs (Kuntner et al., 2019). On praying mantises, SSD is correlated with flower mimicry, which may increase prey consumption and allow female growth (Svenson et al., 2016). Therefore, a more lucrative foraging strategy may lead to the evolution of larger female body sizes due to fecundity selection.

However, SSD would not evolve if the fecundity selection on females led to larger males due to genetic correlations. In the collared flycatcher (*Ficedula albicollis*), for instance, the absence of SSD is attributed to the high genetic correlation between the sexes, even though the predicted selection would result in females four times larger and males half the size that is observed (Merila et al., 1998). In spiders, hypotheses to explain why males may not increase with female size range from differential mortality model (Vollrath & Parker, 1992) and sexual cannibalism (Wilder & Rypstra, 2008) to scrambled competition and gravity (Moya-Laraño et al., 2002, 2009).

Crab spiders (Thomisidae) are sit-and-wait predators that wait for prey on different plant structures and leaf litter. Their most common strategy is to wait for the approach of a potential prey, most commonly small insects. Nonetheless, the most studied crab spiders hunt on flowers. Compared to other substrata, flower crab spiders likely have access to a higher and/or more regular prey intake due to the attractiveness of flowers (Figure 1A). Females of *Misumena vatia*, a flower-foraging crab spider, regularly prey on *Apis mellifera* bees, an abundant and high-quality prey item. Further, females of *Misumena* occasionally capture the even larger *Bombus* bees, which provide higher energy consumption, causing increased growth rate, weight and the number of eggs (Fritz & Morse, 1985). Moreover, UV-reflective female flower crab spiders attract bees (Cheng et al., 2006; Heiling, Cheng, et al., 2005; Heiling, Chittka, et al., 2005; Heiling et al., 2003; Herberstein et al., 2009; Welti

et al., 2016). The contrast between a UV-reflecting *Thomisus spectabilis* female and a non-UV-reflective flower increases the probability of a bee visiting a flower which has a spider present (Heiling, Cheng, et al., 2005; Heiling et al., 2003), and is associated with a better female body condition (Gawryszewski et al., 2012). Some female crab spiders also employ aggressive mimicry, a strategy in which the spider resembles a foraging resource their prey is interested in. For instance, females of the spiders of the *Epicadus* genus have a modified abdomen which resembles flowers. Bees are commonly attracted to these spiders even when the spider is not sitting on the flower (Vieira et al., 2017). The evolution of these exploitative foraging strategies (EFS, hunting on flowers and prey luring) may provide a higher prey capture by exploiting prey foraging behaviour and, consequently, influence the evolution of body sizes and SSD.

In crab spiders, the evolution of EFS might provide a pathway to surpass the energetic limitations of larger sizes and, in turn, allow for fecundity selection to increase female size. Therefore, we hypothesise that EFS species will have larger females than non-EFS crab spider species. Furthermore, selection against larger males may cause a reduction in the genetic correlation of male and female sizes and, consequently, the evolution of increased SSD in EFS species. Therefore, we also tested the evolution of male sizes and the correlation between female and male sizes on EFS species compared to non-EFS species. We tested these ideas in a comparative framework after gathering data from 1360 species from 47 genera worldwide distributed.

2.3 METHODS

2.3.1 Data collection

To evaluate the size evolution of each sex, we used the cephalothorax width and body length from taxonomical papers listed in the World Spider Catalog (WSC). In total, we collected size data from 1360 species from 47 genera. Not all species had both male and female sizes available as some do not have both sexes described, or the author measured only one of the sexes. Also, some authors provide only one of

the size measurements. Therefore, not all species had both measurements available. This resulted in 702 species with only males measured, 1142 with only females, and 627 with both sexes measured. Carapace width (CW) is considered a better measurement of size than body length (BL) because the latter is confounded with body condition (Foellmer & Fairbairn, 2005; Foellmer & Moya-Larano, 2007). However, body length is more readily available in taxonomical works; therefore, we extracted both. We only used the measurements of adult individuals and, when possible, used the most recent taxonomical article which had both sexes described. If none had both sexes measured, we used only the most recent scientific article.

We extracted data from genera present in five different crab spider phylogenies (Benjamin et al., 2008; Benjamin & Clayton, 2016; Gawryszewski et al., 2017; Machado & Teixeira, 2021; Vieira, 2015). We chose to select genera from phylogenies to reduce taxonomical inconsistencies. This phylogenetic diversity resulted in worldwide distributed species encompassing all major biogeographical areas. According to the scientific literature and other sources, we classified as Exploitative Foraging Strategy (EFS) spiders that forage on flowers or employ aggressive mimicry (Appendix I). We performed a genus-level classification, as detailed species-level natural history data is scarce. Therefore, we assumed species within each genus have the same foraging strategy. We excluded from the analyses genera without foraging behaviour data.

2.3.2 Statistical Analysis

We analysed the data through linear mixed models. To evaluate the evolution of male and female body sizes, we used body length or cephalothorax width as response variables; and sex, foraging strategy and its interaction as explanatory variables. The genus and species entered into the random structure. The body length model had a sample size of 1922 individuals divided into 1318 species on 42 genera, while the cephalothorax width model had a sample size of 1381 individuals on 913 species on 38 genera. Model checks and AIC comparison indicated heterogeneous variance; therefore, we included 'Sex', 'EFS' and their interaction into the variance structure.

To evaluate the evolution of the correlation between male and female sizes, we used the male size as the response variable and the female size, foraging strategy and its interaction as explanatory variables; the genus entered into the model random structure. The body length model had 604 species divided into 40 genera, while the cephalothorax had 468 species divided into 35 genera. Model checks indicated heterogeneous variance only on the cephalothorax model; therefore, EFS entered into the variance structure.

In all models, the body length was square root transformed, and the cephalothorax width was log-transformed. However, we present model results on the back-transformed scale for easier visualization, unless specified. Models were run on R version 2.2 through the nlme package (version 3.1-160). Model selection of the fixed effects was performed using a Likelihood Ratio Test with models fitted by Maximum Likelihood. Pairwise comparisons were performed through Tukey HSD implemented on emmeans (version 1.8.2); the containment method was used to estimate the degrees of freedom. Model validation was performed through visual inspection of residual graphs following Zuur et al. (2010) protocol (Zuur et al., 2010).

2.4 RESULTS

Overall, the employment of Exploitative Foraging Strategies (EFS) is associated with the evolution of larger body sizes in females and smaller sizes in males. Model selection clearly indicates that the full model is a better fit than the next most complex model, i.e. the model without interaction between sex and EFS (Likelihood-ratio Test; CW model: LR = 90.395, DF=1, $p < 0.001$; BL model: LR = 135.342, DF=1, $p < 0.001$)

Our model indicates an effect of EFS on the female's carapace width (estimated difference in log-scale = 0.233, $t_{36} = 2.610$, $p = 0.013$) (Figure 1B), although not on body length (estimated difference in square root-scale = 0.122, $t_{40} = 1.616$, $p = 0.114$) (Figure 1C). Model estimations predict a mean carapace width size of 2.67 mm [95%

CI: 2.29 to 3.10] for EFS females and 2.11 mm [95% CI: 1.91 to 2.33] for non-EFS species. Body length predictions are 6.40 mm [95% CI: 5.76 to 7.07] for EFS species and 5.81 mm [95% CI: 5.43 to 6.20] for non-EFS.

The pairwise comparison indicates that males of species that employ EFS have significantly smaller body lengths than those which do not (Tukey HSD; estimated difference in square root-scale= 0.238, $t_{40}= 3.306$, $p= 0.002$) (Figure 1C), but not CW (Tukey HSD; estimated difference in log-scale= 0.126, $t_{36}= 1.385$, $p= 0.175$) (Figure 1B). Model estimates a male body length of EFS species of 3.13 mm [95% CI: 2.72 to 3.61 mm] and 4.04 mm [95% CI: 3.72 to 4.37 mm] for non-EFS species; CW predictions are 1.53 mm [95% CI: 1.31 to 1.79 mm] for EFS species and 1.73 [95% CI: 1.57 to 1.91 mm] for non-EFS species.

For the evolution of SSD to occur, male and female sizes need to be decoupled. As one sex increases in size, the other must reduce, increase at a lower rate or stay the same. In our models that evaluated the association between male and female sizes, there was a significant interaction between female size and EFS using both CW ($t=-3.219$, $DF=431$, $p=0.001$) and BL ($t=-3.352$, $DF=562$, $p<0.001$). For the CW model, the estimated slopes were 0.68 [95% CI: 0.57 to 0.78] and 0.34 [95% CI: 0.03 to 0.65] for non-EFS and EFS, respectively (Figure 1D). For the BL model, estimates were 0.53 [95% CI: 0.43 to 0.63] and 0.24 [95% CI: -0.02 to 0.51] (Figure 1E).

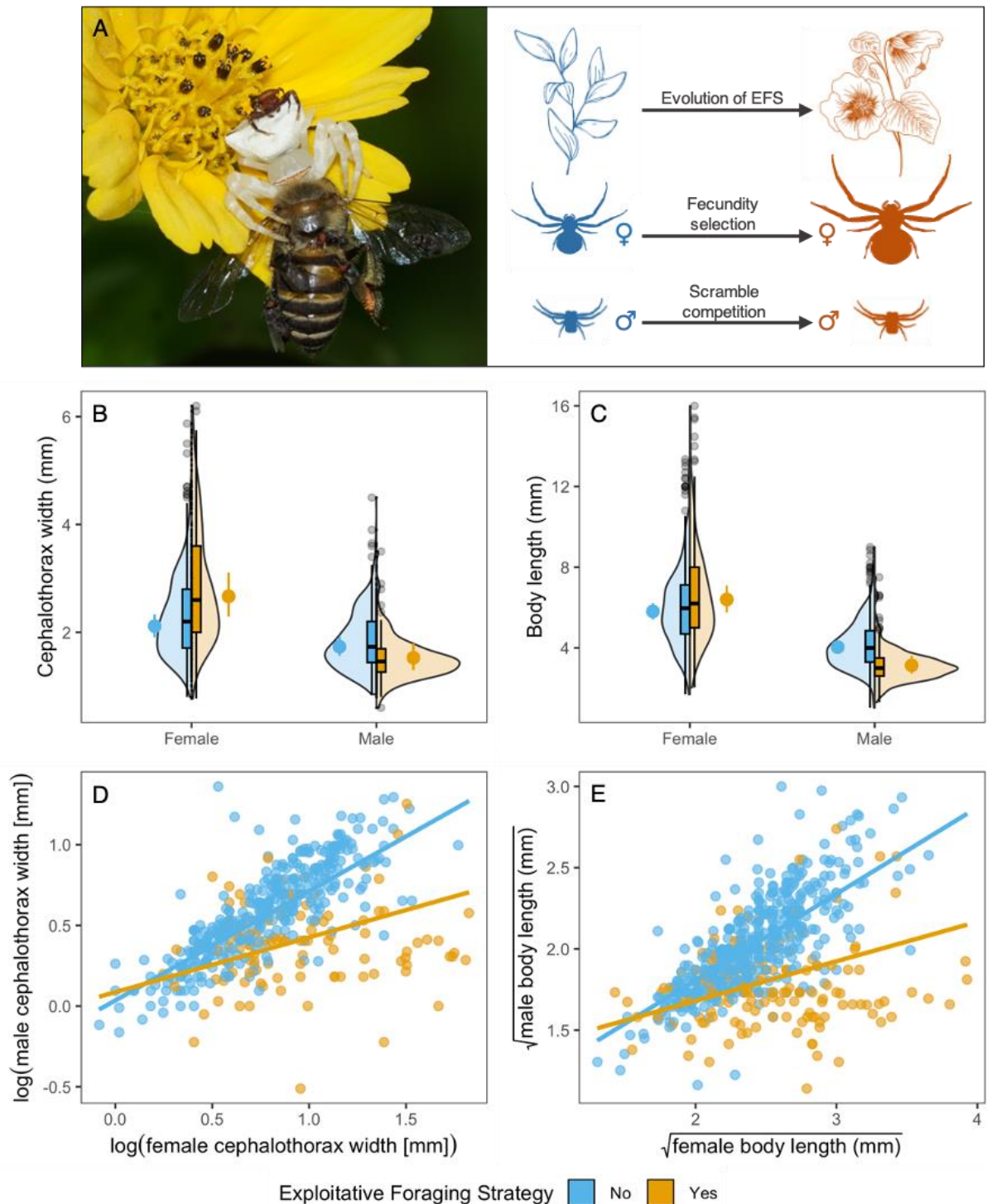


Figure 1. A) A female of *Thomisus* sp. preying on a bee and the male crab spider on top of her. The scheme shows an evolutionary shift to exploitative foraging strategies (EFS), increasing prey consumption and allowing female growth through fecundity selection, over evolutionary time. Scramble competition may check male increase or even decrease its size. These processes should lead to larger sexual size dimorphism in EFS species. Distribution of (B) cephalothorax width and (C) body length of females and males of crab spider species based on the occurrence of exploitative foraging strategies. Dots denote statistical model estimates of mean size with a 95% confidence interval ($N = 1360$ species). Relationship between female and male cephalothorax width (D) and body length (E) of crab spider species based on the occurrence of exploitative foraging strategies. Lines denote the statistical model estimated regressions ($N = 627$ species). Photo by Vineeth Vengolis used under CC BY-SA 4.0 license.

2.5 DISCUSSION

Our results clearly indicate an association between EFS and body size evolution. Females are significantly larger in EFS species, and males decrease in size in EFS species. In addition, for the evolution of SSD to occur, it is also necessary that the males do not increase at the same rate as females (Andersson, 1994; Blanckenhorn, 2005). Our data show a lower slope between male and female sizes on EFS species which, in turn, results in higher SSD on those species.

Fecundity selection is evoked as the primary selective pressure for increased female size in most animal groups with female-biased SSD (Fairbairn et al., 2007). Several studies have provided strong evidence for the reproductive advantages of larger female sizes (Honěk, 1993; Prenter et al., 1999). Our work provides further support in favour of fecundity selection. It suggests a route for the increase in female body size, as the exploitative foraging strategies are a way to surpass the energetic limitations of larger sizes. Therefore, in crab spiders, the evolutionary increase in female size appears to be primarily restrained by dietary reasons.

Although we did not predict the size reduction in ESF males, our models have shown that males of EFS species have significantly smaller body lengths than those who employ other foraging strategies. Foraging strategies have already been suggested as the cause of SSD in spiders due to male dwarfism. Active hunters would have higher mortality rates during mate search resulting in lessened male-male competition and smaller males (i. e. differential mortality model; Morbey & Ydenberg, 2001). However, phylogenetic comparisons and experimental data have shown no association between active and sit-and-wait foraging strategies and SSD occurrence (Prenter et al., 1997, 1998; Walker & Rypstra, 2003).

In crab spiders, increased selective advantages of protandry might play a role in the evolution of smaller EFS males. If female EFS spiders depend on flowers for foraging and survival, those species likely have an aggregated distribution due to the aggregated nature of flowers. Therefore, males with shorter development and consequently smaller size may reach sites with rich female density with little to no male competition [i. e. mate opportunity hypothesis; 43]. Moreover, smaller males

may have higher mobility. The gravity hypothesis states that smaller males climb faster and, therefore, would be favoured in a scrambled competition context (Moya-Laraño et al., 2002). However, the gravity hypothesis has failed to hold itself true in experimental trials with no effect of size on climbing speed (Brandt & Andrade, 2007; Prenter et al., 2010; Quiñones-Lebrón et al., 2019) or larger males having an optimum body size (Foellmer et al., 2011; Moya-Laraño et al., 2009). Nonetheless, we did not find a clear difference in male carapace width. As body length is confounded with body condition (Foellmer & Moya-Larano, 2007), this pattern might suggest that these males have a poorer body condition or that their body shape changes depending on foraging mode. For instance, the genus *Tmarus* is known to sit-and-wait on branches camouflaged with its long and thin bodies (Dippenaar-Schoeman, 1985). Therefore, the difference in body shape may be accounted for by differences in body length.

Furthermore, exploitative foraging strategies might be either the consequence or the cause of SSD. Our hypothesis suggests that the evolution of alternative foraging strategies enables organisms to access increased prey consumption and achieve larger sizes, thus causing SSD. On the other hand, if there is a trend for larger size due to fecundity selection, exploitative foraging strategies may secondarily evolve to fulfil these needs, making them a consequence of SSD. As hunting on flowers has evolved multiple independent times within the family (Gawryszewski et al., 2017), both scenarios may have occurred.

In other groups, the evolution of EFS may also lead to larger SSD. For instance, the spider genera *Mastophora* have some of the most notable cases of female-biased SSD. *Mastophora* has a unique foraging strategy in which they mimic virgin female moths' pheromones, attracting male moths (Eberhard, 1980). This specialised foraging strategy might increase prey consumption allowing for female size increase through fecundity selection. Nonetheless, SSD in *Mastophora* might result from protandry, as males go through only one to two instars before sexual maturity (Eberhard, 1980) or even emerge as adults (Gertsch, 1955). Similarly, the light-emitting modified dorsal fin of anglerfishes might increase the female probability of

catching prey (Pietsch, 2009), contributing to the evolution of extreme SSD in this group.

In conclusion, body size and SSD evolution are associated with foraging strategies in crab spiders. Foraging strategies that supply higher energy intake allow for increased female growth through fecundity selection, while other less profitable foraging strategies may limit female body size. Also, foraging strategies seem to affect male sizes, as males in EFS species were significantly smaller than in species that do not employ EFS. The increased female size and reduced male size result in larger SSD on EFS crab spiders. Therefore, the evolution of more lucrative foraging strategies appears to be a key event for the increase in female sizes, reduction in male sizes, and larger SSD in crab spiders.

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Chapter II

***Trichonephila clavipes* (Araneae: Araneidae) male size evolution: the effect of gravity and protandry**

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3.1 ABSTRACT

Trichonephila clavipes (Araneae, Araneidae) exhibit an extreme case of female-biased sexual size dimorphism, with mean female size being 14 times larger than mean male sizes. *Trichonephila clavipes* males compete in vibratory and/or physical contests for female access, with larger males generally winning. While it is accepted that female gigantism is a key factor in driving this dimorphism, the limitations on male size are still unclear. Several hypotheses have been proposed to explain male size. Two interconnected ones are protandry and the gravity hypothesis. The former suggests that earlier male maturation limits male size but confers mating advantages, while the latter posits that there is a positive relationship between climbing speed and size, up to a threshold beyond which male size is constrained by gravity. We hypothesize a trade-off between the advantages of small sizes (due to protandry) and larger sizes (due to climbing speed and male-male competition). To test these hypotheses, we accompanied *Trichonephila clavipes* from five localities and measured, in total, 264 males through the reproductive season. To evaluate the effect of size on climbing speed, we performed climbing trials with 38 individuals of both sexes. Our results indicate that early males are larger than late ones, conflicting with the protandry hypothesis. Our climbing trials showed an interaction between size and sex, with size and condition positively related to climbing speed for males but not for females. These results illustrate the increased fitness advantages of larger male sizes compared to small ones, while possibly providing a size threshold in which increased size do not result on climbing advantages.

Keywords: sexual size dimorphism; protandry; gravity hypothesis.

3.2 INTRODUCTION

Sexual size dimorphism (SSD) is a widespread phenomenon across animal species and refers to the difference in size between males and females. Its evolutionary pathways might arise from natural or sexual selection on the body sizes of the sexes (Andersson, 1994). Usually, larger males are associated with sexual selection as males compete for female access (Fairbairn, 2007), larger females, on the other hand, are associated with natural selection, as larger females produce more eggs (Honěk, 1993). Spiders are among the most extreme cases of female-biased SSD observed in terrestrial animals. In some spider species, females can weigh up to 40 times more than males (Elgar & Fahey, 1996).

Female-biased SSD on spiders have been historically recognized (Darwin, 1871). Darwin proposed that male spiders are smaller than females as “Had the males been in the habit of fighting together, they would, it is probable, have gradually acquired greater size and strength.” (Darwin, 1871). However, another mechanism proposed by Darwin is now believed to explain increased female size on spiders: fecundity selection. Fecundity selection proposes that larger females produce more eggs, which provides a fitness advantage and drives the evolution of female size. This pattern holds for invertebrates in general (Honěk, 1993; Prenter et al., 1999). In spiders, fecundity selection remains the primary explanation for increased female size (Foellmer & Moya-Larano, 2007), as several studies have shown that the evolution of SSD on spiders is a consequence of increased female size (Coddington et al., 1997; Head, 1995; Hormiga et al., 2000; Prenter et al., 1999) rather than the previously perceived notion of male size reduction (Vollrath, 1998), although both processes can happen in conjunction (Chapter 1). As most genetic influencing genes are autosomal there is usually a correlation between female and male size (Reeve & Fairbairn, 1996). For SSD to evolve, opposing pressures must act upon the size of each sex, breaking this correlation (Andersson, 1994; Blanckenhorn, 2005; Kuntner & Coddington, 2020).

Male spiders have often been referred to as ‘dwarfs’ (Vollrath, 1998), implying a male size reduction over spider evolutionary history. Several hypotheses have been raised over the last century to explain why males have reduced in size. Although current data actually indicates that females increased in size (fecundity selection),

those hypotheses are important in understanding why males have not evolved to become larger alongside females. One of the earliest explanations is related to sexual cannibalism. This hypothesis suggests that smaller males are more agile and can escape females more easily, or are below a size of female interest (Darwin, 1871). Comparative analyses have supported the sexual cannibalism hypothesis (Wilder & Rypstra, 2008). However, some species, such as in *Latrodectus*, the male offers itself for the females, which in turn provides offspring benefits for cannibalized males (Andrade, 1996). Additionally, due to low female density, the chance of a male encountering multiple females is low, so investing more in a single mate may be more beneficial than surviving and searching for another (Andrade, 2003).

Male density has also been of interest in explaining spider SSD (Vollrath & Parker, 1992). Male-male competition is typically thought to drive larger male sizes (Andersson, 1994; Fairbairn, 2007). However, for spiders, it has been suggested that the lower male density and, consequently, the lower male-male competition will provide no fitness advantages for larger male size. In that regard, the differential mortality model (Vollrath & Parker, 1992) suggests that on active hunters males suffer higher mortality when compared to sit and wait species. This would result in lower male density and, consequently, lessened male-male competition. However, both comparative and experimental data have failed to establish any relationship between active hunter foraging mode and SSD (Prenter et al., 1997, 1998; Walker & Rypstra, 2003), leading to the rejection of the differential mortality model as the cause of spider SSD.

Early male development has also been proposed as the cause of spider SSD (Vollrath, 1998). In the absence of sexual selection, male spiders compete in a scrambled context, and individuals that develop more quickly can gain a mating advantage over slower-developing males (Morbey & Ydenberg, 2001). The protandry hypothesis suggests that reduced number of instars, rather than small size, is driving SSD evolution. In some extreme cases the males even emerge as adults from the egg sac (Gertsch, 1955).

However, fast development does not guarantee a mate, males also need to reach the female before others. The Gravity Hypothesis is a complement to protandry due to the scrambled competition context. It states that smaller males are more agile due

to the reduced effect of gravity on them (Moya-Laraño et al., 2002). However, experimental trials have yielded mixed results, especially due to the fact that leg size is correlated with body length, and leg size is correlated with climbing speed (Brandt & Andrade, 2007; Foellmer & Fairbairn, 2005). This criticism led to a refined version of the Gravity Hypothesis, which posits that larger males are faster climbers up to a threshold beyond which size has no further impact on climbing speed (Moya-Laraño et al., 2009). This refined version also received mixed experimental results (Prenter et al., 2010; Quiñones-Lebrón et al., 2019) but provides an explanation to why males remained small.

Nonetheless, not all evolutionary pressures select small body sizes on male spiders. For instance, *Mecolaesthus longissimus* (Araneae, Pholcidae) males have abdomens double the size of females, which are used to compete for female access (Huber, 2005). On *Trichonephila clavipes* larger males are better competitors for female access due to male-male competition (Christenson & Goist Jr, 1979). Further, larger males are faster to return to female webs if removed (Meraz et al., 2012) and, on *Trichonephila plumipes*, larger males are faster climbers (Prenter et al., 2006). If the gravity hypothesis holds true for *T. clavipes*, these larger males have better chances of first arriving on females due to climbing speed and defending females from competitors.

The Nephilinae subfamily is an exception in SSD evolution of spiders. In most cases, a monomorphic ancestral state is assumed; however, in Nephilinae, ancestral state already had female-biased SSD and recently males have increased in size (Kuntner et al., 2019). *T. clavipes* males have a wide range of sizes, from 1.29 mm to 3.38 mm in cephalothorax width (own data). Smaller males are often associated with shorter development due to protandry, so there must be a trade off between larger size and faster development.

Therefore, we hypothesize that protandry plays a significant role in the SSD of *T. clavipes*, as it allows males to reach sexual maturity earlier than females, resulting in smaller early-developing males compared to later ones. Also, we expect that larger males will be faster climbers than the small ones, therefore, there will have a trade-off between fast development and mobility capabilities. Also, we expect that there will be a threshold in which climbing speed is no longer affected by the size,

limiting the increase in male size. This would explain why males have remained small but have, nonetheless, suffered an increase in size on Nephilinae.

3.3 METHODS

3.3.1 *Study species and location*

Trichonephila clavipes is a widespread Araneidae, found from Argentina to the United States of America. *T. clavipes* is a protandrous species, males mature earlier than females and defend the web from possible competitors (Vollrath, 1980). Female *T. clavipes* are much larger than the males and accept males based on the result of male-male contests. Sexual cannibalism is rare in this species (Uhl & Vollrath, 1998). A female can lay multiple eggsacs and the number of eggs is closely linked to female size (L. E. Higgins, 1992). Males, however, have a limited supply of sperm (Michalik & Rittschof, 2011) and do not refill their pedipalps after copulation (Myers & Christenson, 1988).

While juveniles, male and female spiders construct separated webs. When males are an instar from becoming adults, they leave their webs in search for juvenile females and reside on their webs (Hill & Christenson, 1988). During this period males do not feed and suffer significant weight loss during translocation (Meraz et al., 2012). Once on the female's web, multiple males compete in physical and/or vibratory contests to determine which one will stay closest to the hub, and consequently closest to the female. Normally, larger males have advantages on these contests while smaller males stay on the periphery of the web and may even change webs (Christenson & Goist Jr, 1979; Constant et al., 2011), as *T. clavipes* are normally aggregated with several females in close vicinity (Meraz et al., 2012; Motta, 2014).

For this work we accompanied *T. clavipes* from six localities during their reproductive season, including three in natural (-15.943761, -47.942000; and -15.765623, -47.856304), one in urban (-15.763784, -47.869376) and two in rural (-15.948580, -47.934064 and -15.922120, -47.949395) environments in Distrito Federal, Brazil. The study was conducted on a savannah-like vegetation typical from central Brazil. The region has well defined dry and rainy seasons. The reproductive

season of *T. clavipes* occurs once a year, with peak abundance from March to July (Motta, 2014) on the transition from rainy to dry season.

3.3.2 *Protandry and male size*

To investigate the hypothesis that males reach sexual maturity earlier than females, we conducted a field study on the six localities from 06/01/2021 to 07/06/2022. We recorded the number of *Trichonephila clavipes* males, females, pre-males, pre-females, and juveniles on a weekly basis (from 06/01 to 19/03) or every two weeks (from 30/03 to 07/06) which resulted on 5256 data points. We also sought to assess the impact of protandry on male size by randomly selecting and measuring 10 males from each population on the period described. To minimize harm to the spiders, we photographed them on squared paper before returning them to their female's web. We used ImageJ software (version 1.53k) to measure cephalothorax width, length, abdominal area, and leg size of 269 males. If any legs were missing, we measured the leg on the other side; if no leg was present, we randomly selected another male to measure.

3.3.3 *Climbing trials*

To investigate the impact of morphometric parameters on climbing speed, we conducted a laboratory experiment with 38 *Trichonephila clavipes* individuals (5 females, 9 males, 2 pre-males, and 22 pre-females) from two locations that were not included in the protandry and size evaluation (-15.713305, -47.866641 and -15.764311, -47.871353). We decided to add females to expand the upper range of size in our experiments and possibly observe the curvilinear pattern on climbing speed. Prior to the experiment, the individuals were placed on a 50 cm wooden rod for a 5-minute acclimatization period. Subsequently, they were gently encouraged to climb the rod and all climbing attempts were recorded without allowing the individuals to stop at any point. If an individual stopped climbing, it was gently touched on its hind legs with a brush to continue. Between each climbing trial, the wooden rod was cleaned with 70% ethanol.

We photographed all individuals that participated in the climbing trials on squared paper and measured cephalothorax width, length, abdominal area, and leg size using the software ImageJ (version 1.53k). We classified the participating individuals as

males, females, pre-males, and pre-females, but grouped pre-males with males and pre-females with females to due to the small number of pre-male individuals. To evaluate climbing speed, we divided the length of the wooden rod (50 cm) by the time (in seconds) each individual took to reach the top, resulting in speed measurements in cm/s.

3.3.4 *Statistical analyses*

Protandry analyses were made through linear regression with size on the response variable and days since first adult male as explanatory variable. Generalized least squares models were used to create a correlation structure of days, however AICc values indicated that the simple regression without correlation structure was a better fit.

For the climbing trails we first used a principal component analysis (PCA) on cephalothorax width and length and extracted the first principal component (PC1) as a measurement of size. We did that because morphometric parameters are highly correlated with size, which violates an assumption of linear models. To obtain leg size independent of overall size, we preformed four linear regressions of leg size (one through four) with PC1 as an explanatory variable. The residuals of this regression represent leg size independent of overall size. As all leg size residuals were correlated, we preformed another PCA of all four legs, and used the first PC as measurement of leg size. To obtain a measurement of body condition independent of size, we preformed another linear regression of the square root of abdominal area with size as a explanatory variable. Again, we extracted the residuals of this regression as a measurement of condition independent of size. The final model was fitted using generalized least squares with climbing speed as a function of size (PC1 of cephalothorax width and length), leg (PC1 of the leg size residuals) and condition (residuals of square root abdominal area) and their interaction with sex.

All model validation was performed through the visual inspection of residual graphs following Zuur et al., 2010 protocol. Model selection of fixed effects was performed through Likelihood-ratio Test (LRT). Generalized least square model was constructed using the nlme package (version 3.1-160) implemented on R version 2.2.

3.4 RESULTS

3.4.1 *Size and protandry*

Although males matured earlier than females in all populations evaluated, the largest number of adult males coincided with females on day 117 (70 males and 62 females) (Figure 1A). However, after the peak male populations sharply dropped while female populations were more resilient.

Furthermore, we observed that earlier-maturing males were larger than the later-maturing ones. Mean cephalothorax width of males on the first day was 2.36 mm and 1.87 mm on the last day. Our linear regression showed a significant negative effect of time on male size (slope estimation on square root scale= -0.0016, df= 267, $t=-4.536$, $p<0.001$) (Figure 1B).

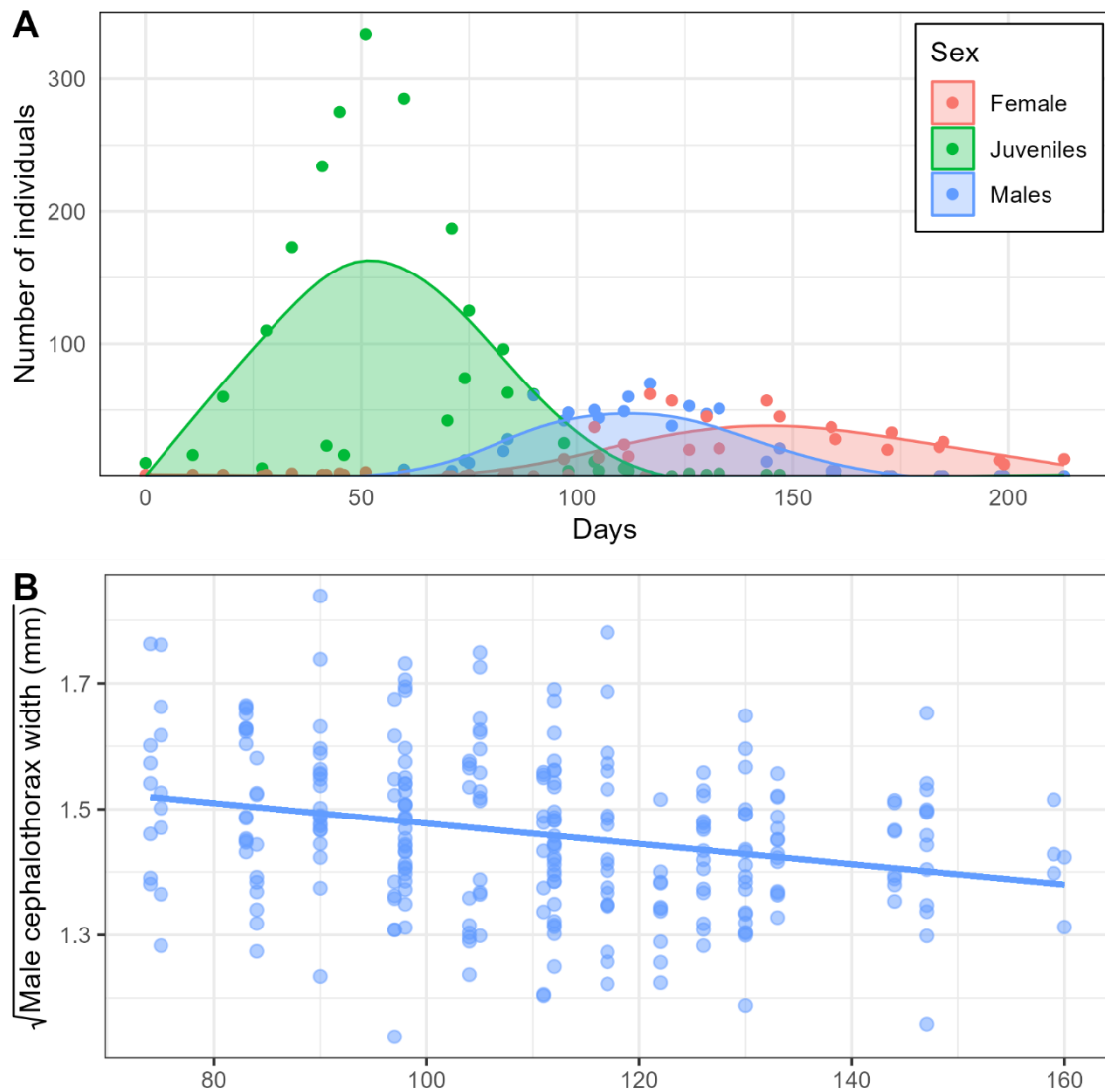


Figure 1. A) Number of individuals of juvenile, males and females of *Trichonephila clavipes* populations by days since the first individual observed, in total, the sum of all observations resulted on 5256 spiders. Curves were generated by General Additive Models implemented on ggplot2 package (version 3.4.0). B) Relationship between the square root of cephalothorax width of male *Trichonephila clavipes* and days since the first individual was observed in the studied populations, in total 269 individuals were measured. The solid line represents the linear regression, which shows a significant negative effect of time on male size.

3.4.2 Climbing trials

We found that the model had a better fit without including leg size as an explanatory variable (LRT; $df=1$, $LR=4.901$, $p=0.086$). The interaction between size (LRT; $df=1$, $LR=11.849$, $p<0.001$) and condition (LRT; $df=1$, $LR=15.707$, $p<0.001$) with sex was significant to explain climbing speed. For males, size and condition were

significant and positively related to climbing speed, but this relationship was not observed for females (Table 1; Figure 2). For females, the model estimated a positive relationship between size and climbing speed, but a negative relationship between condition and climbing speed, but neither relationship was statistically significant (Table 1; Figure 2)

Table 1. Model results of the effect of size, condition and their interaction with sex on climbing speed (cm/s). Model estimations used females as base of comparison.

	Value	Standard error	t	p
Intercept	2.024	0.932	21.712	<0.001
Size	0.064	0.049	1.282	0.209
Condition	-0.115	0.074	-1.540	0.133
Males	1.496	0.454	3.293	0.002
Size:Male	0.807	0.208	3.871	<0.001
Condition:Male	1.137	0.278	4.906	<0.001

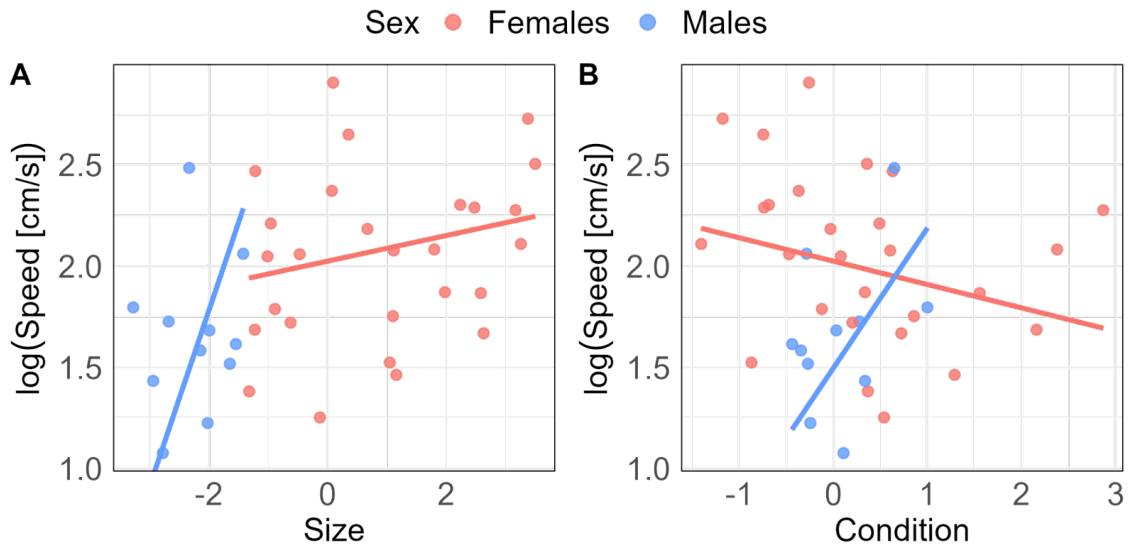


Figure 2. Effect of size (A) and condition (B) on climbing speed (cm/s). The blue line represents the statistical model estimation for males, and the red line represents the model estimation for females

3.5 DISCUSSION

Contrary to our hypothesis, our results suggest that earlier-maturing male *Trichonephila clavipes* are larger than their late-maturing ones (Figure 1B). In addition, we found that size and condition are positively related to climbing speed in male but not female spiders (Figure 2). Both results suggest an overall fitness advantage of larger male sizes compared to smaller ones. Larger males are the first to reach sexual maturity, reach the female and are better competitors on male-male competition. All these fitness advantages might explain the increase in male size in the Nephilinae subfamily (Kuntner et al., 2019). Our climbing trials suggest that there might be limited climbing advantages provided by size, as suggested by the Gravity Hypothesis (Moya-Laraño et al., 2009). Females, much larger than males, do not gain significant advantages to climbing speed by size, however, our experimental design cannot isolate the effect of size and sex on climbing speed, and we did not observe the curvilinear pattern on male sizes. The gravity effect on females, on the other hand, could impact their foraging efficiency as it limits the ability to change foraging sites (Kuntner & Coddington, 2020). However, the increased benefits from fecundity selection may still drive females to larger sizes.

The large early-maturing males could be explained by access to food. In other species, successful foraging increases the speed of reaching sexual maturity and also results in larger females (Higgins & Goodnight, 2011) and males (Vollrath, 1980). *Mecaphesa celler* (Araneae, Thomisidae) follows this pattern. The first adult individuals are larger than late developing ones (Chelini & Hebets, 2017). However, on *M. celler*, populations decrease in the middle of the reproductive season and later reappear with smaller individuals. This timing segregation results in the pairing of high-quality mates. On *T. clavipes*, however, there is a single reproductive event (Figure 1B), so small males compete for female access with larger males.

Larger males are better competitors on male-male contests (Christenson & Goist Jr, 1979; Constant et al., 2011), are faster climbers and also the first males to reach sexual maturity. All these benefits of larger male sizes probably result in directional selection for increased male size on *T. clavipes*. If this pattern holds for other Nephlinea species, it probably explains why males have increased in size in this subfamily (Kuntner et al., 2019). In spider groups where male-male competition is reduced, the advantages of larger size may be less significant, and delayed maturation by an extra instar may not provide enough advantage to overcome slower climbing speed.

Moreover, we found that condition is positively correlated with male climbing speed (Figure 2). Therefore, energy reserves might also be highly selected on males. Further, previous research has shown that male *T. clavipes* pair with females of similar quality, with small males choosing small females and large males choosing large females (Pollo et al., 2019). Moreover, males of *T. clavipes* have a limited supply of sperm and do not refill their pedipalps after mating (Michalik & Rittschof, 2011; Myers & Christenson, 1988), therefore small males do not lose the opportunity to mate, but may have lower fitness as they have to mate with lower quality females. It is also possible that satellite males employ alternative reproductive strategies such as sneak copulation. However, we did not observe this behavior on the field nor it has been documented on this species to our knowledge.

In conclusion, our findings suggest that the early males are larger than late ones, and the Gravity Hypothesis may limit the increase in male size in *Trichonephila clavipes*. The combined effects of faster climbing and male-male competition might explain a

directional selection force to increased male size on the Nephilinae subfamily. While protandry may also play a role on male *T. clavipes* maturation, our results suggest that faster-developing males were larger than late-developing ones. Future studies should include the entire range of sizes of *T. clavipes*, from juveniles to adult females, to better disentangle the effects of size and sex on climbing speed. Additionally, examining female size and copulations throughout the reproductive season may provide insight into the fitness costs of late arriving small males.

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4. CONSIDERAÇÕES FINAIS

Diversos vetores de pressões evolutivas atuam sobre o tamanho corporal de machos e fêmeas. Este trabalho avaliou hipóteses sobre as pressões no tamanho de fêmeas em Thomisidae no Capítulo 1 e pressões sobre o tamanho de machos em *Trichonephila clavipes* no Capítulo 2.

No primeiro capítulo observamos que estratégias alimentares que fornecem maior qualidade ou quantidade de alimento resultam em fêmeas maiores e machos menores. O efeito observado nas fêmeas corrobora nossas hipóteses, porém, a diminuição do tamanho de machos não foi prevista. Para tentar explicar esse padrão de diminuição de machos propomos que *scrambled competition* pode ter um papel. Machos que se desenvolvem antes, conseguem chegar em locais com alta densidade de fêmeas com baixa ou nenhuma competição intrasexual. Futuros trabalhos devem investigar como estratégias de forrageamento podem afetar o tamanho de machos, além do de fêmeas.

Futuros trabalhos podem também complementar esses achados com medidas de animais em coleção para incorporar a variação natural de tamanho nesse padrão. Pela falta de dados de história natural classificamos como se cada gênero adotasse uma mesma estratégia de forrageamento, o que pode não ser verdade para grupos com muitas espécies (por exemplo, *Tmarus* com 215 e *Xysticus* com 268 espécies). Porém, uma melhor categorização dessas estratégias necessitaria de mais dados comportamentais para espécies raras, dados estes, indisponíveis.

No segundo capítulo avaliamos algumas pressões sobre a evolução do tamanho corporal em *T. clavipes*. Diferente do esperado observamos uma relação negativa de dias e tamanho dos machos observados em cinco localidades estudadas. Além disso, observamos uma relação positiva entre tamanho e velocidade de escalada para machos, mas não para fêmeas. Essa relação de tamanho de macho com prioridade na maturação e maior velocidade de escalada somado com maior probabilidade de machos maiores vencerem combates intrasexuais (Christenson & Goist Jr, 1979) indica uma aptidão maior de machos grandes para reprodução. A Hipótese da Gravidade que prevê um padrão curvilíneo entre velocidade de escalada

e tamanho não pôde ser pois nosso desenho experimental não permitiu separar o efeito de sexo e tamanho em nossas análises estatísticas. Dessa forma, não é possível concluir se a redução de velocidade de fêmeas é devido ao tamanho ou outras características morfológicas específicas do sexo. Por outro lado, a condição do macho é positivamente correlacionada com sua velocidade de escalada, mas isso não ocorre para fêmeas.

Aranhas são um grupo com mais de 50.000 espécies (World Spider Catalog, 2023), a maioria destas possuem dimorfismo sexual de tamanho com viés para as fêmeas. É improvável que uma mesma pressão evolutiva seja a causa desse padrão em um grupo tão diverso quanto aranhas. Nosso trabalho foi capaz de lucidar o efeito de estratégias de forrageamento na evolução do dimorfismo sexual de tamanho em tomisídeos e complementar o efeito de protandria e gravidade no sistema de acasalamento de *T. clavipes*, como forma de entender a evolução do tamanho corporal de machos nessa espécie.

4.1 REFERENCES

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APENDIX I – Thomisidae genera classification

Supplementary Table 1. All genera measured during the data collection with Exploitative Foraging Strategy classification, the source of the measurements and the source of the foraging strategy classification.

Genus	EFS classification	Measurement Source	EFS source
Acentroscelus	non-EFS	(E. Keyserling, 1880; C. de Mello-Leitão, 1947; C. F. de Mello-Leitão, 1929a, 1940b, 1943a, 1943c; Rinaldi, 1984; B. M. Soares, 1942)	(Vieira, 2015)
Aphantochilus	non-EFS	(Canals, 1933; C. F. de Mello-Leitão, 1929a; O. Pickard-Cambridge, 1870)	(Cushing, 2012)
Apyretina	Unknown	(E. Simon, 1903b)	-
Australomisidia	EFS	(Szymkowiak, 2008, 2014; Szymkowiak & Dymek, 2012)	(Gawryszewski et al., 2017)
Bomis	non-EFS	(Biswas & Mazumder, 1981; Szymkowiak & Królikowska, 2017; Tikader, 1980; Tikader & Biswas, 1981)	(Gawryszewski et al., 2017)
Borboropactus	non-EFS	(Barrion & Litsinger, 1995; Lawrence, 1937, 1938; Marusik et al., 2013; Meng et al., 2019; E. Simon, 1884a, 1903a; D. X. Song, 1993; G. Tang & Li, 2010b; Tikader, 1980)	(Barrion & Litsinger, 1995; C. M. Yin et al., 2012)

Cebrennius	non-EFS	(Benjamin, 2016; G. Tang et al., 2009; G. Tang & Li, 2010b)	(Benjamin, 2016)
Coenypha	non-EFS	(E. Keyserling, 1880; C. F. de Mello-Leitão, 1929b, 1951; E. Simon, 1887; Tullgren, 1902)	(Machado & Teixeira, 2021)
Coriarachne	non-EFS	(Almquist, 2006; Dondale & Redner, 1978; Ono, 1988)	(Almquist, 2006; Dondale & Redner, 1978; Gawryszewski et al., 2017)
Cymbacha	non-EFS	(Koch, 1874, 1876a; E. Simon, 1895b; Thorell, 1881)	(Gawryszewski et al., 2017)
Diaea	non-EFS	(Almquist, 2006; Barrion & Litsinger, 1995; Biswas & Mazumder, 1981; Bryant, 1933, 1935; Buchar & Thaler, 1984; Dyal, 1935; Fage, 1923; Gertsch, 1939; Guo & Zhang, 2014; H. E. Hogg, 1922; H. R. Hogg, 1915; Jézéquel, 1966; Karsch, 1880b; E. Keyserling, 1880; Koch, 1874; L. Kulczyński, 1901; Kulczynski, 1911; Lessert, 1919; Millot, 1942; Ono, 1985a, 1993; O. Pickard-Cambridge, 1899; Rainbow, 1898, 1902; Roewer, 1938, 1961; E. Simon, 1880, 1882, 1903a; D. X. Song & Hu, 1986; Strand, 1901, 1913b; Szymkowiak, 2014; Thorell, 1877a; Urones, 2000; Xu et al., 2008; C. M. Yin et al., 2012; Zamani &	(Gawryszewski et al., 2017)

		Marusik, 2017; F. Zhang, Song, et al., 2004)	
Ebrechtella	EFS	(J. L. Hu & Wu, 1989; Marusik, 1993; Seo, 2015; E. Simon, 1909; D. X. Song et al., 1997; D. Song & Zhu, 1997; Thorell, 1887, 1895; C. M. Yin et al., 2012)	(S. T. Kim & Lee, 2012)
Epicadinus	non-EFS	(Prado et al., 2018)	(Prado et al., 2018)
Epicadus	EFS	(Bauer, 2020; Machado et al., 2015, 2018; Silva-Moreira & Machado, 2016)	(Vieira et al., 2017)
Epidius	non-EFS	(Badcock, 1917, pp. 1901–2; Benjamin, 2000, 2017; Lessert, 1930, 1943; Ono, 1988; E. Simon, 1897; D. X. Song & Kim, 1992; G. Tang & Li, 2010a; Thorell, 1890b; C. Yin et al., 1999)	(Joseph & Ambalaparambil, 2017)
Geraesta	Unknown	(Benjamin, 2015; U. A. Gajbe, 2007b; E. Simon, 1886b, 1888)	-
Hedana	non-EFS	(Chrysanthus, 1964; H. R. Hogg, 1896; Koch, 1874, 1875b; E. Simon, 1885, 1895a; Thorell, 1890b)	(Gawryszewski et al., 2017)
Heriaeus	non-EFS	(Charitonov, 1946; Komnenov, 2017; Liang et al., 1991; Loerbroks, 1983; Niekerk & Dippenaar-Schoeman, 2013; Sen & Sureshan, 2022; G. Tang & Li, 2010a; Utochkin, 1985)	(Gawryszewski et al., 2017; Niekerk & Dippenaar-Schoeman, 2013)

Isala	non-EFS	(Machado, Teixeira, et al., 2019)	(Machado, Teixeira, et al., 2019)
Mecaphesa	EFS	(Baert, 2013; Banks, 1898; Berland, 1924; Dondale & Redner, 1978; Gertsch, 1939; M. L. Jiménez, 1991; E. Keyserling, 1880; Kraus, 1955; Schick, 1965, 1970; Suman, 1971)	(Hanna & Eason, 2013; Robakiewicz & Daigle, 2004)
Metadiaea	EFS	(C. F. de Mello-Leitão, 1929a)	(Vieira, 2015)
Misumenoides	EFS	(Biswas & Roy, 2008; L. di Caporiacco, 1955; L. D. Caporiacco, 1948; Dondale & Redner, 1978; P. U. Gajbe, 2004; Gertsch, 1939; Gertsch & Davis, 1940; Holmberg, 1881; M. L. Jiménez, 1986; M.-L. Jiménez, 1992; E. Keyserling, 1880, 1881; C. de Mello-Leitão, 1947; C. F. de Mello-Leitão, 1929a, 1938, 1941b, 1943b, 1944, 1949; O. Pickard-Cambridge, 1900; B. A. M. Soares, 1944b; Teixeira & Lise, 2012)	(Dodson et al., 2013; Stellwag & Dodson, 2010; Vieira, 2015)
Misumenops	EFS	(Badcock, 1932; Banks, 1898; Barrion & Litsinger, 1995; Berland, 1927, 1936; Blackwall, 1862; Bristowe, 1930; L. di Caporiacco, 1947b; Denis, 1941; Dippenaar-Schoeman, 1983; Garb, 2007; Holmberg, 1876; J.	(Vieira, 2015)

		Hu, 2001; J.-L. Hu & Li, 1987; E. Keyserling, 1880; L. Kulczyński, 1901; Ledoux & Hallé, 1995; Lehtinen & Marusik, 2008; C. F. de Mello-Leitão, 1925, 1929a, 1929a, 1944, 1949; O. Pickard-Cambridge, 1900; Piza Jr., 1937; Rinaldi, 1983; Schenkel, 1949; B. A. M. Soares, 1943; Tullgren, 1905)	
Monaeses	non-EFS	(Barrion & Litsinger, 1995; Chen & Zhang, 1995; Dippenaar-Schoeman, 1984; U. A. Gajbe & Rane, 1992; Jézéquel, 1964; Koch, 1874; Millot, 1942; Ono, 1985b; Pavesi, 1897; E. Simon, 1907a; Taczanowski, 1872; Thorell, 1895; Tikader, 1980; Yuan et al., 2019; F. Zhang, Song, et al., 2004)	(Dippenaar-Schoeman, 1984)
Onocolus	non-EFS	(Lise, 1979a, 1979b, 1980a, 1980b; C. de Mello-Leitão, 1948; C. F. de Mello-Leitão, 1929a, 1934, 1941a; B. A. M. Soares & Soares, 1946; Teixeira & Machado, 2019)	(Vieira, 2015)
Oxytate	non-EFS	(Benjamin, 2001; L. di Caporiacco, 1940b, 1947a; U. A. Gajbe, 2008; He & Hu, 1999; H. R. Hogg, 1914; Jézéquel, 1964, 1966; Lessert, 1919; K. Liu et al., 2017; Ono,	(Benjamin, 2001)

		1977b; Paik, 1985b; Sen et al., 2015; E. Simon, 1886b, 1906; G. Tang et al., 1999, 2008; G. Tang & Li, 2009a, 2010b; Thorell, 1895; Y. N. Wang et al., 2012; Workman, 1896; Y. J. Zhang & Yin, 1998)	
Ozyptila	non-EFS	(Almquist, 2006; Bell & Merrett, 2000; Blackwall, 1870; L. di Caporiacco, 1935, 1947a; Coşar & Danişman, 2021; Danişman & Coşar, 2021; Deltshev et al., 2016; Demircan & Topçu, 2015; Denis, 1945, 1954; Dondale & Redner, 1975; U. A. Gajbe, 2007b; Grube, 1861; Jézéquel, 1964; Karol, 1966a; Levy, 1975, 1985, 1999, 2007; Lissner & Lissner, 2017; Logunov & Marusik, 1994; Lucas, 1846; Marusik & Logunov, 1990, 2001; Mcheidze, 2014; Ono, 1985a, 1988, 1996a, 2002; Ono & Martens, 2004; Paik, 1985a; Pavesi, 1895; Ponomarev et al., 2011; Ponomarev & Shmatko, 2021; Roberts, 1998; Roewer, 1955, p. 50, 1959; Schmidt, 1980; Sen et al., 2015; Seo, 2015; Seo & Sohn, 1997; E. Simon, 1885, 1886d; E. L. Simon, 1874; D. Song & Zhu, 1997; Strand, 1906; G. Tang & Li, 2010a, 2010b; Thaler, 1987;	(Deltshev et al., 2016; Gawryszewski et al., 2017; Mcheidze, 2014)

		Thaler & Zingerle, 1998; Thorell, 1875a; Tikader, 1961, 1971, 1980; Urones, 1998; Weiss, 1998; Wunderlich, 1995, 2011; Wunderlich & Schultz, 1995; C. M. Yin et al., 2012; F. Zhang, Song, et al., 2004)	
Pagida	non-EFS	(Benjamin & Clayton, 2016)	(Benjamin & Clayton, 2016)
Paratobias	Unknown	(O. Pickard-Cambridge, 1900)	
Pharta	Unknown	(Benjamin, 2014; Ono, 1995; Ono & Song, 1986; Sen et al., 2012; G. Tang et al., 2009; Thorell, 1891a, pp. 1845-1847; C. Wang et al., 2016; Z.-Z. Yang et al., 2006)	
Phrynarachne	EFS	(Berland, 1938; Dash & Sivaperuman, 2021; Jézéquel, 1964; Karsch, 1880b; S. T. Kim & Lee, 2012; Ledoux, 2004; Lessert, 1933; Y. Li et al., 1985; O. Pickard-Cambridge, 1899; Pocock, 1899; Pocock & Rothschild, 1903; Rainbow, 1899; Roy et al., 2010; E. Simon, 1886b, 1903b, 1907a; D. X. Song & Chai, 1990; G. Tang & Li, 2010a; Thorell, 1891a, pp. 1845-1847, 1895; Workman, 1896; C. M. Yin et al., 2012; M. S. Zhu & Song, 2006)	(Yu et al., 2022)

Pistius	non-EFS	(Almquist, 2006; S. T. Kim & Lee, 2012; Kumari & Mittal, 1999; G. Tang & Li, 2010a; Tian et al., 2018; Tikader, 1980)	(Gawryszewski et al., 2017; S. T. Kim & Lee, 2012)
Runcinia	non-EFS	(Dippenaar-Schoeman, 1980, 1983; P. Gajbe, 2004; P. U. Gajbe, 2004; Lessert, 1919; Marusik, 1993; Marusik & Logunov, 1990; Ono, 1988; Roberts, 1998; Roewer, 1961; Schenkel, 1944; E. Simon, 1895a; Thorell, 1891b, 1895; Tikader, 1980)	(Gawryszewski et al., 2017)
Sidymella	non-EFS	(Bryant, 1933; H. R. Hogg, 1910; Koch, 1874; Lise, 1973; Machado, Guzati, et al., 2019; C. Mello-Leitão, 1947; Strand, 1913a)	(Gawryszewski et al., 2017; Vieira, 2015)
Stephanopis	non-EFS	(E. Keyserling, 1880; Koch, 1874; Machado, Teixeira, et al., 2019; C. F. de Mello-Leitão, 1951)	(Gawryszewski et al., 2017; Machado, Guzati, et al., 2019)
Stephanopoides	non-EFS	(Bonaldo & Lise, 2001; Molina-Gómez et al., 2020; Teixeira & Barros, 2015)	(Vieira, 2015)
Stiphropus	non-EFS	(Gerstaecker, 1873; Huang & Lin, 2020; Jézéquel, 1966; Lawrence, 1927, 1928, 1952; Lessert, 1923, 1943; Z.-X. Li et al., 2009; Millot, 1942; Ono, 1980; Sen et al., 2010; E. Simon,	(Z. Z. Yang et al., 2006)

		1886b, 1895a, 1907a; Z. Z. Yang et al., 2006; M. S. Zhu & Shan, 2007)	
Strigoplus	Unknown	(Dhali et al., 2016; Patel, 2003; Saha & Raychaudhuri, 2004; E. Simon, 1884b; C. M. Yin et al., 2012)	-
Strophius	EFS	(E. Keyserling, 1880; C. F. de Mello-Leitão, 1929a; F. O. Pickard-Cambridge, 1897, p. 2; O. Pickard-Cambridge, 1892; B. A. M. Soares, 1943)	(Vieira, 2015)
Synaemops	non-EFS	(C. F. de Mello-Leitão, 1929a, 1941a, 1941c)	(Vieira, 2015)
Synema	EFS	(Barrion & Litsinger, 1995; L. di Caporiacco, 1939, 1947a, 1954, 1955; Demir et al., 2009; U. A. Gajbe, 2007a; Gertsch, 1939; Jézéquel, 1964, 1966; M.-L. Jiménez, 1987; Karsch, 1878; E. Keyserling, 1880, 1891; E. v Keyserling, 1883; Lawrence, 1947; Lessert, 1919, 1923, 1928; Levy, 1975; Marusik & Logunov, 1990, p. 2; Mcheidze, 2014; C. Mello-Leitão, 1947; C. de Mello-Leitão, 1939, 1947; C. F. de Mello-Leitão, 1929a; Millot, 1942; Ono, 1983, 2001; Pavesi, 1883; Petrunkevitch, 1925; F. O. Pickard-Cambridge, 1897, p. 2; O. Pickard-Cambridge, 1900;	(Gawryszewski et al., 2017)

		Piza Jr., 1934; Roewer, 1961; E. Simon, 1886a, 1907a; B. A. M. Soares & Soares, 1946; B. M. Soares, 1943; Strand, 1909, 1913b; G. Tang et al., 2008, 2008; G. Tang & Li, 2010a; L. R. Tang & Song, 1988; Thorell, 1875a, 1895; Workman, 1896; C. M. Yin et al., 2012)	
Tharpyna	non-EFS	(Hickman, 1944; Karsch, 1878; Koch, 1874, 1875b, 1876a; Rainbow, 1920; Tikader & Biswas, 1979)	(Gawryszewski et al., 2017)
Tharrhalea	EFS	(Barrion & Litsinger, 1995; Karsch, 1880a; Koch, 1874, 1875b; W. Kulczyński, 1911a, 1911b; E. Simon, 1886c, 1895a; Szymkowiak, 2014; Thorell, 1877b, 1881)	(Gawryszewski et al., 2017)
Thomisus	EFS	(Adolf Friedrich, 1910; Barrion et al., 2013; Barrion & Litsinger, 1995; Biswas & Roy, 2005; Blackwall, 1866, 1870; L. di Caporiacco, 1941, 1947a; Chrysanthus, 1964; Comellini, 1959; Commellini, 1957; Dippenaar-Schoeman, 1983, 1988; Dippenaar-Schoeman & van Harten, 2007; Dyal, 1935; Fage, 1930; Fox, 1937; P. Gajbe, 2004; P. U. Gajbe, 2004; U. A. Gajbe, 2005, 2007a; E.	(Gawryszewski et al., 2017)

		<p>Keyserling, 1880, 1881; Kiany et al., 2017; Kumari & Mittal, 1997; Lenz, 1891; Lessert, 1943; Levy, 1973; Lucas, 1858; Marusik & Logunov, 1990; C. F. de Mello-Leitão, 1929a; Ono, 1988; Parveen et al., 2008; Peng et al., 2001; Pravalikha & Srinivasulu, 2015; Reddy & Patel, 1991; Roewer, 1961; Saha & Raychaudhuri, 2007b; Schenkel, 1963b; Sen et al., 2015, 2015; E. Simon, 1877b, 1882, 1886d, 1890, 1902, 1906, 1909; Stoliczka, 1869; Strand, 1907b, 1907c, 1916; Sunil & Sebastian, 2001; G. Tang & Li, 2010b; L. R. Tang & Song, 1988; Thorell, 1878, 1887, 1890b, 1891a, pp. 1845–1847, 1895; Tikader, 1971; Workman, 1896; C. M. Yin et al., 2012)</p>	
Tmarus	non-EFS	<p>(Baert, 2013; Banks, 1898; Barrion et al., 2013; Barrion & Litsinger, 1995; Bayram et al., 2007; Bedoya-Roqueme, 2020; Berland, 1913; Butler, 1876; L. di Caporiacco, 1940a, 1941, 1947a, 1949, pp. 1944–1946, 1954; Chickering, 1950, 1965, 1966; Chrysanthus, 1964; Comellini, 1955; Daxiang, 1981; Dippenaar-</p>	<p>(Gawryszewski et al., 2017; Vieira, 2015)</p>

		<p>Schoeman, 1985, 1989; Dondale & Redner, 1978; P. U. Gajbe, 2004; Garcia-Neto, 1986, 1991; Gertsch, 1939; Han & Zhu, 2008; Ileperuma Arachchi & Benjamin, 2019; Jézéquel, 1964, 1966; M.-L. Jiménez, 1987, 1992; E. Keyserling, 1880, 1891; E. G. Keyserling, 1884; E. v Keyserling, 1883; Koch, 1874, 1876a; Lessert, 1919, 1928; Levy, 1973, 2007; Marusik, 1993, 1993; Marusik & Logunov, 2001; C. Mello-Leitão, 1947; C. de Mello-Leitão, 1943, 1944, 1947, 1948; C. F. de Mello-Leitão, 1929a, 1940a, 1941b, 1941a, 1943c, 1949; Millot, 1942; Ono, 1977a, 1988, 1996b, 1997; Paik, 1973; O. Pickard-Cambridge, 1900; Piza Jr., 1935, 1944; Rainbow, 1915; Rao et al., 2006; Schenkel, 1953, 1963b; Schiapelli & Gerschman, 1942; Schick, 1965; Sen et al., 2015; E. Simon, 1878, 1906, 1907a, 1909; E. L. Simon, 1874; B. A. Soares & Camargo, 1948; B. A. M. Soares, 1941, 1944a; B. A. M. Soares & Soares, 1946; B. M. Soares, 1943; D. Song & Zhu, 1997; Taczanowski, 1872; G. Tang & Li, 2010a, 2009b; Thorell, 1890a, 1894,</p>	
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		1895; X. G. Wang & Xi, 1998; Z.-Z. Yang et al., 2005; C. M. Yin et al., 2012; J.-X. Zhang et al., 2006; C. D. Zhu & Wen, 1981)	
Xysticus	non-EFS	(Almquist, 2006; Azarkina & Logunov, 2001; Ballarin et al., 2018; Banks, 1898; Basu, 1979; Bauer et al., 2020; Berland, 1922; Bosmans & Jacobs, 1985; Canestrini, 1873; L. di Caporiacco, 1922, 1933, 1935, 1938, 1939; Carrillo et al., 2016; Cockendolpher & Horner, 1980; Dalmas, 1922; Demir, 2015; Demir et al., 2017; Demir & Koçyiğit, 2016; Demir, 2012; Denis, 1956; Di & Zhu, 2008; Dondale, 2008; Dondale et al., 2006; Dondale & Redner, 1978; P. U. Gajbe, 2004; U. A. Gajbe, 2005; U. A. Gajbe & Gajbe, 1999; Gertsch, 1933, 1934, 1939, 1953; Guo, Ren, et al., 2015; Guo, Zhao, et al., 2015; Helsdingen, 1986; Hepner et al., 2011; J. Hu, 2001; IJLand & van Helsdingen, 2016; Jantscher, 2001; Jézéquel, 1966; Jocqué, 1977; Karol, 1966b, 1968; E. Keyserling, 1880; B.-W. Kim & Lee, 2007; J. P. Kim et al., 2016; S. T. Kim & Lee, 2012; Koch, 1875b, 1875a, 1876b, 1878;	(Gawryszewski et al., 2017)

		<p>Kroneberg, 1875; W. Kulczyński, 1882, 1901; Lawrence, 1927, 1928, 1937, 1938, 1942, 1952; Lee & Kim, 2018; Lessert, 1910, 1919, 1943; Levy, 1976, 2007; Z. X. Li & Yang, 2008; L. Liu et al., 2015; Logunov, 1995, 2006; Logunov et al., 2002; Logunov & Marusik, 1994; Lucas, 1838; Marusik, 1993; Marusik & Azarkina, 2016; Marusik & Chevrizov, 1990; Marusik & Logunov, 1990, 1995, p. 2; Mcheidze, 2014; Ono, 1978, 1988, 2002; Ono & Martens, 2004; Ovtsharenko, 1979; Pavesi, 1883; Rainbow, 1898; Redner & Dondale, 1965; Roberts, 1998; Roewer, 1938, p. 11938, 1962; Ruch et al., 2014; Saha & Raychaudhuri, 2007a; Schenkel, 1936, 1938, 1963a; Schick, 1965; Schmidt, 1968; Seyfulina & Mikhailov, 2004; E. Simon, 1873, 1876, 1877a, 1890, 1903b, 1905, 1907b, 1910; E. L. Simon, 1874; D. Song et al., 1996; D. X. Song & Wang, 1994; D. Song & Zhu, 1995, 1997; Strand, 1906, 1907a; Svaton et al., 2000; G. Tang et al., 2013; Thorell, 1875a, 1875b; Tikader, 1962, 1980; Turnbull et al., 1965; Tystshenko, 1965;</p>	
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		Utochkin, 1968; Utochkin & Savelyeva, 1995; Wunderlich, 1995; C. M. Yin et al., 2012; B. S. Zhang et al., 2004; F. Zhang, Zhu, et al., 2004; Zuo et al., 2014)	
Zygomētis	EFS	(Shield & Strudwick, 2000)	(Gawryszewski et al., 2017; Shield & Strudwick, 2000)

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