Renato Chaves de Macedo Rego

Quando e como ocorrem episódios de seleção sexual em espécies animais?

Uma investigação meta-analítica

When and how do episodes of sexual selection occur in animal species?

A meta-analytical investigation

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Tese apresentada ao Instituto de Biociências da Universidade de São Paulo como parte dos requisitos para obtenção do Título de Doutor em Ciências, na Área de Ecologia de Ecossistemas Terrestres e Aquáticos.

Orientador: Dr. Eduardo da Silva Alves dos Santos

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Aprovado em: ____________________

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___________________________ ___________________________

Eduardo Santos

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Prof. Dr. Eduardo da Silva Alves dos Santos

(Orientador)

Dedicatória

Às pessoas mais importantes da minha vida:

meu pai, minha mãe e minha irmã.

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Resumo

MACEDO-REGO, Renato C. Quando e como ocorrem episódios de seleção sexual em espécies animais? Uma investigação meta-analítica. 2020. Tese (Doutorado) – Instituto de Biociências, Universidade de São Paulo, SP.

No início, a teoria de seleção sexual baseava-se somente em episódios pré-acasalamento de competição por parceiros sexuais. Em alguns sistemas de acasalamento, machos tentam monopolizar parceiras através da defesa de recursos usados pelas fêmeas ou guardando diretamente as fêmeas. Em outros sistemas de acasalamento, esse comportamento de monopolização não existe e as táticas dos machos baseiam-se principalmente em achar ou cortejar fêmeas. Em todos cenários, esperava-se usualmente que fêmeas fossem o sexo criterioso na escolha e acasalassem poucas vezes. Contudo, análises genéticas modernas revelaram que frequentemente fêmeas acasalam com diferentes parceiros sexuais, o que permite a ocorrência de episódios de seleção sexual pós-acasalamento, como escolha críptica da fêmea e competição espermática. Agora, para melhor entender processos de seleção sexual, é necessário estimar seleção sexual em diferentes sistemas de acasalamento, integrando episódios de seleção pré e pós-acasalamento. Dessa forma, apresentamos aqui três meta-análises que integram episódios de seleção pré e pós-acasalamento em animais e combinam estimativas de seleção baseadas em indivíduos e em atributos desses indivíduos. No Capítulo 1, mostramos que medidas de sucesso de acasalamento inferidas a partir de testes genéticos produzem estimativas maiores da oportunidade para seleção sexual pré-acasalamento (I_s) do que medidas diretas de sucesso de acasalamento. Isso mostra que estimativas genéticas de sucesso de acasalamento não devem ser usadas para calcular-se I_s e que elas são mais propícias para o cálculo da oportunidade para seleção sexual pós-acasalamento. Dessa forma, propomos um novo índice de seleção pós-acasalamento: a oportunidade para seleção por fertilização. Sobretudo, nossos resultados mostram também que a oportunidade para seleção sexual pós-acasalamento é comum em animais. No Capítulo 2, mostramos que, quando o comportamento de monopolização ocorre, fêmeas lidam com menor oportunidade para seleção sexual pré-acasalamento e machos lidam com maior oportunidade para seleção sexual pré-acasalamento. Contudo, para ambos sexos, a oportunidade para seleção por fertilização e a oportunidade para seleção total não diferem de acordo com a ocorrência do comportamento de monopolização. Isso mostra que: (i) machos são bem sucedidos em monopolizar fêmeas durante eventos pré-acasalamento, mas fêmeas não são monopolizadas quando se analisa a integralidade dos eventos reprodutivos; (ii) poliandria é comum em animais; e (iii) escolha críptica da fêmea e competição espermática são forças seletivas efetivas. No Capítulo 3, demonstramos pela primeira vez que fêmeas e machos de maior tamanho corporal produzem mais filhotes, corroborando uma antiga hipótese de Charles Darwin sobre a evolução de tamanho corporal em fêmeas. Apesar das vantagens em ser grande quando comportamento de monopolização ocorre, nós também mostramos que indivíduos grandes são igualmente bem sucedidos em diferentes sistemas de acasalamento. Por fim, mostramos que investir em atributos envolvidos em fertilização aumenta o sucesso reprodutivo de machos, demonstrando novamente a relevância de episódios de seleção sexual pós-acasalamento.

Palavras-chave: oportunidade para seleção sexual, poliandria, seleção sexual pós-acasalamento, sistema de acasalamento, sucesso reprodutivo, tamanho corporal.

Abstract

MACEDO-REGO, Renato C. When and how do episodes of sexual selection occur in animal species? A meta-analytical investigation. 2020. Tese (Doutorado) – Instituto de Biociências, Universidade de São Paulo, SP.

The theory of sexual selection was initially based only on pre-mating episodes of intrasexual competition for sexual partners. In some mating systems, males try to monopolize females by guarding them or by defending resource(s) used by females. In other mating systems, such monopolization behavior is absent and male mating tactics are mainly based on finding or courting females. In all scenarios, females were usually expected to be the choosy sex and mate just a few times. However, modern genetic paternity analyses revealed that females frequently mate with different partners, leading to post-mating episodes of sexual selection, such as cryptic female choice and sperm competition. To better understand sexual selection processes, it is necessary to estimate sexual selection in different mating systems, integrating pre- and post-mating episodes of selection. Therefore, here we present three hierarchical meta-analyses that integrate pre- and post-mating selection episodes across animals, and combine individual-based and trait-based estimates of sexual selection. In Chapter 1, we show that mating success measures inferred from genetic analyses produce higher estimates of the opportunity for pre-mating sexual selection (I_s) than measures of actual mating success. This shows that genetic estimates of mating success should not be used to calculate I_s and that they would be better employed to estimate the opportunity for post-mating sexual selection. Therefore, we propose a new post-mating selection index: the opportunity for fertilization selection. More importantly, our results show that the opportunity for post-mating sexual selection is ubiquitous among animals. In Chapter 2, we show that, when monopolization behavior occurs, females face a lower opportunity for pre-mating sexual selection and males face a higher opportunity for pre-mating sexual selection. However, for both sexes, the opportunity for fertilization selection and the opportunity for selection do not differ according to the occurrence of monopolization behavior. This shows that: (i) males succeed in economically monopolizing females during pre-mating events, but females are not monopolized by males when we look at the whole reproductive process; (ii) polyandry is ubiquitous among animals; and (iii) cryptic female choice and sperm competition are effective selective forces. In Chapter 3, we demonstrate for the first time that larger females and males sire more offspring, corroborating a long-standing Darwinian hypothesis on the evolution of female body size. Despite the advantages of being larger when monopolization behavior occurs, we also show that large individuals are equally successful in different mating systems. Finally, we show that investing in fertilization-related traits results in higher fitness for males, demonstrating again the relevance of post-mating sexual selection.

Keywords: body size, mating system, opportunity for sexual selection, polyandry, post-mating sexual selection, reproductive success.

Índice

Guia para esta Tese

Introdução e Conclusão gerais: escrevi essas duas seções com a intenção de promover a divulgação científica. Essas duas seções compõem um conto, através do qual explico o que desenvolvi ao longo de meu curso de doutorado. Com o conto, eu apresento o arcabouço teórico no qual minha tese se baseia, explico as hipóteses que testei, apresento os resultados que obtive e os discuto tendo como base a teoria de Seleção Sexual. Assim, forneço introdução e conclusão gerais para minha tese, ao mesmo tempo em que apresento para a sociedade o trabalho que produzi.

Capítulos: minha tese tem três capítulos, escritos em formato de artigo, para que sejam publicados em periódicos científicos. Cada capítulo é composto por Introdução, Material e Métodos, Resultados, Discussão, Referências e Material Suplementar. Os trabalhos que proveram dados para minhas meta-análises serão listados na íntegra quando da publicação dos artigos em periódicos científicos.

Apêndices: ao fim da apresentação dos três capítulos, encontram-se os apêndices. Esses apêndices apresentam informações adicionais que são do interesse de dois ou mais capítulos.

OBS: in the papers derived from this thesis, we are going to inform the complete list of studies from which we extracted effect sizes.

Introdução geral

Finalmente tinha chegado o grande dia. Para ser sincero, na verdade, não era um grande dia, não. Era um dia como outro qualquer, bem normal. Estava até nublado. E com cara de que ia chover. Mas para Filipinho era um grande dia. Ele estava esperando por este dia havia muito tempo. Mas talvez eu precise avisar que o nome dele não é Filipinho. É que eu tenho que traduzir para que faça sentido, já que vocês são humanos, vivem na Terra e não fazem ideia de que em uma estrela, em outro universo, na dimensão 5,2/β, vive Filipinho. Não que Filipinho seja importante, muito pelo contrário. É que ele pertence a uma outra espécie, e os indivíduos dessa espécie têm uma língua que vocês não entenderiam, pois eles sequer se comunicam por sons ou sinais visuais. Mas eu vou traduzir tudo para que vocês consigam entender. Ah! Sobre isso, preciso comentar que a espécie de Filipinho não conhece o conceito de dia. Afinal de contas, eles vivem em uma estrela, e lá está sempre iluminado. Apesar dos dias nublados. Mas esqueçam os dias que não são dias; a essa altura, vocês devem estar com muitas dúvidas. Talvez eu tenha começado essa história de uma forma um tanto quanto confusa. – Tem mais de um assunto neste mesmo parágrafo! – Mas é que é difícil de explicar mesmo. Então, me limito a responder o mais importante: por que ’Filipinho’? Eu acho simpático como alguns humanos falam o nome de amigos no diminutivo, de forma carinhosa. Aí, eu resolvi imitar. Mas voltando para a história, o que temos até agora é que era um grande dia e o nosso protagonista é o Filipinho. Tirando pelo fato de que ele não se chama Filipinho. E não era bem um grande dia; na verdade, nem dia era. Mas acho que conseguimos seguir a partir daqui.

O quê de tão importante estava acontecendo na vida de Filipinho? Filipinho estava prestes a defender o seu mestrado. Filipinho estava se formando em Ciências – lá, eles não separam as disciplinas em Biologia, Física, Química, Sociais, como vocês humanos fazem. Esse é o grande momento da formação de um estudante no mundo de Filipinho. Embora eu não saiba se posso chamar de ‘mundo’; eu não entendo muito de astronomia e filosofia humanas. Pois bem, na estrela onde Filipinho vive, a defesa de mestrado é muito importante. Todos os habitantes da estrela assistem as defesas pela internet deles. Mas os habitantes não são poucos, na verdade eles são muitos. Mas como eles têm muito tempo livre, toda a estrela assiste as defesas. Apesar dessa grande audiência, a defesa é feita especialmente para uma banca composta por cinco especialistas na área, que fazem perguntas para o estudante que está fazendo a apresentação. Ao fim da apresentação, a população da estrela vota se o estudante deve ser aprovado ou reprovado. Mas isso é só pela espetacularização do evento. Na prática, quem decide se o estudante será aprovado ou não é a banca de especialistas. Se o estudante for reprovado, ele é sumariamente executado em uma corte marcial. O que parece muito radical, mas na espécie de Filipinho isso significa renascer cinco segundos depois e recomeçar os estudos do início.

E Filipinho fez um trabalho bem interessante. Na estrela onde vive Filipinho, muitos estudos têm sido feitos para entender como outras espécies, espalhadas pelos muitos universos, fazem ciência, identificando semelhanças e diferenças nos métodos e na filosofia. E Filipinho se somou a esses esforços estudando vocês, os humanos. O que é, sem sombra de dúvidas, muito controverso, pois... ah, como posso dizer isso? Vocês não são exatamente uma sociedade muito avançada. Não! Isso soa preconceituoso, desculpa. Deixe-me ver... vocês ainda têm muitos problemas a resolver. É, acho que isso traduz bem a situação... Mas pouco importa, pois me estendi muito nessa introdução! Para ir direto ao ponto, vamos pular para a última parte da defesa de Filipinho, quando a chefa da banca avaliadora, a Dra. Claudinha, sentada no centro da banca avaliadora, falou:

– Filipinho, muito boa a sua apresentação sobre como humanos do planeta Terra fazem ciência. Mas se não fui informada erroneamente, você selecionou um trabalho científico feito por humanos para ilustrar toda a argumentação que você acabou de fazer. Estou correta?

– Está, sim. É a tese de doutorado de um humano chamado Renato Chaves de Macedo Rego.

– Bom, para você ter selecionado o trabalho dele, imagino que o...

– Renato.

– ... que ele seja um dos maiores pesquisadores humanos.

– Não, de forma alguma. Definitivamente, não.

– Mas então por que você selecionou o trabalho dele?

– Eu preferi selecionar uma pesquisa humana através de sorteio para evitar que eu gerasse um viés ao escolher algum trabalho de pesquisador muito renomado entre humanos.

Na verdade, Filipinho escolheu o referido trabalho porque o autor humano escreveu uma tese que continha na introdução e na conclusão gerais uma história pretensamente extrovertida. E Filipinho gosta desse tipo de coisa. Mas Filipinho sabia que ele não podia revelar isso, pois boas práticas científicas incluem o esforço de evitar vieses na metodologia de pesquisa, uma vez que vieses podem alterar os resultados obtidos. Nesse sentido, o sorteio é uma forma efetiva de evitar vieses.

– Estou de acordo com o seu procedimento, Filipinho – completou a Dra. Claudinha. – Fale mais sobre esse trabalho.

– Ok. O autor humano estuda como espécies evoluem. Mais especificamente, ele estuda o processo evolutivo chamado seleção sexual.

– Então humanos já conhecem evolução de espécies? – surpreendeu-se a Dra. Tatianinha, sentada diretamente à esquerda da Dra. Claudinha. – Interessante. Você pode explicar para a audiência o que é evolução e, mais especificamente, o que é evolução por seleção sexual?

– Claro. Evolução é o processo através do qual as frequências de determinadas formas genéticas variam ao passar-se de uma geração para a outra. Explicarei melhor. Os genes[1] na Terra são estruturalmente diferentes dos nossos, mas o processo evolutivo lá é o mesmo. Imaginemos uma população em que 50% dos indivíduos apresentam o gene A e os outros 50% dos indivíduos apresentam o gene B. Se, depois de uma geração, 70% dos indivíduos apresentam o gene A e os 30% restantes apresentam o gene B, houve mudança nas frequências dos genes na população e a isso se dá o nome de evolução.

– Certo. E como seria a evolução por seleção sexual, Filipinho? – perguntou a Dra. Tatianinha.

– Imaginemos uma população de uma espécie qualquer em que indivíduos que apresentam um gene A apresentam também uma determinada característica física que os torna mais atraentes para potenciais parceiros sexuais, enquanto indivíduos pouco atraentes têm o gene B. Os indivíduos com o gene A são mais atraentes, terão mais parceiros sexuais, mais filhotes e seus filhotes terão o mesmo gene A (e por isso seus filhotes também serão atraentes). Enquanto isso, os indivíduos com gene B são menos atraentes, terão menos parceiros sexuais, menos filhotes e seus poucos filhotes terão o mesmo gene B (e por isso serão pouco atraentes também). Assim, com o tempo, a tendência é que aumente na população o número de indivíduos com o gene A e diminua o número de indivíduos com o gene B. Como eu comentei anteriormente, a esse processo, com mudança na frequência de genes (no caso, os genes A e B), se dá o nome de evolução. Como esse processo não ocorreu ao acaso, houve evolução por seleção. Como essa seleção ocorreu em contexto sexual, ou seja, alguns indivíduos foram mais bem sucedidos em obter parceiros sexuais e gerar filhotes, constata-se que houve evolução por seleção sexual.

– Ótimo, Filipinho. Ficou bem claro qual é a base do trabalho. Agora, nos conte como é o sexo lá na Terra – solicitou a Dra. Robertinha, sentada à direita da Dra. Claudinha.

– Perdão...?

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[1] Nota de Renato Chaves de Macedo Rego (RCMR): Genes são unidades de informação biológica codificada. Em humanos, assim como em muitas outras formas de vida, em combinação com outros materiais, os genes compõem cadeias de DNA. Essas cadeias de DNA estão contidas em nossas células. Estruturas de nossas células fazem a leitura da informação codificada nos genes, ação essa que se traduz na produção de várias das características que nossos organismos apresentam.

– Como se caracteriza o sexo entre espécies terráqueas? O autor estudou espécies da Terra, certo?

– Ah, sim! Os humanos nem sabem que há vida fora da Terra. Sobre ‘sexo’, há diferentes definições para essa mesma palavra. No projeto que estudei, o autor usa a definição de ‘sexo’ atrelada ao tipo de gameta de cada indivíduo, que pode ser o óvulo ou o espermatozoide. Então, há as fêmeas, que produzem poucos gametas grandes e de baixa mobilidade, os óvulos; e há os machos, que produzem muitos gametas pequenos e de alta mobilidade, os espermatozoides. Quando fêmeas e machos acasalam, os espermatozoides dos machos fertilizam os óvulos das fêmeas, produzindo células que se desenvolverão em novos indivíduos: os filhotes.

– Mas por que ele estudou espécies com somente dois sexos? Só há espécies com dois sexos lá na Terra?

– Não, há espécies de algo chamado fungos, e alguns fungos têm inúmeros sexos. Mas o autor humano estudou somente espécies animais, todas elas apresentando somente dois sexos.

– Então, ele escolheu o que era mais fácil de estudar?

– Talvez, mas é que humanos têm muito mais informações sobre as espécies com somente dois sexos. Os próprios humanos só apresentam dois sexos, segundo essa classificação[2].

– Bom, pelo menos, eles devem ter menos problemas com sexismo do que nós, que temos 176 tipos de sexo – comentou a Dra. Tatianinha.

– Na verdade, não – respondeu Filipinho. – Eles têm muito mais problemas com isso.

– É impressionante que eles sejam mais sexistas que a gente. Talvez o problema deles seja justamente a falta de diversidade – comentou o Dr. Agostinhozinho, sentado na extrema-esquerda da banca.

– Voltando ao que importa, o que o humano estudou sobre seleção sexual? – perguntou o Dr. Hélio, sentado na quinta cadeira, mais à direita.

– Ele dividiu o trabalho dele em três capítulos. No primeiro capítulo, ele usou um índice que estima a intensidade de seleção sexual existente antes que fêmeas e machos de espécies animais acasalem. É um índice de seleção sexual usado por muitos pesquisadores humanos. Basicamente, esse

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[2] Nota de RCMR: Aqui, Filipinho estava falando do conceito de sexo em termos estritamente biológicos. Em animais, o sexo (fêmea ou macho) é definido tão somente de acordo com o tipo de gameta produzido pelo indivíduo. É importantíssimo não confundir a definição biológica de sexo com o conceito de gênero em humanos. Os conceitos ‘mulher’ e ‘homem’ referem-se a gênero e não a sexo biológico. Esta tese não trata de gêneros. Esta tese trata de ‘sexo’ sob a definição estritamente biológica.

índice mostra o quanto que os indivíduos de um mesmo sexo e de uma mesma população variam em relação ao sucesso de acasalamento. Se alguns indivíduos são muito bem sucedidos e outros são mal sucedidos, há entre eles uma grande variação no sucesso de acasalamento. Quanto maior for a variação no sucesso de acasalamento, maior é a intensidade de seleção sexual.

– E o que seria sucesso de acasalamento? – perguntou o Dr. Agostinhozinho.

– Essa é a chave do Capítulo 1. Sucesso de acasalamento é uma variável científica teórica, mas para medi-la, cientistas precisam encontrar uma variável operacional de sucesso de acasalamento. Diferentes autores estimam sucesso de acasalamento usando diferentes variáveis operacionais. Por exemplo, há autores que estimam sucesso de acasalamento contando diretamente o número de parceiros sexuais de cada indivíduo. Mas há autores que usam testes de maternidade e paternidade para inferir quem acasalou com quem e quantificar o sucesso de acasalamento dos indivíduos. Então, o autor humano do trabalho que eu selecionei quantificou se essas diferentes formas de medir sucesso de acasalamento geram diferentes estimativas da intensidade de seleção sexual.

– E o que o autor fez no Capítulo 2? – perguntou a Dra. Robertinha.

– No Capítulo 2, o autor estudou como os diferentes sistemas de acasalamento existentes em animais terráqueos influenciam a intensidade de seleção sexual para fêmeas e machos. Em algumas espécies, os machos tentam monopolizar o acesso a fêmeas, seja guardando as fêmeas da investida de outros machos ou seja defendendo algum recurso utilizados pelas fêmeas, como comida ou abrigos. Nessas espécies, alguns machos tendem a ter muito acesso às fêmeas enquanto outros machos não, o que deve gerar uma grande variação tanto no sucesso de acasalamento, como no sucesso reprodutivo de machos, aumentando a intensidade de seleção sexual entre eles. Já as fêmeas, ao serem guardadas pelos machos, tendem a ter o mesmo sucesso de acasalamento (todas acasalam com o macho guardião), o que significa que a intensidade de seleção sexual para fêmeas será baixa.

– Por que você fala que os machos guardiões tendem a ter mais parceiras e mais filhotes e que as fêmeas tendem a ter o mesmo sucesso de acasalamento nessas espécies? – perguntou a Dra. Robertinha.

– Por que essa é a previsão feita pelos cientistas humanos a partir do que eles observam na natureza. Mas isso não significa que os machos são bem sucedidos ao tentar monopolizar as fêmeas. E o trabalho que selecionei ajuda a responder isso.

– Como? – perguntou a Dra. Claudinha.

– Como eu estava explicando, o autor estudou diferentes sistemas de acasalamento em animais terráqueos. Em algumas espécies, o sistema de acasalamento é caracterizado pelo fato de machos tentarem monopolizar parceiras sexuais. Mas há espécies em que esse comportamento não existe. Nessas espécies, machos tentam obter parceiras investindo mais em encontrar fêmeas antes de seus competidores ou em se exibir para fêmeas em arenas de cortejo. Ao não haver tentativa de monopolização por parte dos machos, fêmeas têm menos restrição para acasalar, o que deve aumentar a variação no sucesso de acasalamento de fêmeas e, consequentemente, aumentar a intensidade de seleção sexual para elas. Por outro lado, se machos não tentam monopolizar fêmeas, a variação no sucesso de acasalamento entre machos deve ser baixa, o que resulta em baixa intensidade de seleção sexual nesse tipo de sistema de acasalamento. Comparando sistemas de acasalamento de acordo com a ocorrência ou ausência do comportamento de monopolização, o autor pôde verificar como sistemas de acasalamento influenciam a seleção sexual e pôde avaliar se machos são realmente bem sucedidos ao tentar monopolizar parceiras sexuais.

– E você comentou que o autor estudou espécies animais terráqueas. Humanos também são animais. Ele incluiu a própria espécie no estudo? – perguntou o Dr. Agostinhozinho.

– Humanos são animais como outros quaisquer, sem dúvidas, estando sujeitos a processos evolutivos como qualquer outra espécie animal. Mas em termos comportamentais, humanos diferem bastante de outras espécies e então o autor julgou que seria melhor não incluir a própria espécie em sua tese. Assim, ele está estudando espécies animais não-humanas e as previsões e conclusões do estudo são baseadas tão somente em animais não-humanos.

– E quanto ao Capítulo 3? – perguntou o Dr. Hélio.

– No terceiro capítulo, o autor novamente comparou sistemas de acasalamento com e sem o comportamento de monopolização. Mas nesse capítulo, ele testou como atributos físicos e comportamentais influenciam o sucesso reprodutivo de fêmeas e machos. Ele coletou medidas de tamanho corporal, de investimento em ornamentos atrativos para o sexo oposto, de investimento em estruturas para fertilização de óvulos e de investimento em armamentos para lutas.

– E o que seria investir em estruturas para fertilização de óvulos e investir em armamentos? – perguntou a Dra. Claudinha.

– Investimento em estruturas para fertilização de óvulos pode ser feito, por exemplo, aumentando-se o número de espermatozoides ou a qualidade dos espermatozoides produzidos, o que deve aumentar as chances de o macho fertilizar os óvulos das fêmeas com que acasala. Investir em armamentos pode ser aumentar o tamanho de chifres, por exemplo.

– E o autor tinha hipóteses de trabalho para esse capítulo 3? – perguntou a Dra. Robertinha.

– Sim. Ele previa que maior tamanho corporal e maiores armamentos seriam mais importantes para machos nas espécies em que o comportamento de tentativa de monopolização existe, já que ser maior e mais bem armado deve ajudar nas brigas entre os machos para tentar monopolizar fêmeas. Ainda para machos, ele previa que investimento em ornamentos e em fertilização seriam mais importantes nas espécies em que o comportamento de tentativa de monopolização não ocorre, dado que a disputa entre machos nessas espécies se dá de formas que não requerem contato físico direto entre eles. Para fêmeas, ele esperava que tamanho corporal fosse mais relevante nas espécies em que o comportamento de tentativa de monopolização existe, pois fêmeas maiores devem ser mais hábeis em se desvencilhar das tentativas de monopolização dos machos.

– E como o autor coletou os dados para esses três capítulos? – perguntou o Dr. Agostinhozinho.

– Ele utilizou um método conhecido como meta-análise. A ideia é coletar dados de diversos trabalhos diferentes e sintetizá-los de forma quantitativa. Então, o autor pegou medidas de seleção sexual disponíveis na literatura científica de seu planeta, tendo como critério básico que fossem medidas de seleção sexual referentes a espécies animais não-humanas. Usando modelagem matemática, ele testou as hipóteses que acabei de descrever.

– E quantos trabalhos ele triou para fazer isso? – perguntou a Dra. Tatianinha.

– Mais de 8.000 artigos científicos.

– Só isso?

– Para humanos, seria o equivalente a ler cerca de 30.000 *querkelecs*[3].

– Ah! Então ele realmente leu uma quantidade grande de trabalhos. Isso certamente aumenta a robustez dos resultados – concluiu a Dra. Robertinha.

– Filipinho, já que chegamos aos resultados, você pode nos entregar as cópias da Tese humana selecionada, por favor? Precisamos ver o material – disse a Dra. Claudinha.

Filipinho entregou então cópias da tese para os cinco membros da banca avaliadora. As cópias estavam traduzidas, afinal de contas, quase ninguém na estrela de Filipinho conhece qualquer língua humana.

Agora, estimada leitora ou leitor, você também pode ler os três capítulos da Tese do tal Renato. Os três capítulos estão anexados aqui também, na sequência desta introdução geral. Mas caso você não queira lidar com a nomenclatura científica mais técnica, você pode pular direto para a conclusão geral (página 188), ver como esta história continua e descobrir se Filipinho foi aprovado ou reprovado

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[3] Nota do narrador: Eu não sei como traduzir *querkelecs*.

na sua defesa de mestrado. Será que a banca avaliadora gostou do trabalho dele? Será que Filipinho foi sumariamente executado e obrigado a fazer todo o trabalho de novo, ao renascer cinco segundos depois? Bom, descubra a seguir.

Capítulo 1

Post-mating episodes of sexual selection are ubiquitous in animal species and the way we measure mating success matters: a meta-analysis

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Abstract

At first, sexual selection theory was mainly based on intrasexual pre-mating competition and its effects on animal reproductive success. Later, the theory was expanded with the inclusion of post-mating selection episodes such as sperm competition and cryptic female choice. Through the last decades, many indexes were created to measure sexual selection intensity, but they are mainly restricted to estimates of sexual selection based on mating success (i.e. pre-mating episodes of selection), but not on fertilization success (i.e. post-mating episodes of selection). Here, using a meta-analytical procedure, comprising 129 animal species, that provided more than 596 effect sizes, we test if different proxies for mating success influence the estimates of sexual selection intensity. We show that, for both females and males, quantifying the mating success by counting the number of sexual events or the number of sexual partners does not influence the estimate of the opportunity for sexual selection. We also show that, regardless of the sex, inferring mating success from genetic analyses alter the estimate of the opportunity for sexual selection, but does not change the estimated slope of the Bateman gradient. The different opportunities for sexual selection generated by actual mating success and genetically inferred mating success demonstrate the ubiquitous occurrence of post-mating sexual selection across animals, for females and males. Therefore, we should be cautious about inferring mating success from genetic analyses and on how to interpret selection indexes derived from these mating success estimates. As a solution, we propose a post-mating sexual selection index, the opportunity for fertilization selection.

Keywords (alphabetical order): Bateman gradient, body condition, condition-dependent, cryptic female choice, fertilization success, male dominance, mate choice, opportunity for post-mating sexual selection, opportunity for selection, opportunity for sexual selection, reproductive alternative tactics, reproductive success, selection index, sperm competition.

Introduction

At its first proposition, sexual selection theory was focused on pre-mating events of mate choice and competition for sexual partners, with females usually being expected to be the choosy sex and males being expected to court females and/or fight each other for mating opportunities (Darwin 1871; Dewsbury 2005). More than a century later, the sexual selection field was expanded by the proposition and development of theories focused on what happens after mating/copulation takes place. If a female mates with more than one male, the sperm transferred by her partners may compete to fertilize her ova (Parker 1970a,b), and the female may also trade fertilization in favor of the sperm of (a) particular male(s), cryptically choosing the best male(s) (Thornhill 1983). The subsequent improvement of genetic analyses allowed us to better understand paternity patterns. Such information fueled research interests in post-mating episodes of sexual selection, because of the discovery that polyandry (i.e. females mating with more than one male) is common among animals (Gowaty 2006; Taylor et al. 2014). This widespread occurrence of polyandry challenges previous expectations about the sexual behavior of females (Parker and Birkhead 2013). Because females usually mate multiple times, it is likely that cryptic female choice and sperm competition frequently occur in nature. Accordingly, the occurrence of post-mating events of sexual selection has been demonstrated for many *taxa* (Birkhead and Møller 1998; Parker and Pizzari 2010; Peretti and Aisenberg 2015; Firman et al. 2017). Moreover, with the increasing perception that post-mating events influence the strength of total selection, attempts to integrate pre- and post-mating events of selection became common (e.g. Keogh et al. 2013; Rose et al. 2013; McCullough et al. 2018; Tuni et al. 2018; Filice and Dukas 2019). Now, modern sexual selection theory encompasses both pre- and post-mating episodes of selection.

The inclusion of post-mating events in the theory was initiated by (Parker 1970a,b,c,d,e, 1974), that introduced how sperm competition can operate. Since then, additional studies extended the theoretical basis and provided numerous empirical evidence (Smith 1984; Birkhead and Møller 1998; Shackelford and Pound 2006; Parker and Pizzari 2010; Civetta and Ranz 2019). Among animals, males deal with sperm competition by trying to reduce the risk of sperm competition, and/or investing in being a good post-mating competitor (Simmons 2014). Males may reduce the risk of sperm competition by prolonging copula duration (e.g. del Castillo 2003; Friesen et al. 2017), and guarding females before (e.g. Jormalainen 1999; Kuramitsu et al. 2019), or after (e.g. Bussière et al. 2006; Balenger et al. 2009) mating occurs. Other strategies do not include physical attempts to restrict female polyandrous behavior. For example, some males insert genital plugs that prevent competitors from copulating with the female (e.g. Polak et al. 1998; Kralj-Fišer et al. 2011). Additionally, males may remove from female sperm storages the sperm deposited by other males (e.g. Cordero-Rivera 2016; Sekizawa et al. 2019). Finally, as previously said, male may also engage in being a good post-mating competitor. This engagement may happen through investments in the production of more sperm and/or sperm of higher quality (e.g. Møller 1988; Simmons et al. 2007; DelBarco-Trillo 2011; Lüpold et al. 2011b,a; Rowe and Pruett-Jones 2011). Not surprisingly, among rodent species, the increase in sperm competition intensity is correlated with an increase in sperm quality (Gomendio et al. 2006). However, high investments in sperm production are costly, which may lead to a trade-off between investing in sperm production and investing in traits involved in pre-mating intrasexual competition (e.g. Ferrandiz-Rovira et al. 2014; García-Navas et al. 2014; Dines et al. 2015; Dunn et al. 2015; Lüpold et al. 2019; but see Lüpold et al. 2015).

As highlighted before, post-mating episodes of sexual selection are not restricted to sperm competition, but also include cryptic female choice. After the introduction of the idea of cryptic female choice (Thornhill 1983), the study of female post-mating choice was mainly advocated by Eberhard (1996). Cryptic female choice has been demonstrated in different contexts, but because it occurs inside the female reproductive tract, there are some difficulties in demonstrating its occurrence (Firman et al. 2017). One clear occurrence of cryptic female choice comes from species in which females eject the sperm from particular males (e.g. Pizzari and Birkhead 2000; Peretti and Eberhard 2010; Dean et al. 2011; Droge-Young et al. 2016; Sato et al. 2017), favoring the sperm of preferred males. Cryptic female choice may also rely on morphological variation in female reproductive traits, as for the yellow dung fly, in which a greater number of female sperm storage organs allows high-quality females to better control the proportion of offspring sired by their last sexual partners (Ward 2000). Females may also favor particular males by secreting compounds that affect sperm activity (Gasparini and Pilastro 2011; Alonzo et al. 2016) or by ovipositing sooner after mating with a high-quality male (e.g. Barbosa 2009). In an earwig, the morphology of female sperm storages precludes males from removing much of the sperm already found inside the female. Because larger males mate more times, females tend to accumulate sperm from larger males and, therefore, tend to produce larger sons (Kamimura 2015). This production of high-quality offspring is predicted to maintain cryptic female choice, once post-mating choice is expected to solely rely on genetic benefits (Firman et al. 2017). Accordingly, post-mating inbreeding avoidance has been demonstrated for different *taxa* (Gasparini and Pilastro 2011; Lovlie et al. 2013; Firman and Simmons 2015; Burgess et al. 2019; Pineaux et al. 2019; Speechley et al. 2019).

Given the large evidence of the occurrence of sperm competition and cryptic female choice, one may ask how these post-mating events shape sexual selection. Various indexes to estimate the intensity or the opportunity for sexual selection have been developed (Croshaw 2010; Henshaw et al. 2016), focusing on the variance in mating success (e.g. the opportunity for sexual selection, mating differentials), the variance in reproductive success (e.g. the opportunity for selection, selection differentials), or integrating mating and reproductive success (e.g. Bateman gradient, Jones index) (see Henshaw et al. 2016). However, little attention has been given to quantify the opportunity for post-mating sexual selection (but see Shuster et al. 2013; Pélissié et al. 2014). Here, using quantifications of the opportunity for pre-mating sexual selection and employing meta-analytical techniques, we quantify the opportunity for sexual selection during post-mating events, accessing how cryptic female choice and sperm competition shape sexual selection across animals. This investigation was possible because several studies calculate the opportunity for sexual selection by inferring mating success from genetic analyses (i.e. mating success would then equate to fertilization success). However, it is plausible to expect that fertilization success fails to properly predict mating success because not all matings result in fertilization. Additionally, mating success measures what happens before fertilization occurs, and fertilization success quantifications could probably be better used if employed to access post-mating sexual selection. Therefore, we contrasted estimates of the opportunity for sexual selection obtained through mating success and fertilization success measures, demonstrating that these estimates numerically differ from each other, and suggesting that they provide complementary information on different episodes of sexual selection. Additionally, we tested whether estimates of mating and fertilization success provide different estimates of the Bateman gradient (i.e. the correlation between mating and reproductive success; Bateman 1948; Arnold and Duvall 1994). We also tested whether quantifying mating success by counting the number of mating events or the number of mate partners lead to different estimates of the opportunity for sexual selection, as mating with different sexual partners or repeatedly with the same partner may bring different fitness outputs (e.g. Ronkainen et al. 2010).

Methods

Data search and collection

This study is one ramification of a broader study (Chapters 2 and 3) and it is presented first as its results have implications for the rest of the project. The data used here is a subset of the larger project's dataset and derives from a meta-analytical search procedure. We searched for original studies that measured sexual selection intensity/opportunity or that report data that allowed us to estimate it (see below). We conducted the literature search on *Web of Science* (all databases) and *Scopus* databases, using the following combination of keywords: "reproductive success" AND "mating success" OR "fitness" AND "mating success" OR "paternity" AND "mating success" OR "offspring" AND "mating success" OR "litter" AND "mating success" OR "fertilization success" AND "mating success" OR "breeding success" AND "mating success" OR "fecundity" AND "mating success" OR "reproductive rate" AND "mating success" OR "post-mating sexual selection" OR "post-mating selection" OR

"Bateman*" OR "opportunit* for selection" OR "opportunit* for sexual selection" OR "selection gradient*" OR "Morisita index" OR "monopolization index for reproductive success" OR "Jones index" OR "copulation success" OR "opportunit* for natural selection" OR "intensit* of sexual selection" OR "mating success" AND "survival rate" OR "reproductive success" AND "number of mat*" OR "mixed paternity" OR "mating and reproductive success" OR "opportunit* for natural selection and sexual" OR "natural and sexual selection" OR "sexual and natural selection". We last updated the search on May 28th 2017.

We built the dataset of the larger project by searching the literature for studies on non-human animals that provided at least one measure of the opportunity for sexual selection – I_s, the mating success variance in a given population divided by the squared population mean mating success (Crow 1958) – and one measure of the opportunity for selection – I, the reproductive success variance in the given population divided by the squared population mean reproductive success (Wade 1979). From this subset of approved studies, we also collected estimates of the Bateman gradient – the slope of the least square regression between mating success and reproductive success (Bateman 1948; Arnold and Duvall 1994) – if this index of selection was available. From the larger dataset, we used for this study only estimates of the opportunity for sexual selection and the Bateman gradient. Because I_s is a standardized measure, it can be used for interspecies comparisons (Moura and Peixoto 2013); i.e. these estimates can be used as effect sizes in a meta-analysis. We standardized Bateman gradient estimates following Jones (2009). For each selection index extracted from the literature, we recorded the respective sample size and the sex of the sampled individuals. For estimates of I_s, we qualified the data that provided the measures of mating success into two types: (1) the authors measured the actual mating success; or (2) the authors inferred mating success by obtaining the fertilization success prevenient from genetic paternity analyses.

We divided the I_s estimates obtained from actual measures of mating success into two classes (hereafter, “mating success meaning”): (1a) the authors measured for each individual the number of times it was seen mating; or (1b) the authors measured the number of sexual partners for each individual (the individual with whom a female or male mates is her/his sexual partner). Finally, we classified Bateman gradients in two types: (I) Bateman gradients in which the *x*-axis shows the actual mating success of the individuals; (II) Bateman gradients in which the *x*-axis shows individual mating success inferred from genetic paternity analyses.

While screening the literature, we did not extract data from studies in which the authors precluded variation in mating success (i.e. all individuals had the same mating success). We also rejected studies when authors could not assure that they managed to identify the genetic mothers and/or fathers of the sampled offspring. This is important because, for several species, and specially for males, the social parent may not always be the genetic parent (e.g. Ketterson et al. 1997; Poesel et al. 2011; Schlicht and Kempenaers 2013). Moreover, we did not include_studies in which the experimental procedure somehow changed the reproductive performance of the organisms. We extracted data from the main text and supplementary materials of the original studies. In case data were available in figures, we used the program WebPlotDigitizer (Rohatgi 2015). When data could not be extracted from the main sources, we searched for related data on the Dryad© and Figshare repositories. Additionally, we contacted authors, asking for data when this was not available in any reachable source (see Appendix 1 for more information and to see the template of the e-mail sent to the authors). We followed PRISMA procedure and the PRISMA diagram for this project can be found in Chapter 2.

In order to account for the known heterogeneity in biological data (Senior et al. 2016) and deal with specificities of the data structure, we also qualified the extracted data through many ways. We recorded how fertilization success was measured by the authors (“fertilization success meaning”), accounting if they measured how many times each individual fertilized or was fertilized (only one study in our data set) or if they measured, for each individual, the number of partners with whom they produced at least one offspring. We recorded if authors included in their studies individuals that failed to mate (“inclusion of zeros”), because failing to include them may lead to erroneous estimates of selection (Klug et al. 2010b). We also recorded if authors influenced/determined mating success of (at least part of the) individuals, ("mating success interference") and if authors did not allow intrasexual competition to occur before mating events in the sex being studied. Finally, we recorded the offspring age, because the older the offspring, the higher are the chances of natural selection noise occurrence among the data (Bergeron et al. 2013). For more details on how we screened the studies and how we extracted the data, see Chapter 2.

Hypotheses

We mainly tested different ways to measure/estimate sexual selection, with one of these tests also allowing us to contrast the opportunities of pre- and post-mating sexual selection (Test #2, below). The tests were as follows:

Test #1: we tested, for both sexes, whether estimates of the opportunity for sexual selection differ according to the way mating success was measured by the authors of the original studies: number of mating occurrences *vs*. number of sexual partners. When mating success is measured by counting the number of sexual partners, mating several times or just once with a specific additional sexual partner increases the mating success in one unity. However, when mating success is measured by counting the number of mating occurrences, mating several times with a specific additional sexual partner means a much higher mating success than mating just once with this specific additional sexual partner. Because individuals may differ in the average number of times they mate with each sexual partner, we expected higher estimates of the opportunity for sexual selection when mating success was measured by quantifying the number of mating occurrences, than when quantifying the number of sexual partners;

Test #2: we tested, for both sexes, whether estimates of the opportunity for sexual selection differ according to the way mating success was estimated: directly (authors measured the actual mating success) *vs*. indirectly (authors inferred mating success from genetic analyses). Pre-mating episodes of sexual selection, by definition, precede post-mating episodes of sexual selection (such as fertilization), which means that selection episodes happening before a mating event influence the opportunity for selection after mating, but the opposite is not true (i.e. post-mating episodes of sexual selection cannot change the opportunity for pre-mating sexual selection). Given that individuals with higher mating success have more opportunities to increase their fertilization success, we expected a positive correlation between mating success and fertilization success. Moreover, because pre-mating episodes of selection precede post-mating episodes of selection and assuming a positive correlation between mating and fertilization success, we expected that the opportunity for sexual selection would be higher when authors estimated the mating success indirectly (through fertilization success measures obtained from genetic analyses) than when authors directly estimated the actual mating success;

Test #3: we tested, for both sexes, whether estimates of Bateman gradient differ according to the way mating success was estimated: directly (authors measured the actual mating success) *vs*. indirectly (authors inferred mating success from genetic analyses). Because genetic quantifications of mating success are derived from fertilization success estimates and fertilization success involves producing offspring with sexual partners (i.e. reproductive success), we expected a steeper Bateman gradient when mating success is genetically estimated than when it is directly estimated.

Statistical analysis

Because our estimates come from different species, but those species share an evolutionary history, and because one study may provide more than one effect size estimate (i.e. data are not independent), we used multilevel (hierarchical) meta-regression models. For Test 1, we included as random variables the effect sizes pair identity and the phylogeny. For Test 3, every study provided at least two measures for a given group of individuals: one measure for directly estimated mating success and the other for indirectly estimated mating success. Therefore, we included as random variables for Test 3 the effect sizes pair identity (there is at least one pair per study) and phylogeny. We ran Test 2 two times: Test 2A contained only studies that provided at least two measures for a given group of individuals (one measure for directly estimated mating success and the other for indirectly estimated mating success, as we did for Test 3); Test 2B contained all studies that provided at least one measure of I_s, regardless of its class (if mating success was directly estimated or not). For Tests 2A and 2B, we also included effect sizes pair identity and phylogeny as random variables (for Test 2 B, I_s estimates with no pair estimate received a pair identity that was not designated for any other effect size). Most of the phylogeny (including times of divergence between species) was obtained from the *TimeTree Database* (Hedges et al. 2006). For the missing species in the *TimeTree Database*, we expanded the phylogeny and calculated the remaining times of divergence by using *Mesquite* software (Maddison and Maddison 2019) and *Phylocon* (Webb et al. 2008). The phylogeny constructed contains all the species included in our research project (see phylogeny in Appendix 2). We pruned the phylogeny to restrict the analyses for the species included in each model of the present study.

For Tests 1 and 2, the response variable was the I_s, and we weighted each estimate measure by using their respective sample sizes. For Test 3, the response variable was the standardized slope of the Bateman gradient, and we obtained the sampling variance of each Bateman gradient slope estimate by calculating Pearson's product-moment correlation coefficient (r): $(1 – r^2)^2$ / (sample size – 2) (Lajeunesse et al. 2013). For Test 1, we included the class of mating success as moderator (mating success as number of mating events *vs*. mating success as number of sexual partners). For Tests 2 and 3, we included as moderator the way mating success was estimated (directly *vs*. indirectly through genetic analyses). For all tests, to better explain the variation in effect sizes estimates, we included as random factors (when it was pertinent): mating success meaning, fertilization success meaning, inclusion of zeros, mating success interference, intrasexual competition, and offspring age. We calculated data heterogeneity (I^2; following Nakagawa and Santos 2012), and the proportion of data variance explained by each random variable included per model. To estimate whether the data we collected may be influenced by publication bias, given that animal behavior studies commonly present publication bias (Rosenthal et al. 2017), we calculated Egger's regression (Egger et al. 1997).

Finally, we ran sensitivity analyses, excluding specific data subsets in order to check how these would influence the results. For sensitivity analyses, effect sizes identity and phylogeny were included as random factors. We performed sensitivity analyses by excluding:

i) I_s (only Test 2) and Bateman gradient slope estimates in which mating success represents the number of mating events (not the number of sexual partners);

ii) I_s and Bateman gradient slope estimates that do not include individuals with mating success equal 0;

iii) I_s and Bateman gradient slope estimates from studies in which experimental design influenced/determined mating success of individuals;

iv) and I_s and Bateman gradient slope estimates from studies in which experimental procedure prevented the occurrence of intrasexual competition among individuals of the sex being studied.

In order to better understand how mating and fertilization success measures influence the estimates of the opportunity for sexual selection (Test 2), we calculated the average correlation between mating success and fertilization success for both sexes for studies that provided both fitness measures. We included as random variables the phylogeny and the study identity.

We fit all meta-regression models using the function rma.mv from the *metafor* package (Viechtbauer 2010; R Core Team 2017). We present estimated parameters along with their 95% compatibility intervals (CIs) and discuss our findings interpreting the parameter point estimates, while at the same time acknowledging their uncertainty (Wasserstein et al. 2019).

Results

Test 1 – I_s estimates are similar whether counting the number of matings or the number of sexual partners

For females, from 17 different species, we extracted 23 different estimates of I_s in which mating success is the number of times the female was observed mating. Still for females, from 26 different species, we extracted 36 different estimates of I_s in which mating success is the respective number of sexual partners for each female (Figure S1). Different classes of mating success generate similar estimates of I_s (number of times seen mating: $I_s = 0.667$, 95% CI = -0.624 to 1.959; number of sexual partners: $I_s = 0.706$, 95% CI = -0.753 to 2.167; contrast: $I_s = 0.040$, CI lower end = -0.129, CI upper end = 0.208). The result remains the same in all sensitivity analyses Table S1). Random variables account for a small part of the variation in our data ($I^2 = 6.52\%$; I^2 phylogeny: 5.45%; I^2 effect sizes pair identity = $2.75 \times 10^{-11}\%$; I^2 mating success interference = 1.07%; I^2 inclusion of zeros = $1.05 \times 10^{-12}\%$; I^2 intrasexual competition occurrence = $3.42 \times 10^{-11}\%$). Egger's regression test indicates the possibility of publication bias in the data (Egger's regression: $I_{s\ intercept} = -0.288 \pm 0.100$ SE, $t = -2.863$, $p < 0.05$).

For males, from 18 different species, we extracted 22 different estimates of I_s in which mating success is the number of times the male was observed mating. Still for males, from 22 different species, we extracted 34 different estimates of I_s in which mating success is male's number of sexual partners (Figure S2). Different classes of mating success generate similar estimates of I_s (number of times seen mating: $I_s = -2.750$, 95% CI = -12.212 to 6.710; number of sexual partners: $I_s = -2.420$, 95 % CI = -13.756 to 8.915; contrast: $I_s = 0.331$, CI lower end = -1.544, CI upper end = 2.205). The result remains the same in all sensitivity analyses (Table S3). Random variables account for a small part of the variation in our data ($I^2 = 6.52\%$; I^2 phylogeny: 5.45%; I^2 effect sizes pair identity = $2.75 \times 10^{-11}\%$; I^2 mating success interference = 1.07%; I^2 inclusion of zeros = $1.05 \times 10^{-12}\%$; I^2 intrasexual competition occurrence = $3.42 \times 10^{-11}\%$). Egger's regression test indicates the possibility of publication bias in the data (Egger's regression: $I_{s\ intercept} = -0.288 \pm 0.100$ SE, $t = -2.863$, $p < 0.05$).

Test 2 – Genetic measures of mating success produce higher estimates of I_s (females)

For females, from 14 different species, we extracted from a given group of females at least two measures of I_s, one measure in which mating success was directly estimated and one measure of I_s in which mating success was indirectly estimated. In total, we extracted 17 pairs of I_s estimates (Figure S3). Estimates of I_s differ according to the way mating success is estimated (mating success directly estimated: $I_s = 1.440$, 95% CI = -0.815 to 3.695; mating success inferred from genetic analyses: $I_s = 1.581$, 95% CI = -0.555 to 3.717; contrast: $I_s = 0.141$, CI lower end = 0.260, CI upper end = 0.022). The result remains the same in all sensitivity analyses, except after excluding studies that sampled older offspring, when the absolute estimate value is still higher for mating success genetically estimated, but the difference is only marginally significant (Table S3). Random variables account for a small part of the variation in our data ($I^2 = 14.89\%$; I^2 phylogeny: 5.24%; I^2 effect sizes pair identity = $1.22 \times 10^{-10}\%$; I^2 mating success interference = 6.69%; I^2 inclusion of zeros = 0.54%; I^2 intrasexual competition occurrence = 2.42%; I^2 offspring age = 0%). Egger's regression test indicates the possibility of publication bias in the data (Egger's regression: $I_{s\ intercept} = -0.802 \pm 0.229$ SE, $t = -3.498$, $p < 0.05$). Finally, we detected a positive correlation between mating success and fertilization success for females ($r = 0.645 \pm 0.229$ SE, $z = 5.988$, $n = 15$ species, $p < 0.0001$).

For females, from 42 different species, we extracted 59 estimates of I_s in which mating success was directly estimated; and, from 73 different species, we extracted 141 estimates of I_s in which mating success was indirectly estimated (Figure S3). Estimates of I_s do not differ according to the way mating success was estimated when data coming from all studies are included (mating success directly estimated: $I_s = 0.748$, 95% CI = -2.631 to 4.125; mating success inferred from genetic analyses: $I_s = 0.670$, 95% CI = -2.522 to 3.861; contrast: $I_s = 0.078$, CI lower end = -0.109, CI upper end = 0.264). However, this result is not replicated across sensitivity analyses (Table S4). For all sensitivity analyses, I_s estimates derived from genetically estimating mating success are higher than I_s estimates derived from directly estimated mating success, except after excluding studies in which there was no intrasexual competition among sampled females (in this case, the absolute estimate value is still higher for mating success genetically estimated, but the difference is only marginally significant) and after excluding studies that sampled older offspring (Table S4). Random variables account for a considerable part of the variation in our data (I^2 = 56.46%; I^2 phylogeny: 55.04%; I^2 effect sizes pair identity = 0.61%; I^2 mating success interference = 0.66%; I^2 inclusion of zeros = 0.02%; I^2 intrasexual competition occurrence = 1.16 x 10^{-8}%; offspring age = 0.14%). Egger's regression test indicates that there is little evidence of publication bias in the data (Egger's regression: $I_{s\ intercept}$ = -0.050 ± 0.112 SE, t = -0.444, p > 0.05).

Test 2 – Genetic measures of mating success produce higher estimates of I_s (males)

For males, from 13 different species, we extracted from a given group of females at least two measures of I_s, one measure in which mating success was directly estimated and one measure of I_s in which mating success was indirectly estimated. In total, we extracted 16 pairs of I_s (Figure S4). Estimates of I_s differ according to the way mating success is estimated (mating success directly estimated: I_s = 0.233, 95% CI = -0.816 to 1.280; mating success inferred from genetic analyses: I_s = 0.490, 95% CI = -0.442 to 1.421; contrast: I_s = 0.257, CI lower end = 0.374, CI upper end = 0.141). The result remains the same after all sensitivity analyses, except after excluding studies that sampled older offspring, when the absolute estimate value is still higher for mating success genetically estimated, but the difference is only marginally significant (Table S5). Random variables account for a small part of the variation in our data (I^2 = 4.92%; I^2 phylogeny: 1.47%; I^2 effect sizes pair identity = 1.98^0%; I^2 mating success interference = 1.83 x 10^{-10}%; I^2 inclusion of zeros = 1.48%; I^2 intrasexual competition occurrence = 1.83 x 10^{-10}%; I^2 offspring age = 3.55 x 10^{-8}%). Egger's regression test indicates that there is no publication bias in the data (Egger's regression: $I_{s\ intercept}$ = 0.164 ± 0.185 SE, t = 0.884, p > 0.05). Finally, we detected a positive correlation between mating success and fertilization success for males (r = 0.638 ± 0.152 SE, z = 4.207, n = 15 species, p < 0.0001).

For males, from 39 different species, we extracted 56 estimates of I_s in which mating success was directly estimated; and, from 80 different species, we extracted 171 estimates of I_s in which mating success was indirectly estimated (Figure S4). Estimates of I_s continue to differ according to the way mating success was estimated when data coming from all studies are included (mating success directly estimated: I_s = -0.528, 95% CI = -7.254 to 6.193; mating success inferred from genetic analyses: I_s = -0.289, 95% CI = -6.900 to 6.317; contrast: I_s = 0.239, CI lower end = 0.354, CI upper end = 0.124). The result is the same for all sensitivity analyses (Table S6). Random variables accounted for most of the variation in our data (I^2 = 74.846%; I^2 phylogeny: 69.14%; I^2 effect sizes pair identity = 1.30%; I^2 mating success interference = 0.94%; I^2 inclusion of zeros = 0.22%; I^2 intrasexual competition occurrence = 3.24%; I^2 offspring age = 4.36 x 10^{-7}%). Egger's regression test indicates the possibility of publication bias in the data (Egger's regression: $I_{s\ intercept}$ = 1.786 ± 0.209 SE, t = -8.563, $p < 0.05$).

Test 3 – Estimates of the Bateman gradient are similar whether measuring actual mating success or inferring mating success from genetic analyses

For females, we were able to extract at least one measure of both types of Bateman gradient for 11 species, from 11 different studies. In total, we extracted 14 pairs of Bateman gradient slopes (Figure S5). Estimates of the Bateman gradient do not differ according to the way mating success is estimated (mating success directly estimated: slope = 0.541, 95% CI = 0.117 to 0.964; mating success inferred from genetic analyses: slope = 0.541, 95% CI = 0.118 to 0.963; contrast: I_s = 0.000, CI lower end = 0.001, CI upper end = -0.001). The result remains the same in all sensitivity analyses, except after excluding studies in which females faced no intrasexual competition, when the slope of the Bateman gradient is slightly steeper when mating success is directly estimated (Table S7). Random variables account for a small part of the variation in our data (I^2 = 1.31%; I^2 phylogeny: 7.07 x 10^{-6}%; I^2 effect sizes pair identity = 1.03%; I^2 mating success interference = 2.59 x 10^{-6}%; I^2 inclusion of zeros = 0.28%; I^2 intrasexual competition occurrence = 8.45 x 10^{-6}%; I^2 offspring age = 2.41 x 10^{-11}%). Egger's regression indicates no publication bias in the data (Egger's regression: $I_{s\ intercept}$ = -7.098 x 10^{-2}% ± 0.116 SE, t = -0.610, $p > 0.05$).

For males, we were able to extract at least one measure of both types of Bateman gradient for 10 species, from 10 different studies. In total, we extracted 13 pairs of Bateman gradient slopes (Figure S6). Estimates of the Bateman gradient do not differ according to the way mating success is estimated (mating success directly estimated: slope = 0.928, 95% CI = 0.786 to 1.069; mating success inferred from genetic analyses: slope = 0.928, 95% CI = 0.787 to 1.068; contrast: I_s = 0.000, CI lower end = 0.001, CI upper end = -0.001). The result remains the same in all sensitivity analyses. There was no need to run sensitivity analyses excluding studies with mating success interference and studies with no male intrasexual competition (Table S8). Random variables account for almost no variation in our data (I^2 = 0.02%; I^2 phylogeny: 1.94 x 10^{-11}%; I^2 effect sizes pair identity = 0.01%; I^2 inclusion of zeros = 0.02%; I^2 offspring age = 1.37 x 10^{-10}%). Egger's regression indicates no publication bias in the data (Egger's regression: $I_{s\ intercept}$ = 2.602 x 10^{-2}% ± 0.060 SE, t = 0.429, p > 0.05).

Discussion

General results

Here, we show that inferring mating success directly or from parentage genetic analyses leads to different estimates of the opportunity for sexual selection for both females and males. This finding suggests that fertilization success is not a good predictor of mating success and, as we expected, estimates of the opportunity for sexual selection (I_s) based on quantifications of fertilization success probably tell us more about post-mating sexual selection than about pre-mating sexual selection. Consequently, we demonstrate that post-mating events promote an opportunity for selection across animal *taxa*, showing the evolutionary relevance of mechanisms such as cryptic female choice and sperm competition. For males, this result is consistent, regardless of the data included in the analysis. For females, however, the result is found when analyzing only the studies that estimated mating success both directly and genetically. Despite the smaller sample size, we consider this model to provide more reliable results because it provides at least two contrasting estimates of the opportunity for sexual selection per study, allowing us to perform pairwise comparisons. The model including studies that estimated mating success by only one way (directly or genetically) is less reliable because the variance in the estimates of the opportunity for sexual selection may be due to factors other than the way mating success was estimated. Finally, we also show that, for both sexes, Bateman gradient estimates do not differ according to the way mating success was estimated, and estimating mating success by measuring the number of mating occurrences or the number of mating partners does not lead to different estimates of the opportunity for sexual selection. Below, we discuss how to improve the procedures to measure sexual selection and to interpret the different proxies of sexual selection. In this way, we propose a new index to estimate post-mating sexual selection. More importantly, we discuss how all our findings contribute to sexual selection theory, with special focus on cryptic female choice and sperm competition.

On how to estimate different episodes of sexual selection

Estimating mating success through genetic analyses (instead of directly estimating mating success) leads to higher estimates of the opportunity for sexual selection, I_s. Two facts explain this pattern. First, while the variation in actual mating success in a given population is not due to any post-mating selection episode, the variation in genetically estimated mating success may be due to post-mating sexual selection, because this estimate of mating success is actually a measure of fertilization success. Post-mating sexual selection may alter the variation in fertilization success among individuals, increasing the total selection faced by them and explaining why genetic estimates of mating success produce higher estimates of the opportunity for sexual selection. Second, if mating success is equated to fertilization success, when no offspring is produced, a mating event is not detected by the genetic procedure (Parker and Tang-Martinez 2005; Arnqvist 2013), leading to an underestimation of the number of mating events and probably to a lower estimate of the opportunity for sexual selection. This highlights the relevance of properly interpreting selection indexes, evaluating their applicability and limitations (see Kokko et al. 1999; Croshaw 2010; Klug et al. 2010a; Fitze and Le Galliard 2011;

Jennions et al. 2012b; Henshaw et al. 2016). Here, we contribute to this debate by showing that, for any species, if the only option is to infer mating success from fertilization success, it is important to consider that this procedure leads to erroneous estimations of the opportunity for pre-mating sexual selection. If we calculate the relative variance in fertilization success in a given population, we obtain a proxy for the *opportunity for fertilization selection*, but not a proxy for the opportunity for pre-mating sexual selection (I_s). This opportunity for fertilization selection (hereafter, I_f) does not quantify the opportunity for sexual selection due only to post-mating events (for such, see Shuster et al. 2013; Pélissié et al. 2014), the I_f presents the opportunity for selection until fertilization takes place.

While the way mating success is estimated generates different estimates of I_s and I_f, the same does not apply for the Bateman gradient. Therefore, if it is not possible to directly quantify mating success, a standardized Bateman gradient between fertilization success and reproductive success will return a similar selection gradient. However, three important observations must be made. First, we show here that standardized Bateman gradients provide similar findings, but one should not infer that Bateman gradients containing raw data will work in the same way. Second, a Bateman gradient for which mating success is inferred from fertilization success presents autocorrelated axes (Arnqvist 2013), because reproduction influences the fitness proxies found in both axes. Third, Bateman gradients based on mating or fertilization success give us different information. Bateman gradients are meant to describe the increase in reproductive success obtained from each unity increase in mating success (Arnold and Duvall 1994; Jones 2009). However, the least square regression between fertilization and reproductive success shows the fitness return obtained from each reproductive partner. In conclusion, while fertilization success measures may be useful to infer the slope of the Bateman gradient when directly estimating mating success is not feasible, we have to be careful when deriving conclusions from Bateman gradients that correlate fertilization and reproductive success. Finally, we also found that quantifying mating success by counting the number of mating events or number of sexual partners does not change the I_s estimate. This does not mean that mating success estimates are not influenced by the way we quantify it; our result only shows that the opportunity for pre-mating sexual selection is not influenced by the way we directly measure mating success. This information is useful when a species' mating system or the methodological procedure make it difficult or not possible to count the number of sexual partners (e.g. Kehat and Gordon 1977; Townsend 1989; Forsman and Hagman 2006; Marie-Orleach et al. 2016).

Why mating and fertilization success generate different estimates of the opportunity for sexual selection among females?

For females, estimates of the opportunity for fertilization selection are greater than the estimates of the opportunity for pre-mating sexual selection, indicating the occurrence of post-mating sexual selection. If that is the case, both sperm competition and cryptic female choice may explain the results. For example, pre-mating choice imposes costs for females (e.g. Pomiankowski 1987; Vitousek et al. 2007; Booksmythe et al. 2008), and the same applies for some forms of post-mating/cryptic female choice (Firman et al. 2017; e.g. Ward et al. 2008). Because females differ in body condition, and females with good body condition have more energy for reproductive and somatic investments, it is reasonable to expect that the expression of cryptic female choice may be condition-dependent (see Vermeulen et al. 2008). And cryptic female choice not only allows females to prevent genetic incompatibilities with sexual partners (Welke and Schneider 2009; Slatyer et al. 2012), but also allows females to increase the genetic diversity of their offspring by producing offspring with more than one male (e.g. Foerster et al. 2003; Garant et al. 2005), which tends to translate into an increase in female fitness. When cryptic female choice is condition-dependent, high-quality females are more prone to cryptically choose sexual partners, increasing their own fitness, while low-quality females are not able to equally increase their fitness through the same manner. This probable difference in post-mating choice ability may promote post-mating sexual selection, which can explain why the mean I_f estimate is higher than the mean I_s estimate for females across animals.

Similarly to cryptic female choice, sperm competition may also explain why mating and fertilization success generate different estimates of the opportunity for sexual selection among females. Given that males compete to mate with high-quality females (Andersson 1994; Bonduriansky 2001), it is reasonable to expect that males also compete for the fertilization of high-quality females' ova - and, in accordance, we found here a positive high correlation between female mating success and female fertilization success. As producing sperm in higher quantity and/or quality is energy-demanding (e.g. Olsson et al. 1997; Burness et al. 2008; Tourmente and Roldan 2015), one possibility is that males enhance their fitness by modulating the sperm quantity and/or quality according to female quality (i.e. strategic ejaculation) (Parker and Pizzari 2010; Kelly and Jennions 2011). For instance, males may strategically adjust the sperm they transfer, favoring larger females (e.g. Gage 1998; Galeotti et al. 2008; Teuschl et al. 2010), younger females (e.g. Cook and Gage 1995; Lüpold et al. 2011a), or more attractive females, even if attractiveness is not accessed through body size or age (e.g. Cornwallis and Birkhead 2007; Cornwallis and O'Connor 2009; Leivers et al. 2014). A meta-analysis comprising many animal species has shown that males transfer larger ejaculates when mating with virgin females and when mating with higher quality females (quality was accessed using several proxies) (Kelly and Jennions 2011). If males invest more and/or better sperm when mating with particular females in a given population, this tends to increase the variance in fertilization success among females, explaining the results we obtained when contrasting I_s and I_f estimates.

Why mating and fertilization success generate different estimates of the opportunity for sexual selection among males?

Regardless of the origin of the data, estimates of the opportunity for sexual selection for males consistently differed according to the way mating success was estimated (directly or genetically). This finding supports the ubiquitous occurrence of the opportunity for post-mating sexual selection among males. If females from a given species consistently favor the sperm of males that were the most successful in pre-mating competition – e.g. the most attractive males, good fathers, dominant males, larger males, healthier males - this will lead to an increase in the opportunity for post-mating sexual selection, as shown here. This possibility is corroborated by the positive (and high) correlation between male mating success and male fertilization success across animal *taxa* found here. In fowls, for example, males compete to access females, establishing dominance hierarchies. While dominant males achieve high mating success, subordinate males are prevented from accessing females and mate by coercive copulation attempts. Females respond by ejecting the sperm of subordinate males and preserving the sperm deposited by dominant males (Parker and Pizzari 2010; Dean et al. 2011). Given that dominant behavior is heritable (Craig et al. 1965), these females will produce male offspring that will inherit this dominant behavior, characterizing the post-mating sexual selection of a particular trait that makes males more prone to mate and fertilize females. Taking into account that similar patterns are found for other species (e.g. Kamimura 2015; Sato 2017; Sato et al. 2017), it is clear how cryptic female choice may promote an opportunity for post-mating sexual selection among males.

As stated above, sperm competition may also explain why I_f estimates are higher than I_s estimates for males. One possibility is that males that achieve higher levels of mating success are also good post-mating competitors (e.g. Cornwallis and Birkhead 2007; Lemaître et al. 2012; García-Granados et al. 2019; Losdat et al. 2019), enhancing their relative success by winning sperm competition against other males. This possibility is corroborated by the high positive correlation between mating and fertilization success in our data. Maybe, these successful males produce sperm in higher quantity and/or quality, succeeding in sperm competition (e.g. Engqvist et al. 2007; Mellström and Wiklund 2009) and preventing sperm depletion/limitation caused by multiple matings (e.g. Weir and Grant 2010; Schütz et al. 2017). Nevertheless, while our results may indicate that good pre-mating male competitors are also good post-mating competitors, increasing evidence has shown a trade-off between investing in traits involved in pre-mating intrasexual competition and investing in sperm competition (Ferrandiz-Rovira et al. 2014; García-Navas et al. 2014; Dines et al. 2015; Dunn et al. 2015; Lüpold et al. 2019). One possible explanation for this discrepancy between our results and the mentioned evidences from the literature is that subdominant males do invest more in sperm competition (e.g. Locatello et al. 2007; Iwata et al. 2011), but this does not suffice to compensate for the higher mating success of dominant males (e.g. Müller et al. 2007; Mascolino et al. 2016; Balmer et al. 2019; but see Magalhaes et al. 2017), with dominant males achieving higher fertilization success anyway. Thus, in this case, when subdominant males invest more in sperm competition than dominant males, the opportunity for post-mating sexual selection is prevented from being even higher.

Future research and conclusions

Given the ubiquitous presence of the opportunity for post-mating sexual selection shown here, future studies should continue to analyze how cryptic female choice and sperm competition influence sexual selection, including how post-mating sexual selection operates in different social mating systems (Chapter 2). More studies on cryptic female choice and sperm competition will allow the development of more meta-analyses on post-mating selection episodes (that are now underrepresented in sexual selection research, see Jennions et al. 2012a), expanding our knowledge on evolution through sexual selection. Here, using a meta-analytical procedure, we demonstrate the ubiquity of the opportunity for post-mating sexual selection for females and males across animals. Additionally, we propose an alternative selection index, the opportunity for fertilization selection (completely derived from another standard index, I_s - Crow 1958), useful to estimate post-mating sexual selection and that does not require any source of data other than the ones usually collected to quantify sexual selection. The acknowledgment of the conceptual difference between I_s and I_f is methodologically important and helps to fill a gap in sexual selection research, given that most sexual selection indexes focus mainly on male mating success (Kvarnemo and Simmons 2013). The opportunity for fertilization selection comprises post-mating events and can be applied to both sexes (as done here), which increases its applicability. Regardless of the use of the opportunity for fertilization selection index, we encourage authors to measure both mating and fertilization success when possible, because this will allow us to better integrate pre- and post-mating events of sexual selection, as we demonstrate.

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Supplementary material

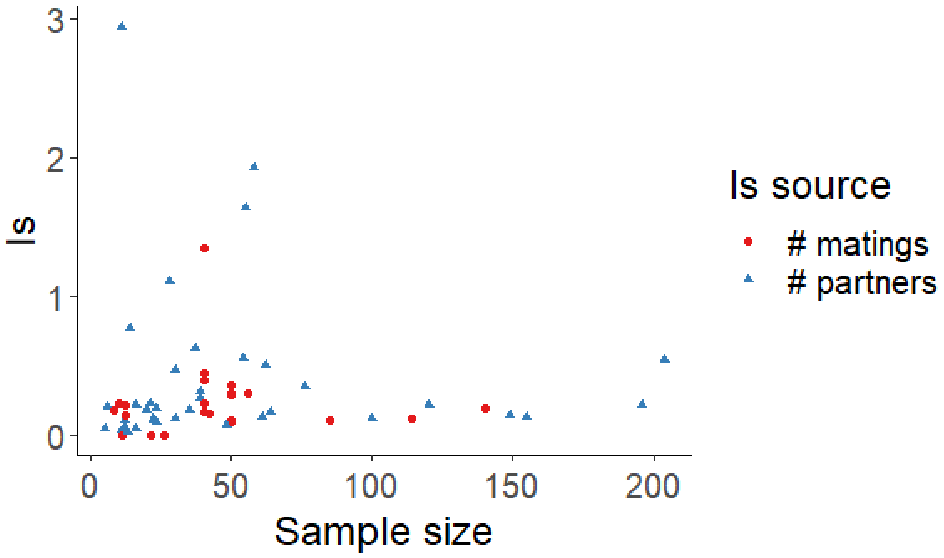

Figure S1. Estimates of the opportunity for sexual selection for females and their respective sample sizes obtained from two classes of mating success (red circles: mating success calculated as the number of mating events; blue triangles: mating success calculated as the number of sexual partners).

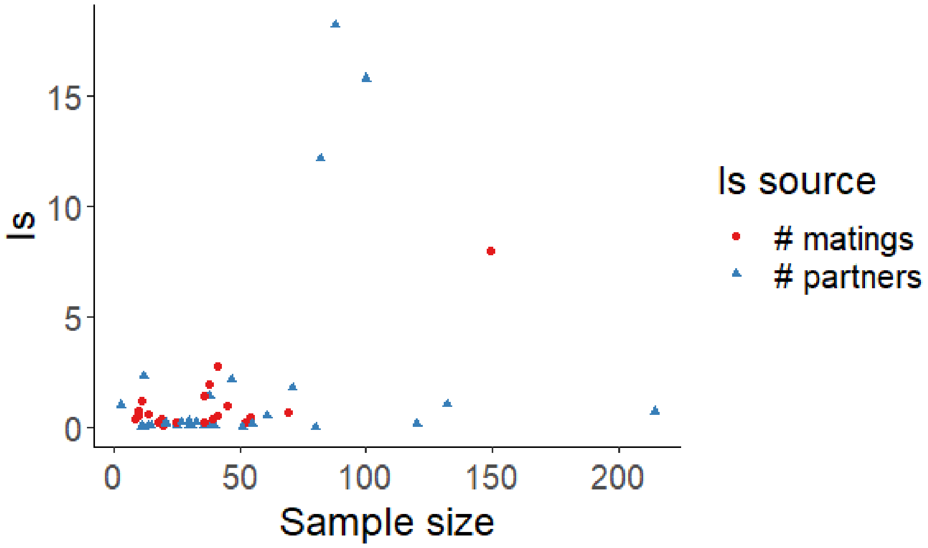

Figure S2. Estimates of the opportunity for sexual selection for males and their respective sample sizes obtained from two classes of mating success (red circles: mating success calculated as the number of mating events; blue triangles: mating success calculated as the number of sexual partners).

Table S1. Results for all models run in order to test the effects of different classes of mating success on the calculation of the opportunity for sexual selection (I_s) for females. There are two classes of mating success: (i) mating success quantified as number of mating occurrences per individuals; (ii) mating success quantified as number of sexual partners per individual. First model includes all data and all pertinent random variables. Sensitivity analyses were performed by excluding particular data. The confidence interval (2.5% CI to 97.5% CI) for each mean estimate is informed per mating success class. Number of estimates and number of sampled species are informed per mating success class.

Model	mating success meaning	I_s	2.5% CI	97.5% CI	Estimates	Species
All data; Random variables: phylogeny, effect sizes pair identity, mating success interference, inclusion of zeros, and intrasexual competition occurrence	no. sexual partners	0.706	-0.753	2.167	36	26
	no. mating occurrences	0.667	-0.624	1.959	23	17
All data; Random variables: phylogeny and effect sizes pair id	no. sexual partners	0.437	-0.167	1.041	36	26
	no. mating occurrences	0.358	0.035	0.681	23	17
Data: excluding studies in which authors determined mating success; Random variables: phylogeny and effect sizes pair id	no. sexual partners	0.466	-0.627	1.559	31	22
	no. mating occurrences	0.410	-0.518	1.339	23	17
Data: excluding effect sizes that do not include mating success = 0; Random variables: phylogeny and effect sizes pair id	no. sexual partners	0.518	-0.394	1.428	20	15
	no. mating occurrences	0.535	-0.211	1.280	19	14
Data: excluding studies with no intrasexual competition; Random variables: phylogeny and effect sizes pair id	no. sexual partners	0.501	-0.637	1.640	27	20
	no. mating occurrences	0.444	-0.526	1.414	18	15

Table S2. Results for all models run in order to test the effects of different classes of mating success on the calculation of the opportunity for sexual selection (I_s) for males. There are two classes of mating success: (i) mating success quantified as number of mating occurrences per individuals; (ii) mating success quantified as number of sexual partners per individual. First model includes all data and all pertinent random variables. Sensitivity analyses were performed by excluding particular data. The confidence interval (2.5% CI to 97.5% CI) for each mean estimate is informed per mating success class. Number of estimates and number of sampled species are informed per mating success class.

Model	mating success meaning	I_s	2.5% CI	97.5% CI	Estimates	Species
All data; Random variables: phylogeny, effect sizes pair identity, mating success interference, inclusion of zeros, and intrasexual competition occurrence	no. sexual partners	-2.420	-13.756	8.915	34	22
	no. mating occurrences	-2.750	-12.212	6.710	22	18
All data; Random variables: phylogeny and effect sizes pair id	no. sexual partners	1.187	-3.396	5.771	34	22
	no. mating occurrences	0.658	-1.913	3.229	22	18
Data: excluding studies in which authors determined mating success; Random variables: phylogeny and effect sizes pair id	no. sexual partners	1.237	-3.608	6.082	32	20
	no. mating occurrences	0.612	-2.161	3.385	22	18
Data: excluding effect sizes that do not include mating success = 0; Random variables: phylogeny and effect sizes pair id	no. sexual partners	1.013	-6.656	8.681	26	17
	no. mating occurrences	0.733	-5.252	6.717	22	18
Data: excluding studies with no intrasexual competition; Random variables: phylogeny and effect sizes pair id	no. sexual partners	1.264	-3.749	6.278	30	19
	no. mating occurrences	0.583	-2.262	3.429	22	18

Table S3. Results for all models run in order to test if the way researchers estimate mating success (directly vs. indirectly/genetically) influences the estimate of the opportunity for sexual selection (I_s) for females, using only studies that provided two measures of I_s per group of females (one measure derived from directly estimated mating success and the other measure derived from indirectly estimated mating success). Directly estimated mating success are the measures derived from studies in which the authors measured the actual mating success for each individual, and indirectly estimated mating success are the measures derived from studies in which the authors inferred mating success from genetic analyses. First model includes all data and all pertinent random variables. Sensitivity analyses were performed by excluding particular data. The confidence interval (2.5% CI to 97.5% CI) for each mean estimate is informed per way of estimating mating success. Number of estimates and number of sampled species are informed per way of estimating mating success. Statistically significant differences ($p < 0.05$) between measured estimates are represented with two asterisks (**). Statistically marginal significant differences ($0.05 < p < 0.10$) between measured estimates are represented with one asterisk (*).

Model	How mating success was estimated	I_s	2.5% CI	97.5% CI
All data; Random variables: phylogeny, effect sizes pair identity, mating success interference, inclusion of zeros, intrasexual competition occurrence, and offspring age	directly	1.440**	-0.815	3.695
	genetically	1.581**	-0.555	3.717
All data; Random variables: phylogeny and effect sizes pair id	directly	0.460**	-0.139	1.059
	genetically	0.601**	0.121	1.081
Data: excluding mating/fertilization success as number of mating/fertilization occurrences; Random variables: phylogeny and effect sizes pair id	directly	0.479**	-0.183	1.140
	genetically	0.639**	0.104	1.174
Data: excluding studies in which authors determined mating success; Random variables: phylogeny and effect sizes pair id	directly	0.346**	-0.086	0.779
	genetically	0.49**	0.178	0.803
Data: excluding effect sizes that do not include mating success = 0; Random variables: phylogeny and effect sizes pair id	directly	0.626**	-0.304	1.557
	genetically	0.851**	0.066	1.637
Data: excluding studies with no intrasexual competition; Random variables: phylogeny and effect sizes pair id	directly	0.294*	-0.131	0.719
	genetically	0.417*	0.115	0.719

Table S4. Results for all models run in order to test if the way researchers estimate mating success (directly vs. indirectly/genetically) influences the estimate of the opportunity for sexual selection (I_s) for females, using all studies that provided at least one measure of I_s, regardless of the way mating success was estimated. Directly estimated mating success are the measures derived from studies in which the authors measured the actual mating success for each individual, and indirectly estimated mating success are the measures derived from studies in which the authors inferred mating success from genetic analyses. First model includes all data and all pertinent random variables. Sensitivity analyses were performed by excluding particular data. The confidence interval (2.5% CI to 97.5% CI) for each mean estimate is informed per way of estimating mating success. Number of estimates and number of sampled species are informed per way of estimating mating success. Statistically significant differences ($p < 0.05$) between measured estimates are represented with two asterisks (**). Statistically marginal significant differences ($0.05 < p < 0.10$) between measured estimates are represented with one asterisk (*).

Model	How mating success was estimated	I_s	2.5% CI	97.5% CI
All data; Random variables: phylogeny, effect sizes pair identity, mating success interference, inclusion of zeros, intrasexual competition occurrence, and offspring age	directly	0.748	-2.631	4.125
	genetically	0.670	-2.522	3.861
All data; Random variables: phylogeny and effect sizes pair id	directly	0.353**	-2.897	3.604
	genetically	0.474**	-2.662	3.610
Data: excluding mating/fertilization success as number of mating/fertilization occurrences; Random variables: phylogeny and effect sizes pair id	directly	0.313**	-3.228	3.852
	genetically	0.477**	-2.939	3.892
Data: excluding studies in which authors determined mating success; Random variables: phylogeny and effect sizes pair id	directly	0.344**	-2.978	3.664
	genetically	0.466**	-2.740	3.670
Data: excluding effect sizes that do not include mating success = 0; Random variables: phylogeny and effect sizes pair id	directly	0.873**	-0.334	0.988
	genetically	0.934**	0.561	1.306
Data: excluding studies with no intrasexual competition; Random variables: phylogeny and effect sizes pair id	directly	0.439*	-3.157	4.018
	genetically	0.543*	-2.934	4.003
Data: excluding studies with older offspring; Random variables: phylogeny and effect sizes pair id	directly	0.401	-0.239	1.004
	genetically	0.475	0.025	0.889

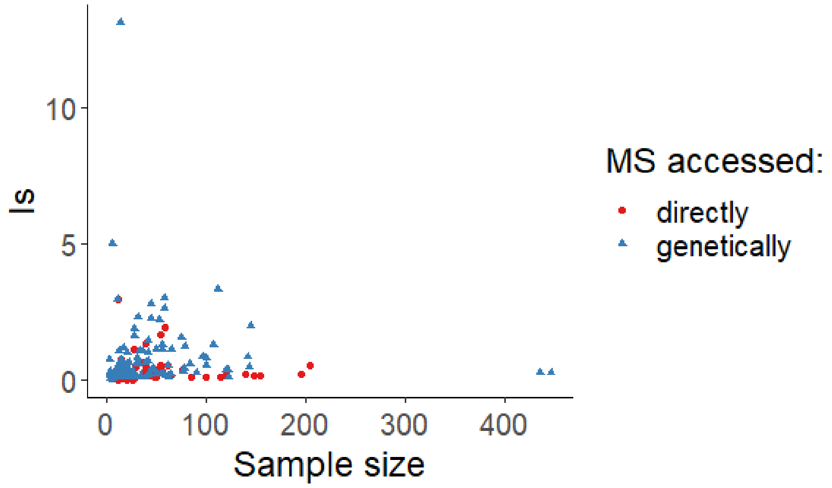

Figure S3. Estimates of the opportunity for sexual selection (and their respective sample sizes) for females, according to the way mating success (MS) was estimated: red circles - mating success directly estimated; blue triangles - mating success inferred from genetic analyses.

Table S5. Results for all models run in order to test if the way researchers estimate mating success (directly vs. indirectly/genetically) influences the estimate of the opportunity for sexual selection (I_s) for males, using only studies that provided two measures of I_s per group of males (one measure derived from directly estimated mating success and the other measure derived from indirectly estimated mating success). Directly estimated mating success are the measures derived from studies in which the authors measured the actual mating success for each individual, and indirectly estimated mating success are the measures derived from studies in which the authors inferred mating success from genetic analyses. First model includes all data and all pertinent random variables. Sensitivity analyses were performed by excluding particular data. The confidence interval (2.5% CI to 97.5% CI) for each mean estimate is informed per way of estimating mating success. Number of estimates and number of sampled species are informed per way of estimating mating success. Statistically significant differences ($p < 0.05$) between measured estimates are represented with two asterisks (**).

Model	How mating success was estimated	I_s	2.5% CI	97.5% CI
All data; Random variables: phylogeny, effect sizes pair identity, mating success interference, inclusion of zeros, intrasexual competition occurrence, and offspring age	directly	0.233**	-0.816	1.280
	genetically	0.490**	-0.442	1.421
All data; Random variables: phylogeny and effect sizes pair id	directly	0.441**	-0.257	1.137
	genetically	0.698**	0.117	1.278
Data: excluding mating/fertilization success as number of mating/fertilization occurrences; Random variables: phylogeny and effect sizes pair id	directly	0.496**	-1.137	2.131
	genetically	0.711**	-0.792	2.215
Data: excluding studies in which authors determined mating success; Random variables: phylogeny and effect sizes pair id	directly	0.442**	-0.268	1.152
	genetically	0.701**	0.107	1.294
Data: excluding effect sizes that do not include mating success = 0; Random variables: phylogeny and effect sizes pair id	directly	0.533**	-0.203	1.270
	genetically	0.825**	0.220	1.430
Data: excluding studies with no intrasexual competition; Random variables: phylogeny and effect sizes pair id	directly	0.442**	-0.268	1.152
	genetically	0.701**	0.107	1.294

Table S6. Results for all models run in order to test if the way researchers estimate mating success (directly vs. indirectly/genetically) influences the estimate of the opportunity for sexual selection (I_s) for males, using all studies that provided at least one measure of I_s, regardless of the way mating success was estimated. Directly estimated mating success are the measures derived from studies in which the authors measured the actual mating success for each individual, and indirectly estimated mating success are the measures derived from studies in which the authors inferred mating success from genetic analyses. First model includes all data and all pertinent random variables. Sensitivity analyses were performed by excluding particular data. The confidence interval (2.5% CI to 97.5% CI) for each mean estimate is informed per way of estimating mating success. Number of estimates and number of sampled species are informed per way of estimating mating success. Statistically significant differences (p < 0.05) between measured estimates are represented with two asterisks (**). Statistically marginal significant differences (0.05 < p < 0.10) between measured estimates are represented with one asterisk (*).

Model	How mating success was estimated	I_s	2.5% CI	97.5% CI
All data; Random variables: phylogeny, effect sizes pair identity, mating success interference, inclusion of zeros, intrasexual competition occurrence, and offspring age	directly	-0.528**	-7.254	6.193
	genetically	-0.289**	-6.900	6.317
All data; Random variables: phylogeny and effect sizes pair id	directly	0.572**	-5.918	7.062
	genetically	0.811**	-5.564	7.186
Data: excluding mating/fertilization success as number of mating/fertilization occurrences; Random variables: phylogeny and effect sizes pair id	directly	0.651**	-6.252	7.553
	genetically	0.848**	-5.925	7.621
Data: excluding studies in which authors determined mating success; Random variables: phylogeny and effect sizes pair id	directly	0.579**	-5.897	7.055
	genetically	0.820**	-5.541	7.180
Data: excluding effect sizes that do not include mating success = 0; Random variables: phylogeny and effect sizes pair id	directly	0.675**	-4.654	6.006
	genetically	0.938**	-4.261	6.138
Data: excluding studies with no intrasexual competition; Random variables: phylogeny and effect sizes pair id	directly	0.663**	-6.061	7.386
	genetically	0.904**	-5.704	7.512
Data: excluding studies with older offspring; Random variables: phylogeny and effect sizes pair id	directly	0.541**	-6.326	7.407
	genetically	0.768**	-5.904	7.440

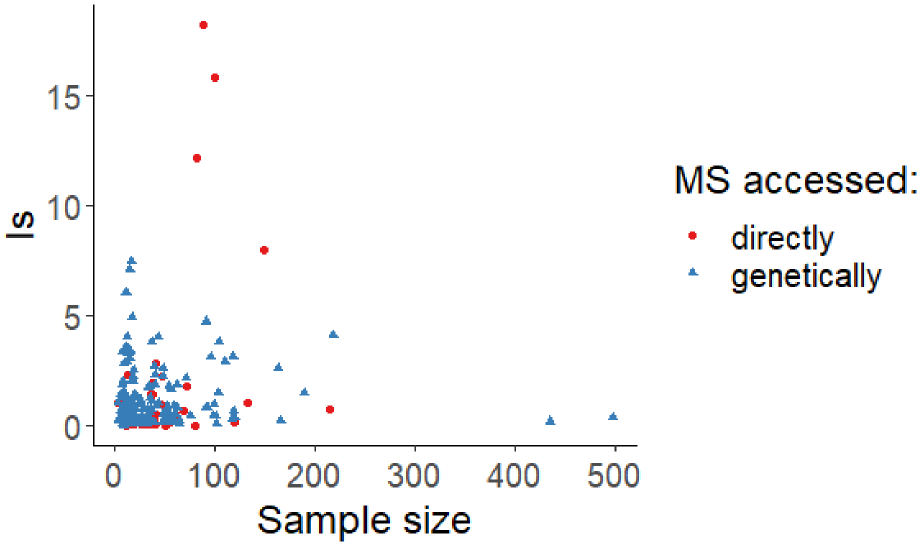

Figure S4. Estimates of the opportunity for sexual selection (and their respective sample sizes) for males, according to the way mating success (MS) was estimated: red circles - mating success directly estimated; blue triangles - mating success inferred from genetic analyses.

Table S7. Results for all models run in order to test if the way researchers estimate mating success (directly vs. indirectly/genetically) influences the estimate of the slope of the Bateman gradient for females, using only studies that provided two measures of the Bateman gradient per group of females (one measure derived from directly estimated mating success and the other measure derived from indirectly estimated mating success). Directly estimated mating success are the measures derived from studies in which the authors measured the actual mating success for each individual, and indirectly estimated mating success are the measures derived from studies in which the authors inferred mating success from genetic analyses. First model includes all data and all pertinent random variables. Sensitivity analyses were performed by excluding particular data. The confidence interval (2.5% CI to 97.5% CI) for each mean estimate is informed per way of estimating mating success. Number of estimates and number of sampled species are informed per way of estimating mating success. Statistically significant differences (p < 0.05) between measured estimates are represented with two asterisks (**). Statistically marginal significant differences (0.05 < p < 0.10) between measured estimates are represented with one asterisk (*).

Model	**How mating success was estimated**	**slope**	**2.5% CI**	**97.5% CI**
All data; Random variables: phylogeny, effect size identity, mating success meaning, inclusion of zeros, and intrasexual competition occurrence	directly	0.541	0.117	0.964
	genetically	0.541	0.118	0.963
All data; Random variables: phylogeny and effect size id	directly	0.581	0.316	0.845
	genetically	0.581	0.317	0.844
Data: excluding mating/fertilization success as number of mating/fertilization occurrences; Random variables: phylogeny and effect size id	directly	0.550	0.268	0.832
	genetically	0.550	0.269	0.831
Data: excluding studies in which authors determined mating success; Random variables: phylogeny and effect size id	directly	0.559*	0.252	0.867
	genetically	0.537*	0.256	0.819
Data: excluding effect sizes that do not include mating success = 0; Random variables: phylogeny and effect size id	directly	0.734	0.426	1.041
	genetically	0.734	0.427	1.040
Data: excluding studies with no intrasexual competition; Random variables: phylogeny and effect size id	directly	0.528**	0.202	0.855
	genetically	0.500**	0.200	0.801

Table S8. Results for all models run in order to test if the way researchers estimate mating success (directly vs. indirectly/genetically) influences the estimate of the slope of the Bateman gradient for females, using only studies that provided two measures of the Bateman gradient per group of females (one measure derived from directly estimated mating success and the other measure derived from indirectly estimated mating success). Directly estimated mating success are the measures derived from studies in which the authors measured the actual mating success for each individual, and indirectly estimated mating success are the measures derived from studies in which the authors inferred mating success from genetic analyses. First model includes all data and all pertinent random variables. Sensitivity analyses were performed by excluding particular data. The confidence interval (2.5% CI to 97.5% CI) for each mean estimate is informed per way of estimating mating success. Number of estimates and number of sampled species are informed per way of estimating mating success. Statistically significant differences (p < 0.05) between measured estimates are represented with two asterisks (**). Statistically marginal significant differences (0.05 < p < 0.10) between measured estimates are represented with one asterisk (*).

Model	**How mating success was accessed**	**slope**	**2.5% CI**	**97.5% CI**
All data; Random variables: phylogeny, effect size id, mating success meaning, inclusion of zeros, and intrasexual competition occurrence	directly	0.928	0.786	1.069
	genetically	0.928	0.787	1.068
All data; Random variables: phylogeny and effect size id	directly	0.978	0.904	1.053
	genetically	0.978	0.905	1.052
Data: excluding mating/fertilization success as number of mating/fertilization occurrences; Random variables: phylogeny and effect size id	directly	0.964	0.882	1.046
	genetically	0.964	0.883	1.045
Data: excluding effect sizes that do not include mating success = 0; Random variables: phylogeny and effect size id	directly	0.994	0.974	1.014
	genetically	0.994	0.975	1.013

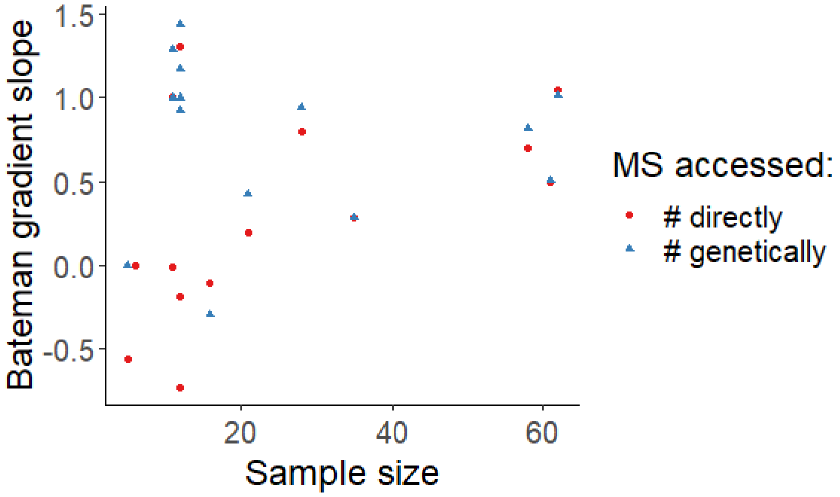

Figure S5. Estimates of the slope of the Bateman gradient (and their respective sample sizes) for females, according to the way mating success (MS) was estimated: red circles - mating success directly estimated; blue triangles - mating success inferred from genetic analyses.

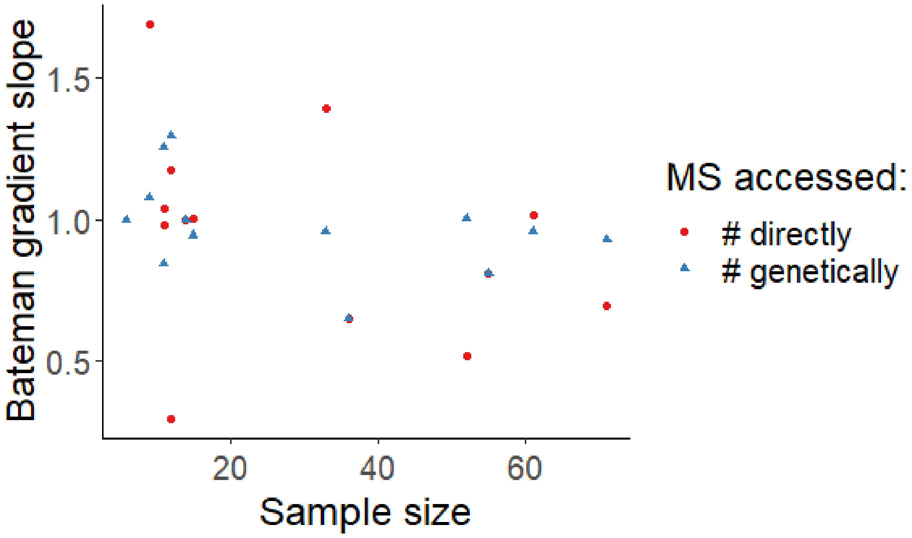

Figure S6. Estimates of the slope of the Bateman gradient (and their respective sample sizes) for males, according to the way mating success (MS) was estimated: red circles - mating success directly estimated; blue triangles - mating success inferred from genetic analyses.

Capítulo 2

Females are not monopolized by males: a meta-analysis contrasting mating systems in non-human animals

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Abstract

The seminal Darwin-Bateman paradigm predicts females to be choosy and enhance their fitness by mating with few high-quality males, and predicts that males should compete intrasexually to mate with as many females as possible. In many species, males attempt to enhance their fitness by defending a harem and/or a resource used by females, and, supposedly, directly monopolize females. However, the advent of parentage analyses showed that females from many species mate more frequently than previously expected, which contradicts traditional expectations of the outcome of male monopolization behavior. Here, in an extensive meta-analysis, encompassing 114 species, across all animal kingdom, and including more than 1,200 effect sizes, we tested how the occurrence of monopolization behavior modulates sexual selection on females and males, answering if males really succeed in economically monopolizing females. We answered this question by using four different indexes of sexual selection that comprise pre-mating, post-mating or both episodes of sexual selection. We found that the occurrence of monopolization behavior results in lower estimates of the opportunity for pre-mating sexual selection for females and higher estimates for males than when monopolization behavior is absent. However, for both sexes, we found that the occurrence/absence of monopolization behavior does not modulate the opportunity for fertilization selection, the opportunity for selection, nor the slope of the Bateman gradient. These results show that males do succeed in restricting females' re-mating ability when monopolization behavior occurs. However, the effectiveness of monopolization behavior is restricted to the pre-mating phase, and females are not restricted during the post-mating period. The pattern found here reinforces the notion that post-mating episodes of selection, such as cryptic female choice and sperm competition, are important factors influencing the opportunity for selection among animals. We discuss how post-mating events influence sexual selection and how females are active actors in sexual selection processes. We also highlight how poor data reports in scientific literature prevented us from extracting a considerable quantity of effect sizes.

Keywords (alphabetical order): Bateman gradient, cryptic female choice, female defense polygyny, fertilization success, harem, Jones index, lek, male dominance, mate choice, mating success, monopolization, opportunity for selection, opportunity for fertilization selection, opportunity for sexual selection, reproductive alternative tactics, reproductive success, resource defense polygyny, scramble competition, sexual selection, sperm competition, territory defense polygyny.

Introduction

The Darwin-Bateman paradigm predicts that males will maximize their reproductive success by mating with as many females as possible, in a way that any additional mating opportunity can increase male fitness (Darwin 1871; Bateman 1948; Dewsbury 2005). Female fitness, on the other hand, depends more on the quality of her sexual partners, which means that females benefit more by being choosy than by seeking multiple sexual partners (Darwin 1871; Bateman 1948; Dewsbury 2005). This rationale was first introduced by Darwin himself (Darwin 1871) and later empirically tested by Bateman (1948) in a series of experiments with fruit flies. Bateman (1948) showed that multiple matings result in a negligible increase in reproductive success for females and in a high increase for males, which sustains the expectation that choosiness will evolve more frequently among females than among males. In the following decades, Bateman's approach to relate mating and reproductive success was replicated for several species, across many *taxa* - e.g. Actinopterygii (Wacker et al. 2014); Amphibia (Mangold et al. 2015); Coleoptera (Fritzsche and Arnqvist 2013); *Drosophila melanogaster*, again (Bjork and Pitnick 2006); Gastropoda (Johannesson et al. 2016); Hemiptera (Gagnon et al. 2012); Mammalia (Wells et al. 2017); Passeriformes (Apakupakul and Rubenstein 2015), Pycnogonida (Barreto and Avise 2010), and Reptilia (Halliwell et al. 2017). Finally, a recent meta-analysis has shown that the pattern found for fruit flies is the same across the animal kingdom (Janicke et al. 2016), with males presenting a steeper correlation between mating and reproductive success than females, giving strong support for the Darwin-Bateman paradigm.

In an effort to understand the uneven distribution of mating opportunities among individuals of a species, Emlen and Oring (1977) presented a classification of ecological mating systems that guided research in the field since then. In many species, males try to economically monopolize the access to sexual partners by defending a resource used by females (i.e. resource defense polygyny; e.g. Noble et al. 2013; York and Baird 2015) or by directly defending the females (i.e. female defense polygyny or harems - Macedo-Rego and Santos 2017; e.g. Cotton et al. 2015; Tentelier et al. 2016). In other systems, males do not directly monopolize females. For example, males may exhibit ornaments to potential sexual partners and outcompete rivals in leks (Broquet et al. 2009; Sardell and DuVal 2013). In other species, males maximize their reproductive success by investing in finding as many mates as possible and/or finding mates faster than their rivals, in a scramble competition (e.g. Prosser et al. 2002; Dougherty and Shuker 2016). The theoretical expectation is that the intensity of sexual selection (i.e. the non-random variance in mating and/or reproductive success) will be higher among males in species in which male monopolization behavior occurs than in species with no such behavior (Emlen and Oring 1977), because these males try to prevent competitors from gaining mating opportunities. Complementarily, because males try to directly monopolize females, which may restrict a female's potential to mate multiply, one can predict that the intensity of sexual selection among females will be lower in species in which male monopolization behavior occurs than in species with no such behavior (partially following the rationale presented by the constrained female hypothesis - see Gowaty 2006).

For several species, it was traditionally reasonable to infer that dominant males fathered the offspring born in their territories and/or harems. However, with the development of genetic parentage analyses, this inference changed. We now know that successful males in securing territories, and/or harems, are losing paternity to less dominant males and/or neighbors (e.g. Dixson et al. 1993; Ellis and Bercovitch 2011). Now, this does not seem odd, because increasing evidence show that females benefit from multiple matings (Jennions and Petrie 2000; Slatyer et al. 2012) and do mate polyandrously in many species (Gowaty 2006; Taylor et al. 2014). If some males try to prevent their rivals from accessing fertile females and they (partially) fail, the identified social (ecological) mating system differs from the genetic mating system (Møller and Birkhead 1994). This means that, despite their unquestionable utility, social mating systems do not tell us the whole story. First, for many species, more individuals may achieve matings than we can access and record in the field, and it is possible that this severely influences the distribution of matings and offspring among females and males (i.e. the intensity of sexual selection). Second, it is usually more difficult to study what happens in post-mating episodes of selection than in pre-mating episodes, and processes like sperm competition (i.e. the competition among sperm from different males that mated with the same female; Parker 1970b) and cryptic female choice (i.e. female post-mating choice on male sperm; Thornhill 1983) seem to play a big role in post-mating (and total) selection (Chapter 1). Because sperm competition and cryptic female choice probably play a key role, the distribution of matings and offspring in nature may differ from our standard expectations, justifying further investigation on the relative impact of different episodes of selection.

The picture now is: (1) from Darwin (1871) to Parker (1970a), we solely focused on what happens before mating and, consequently, we produced an asymmetry in the scientific knowledge that may affect our perception of the relative role played by pre- and post-mating events; (2) sometimes females mate multiply, which increases the opportunity for post-mating sexual selection, through sperm competition and cryptic female choice (Kvarnemo and Simmons 2013); and (3) some non-dominant males that achieve low mating success are good post-mating competitors, achieving high reproductive success (e.g. Fu et al. 2001; Buzatto et al. 2014), and defying the most parsimonious predictions on male reproductive success made by observing social mating systems. Given this scenario, one may ask how effective are dominant males in monopolizing females. How does the attempt to monopolize sexual partners influence sexual selection intensity/opportunity among both sexes? Because monopolization behavior should restrict female re-mating potential and, consequently, reduce the variance in female mating, fertilization and reproductive success, we tested the hypothesis that females face a lower opportunity for sexual selection in species in which monopolization behavior occurs than in species with no such behavior. Complementarily, because the occurrence of monopolization behavior should enhance the variance in male mating, fertilization and reproductive success, we tested the hypothesis that males face a higher opportunity for sexual selection in species in which monopolization behavior occurs than in species with no such behavior. In order to test these hypotheses, we conducted an extensive meta-analysis across animals, providing more than 1,200 effect sizes estimates and combining four different indexes of selection that focus on three different episodes of selection, allowing us to integrate seminal theoretical bases of sexual selection research, from Darwin (1871) to current times.

Methods

Literature search

We developed an extensive and systematic search of the literature for studies that quantified mating and reproductive success among individuals of a given animal population. We used the following combination of keywords: "reproductive success" AND "mating success" OR "fitness" AND "mating success" OR "paternity" AND "mating success" OR "offspring" AND "mating success" OR "litter" AND "mating success" OR "fertilization success" AND "mating success" OR "breeding success" AND "mating success" OR "fecundity" AND "mating success" OR "reproductive rate" AND "mating success" OR "post-mating sexual selection" OR "post-mating selection" OR "Bateman*" OR "opportunit* for selection" OR "opportunit* for sexual selection" OR "selection gradient*" OR "Morisita index" OR "monopolization index for reproductive success" OR "Jones index" OR "copulation success" OR "opportunit* for natural selection" OR "intensit* of sexual selection" OR "mating success" AND "survival rate" OR "reproductive success" AND "number of mat*" OR "mixed paternity" OR "mating and reproductive success" OR "opportunit* for natural selection and sexual" OR "natural and sexual selection" OR "sexual and natural selection". The search was performed on *ISI Web of Science* (all databases) and *Scopus*, and was last updated on 28th May 2017.

Screening studies

First, by reading titles and abstracts of the studies found, we selected those studies that seemed to quantify the mating success and the reproductive success of females and/or males. These included studies that calculated the opportunity for sexual selection (I_s), the opportunity for fertilization selection (I_f; Chapter 1), the opportunity for selection (I), and the Bateman gradient. We excluded studies that did not allow mating success to vary, as variation is a prerequisite for selection (for example, we excluded all studies in which all individuals had the chance to mate with only one sexual partner). We restricted our study to non-human animals, because humans are a species with highly complex cultural development, presenting behaviors that strikingly differ from other animal species. The procedure to identify the occurrence of monopolization behavior (see below) cannot be directly applied to humans and doing so would potentially result in misleading (probably sexist) interpretations of available information on human behavior.

Second, we read all studies approved in the first step in order to check their eligibility and extract the data. Again, we excluded all studies that did not allow mating success to vary. Additionally, we excluded data in which maternity and/or paternity could not be reasonably assured. For example, in a socially monogamous bird species in which there is no nest-parasitism (i.e. nests belonging to this species do not contain eggs from conspecific females or from other species), we can be confident that the sampled offspring were produced by the female tending the nest. Otherwise, because extra-pair paternity is common among birds (Westneat and Sherman 1997; Macedo et al. 2008; Lifjeld et al. 2010), usually, we could only be confident of paternity if the authors performed genetic parentage analysis. However, if the authors prevented nest parasitism or the authors were able to record every single mating event, male reproductive success could be directly quantified by counting the number of offspring produced per nest (with no need for genetic parentage analysis). Finally, for experimental studies, we also excluded data coming from experimental groups in which individuals faced a treatment that changed their reproductive performance.

Data collection – effect sizes

From the studies selected in the previous screenings, we extracted data to calculate, for both sexes, effect sizes that are proxies to estimate the intensity of sexual selection. Because it is important to access different selective events in order to study sexual selection (Fitze and Le Galliard 2011; Kvarnemo and Simmons 2013), including components of pre-mating, post-mating and total sexual selection, we selected as effect sizes five different proxies of sexual selection. As these proxies require simple data to be calculated (Henshaw et al. 2016) and are commonly used in sexual selection studies, we opted to use as effect sizes:

- I_s, the opportunity for sexual selection - i.e. the mating success variance divided by the squared mean mating success (Crow 1958);
- I_f, the opportunity for fertilization selection, - i.e. the fertilization success variance divided by the squared mean fertilization success (Chapter 1);
- I, the opportunity for selection - i.e. the reproductive success variance divided by the squared mean reproductive success (Wade 1979);
- the Bateman gradient - i.e. the slope of the least square regression between mating success and reproductive success (Bateman 1948; Arnold and Duvall 1994);
- the Jones index (s'_{max}), an upper limit of the intensity of sexual selection acting upon a specific trait correlated with mate acquisition - i.e. the square root of I_s multiplied by the respective Bateman gradient (see Jones 2009; Henshaw et al. 2016).

Here, the mean reproductive success is the mean number of offspring produced by individuals in a given population, an information that may have been obtained from different sources (e.g. number of embryos in a pouch, number of eggs in a nest, or the number of young produced). For each individual, mating success is the number of times this individual was observed mating, or the number of sexual partners with whom this individual mated. Due to methodological limitations, several studies calculate I_s by inferring mating success from genetic analyses (i.e. the female mating success would then be the number of males that fertilized her eggs, and the male mating success would be the number of females he fertilized). However, as previously demonstrated, I_s estimates calculated from genetic analyses differ from I_s estimates obtained by observing and recording mating events (Chapter 1). Because the majority of the data available in the literature comes from studies that performed genetic analyses, but did not register mating events *per se*, here we use an additional index of sexual selection, analogous to I_s and I: the opportunity for fertilization selection, I_f. Fertilization success is the number of individuals that fertilize a focal individual or the number of individuals fertilized by a focal individual. Despite the existence of other indexes to estimate post-mating sexual selection (e.g. Shuster et al. 2013), we opted to use the analogous I_f, as it allows us to compare three indexes that are calculated exactly in the same manner, but that provide us with different information.

Being standardized and dimensionless, I_s and I allow the comparison among data from different studies (Moura and Peixoto 2013), and the same applies for I_f. In order to also use Bateman gradient as an effect size and compare measures coming from different species, we standardized the Bateman gradients by obtaining the slope of the least square regression between the relative mating success and the relative reproductive success (following Jones 2009). We calculated relative measures of mating and reproductive success by dividing every individual measure of success by the mean success in the studied population. A study was only included in our meta-analysis if it provided at least one measure of I and one measure of I_s or I_f, in order to allow us to investigate different events of selection (pre-mating, post-mating, and total selection). Additionally, for each effect size, we also recorded the sex of the individuals sampled and the sample size.

We calculated the effect sizes from information provided in the text or tables of the manuscript and/or the supplementary material. We also extracted data from figures, using the program WebPlotDigitizer (Rohatgi 2015). For many studies, we were unable to extract data from the information available in the main sources. When this was the case, we actively searched for the data on two repositories: Dryad© and Figshare. After this step, there were still several studies from which we could identify that the needed data was collected by the authors, but that we could not extract it from the published manuscript. From these remaining studies, we selected 152 studies, and contacted at least one of the authors to ask for the data (see Appendix 1 for more information and to see the template of the e-mail sent to the authors).

Data collection – moderators

To investigate the causes of variation in sexual selection intensity/opportunity, and test our hypotheses, we included as moderators the absence (0) or occurrence (1) of monopolization behavior in the species. We preferentially used information on social monopolization coming from the original papers that provided selection indexes estimates. Then, if necessary, we used additional information available in the literature (for search protocol, see Appendix 3), screening more than 2,000 studies during this task alone.

We considered that individuals try to socially monopolize mates when: (i) individuals actively defend the access to at least one mature individual of the opposite sex; and (ii) when individuals defend the access to a particular resource (including territories) used by the opposite sex and, by doing this, indirectly defend access to mature individuals of the opposite sex. We considered that individuals do not try to monopolize mates when: (i) it is said that neither sex directly or indirectly defend the access to mature individuals of the opposite sex; (ii) when the mating system described is a scramble competition or a lek (see Appendix 4 for more on monopolization behavior). For lek mating systems, one may predict that some males will achieve higher mating success than his competitors will, once females are clumped and high-quality males may outcompete their rivals in the communal display arenas (Emlen and Oring 1977; Mackenzie et al. 1995). However, in leks, resources and sexual partners are not economically monopolizable (Emlen and Oring 1977; Thornhill and Alcock 1983) (therefore, males cannot directly preclude competitors from seeking mates), female choice plays a big role (see Queller 1987; Kirkpatrick and Ryan 1991), and attractive males may even reject sexual receptive females (e.g. Sæther et al. 2001). Therefore, given that our task is to test if the attempt to economically/physically monopolize females modulates sexual selection, we include leks as a mating system with no monopolization attempt behavior. Additionally, we did not exclude from our data collection species presenting hermaphroditism, given that hermaphrodites may present monopolization behavior (Oliver 1997; Dillen et al. 2009) and it is possible to calculate fitness for individuals acting as females or males (e.g. Anthes et al. 2010; Janicke et al. 2015).

<u>Data collection – random variables</u>

Given the heterogeneous nature of our data, while extracting the effect sizes and characterizing the social mating systems of the species, we also recorded additional variables that may influence the results and the variation among different effect size estimates. We recorded:

I) (“mating success meaning”) how the author(s) measured mating success; more specifically, if authors counted the number of mating events or the number of mate partners for each individual, once mating repeatedly with different sexual partners or repeatedly with the same partner may lead to different fitness outputs (e.g. Ronkainen et al. 2010) – but note that we already demonstrated that different forms of measuring mating success do not produce different estimates of I_s (Chapter 1);

II) (“fertilization success meaning”) how the author(s) measured fertilization success – if they counted the number of fertilization events (less than 0.01% of all cases in our dataset) or if they counted the number of individuals with whom each individual produced at least one offspring;

III) (“inclusion of zeros”) if the data presumably included individuals with mating success equal to 0, given that inclusion or exclusion of individuals that fail in a particular step of selection episodes may lead to different estimates of selection (Klug et al. 2010; Arnqvist 2013);

IV) (“mating success interference”) if the authors somehow influenced/determined mating success of (some) individuals;

V) (“intrasexual competition occurrence”) if the authors prevented intrasexual competition from happening among individuals of the focal sex;

VI) (offspring age) when reproductive success was measured (we separated offspring in four classes: eggs/embryos, newborn, juveniles, and adults), because as older are the offspring sampled, the effects of natural selection tend to be higher, which may influence measures of sexual selection intensity/opportunity (Bergeron et al. 2013);

VII) if the social mating system is a female defense polygyny, a male defense polyandry, a resource defense polyandry/polygyny, a lek, a monogamous defense, a scramble competition, or other.

When pertinent and possible, these random variables were included in the statistical analyses (see below).

Data analyses – hypotheses and predictions

We tested the following predictions:

1A) because male monopolization behavior tends to prevent (some) females from mating multiply, we predict that the opportunity for sexual selection (I_s) will be lower among females when monopolization behavior occurs than when this behavior is absent;

1B) because male monopolization behavior tends to prevent (some) males from mating, we predict that the opportunity for sexual selection will be higher among males when monopolization behavior occurs than when this behavior is absent;

2A) because male monopolization behavior prevents females from mating multiply, and, the more a female mates, the larger will be the chances of siring offspring from multiples males, we predict that the opportunity for fertilization selection (I_f) will be lower among females when monopolization behavior occurs than when this behavior is absent;

2B) because male monopolization behavior prevents some males from mating, and few or no mating opportunities tends to lead to zero or few eggs fertilized, we predict that the opportunity for fertilization selection (I_f) will be higher among males when monopolization behavior occurs than when this behavior is absent;

3A) because male monopolization behavior prevents females from mating multiply, and, the more a female mates, the lower are the chances of gamete incompatibility (Tregenza and Wedell 2000), we predict that the opportunity for selection (I) will be lower among females when monopolization behavior occurs than when this behavior is absent;

3B) because male monopolization behavior prevents some males from mating, and few or no mating opportunities tends to lead to zero offspring, we predict that the opportunity for selection (I) will be higher among males when monopolization behavior occurs than when this behavior is absent;

4) because monopolization behavior reduces the total amount of sexual coupling events, the higher is the intensity of monopolization behavior, the greater should be the selective pressure upon increasing the number of offspring produced per mating event. Therefore, for both sexes, we predict that the Bateman gradients will be steeper when monopolization behavior occurs than when this behavior is absent.

Due to the small sample sizes, we could not test any of the hypotheses for the Jones index. Hypotheses for the Jones index would follow the same rationale and pattern presented for I_s. All predictions are summarized in Table 1.

Table 1. Summary of predictions regarding the contrast in potential sexual selection strength between mating systems in which monopolization behavior occurs (MO) and mating systems in which monopolization behavior does not occur (NM). The predictions are made separately for females and males, and concern four selection indexes: the opportunity for sexual selection (I_s), the opportunity for fertilization selection (I_f), the opportunity for selection (I), and the Bateman gradient. In green, we highlight the occasions in which we expect that the average estimate for the selection index will be higher when monopolization behavior occurs. In yellow, we highlight the occasions in which we expect that the average estimate for the selection index will be higher when the monopolization behavior does not occur.

Selection index	**Females**	**Males**
I_s	NM > MO	MO > NM
I_f	NM > MO	MO > NM
I	NM > MO	MO > NM
Bateman gradient	MO > NM	MO > NM

Statistical analysis

To analyze the role played by monopolization behavior on sexual selection, we used multilevel (hierarchical) meta-regression models, as this type of model allows for the inclusion of random effects and does not assume independence among data (Nakagawa et al. 2017). One model was run for each selection index (i.e. the opportunity for sexual selection, I_s; the opportunity for fertilization selection, I_f; the opportunity for selection, I; and the Bateman gradient). In all models, the response variable was the selection index, and their sampling variance was included in different ways. Because the Bateman gradient is a least square regression, we calculated the sampling variance correspondent for Pearson's product-moment correlation coefficient (r): $(1 – r^2)^2$ / (sample size - 2) (Lajeunesse et al. 2013). For I_s, I_f and I, because these indexes do not have an associated standard variance, we used the sample size of each estimate as a weight (following Kraaijeveld et al. 2011; Moura and Peixoto 2013). For I_s and I_f models, we excluded all effect sizes from studies in which the authors somehow influenced/determined mating success of (some) individuals. All meta-regression models were fit using the function *rma.mv* from the *metafor* package (Viechtbauer 2010; R Core Team 2017).

Because (a) our main aim was to evaluate how (and whether) the monopolization behavior influences the opportunity for sexual selection faced by females and males, and because (b) heterogeneity among data is expected in biological meta-analyses (Senior et al. 2016), all meta-analytical multilevel models performed included monopolization behavior as a moderator. Monopolization behavior was coded as a categorical variable with two levels (i.e. populations that present monopolization behavior or not). We excluded data from our analyses for which we could not establish the existence or non-existence of monopolization behavior.

We treated additional non-independence of data (avoiding type I error; Nakagawa et al. 2017) by including as random effects the effect size identity and the phylogeny (see phylogeny in Appendix 2). We obtained the phylogeny from the *TimeTree Database* (Hedges et al. 2006). Using the softwares *Mesquite* (Maddison and Maddison 2019) and *Phylocon* (Webb et al. 2008), we included in the phylogeny the species whose times of divergence were not provided by the *TimeTree Database*. Then, we pruned the phylogeny according to the species included in each of the models. To better explain the variance among the data, when it was pertinent and feasible, we also included as random variables: mating success meaning, fertilization success meaning, inclusion of zeros, mating success interference, intrasexual competition occurrence, and offspring age. We assessed data heterogeneity using I^2 and we calculated the proportion of variance explained by each random variable. Additionally, we also performed sensitivity tests to investigate results consistency (see Supplementary Material 1 - Sensitivity tests).

Because publication bias is common in animal behavior research (Rosenthal et al. 2017), we used Egger's regression to assess publication bias. Finally, because we also obtained data from species in which females try to physically monopolize males, when pertinent and possible, we ran additional models (following the exact procedure described above) including in the analyses both females that guard and males that are guarded. This procedure led to the creation of two classes for these additional models: males and females that guard (from now on "guardians") and females and males that are targets of monopolization (from now on "targets"). The predictions for these models including guardians and targets are the same presented above (i.e. females and targets share the same predictions, and males and guardians share the same predictions), once we were also testing the role played by the monopolization behavior.

Complementarily, we calculated average effect sizes for all selection indexes. The models for average effect size calculation included all data available and all random variables pertinent and possible, with no inclusion of monopolization behavior as moderator. For the Jones index, we only ran models to calculate the average effect size among females and males. To obtain average measures of the Jones index, first, we excluded all effect sizes coming from studies in which the authors determined/influenced mating success, once the Jones index requires the use of Bateman gradients calculated from observational estimates of mating success (Henshaw et al. 2016).

Results

Data collection

For our search, *Web of Science* provided 6,414 studies and *Scopus* provided 5,288 studies (4,078 studies were provided by both *Scopus* and *Web of Science*). After removing duplicates, our search resulted in an initial list of 7,624 studies. By reading the titles and abstracts of the 7,624 studies, we selected 1,580 studies and rejected the remaining (Table 2). From the rejected studies, we selected 79 studies that could potentially provide citations to useful publications not included in our initial list. We read the references of those 79 studies, and selected 181 additional studies to read. While contacting authors, asking for more data, we also received the suggestion of four potential useful studies. Therefore, we read 1,844 studies in full, to check data availability and extract effect sizes (the whole process of data collection is described in Figure 1).

Table 2. The reasons that motivated the rejection of studies by reading their titles and abstracts and the quantity of studies rejected per each different reason. Once at least one reason to reject a study was identified, we did not try to analyze if the study could be rejected for other reasons. Therefore, for every study, we recorded the first reason(s) that caused its rejection.

Reasons for rejection	Number of studies
study on a completely unrelated topic	2,987
study only addresses pre-mating events (no measure of reproductive success)	928
study on plants	452
study on sexual selection but with no measurement of mating and reproductive success	407
study is not on sexual selection or sexual selection is a minor issue; includes studies on natural selection, speciation, and phylogeny	298
study only addresses post-mating events (no measure of mating success)	274
study on humans	188
mathematical model on sexual selection that does not provide useful data	147
qualitative review	126

Reasons for rejection	**Number of studies**
non-empirical study on sexual selection (but not a review or mathematical model) that does not provide useful data	95
title indicates that the study could be useful, but the abstract (and the whole study) could not be found)	45
title indicates that the study could be useful, but the abstract (and the whole study) could not be found	42
study on fungi, bacteria, virus, and any *taxa* not included in other exclusion criteria	25
descriptive study on sexual selection with no measurement of fitness	24
study strictly on parental care	20
report of a conference presentation on sexual selection	14
study does not allow mating success to vary	14
study uses artificial insemination in its protocol	4
comment on other studies	4
book review	2
others	2

After reading all 1,844 studies, we were able to extract at least one measure of I and one measure of I_s or I_f for at least one of the sexes from 144 studies. We contacted 121 authors to ask for additional data, receiving 20 positive answers and 55 negative answers. E-mails sent to seven additional authors were not delivered. From the positive answers, we were able to extract 41 additional effect size estimates for females (I_s: 8, I_f: 8, I: 13, Bateman gradient: 12) and 63 additional effect size estimates for males (I_s: 7, I_f: 17, I: 19, Bateman gradient: 20), totaling 104 additional effect sizes from 11 different studies. Therefore, we extracted data from 155 studies and discarded 1,689 studies (Table 3 shows the reasons for studies rejection at this step). From the 1,689 rejected studies, 454 studies present methods and/or results that show that their data would be useful for our meta-analysis (but the data is not reported in a way that we were able to extract the effect sizes). Altogether, from the 130 species that provided at least one measure of I and one measure of I_s or I_f for at least one of the sexes, we extracted 1,243 effect sizes (see Table 4 for summary of effect sizes per selection index). From the available literature, we could identify if monopolization occurs or not for 114 species of these 130 species (see Table 4).

Table 3. The reasons that motivated the rejection of studies after data extraction attempt and the quantity of studies rejected per each different reason. A study can be rejected by more than one reason. Quantities are presented for sexes and a study rejected for one sex may have been approved for the other sex. In bold letters, studies that have useful data but do not report the data in a useful way for meta-analytical purposes (according to our evaluation and data extraction attempt).

Reasons for rejection	**Females**	**Males**
study on sexual selection or animal behavior that does not quantify reproductive success	305	336
study contains useful data, but the data is not available (and we did not contact the authors)	**317**	**313**
experimental procedure prevents individuals from mating with more than one fertile sexual partner	166	215
study on an unrelated topic	147	147
study contains useful data, but the data is not available. We contacted the authors but received no answer	**119**	**108**
mating events are not registered neither is maternity and/or paternity determined, hindering the possibility of Is or If calculation	82	82
study focus only on males	52	-
study focus only on females	-	50
study is not available online	50	50
experimental procedure prevents some individuals from mating with more than one fertile sexual partner and restricts the mating success of the remaining individuals to a specific quantity z (being z > 1)	49	19
all individuals mated the same z number of times (being z > 1)	47	16
study allows us to calculate I, but not to calculate Is or If	45	31
study quantifies reproductive success for a group of individuals but not per individual	44	43
study on kinship, heritability, mutation or selection of traits that does not include any measure of reproductive success	37	37
study (other than quantitative reviews) that does not present original data	37	37
qualitative review on sexual selection	29	29
mathematical model on sexual selection that does not provide useful data	25	25
meta-analysis, other quantitative reviews or comparative analysis on sexual selection	14	14

Reasons for rejection	**Females**	**Males**
study contains useful data, author(s) sent us some data, but the data sent was not useful	**6**	**6**
study on animal reproduction that does not quantify reproductive success	5	6
authors inform that they failed to access maternity/paternity through genetic analyses	4	4
unreliable determination of maternity/paternity	1	10
we thought the study would contain useful data but authors informed us otherwise	1	2
other	72	72

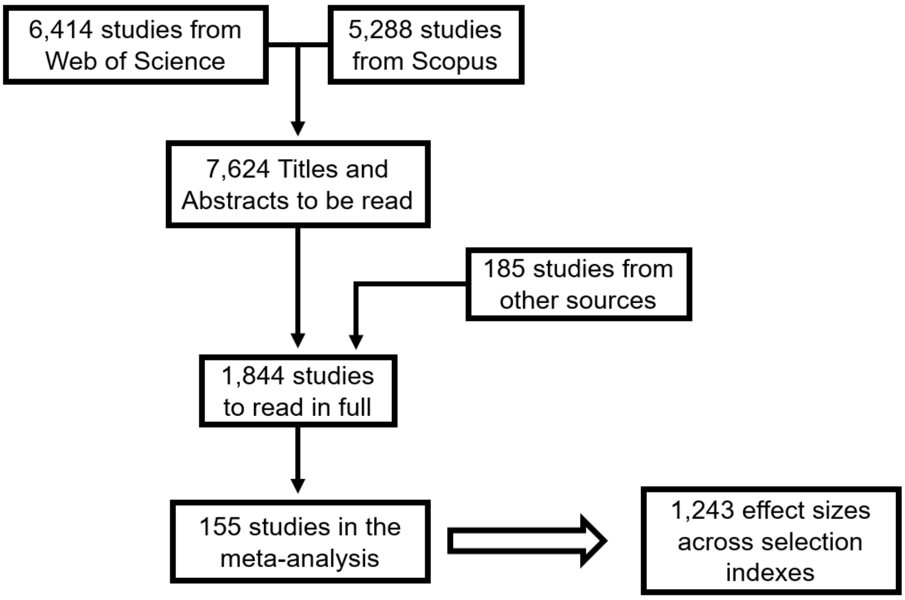

Figure 1. PRISMA diagram, depicting the steps of this meta-analysis, from data search to data collection. The selection indexes collected are the opportunity for sexual selection (I_s), the opportunity for fertilization selection (I_f), the opportunity for selection (I), the Bateman gradient, and the Jones index.

Table 4. Number of estimates per selection index, per class, and the respective number of species. The selection indexes included here are: the opportunity for sexual selection (I_s), the opportunity for fertilization selection (I_f), the opportunity for selection (I), and the Bateman gradient. We run models for four different classes of individuals. The classes are: females, targets (guarded females and guarded males, combined), males, and guardians (females and males that guard, combined). The total number of estimates are depicted, and between parentheses is informed the number of estimates included in each model, after exclusion of species for which we could not identify if the monopolization behavior occurs or not (exception: for the Jones index, we could not contrast mating systems according to the occurrence of monopolization behavior, therefore, there are no excluded species for the Jones index). The number of species that provided estimates are also informed, according to a classification based on monopolization behavior (MB). Species are divided in three types: MB occurs ("MB: yes"), MB does not occur ("MB: no"), and we could not identify if MB occurs or not ("MB: ?").

			Species		
Selection index	**Class**	**Estimates**	**MB: yes**	**MB: no**	**MB: ?**
Is	Females	59 (53)	17	19	6
Is	Males	53 (46)	17	13	6
If	Females	129 (112)	39	24	8
If	Targets	140 (123)	41	24	8
If	Males	160 (141)	42	30	7
If	Guardians	181 (162)	43	30	7
I	Females	186 (163)	47	38	13
I	Targets	198 (175)	50	38	13
I	Males	210 (184)	53	39	12
I	Guardians	221 (195)	54	39	12
Bateman gradient	Females	140 (117)	40	20	12
Bateman gradient	Targets	151 (128)	43	20	12
Bateman gradient	Males	171 (150)	44	23	11
Bateman gradient	Guardians	177 (156)	45	23	11
Jones index	Females	29	10	9	-
Jones index	Males	34	12	9	-

The opportunity for sexual selection (I_S) is influenced by monopolization behavior among females

The average I_s estimate for females is not different from zero (average $I_s = 0.355$, 95% CI = -0.635 to 1.345). Yet, in our meta-regression model, monopolization behavior explains considerable variation in I_s estimates for females. More specifically, females that undergo monopolization attempts face lower opportunity for sexual selection than females that do not undergo monopolization behavior (occurrence of monopolization behavior: $I_s = 0.079$, 95% CI = -1.231 to 1.390; no monopolization behavior: $I_s = 0.452$, 95% CI = -0.530 to 1.434; contrast: $I_s = 0.373$, CI lower end = 0.701, CI upper end = 0.044; for effect sizes, see Supplementary Material 2 - Figure S1). But see sensitivity analyses in Supplementary Material 2 (Table S1). Publication bias for I_s among females was not detected by Egger's regression (Egger's regression: $I_{s\ \mathrm{intercept}} = 0.151 \pm 0.099$ SE, $t = 1.522$, $p > 0.05$). Finally, the included random variables explained a small portion of the variation in the data ($I^2 = 4.07\%$; I^2 phylogeny: 3.65%; I^2 effect size identity = $2.92 \times 10^{-14}\%$; I^2 mating success meaning = $3.67 \times 10^{-11}\%$; I^2 inclusion of zeros = 0.42%; I^2 intrasexual competition occurrence = $3.18 \times 10^{-11}\%$).

The opportunity for sexual selection (I_S) is influenced by monopolization behavior among males

The average I_s estimate for males is not different from zero (average $I_s = -0.969$, 95% CI = -10.260 to 8.321). Yet, in our meta-regression model, monopolization behavior explains considerable variation in I_s estimates for males. We found that in species in which monopolization behavior occurs, there is a higher opportunity for sexual selection among males than in species in which this behavior is absent (occurrence of monopolization behavior: $I_s = 2.390$, 95% CI = -9.301 to 14.081; no monopolization behavior: $I_s = -1.729$, 95% CI = -10.293 to 6.836; contrast: $I_s = -4.118$, CI lower end = -0.992, CI upper end = -7.245; for effect sizes, see Supplementary Material 3 - Figure S2). For results provided by sensitivity analyses, see Supplementary Material 3 (Table S2). Egger's regression revealed publication bias for I_s among males (Egger's regression: $I_{s\ \mathrm{intercept}} = 2.747 \pm 0.839$ SE, $t = 3.276$, $p < 0.05$). Finally, the included random variables explained most of the variation in the data ($I^2 = 75.32\%$; I^2 phylogeny:

69.54%; I^2 effect size identity = 1.24%; I^2 inclusion of zeros = 4.54%; I^2 intrasexual competition occurrence = 6.52 x 10^{-7}%).

The opportunity for fertilization selection (I_f) is not influenced by monopolization behavior among females

The average I_f estimate for females is not different from zero (average I_f = 0.692, 95% CI = -3.851 to 5.235). Moreover, we found that I_f estimates among females do not differ according to the occurrence of monopolization behavior (occurrence of monopolization behavior: I_f = 0.444, 95% CI = -4.928 to 5.815; no monopolization behavior: I_f = 0.463, 95% CI = -3.939 to 4.865; contrast: I_f = 0.019, CI lower end = 0.989, CI upper end = -0.950; for effect sizes, see Supplementary Material 4 - Figure S3). This pattern is the same for all sensitivity analyses (Supplementary Material 4 - Table S3). Egger's regression revealed publication bias for I_f among females (Egger's regression: $I_{f\ intercept}$ = 0.375 ± 0.189 SE, t = 1.988, $p < 0.05$). Finally, the included random variables explained most of the variation in the data (I^2 = 62.64%; I^2 phylogeny: 62.07%; I^2 effect size identity = 0.57%; I^2 inclusion of zeros = 2.90 x 10^{-9}%; I^2 intrasexual competition occurrence = 8.77 x 10^{-15}%). Almost all results are not changed after inclusion of data coming from species in which males are guarded. The only exception is that Egger's regression revealed no publication bias for I_f among targets. For results on targets (i.e. guarded females and guarded males), see Supplementary Material 4 (Figure S3, Box S1, and Table S4).

The opportunity for fertilization selection (I_f) is not influenced by monopolization behavior among males

The average I_f estimate for males is not different from zero (average I_f = 0.368, 95% CI = -2.156 to 2.892). Moreover, we found that I_f estimates among males do not differ according to the occurrence of monopolization behavior (occurrence of monopolization behavior: I_f = -0.029, 95% CI = -3.078 to 3.020; no monopolization behavior: I_f = 0.525, 95% CI = -1.937 to 2.986; contrast: I_f = 0.553, CI lower end = 1.141, CI upper end = -0.034; for effect sizes, see Supplementary Material 5 - Figure S4).

However, the absolute I_f estimate value is much lower when monopolization behavior occurs. After removing the estimates from lek mating systems, this difference between absolute I_f estimate values is negligible (for this and other sensitivity analyses, see Supplementary Material 5 - Table S5). Egger's regression revealed publication bias for I_f among males (Egger's regression: $I_{f\ intercept}$ = 1.272 ± 0.189 SE, t = 6.722, $p < 0.05$). Finally, the included random variables explained part of the variation in the data (I^2 = 27.81%; I^2 phylogeny: 17.25%; I^2 effect size identity = 3.88%; I^2 fertilization success meaning: 4.28 x 10^{-5}%; I^2 inclusion of zeros = 1.60%; I^2 intrasexual competition occurrence = 3.42%; I^2 offspring age: 1.67%). The results are not changed after inclusion of data coming from species in which females guard. For results on guardians (i.e. males and females that guard), see Supplementary Material 5 (Figure S4, Box S2, and Table S6).

<u>The opportunity for selection (I) is not influenced by monopolization behavior among females</u>

The average I estimate for females is not different from zero (average I = 0.931, 95% CI = -2.798 to 4.660). Moreover, we found that I estimates among females do not differ according to the occurrence of monopolization behavior (occurrence of monopolization behavior: I = 0.750, 95% CI = -3.800 to 5.301; no monopolization behavior: I = 1.071, 95% CI = -2.700 to 4.842; contrast: I = 0.321, CI lower end = 1.100, CI upper end = -0.459; for effect sizes, see Supplementary Material 6 - Figure S5). For sensitivity analyses, see Supplementary Material 6 (Table S7). Egger's regression revealed no publication bias for I among females (Egger's regression: $I_{intercept}$ = 0.090 ± 0.154 SE, t = 0.588, $p > 0.05$). Finally, the included random variables explained most of the variation in the data (I^2 = 54.24%; I^2 phylogeny: 51.94%; I^2 effect size identity = 0.90%; I^2 mating success interference = 4.71 x 10^{-8}%; I^2 inclusion of zeros = 0.83%; I^2 intrasexual competition occurrence = 2.10 x 10^{-8}%; I^2 offspring age: 0.58%). The results are not changed after inclusion of data coming from species in which males are guarded. For results on targets (i.e. guarded females and guarded males), see Supplementary Material 6 (Figure S5, Box S3, and Table S8).

The opportunity for selection (I) is not influenced by monopolization behavior among males

The average I estimate for males is not different from zero (average I = 0.878, 95% CI = -6.498 to 8.253). Moreover, we found that I estimates among males do not differ according to the occurrence of monopolization behavior (occurrence of monopolization behavior: I = 1.178, 95% CI = -7.786 to 10.142; no monopolization behavior: I = 0.735, 95% CI = -6.726 to 8.196; contrast: I = -0.443, CI lower end = 1.060, CI upper end = -1.946; for effect sizes, see Supplementary Material 7 - Figure S6). Across almost all sensitivity analyses, the pattern is the same (Supplementary Material 7 - Table S9). Egger's regression revealed publication bias for I among males (Egger's regression: $I_{intercept}$ = 1.767 ± 0.392 SE, t = 4.505, $p < 0.05$). Finally, the included random variables explained most of the variation in the data (I^2 = 80.05%; I^2 phylogeny: 72.82%; I^2 effect size identity = 4.98%; I^2 mating success interference = 9.21 x 10^{-7}%; I^2 inclusion of zeros = 0.65%; I^2 intrasexual competition occurrence = 1.04%; I^2 offspring age: 0.56%). The results are not changed after inclusion of data coming from species in which females guard. For results on guardians (i.e. males and females that guard), see Supplementary Material 7 (Figure S6, Box S4, and Table S10).

The Bateman gradient is not influenced by monopolization behavior among females

The average Bateman gradient for females is positive and different from zero (average slope = 0.487, 95% CI = 0.197 to 0.777). Moreover, we found that Bateman gradient estimates among females do not differ according to the occurrence of monopolization behavior (occurrence of monopolization behavior: slope = 0.433, 95% CI = -0.102 to 0.968; no monopolization behavior: slope = 0.522, 95% CI = 0.182 to 0.863; contrast: slope = 0.089, CI lower end = 0.283, CI upper end = -0.105; for effect sizes, see Supplementary Material 8 - Figure S7). The pattern is the same, regardless of the sensitivity analysis run (Supplementary Material 8 - Table S11). Egger's regression revealed publication bias for Bateman gradient among females (Egger's regression: Bateman gradient $slope_{intercept}$ = 0.150 ± 0.048 SE, t = 3.121, $p < 0.05$). Finally, the included random variables explained almost no variation in the data (I^2 =

1.20%; I^2 phylogeny: 0.33%; I^2 effect size identity = 0.70%; I^2 mating success interference = 8.45×10^{-7}%; I^2 inclusion of zeros = 0.16%; I^2 intrasexual competition occurrence = 1.17×10^{-10}%; I^2 offspring age: 2.51×10^{-14}%). The results are not changed after inclusion of data coming from species in which males are guarded. For results on targets (i.e. guarded females and guarded males), see Supplementary Material 8 (Figure S7, Box S5, and Table S12).

The Bateman gradient is not influenced by monopolization behavior among males

The average Bateman gradient for males is positive and different from zero (average slope = 1.046, 95% CI = 0.671 to 1.422). Moreover, we found that Bateman gradient estimates among males do not differ according to the occurrence of monopolization behavior (occurrence of monopolization behavior: slope = 1.025, 95% CI = 0.586 to 1.465; no monopolization behavior: slope = 1.053, 95% CI = 0.675 to 1.432; contrast: slope = 0.028, CI lower end = 0.089, CI upper end = -0.033; for effect sizes, see Supplementary Material 9 - Figure S8). The pattern is the same, regardless of the sensitivity analysis run (Supplementary Material 9 - Table S13). Egger's regression revealed publication bias for Bateman gradient among males (Egger's regression: Bateman gradient $\text{slope}_{\text{intercept}} = -0.093 \pm 0.023$ SE, $t = -4.007$, $p < 0.05$). Finally, the included random variables explained almost no variation in the data (I^2 = 0.31%; I^2 phylogeny: 0.09%; I^2 effect size identity = 0.03%; I^2 mating success interference = 0.19%; I^2 inclusion of zeros = 0.01%; I^2 intrasexual competition occurrence = 5.11×10^{-10}%; I^2 offspring age: 6.86×10^{-11}%). The results are not changed after inclusion of data coming from species in which females guard. For results on guardians (i.e. males and females that guard), see Supplementary Material 9 (Figure S8, Box S6, and Table S14).

The Jones index – both sexes

The average Jones index among females is positive and different from zero (average Jones index = 0.219, 95% CI = 0.034 to 0.405; Supplementary Material 10 - Figure S9). The average Jones index among males is not different from zero (average Jones index = 0.564, 95% CI = -1.412 to 2.540; Supplementary Material 10 - Figure S10).

Discussion

This meta-analysis provides important information for the theory of sexual selection as it demonstrates that females are not ultimately monopolized by males. Despite the effectiveness of male monopolization behavior in restricting females' re-mating potential, which influences the opportunity for pre-mating sexual selection, the same does not apply for the opportunity for fertilization selection nor the opportunity for selection, for both sexes. This is especially relevant because variance in mating success will only matter in terms of evolutionary selection if it translates into variance in reproductive success (Henshaw et al. 2016), which is demonstrated by the fact that reproductive success is the best proxy for Darwinian fitness (Jones 2009). If monopolization behavior does not influence the relative variance in Darwinian fitness, this behavior is less relevant for non-random evolutionary processes than it is usually expected. In addition to collecting data for species in which males guard females, we also collected data for species in which females are the sex performing the monopolization behavior. However, species presenting female monopolization behavior seem to be rare in nature (if they are common in nature but rare in the scientific literature, a bias is produced by researchers), which made it impossible to test hypotheses for those species alone. Therefore, those species were included in the additional models for targets (guarded females and guarded males combined) and guardians (females and males that guard combined). Because these models never returned different results from the models including females alone or males alone, we here discuss the results only for females and males, for clarity. Nevertheless, the arguments presented below to explain results for females and males usually apply for targets and guardians, respectively.

As highlighted above, here, we confirm a fundamental prediction made by sexual selection theory (following Emlen and Oring 1977): if males monopolize females, females face a lower opportunity for sexual selection and males face a higher opportunity for sexual selection. In other words, when males try to monopolize females, females of a population generally mate with a similar number of partners (e.g. Howard 1983; Gullberg et al. 1997; Benken et al. 1999; LaBarbera et al. 2012; Devost and Turgeon 2016), while the absence of male monopolization attempts allows females to mate with no restriction, which leads to the emergence of a higher variance in female mating success (e.g. Minoretti et al. 2011; Levine et al. 2015; Toft and Albo 2015). With males, on the other hand, there is high variance in male mating success when monopolization behavior occurs, and some males achieve a higher mating success than the others (e.g. Dixson et al. 1993; Paul et al. 1993; Say et al. 2003; Fabiani et al. 2004; Rodríguez-Muñoz et al. 2010). However, when monopolization behavior is absent, the variance in mating success among males is low (e.g. Fitzpatrick and McNeil 1989; Coltman et al. 1999; Pélissié et al. 2012; Turnell and Shaw 2015; Marie-Orleach et al. 2016), which is probably a result of no individual directly restricting mating activity of its competitors. Altogether, these results on the opportunity for sexual selection show that, across animals, in systems such as female or resource defense polygyny, dominant males that try to economically monopolize females succeed in precluding females from mating multiply and, as a consequence, succeed in precluding male competitors to mate (once or multiple times). This highlights the usefulness of the mating systems described by Emlen and Oring (1977), which are good predictors of pre-mating episodes of sexual selection.

Knowing now that monopolization behavior not only restricts the degree of polyandry (which should reduce the risk of sperm competition – Parker et al. 2012), but that it also enhances the variance in male mating success (and males that mate less have fewer opportunities to fertilize female's ova), it would be even more reliable to predict a higher variance in male fertilization and reproductive success when monopolization behavior occurs than when it does not. However, unexpectedly, our results show that, among males, both opportunities for selection (I_f and I) do not differ according to the occurrence of monopolization behavior. Complementarily, the same applies for females, and the restriction imposed by males when monopolization behavior occurs does not manifest into a higher opportunity for fertilization selection or a higher opportunity for selection among females. These findings show us that post-mating episodes are strong enough to erase the outcome of pre-mating intra and intersexual competitions in animals, corroborating the previous evidence of a ubiquitous occurrence of opportunity for post-mating sexual selection among animals (Chapter 1). For example, given that females may cryptically select the sperm from particular males (Firman et al. 2017) and that enhancing offspring genetic diversity tends to be favored by natural selection (Trivers 1972; see examples in Jennions and Petrie 2000 and Mays and Hill 2004), it is possible that females circumvent the monopolization attempts of their sexual partners by selecting the sperm (and, indirectly, the genes) of other males (if the female managed to mate with at least one additional male). Complementarily, for species in which monopolization behavior does not occur, and mean mating success is high, females deal with various candidate sperms that they can cryptically select or reject. Altogether, the high chance of cryptic female choice probably explains (at least partially) why neither the opportunity for fertilization selection, nor the opportunity for selection differ according to the occurrence/absence of monopolization behavior.

Along with cryptic female choice, sperm competition may also may explain why the opportunity for fertilization selection and the opportunity for selection do not differ according to the occurrence/absence of monopolization behavior (however, it may be difficult to disentangle what is the outcome from each of these post-mating processes; Birkhead 1998). Because in scramble competition males do not preclude females from mating multiply, scramble competition may promote a high degree of polyandry and, therefore, enhance the relevance of sperm competition (Kappeler 1997; Holwell et al. 2016). As sperm competition takes place, some males may be more efficient in fertilizing females, increasing the relative variance in fertilization success among males, and increasing the opportunity for selection when monopolization behavior does not occur. Accordingly, it is not surprising that, after sperm competition takes place, the previous difference in the opportunity for sexual selection among social mating systems is not converted into a difference in the other opportunities for selection (fertilization and total selection). Complementarily, for species in which monopolization behavior occurs, from pre-mating phase (I_s) to post-mating phase (I_f), there is a decrease in the potential intensity of sexual selection, indicating that sperm competition intensity is also high when monopolization behavior occurs. Following this, in many *taxa* males face a trade-off between investing in pre- and post-mating competition (e.g. Fitzpatrick et al. 2012; Ferrandiz-Rovira et al. 2014; Dines et al. 2015; Lüpold et al. 2019), with dominant males that invest most of their energy on monopolizing females losing paternity for non-dominant competitors, that invest more on post-mating competition (e.g. Fu et al. 2001; Buzatto et al. 2014). The most common is this trade-off, the greater are the chances that non-dominant males investing more on post-mating competition prevent I_f and I from differing across mating systems.

Across models on the opportunity for fertilization selection, the absolute I_f estimate value is almost always higher when monopolization behavior does not occur. The only exception is when we excluded data coming from lek mating systems. In this latter case, the absolute value of I_f estimate is similar between the two classes of mating system. Because females in lek mating systems are extremely selective before mating, little selective pressure favoring cryptic female choice is expected (Møller 1998). Therefore, the result obtained by excluding lek mating systems indicates that sperm competition not only plays a big role in scramble competition, but also in leks. This suggests an evolutionary response of less attractive males in leks, which probably invest more on sperm competition related traits, in order to surpass the difficulties coming from the high concentration of mating opportunities among attractive males. In a lek-forming *Drosophila* species, it has been demonstrated that males with larger testes sire more offspring (Droney 2001). In other lekking moth species, males mating with a non-virgin female copulate longer than when mating with a virgin female (Engqvist et al. 2014) and males facing the risk of sperm competition transfer more sperm to the female tract (Jarrige et al. 2015). In a manakin bird species, females seem to mate multiply after mating with inexperienced alpha males (Rivers and DuVal 2019) - promoting sperm competition. Additionally, as alpha males get older, they produce less sperm, which leads to the rise of multiple paternity (Sardell and DuVal 2014), as younger individuals fertilize more eggs. However, as sperm competition is not usually considered an important selective pressure in lek mating systems (Sardell and DuVal 2014), few studies on lekking species focus on sperm competition. Contrary, our results indicate that more research should address sperm competition in lek mating systems, as sperm competition seems to be effective in shaping sexual selection in lekking species.

We predicted that producing more offspring per mating event (i.e. a steeper Bateman gradient) would be favored by selection when monopolization behavior occurs, for both sexes, because monopolization behavior restricts female choice and reduces mating success among non-dominant males (a pattern corroborated by our results for the opportunity for sexual selection). However, the fitness return from each mating event is similar for females and males, regardless of the occurrence/absence of monopolization behavior. This indicates that post-mating processes as cryptic female choice and sperm competition suffice to bypass the restrictions imposed by monopolization behavior (as discussed above), and there is no selective pressure upon any additional response to monopolization behavior. However, for both sexes, while Bateman gradient estimates do not differ according to the occurrence of monopolization behavior, the average Bateman gradient in animals is positive regardless of the social mating system. A positive Bateman gradient for males conforms with the standard Darwin-Bateman paradigm (Bateman 1948; Dewsbury 2005), but a positive Bateman gradient for females does not (Kvarnemo and Simmons 2013). The positive Bateman gradient combined with the also positive average Jones index for females reinforce the relevance (and universality) of polyandry and the relevance of the debate on the evolution of polyandry (e.g. Zeh and Zeh 1996, 1997; Arnqvist and Nilsson 2000; Jennions and Petrie 2000; Slatyer et al. 2012; Kvarnemo and Simmons 2013). Complementarily, the average measures for all other sexual selection indexes (I_s, I_f, and I) did not differ from zero, for both sexes. If the opportunities for sexual, fertilization and total selection, on average, do not differ from zero across animals, a considerable portion of animals in nature are currently not facing selection processes, which is expected (Bradshaw 1993).

Publication biases towards higher values were found for the opportunity for sexual selection (only males), the opportunity for fertilization selection (females, guardians, and males), and the opportunity for selection (guardians and males). And a publication bias towards negative values was found for Bateman gradient (guardians and males). This does not bring any special concern on our results because our data presents a high variance in the estimates of all selection indexes across targets, females, guardians, and males and the biases here reported are not expected to influence the contrast of mating systems we propose here. These biases may be a concern on how the scientific community is studying the topic and making the results public (Møller and Jennions 2001). Maybe there would be no publication bias if, across scientific literature, results were often reported in a way useful for meta-analytical approaches. It is important to stress out that we found 609 studies containing useful data, but we succeeded in extracting effect sizes from only 155 studies (25.45%). If more data were made available, we could certainly have tested our hypotheses for the Jones index (Jones 2009). Therefore, better data reporting practices can surely contribute to a more accurate understanding of sexual selection processes (see Haddaway 2015; Greenacre 2016). Additionally, we note that sometimes it was not easy to identify the social mating system of the species included in our meta-analysis, and we could not find any information to confirm or reject the occurrence of monopolization behavior for 12.31% species. Therefore, we recommend that, despite the usefulness of paternity analyses and the relevance of genetic mating systems, authors continue to characterize the social/ecological mating systems of species, especially after the demonstration we provide here that the opportunity for sexual selection differs according to the occurrence/absence of monopolization behavior.

Through an extensive meta-analytical revision of the literature, we demonstrate that male monopolization behavior influences pre-mating sexual selection, but has little influence upon post-mating and total selection. We also show that males may successfully (directly or indirectly) guard females during pre-mating episodes of selection, but they do not completely refrain females from producing offspring with different fathers (i.e. females are not monopolized). This reinforces the notion that females are not passive (Gowaty 1997). All these conclusions are achieved thanks to the efforts of several authors, whose work provided more than 1,200 effect sizes, comprising many animal *taxa* (including Actinopterygii, Amphibia, Arachnida, Aves, Cephalopoda, Chondrichthyes, Gastropoda, Insecta, Mammalia, Maxillopoda, Pycnogonida, Reptilia, and Turbellaria). The large taxonomic scope of the data and the diversity of the proxies to measure sexual selection (comprising all episodes of sexual selection) bolster the findings we report here. Based on our results, it is now important to understand how cryptic female choice and sperm competition operate according to the occurrence or absence of monopolization behavior, with special attention to lek mating systems. Additionally, it is interesting to contrast the selective pressures imposed by monopolization behavior, cryptic female choice and sperm competition in different animal *taxa*, because the phylogeny was the only random variable that considerably explained variation in some models. Because non-random variance in animal fitness relies on behavioral, morphological, and physiological attributes of individuals, the questions we answered here should also be applied focusing on traits that enable individuals to successfully reproduce (Chapter 3). Finally, to avoid the existent gender bias in studies of animal behavior and sexual selection (Ah-King and Nylin 2010; Ah-King et al. 2014), it is important that the future studies here suggested include not only males' perspective, but also females' perspective (see Hare and Simmons 2019). Our results and the arguments we present to discuss these findings emphasize that females are active players in sexual selection processes and that, as a research field, we greatly benefit from including female's perspectives in our analyses, especially if we manage to integrate both pre-mating and post-mating episodes of sexual selection, as done here.

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Supplementary Materials

Supplementary materials are presented according to the order in which they are presented in the main text.

Supplementary Material 1 - Sensitivity tests

We performed sensitivity tests to investigate results consistency. In these tests, we included the phylogeny and effect sizes identity as random effects and we excluded some classes of effect sizes (each at a time):

i) estimates coming from studies in which mating success was measured by counting the number of mating events;

ii) estimates coming from studies in which fertilization success was measured by counting the number of fertilization events;

iii) estimates coming from studies in which individuals with mating success equal to 0 were not included;

iv) estimates coming from studies in which the authors somehow influenced/determined mating success of (some) individuals;

v) estimates coming from studies in which the authors prevented intrasexual competition to happen among the focal sex;

vi) estimates coming from lek systems, once it is expected that this mating system also presents high intensities of sexual selection (Payne 1984; Andersson 1994; Székely et al. 2007);

vii) and estimates coming from studies in which reproductive success was measured on older offspring (i.e. juveniles, and adults).

Supplementary Material 2 – I_s (females)

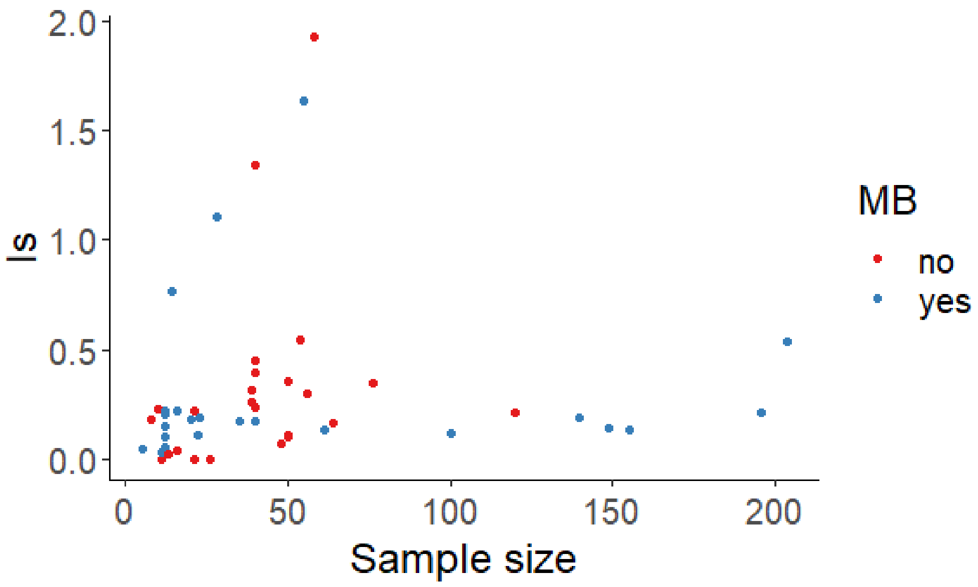

Figure S1. Estimates of the opportunity for sexual selection (I_s) and the respective sample sizes obtained for females across animals. Estimates are divided in two classes, according to monopolization behavior (MB) occurrence. Estimates coming from species that present monopolization behavior (when males try to economically monopolize females) are represented in blue. Estimates coming from species that do not present monopolization behavior are represented in red.

Table S1. Results regarding the difference in female I_s estimates between species in which monopolization behavior occurs and species in which this behavior is absent (yes: 1; no: 0). Each model run may contain all data available or part of it (sensitivity analyses). This table presents the estimate of I_s value per type of social mating system and their respective interval of confidence (2.5% CI to 97.5% CI). The number of species and estimates included per social mating system per model is also informed. Statistically significant differences ($p < 0.05$) between social mating systems are indicated with two asterisks (**). There are no marginally significant differences ($0.05 < p < 0.10$).

Model	Monopolization	I_s	2.5% CI	97.5% CI	Estimates	Species
All data; Random variables: phylogeny, effect size identity, mating success meaning, inclusion of zeros, and intrasexual competition occurrence	1: yes	0.079**	-1.231	1.390	23	16
	0: no	0.452**	-0.530	1.434	25	16
All data; Random variables: phylogeny and effect size identity	1: yes	0.275	-1.119	1.669	23	16
	0: no	0.500	-0.541	1.541	25	16
Data: excluding mating success as number of mating occurrences; Random variables: phylogeny and effect size identity	1: yes	0.326	-0.333	0.986	19	13
	0: no	0.392	0.099	0.685	11	8
Data: excluding effect sizes that do not include mating success = 0; Random variables: phylogeny and effect size identity	1: yes	0.857	-0.940	2.053	16	10
	0: no	0.523	-0.389	1.434	18	11
Data: excluding studies with no intrasexual competition; Random variables: phylogeny and effect size identity	1: yes	0.322	-1.185	1.830	21	15
	0: no	0.577	-0.564	1.719	17	13
Data: excluding lek systems; Random variables: phylogeny and effect size identity	1: yes	0.282	-1.149	1.712	23	16
	0: no	0.483	-0.581	1.546	24	15

Supplementary Material 3 – I_s (males)

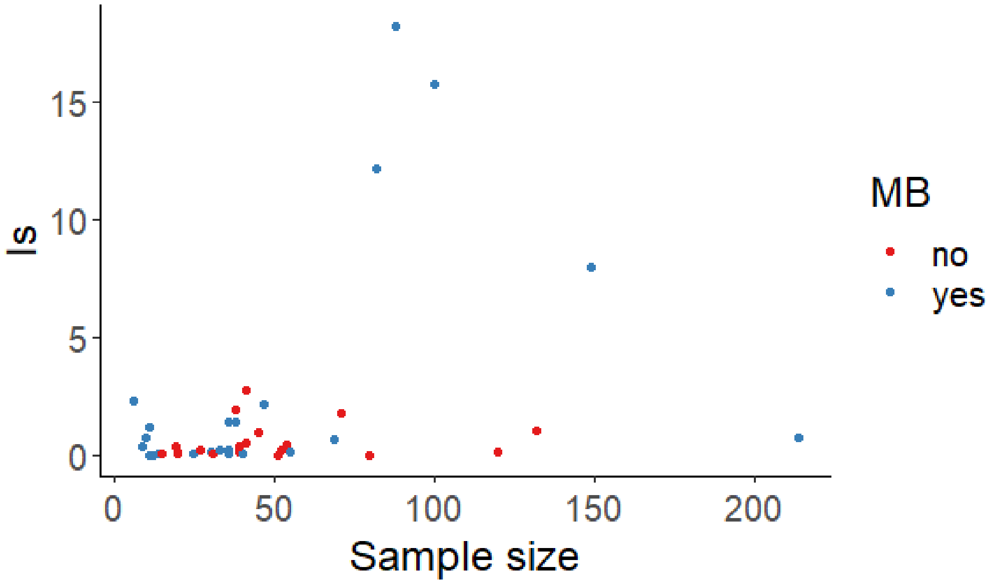

Figure S2. Estimates of the opportunity for sexual selection (I_s) and the respective sample sizes obtained for males across animals. Estimates are divided in two classes, according to monopolization behavior (MB) occurrence. Estimates coming from species that present monopolization behavior (when males try to economically monopolize females) are represented in blue. Estimates coming from species that do not present monopolization behavior are represented in red.

Table S2. Results regarding the difference in male I_s estimates between species in which monopolization behavior occurs and species in which this behavior is absent (yes: 1; no: 0). Each model run may contain all data available or part of it (sensitivity analyses). This table presents the estimate of I_s value per type of social mating system and their respective interval of confidence (2.5% CI to 97.5% CI). The number of species and estimates included per social mating system per model is also informed. Statistically significant differences ($p < 0.05$) between social mating systems are indicated with two asterisks (**). There are no marginally significant differences ($0.05 < p < 0.10$).

Model	**Monopolization**	**I_s**	**2.5% CI**	**97.5% CI**	**Estimates**	**Species**
All data; Random variables: phylogeny, effect size identity, inclusion of zeros, and intrasexual competition occurrence	1: yes	2.390**	-9.301	14.081	26	17
	0: no	-1.729**	-10.293	6.836	20	13
All data; Random variables: phylogeny and effect size identity	1: yes	4.482**	-7.937	16.900	26	17
	0: no	-0.958**	-10.046	8.130	20	13
Data: excluding mating success as number of mating occurrences; Random variables: phylogeny and effect size identity	1: yes	5.136**	-10.495	20.766	19	12
	0: no	-3.13**	-14.169	7.909	10	6
Data: excluding effect sizes that do not include mating success = 0; Random variables: phylogeny and effect size identity	1: yes	0.938	-8.713	10.588	22	14
	0: no	1.09	-5.316	7.495	16	11
Data: excluding studies with no intrasexual competition; Random variables: phylogeny and effect size identity	1: yes	4.466**	-8.232	17.164	26	17
	0: no	-1.026**	-10.315	8.263	19	12
Data: excluding lek systems; Random variables: phylogeny and effect size identity	1: yes	4.625**	-7.984	17.233	26	17
	0: no	-1.15**	-10.303	8.003	18	12

Supplementary Material 4 – I_f (females and targets)

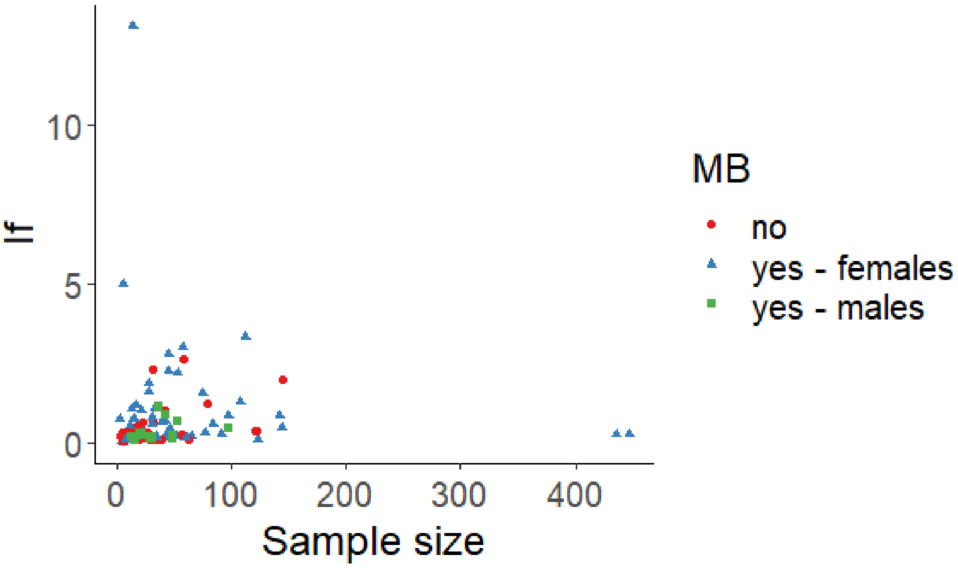

Figure S3. Estimates of the opportunity for fertilization selection (I_f) and the respective sample sizes obtained for targets (females and guarded males) across animals. Estimates are divided in three classes, according to monopolization behavior (MB) occurrence and sex. Estimates of I_f among females of species that present monopolization behavior (when males try to economically monopolize females) are represented with blue triangles. Estimates of I_f among guarded males are represented with green squares. Estimates of I_f among females of species that do not present monopolization behavior are represented with red circles.

Table S3. Results regarding the difference in female I_f estimates between species in which monopolization behavior occurs and species in which this behavior is absent (yes: 1; no: 0). Each model run may contain all data available or part of it (sensitivity analyses). This table presents the estimate of I_f value per type of social mating system and their respective interval of confidence (2.5% CI to 97.5% CI). There are no statistically significant differences ($p < 0.05$) or marginally significant differences ($0.05 < p < 0.10$) between social mating systems.

Model	**Monopolization**	I_f	**2.5% CI**	**97.5% CI**	**Estimates**	**Species**
All data; Random variables: phylogeny, effect size identity, inclusion of zeros, intrasexual competition occurrence, and offspring age	1: yes	0.444	-4.928	5.815	69	39
	0: no	0.463	-3.939	4.865	43	24
All data; Random variables: phylogeny and effect size identity	1: yes	0.444	-4.928	5.815	69	39
	0: no	0.463	-3.939	4.865	43	24
Data: excluding fertilization success as number of fertilization occurrences; Random variables: phylogeny and effect size identity	1: yes	0.450	-5.007	5.907	69	39
	0: no	0.473	-4.000	4.946	42	23
Data: excluding effect sizes that do not include mating success = 0; Random variables: phylogeny and effect size identity	1: yes	0.856	-1.558	3.271	48	28
	0: no	0.647	-0.655	1.949	14	10
Data: excluding studies with no intrasexual competition; Random variables: phylogeny and effect size identity	1: yes	0.485	-5.172	6.142	67	37
	0: no	0.509	-4.143	5.161	41	23
Data: excluding lek systems; Random variables: phylogeny and effect size identity	1: yes	0.431	-5.267	6.129	69	39
	0: no	0.573	-4.042	5.188	35	19
Data: excluding older offspring; Random variables: phylogeny and effect size identity	1: yes	0.835	-0.732	2.402	29	19
	0: no	0.377	-0.283	1.037	28	13

Box S1 - The opportunity for fertilization selection (If) is not influenced by monopolization behavior among targets (i.e. guarded females and guarded males)

The average I_f estimate for targets is also not different from zero (average $I_f = 0.454$, 95% CI = -3.847 to 4.756). Moreover, we also found that I_f estimates among targets do not differ according to the occurrence of monopolization behavior (occurrence of monopolization behavior: $I_f = 0.632$, 95% CI = -4.894 to 6.158; no monopolization behavior: $I_f = 0.647$, 95% CI = -3.906 to 5.200; contrast: $I_f = 0.015$, CI lower end = -0.988, CI upper end = -0.958; for effect sizes, see Supplementary Material 4 - Figure S3). This pattern is the same across all sensitivity analyses (Supplementary Material 4 - Table S4). Egger's regression revealed no publication bias for I_f among targets (Egger's regression: $I_{f\ \mathrm{intercept}} = 0.145 \pm 0.171$ SE, $t = 0.846$, $p > 0.05$). Finally, the included random variables explained most of the variation in the data ($I^2 = 62.96\%$; I^2 phylogeny: 61.95%; I^2 effect size identity = 0.38%; I^2 inclusion of zeros = $1.16 \times 10^{-9}\%$; I^2 offspring age: 0.63%).

Table S4. Results regarding the difference in targets' I_f estimates between species in which monopolization behavior occurs and species in which this behavior is absent (yes: 1; no: 0). Each model run may contain all data available or part of it (sensitivity analyses). This table presents the estimate of I_f value per type of social mating system and their respective interval of confidence (2.5% CI to 97.5% CI). The number of species and estimates included per social mating system per model is also informed. There are no statistically significant differences ($p < 0.05$) or marginally significant differences ($0.05 < p < 0.10$) between social mating systems.

Model	Monopolization	I_f	2.5% CI	97.5% CI	Estimates	Species
All data; Random variables: phylogeny, effect size identity, inclusion of zeros, and offspring age	1: yes	0.632	-4.894	6.158	80	41
	0: no	0.647	-3.906	5.200	43	24
All data; Random variables: phylogeny and effect size identity	1: yes	0.443	-4.881	5.767	80	41
	0: no	0.467	-3.901	4.836	43	24
Data: excluding fertilization success as number of fertilization occurrences; Random variables: phylogeny and effect size identity	1: yes	0.450	-4.957	5.856	80	41
	0: no	0.478	-3.959	4.914	42	23
Data: excluding effect sizes that do not include mating success = 0; Random variables: phylogeny and effect size identity	1: yes	0.439	-7.673	8.555	55	29
	0: no	0.995	-5.255	7.249	14	10
Data: excluding studies with no intrasexual competition; Random variables: phylogeny and effect size identity	1: yes	0.485	-5.116	6.086	78	39
	0: no	0.514	-4.097	5.125	41	23
Data: excluding lek systems; Random variables: phylogeny and effect size identity	1: yes	0.431	-5.211	6.072	80	41
	0: no	0.577	-3.999	5.153	35	19
Data: excluding older offspring; Random variables: phylogeny and effect size identity	1: yes	0.425	-6.901	7.751	40	21
	0: no	0.337	-5.190	5.865	28	13

Supplementary Material 5 – I_f (males and guardians)

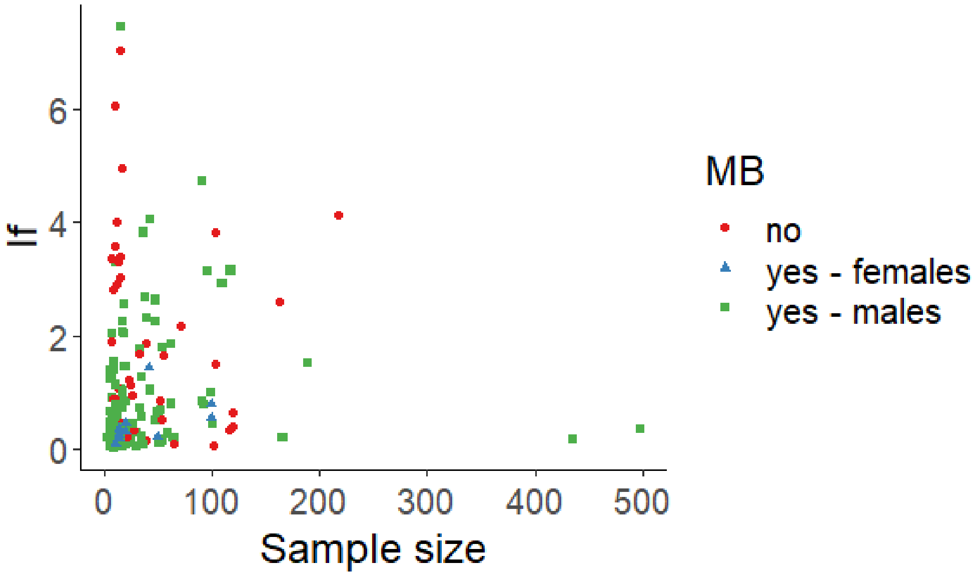

Figure S4. Estimates of the opportunity for fertilization selection (I_f) and the respective sample sizes obtained for guardians (males and females that guard) across animals. Estimates are divided in three classes, according to monopolization behavior (MB) occurrence and sex. Estimates of I_f among males of species that present monopolization behavior (when males try to economically monopolize females) are represented with green squares. Estimates of I_f among females that guard are represented with blue triangles. Estimates of I_f among males of species that do not present monopolization behavior are represented with red circles.

Table S5. Results regarding the difference in male I_f estimates between species in which monopolization behavior occurs and species in which this behavior is absent (yes: 1; no: 0). Each model run may contain all data available or part of it (sensitivity analyses). This table presents the estimate of I_f value per type of social mating system and their respective interval of confidence (2.5% CI to 97.5% CI). The number of species and estimates included per social mating system per model is also informed. Marginally significant differences (0.05 < p < 0.10) between social mating systems are indicated with one asterisk (*). There are no statistically significant differences (p < 0.05) between social mating systems.

Model	Monopolization	I_f	2.5% CI	97.5% CI	Estimates	Species
All data; Random variables: phylogeny, effect size identity, mating success meaning, inclusion of zeros, intrasexual competition occurrence, and offspring age	1: yes	-0.029*	-3.078	3.020	90	42
	0: no	0.525*	-1.937	2.986	51	30
All data; Random variables: phylogeny and effect size identity	1: yes	0.478	-1.975	2.931	90	42
	0: no	0.914	-0.933	2.760	51	30
Data: excluding fertilization success as number of fertilization occurrences; Random variables: phylogeny and effect size identity	1: yes	0.481	-2.036	2.997	90	42
	0: no	0.952	-0.944	2.848	49	28
Data: excluding effect sizes that do not include mating success = 0; Random variables: phylogeny and effect size identity	1: yes	0.384*	-2.304	3.071	62	34
	0: no	1.092*	-0.807	2.990	37	21
Data: excluding studies with no intrasexual competition; Random variables: phylogeny and effect size identity	1: yes	0.592	-2.185	3.370	88	40
	0: no	1.013	-1.122	3.148	47	28
Data: excluding lek systems; Random variables: phylogeny and effect size identity	1: yes	0.741	-1.261	2.744	90	43
	0: no	0.759	-0.644	2.161	38	24
Data: excluding older offspring; Random variables: phylogeny and effect size identity	1: yes	0.547	-2.780	3.875	52	25
	0: no	0.706	-1.858	3.269	28	19

Box S2 - The opportunity for fertilization selection (If) is not influenced by monopolization behavior among guardians (i.e. males and females that guard)

The average I_f estimate for guardians is not different from zero (average $I_f = 0.350$, 95% CI = -2.330 to 3.029). Moreover, we found that I_f estimates among guardians do not differ according to the occurrence of monopolization behavior (occurrence of monopolization behavior: $I_f = -0.057$, 95% CI = -3.242 to 3.128; no monopolization behavior: $I_f = 0.512$, 95% CI = -2.089 to 3.112; contrast: $I_f = 0.568$, CI lower end = 1.153, CI upper end = -0.017; for effect sizes, see Supplementary Material 5 - Figure S4), with the absolute I_f estimate value being much lower when monopolization behavior occurs. This pattern is the same across almost all sensitivity analyses (Supplementary Material 5 - Table S6) and, once again, the exception arises after removing the estimates coming from lek systems, which considerably reduces the difference in absolute I_f estimate values between social mating systems (Supplementary Material 5 - Table S6). Egger's regression revealed publication bias for I_f among guardians (Egger's regression: $I_{f\ \mathrm{intercept}} = 1.230 \pm 0.177$ SE, $t = 6.934$, $p < 0.05$). Finally, the included random variables explained part of the variation in the data ($I^2 = 29.40\%$; I^2 phylogeny: 18.98%; I^2 effect size identity = 3.26%; I^2 fertilization success meaning: $1.24 \times 10^{-6}\%$; I^2 inclusion of zeros = 1.25%; I^2 offspring age: 3.99%).

Table S6. Results regarding the difference in guardians' I_f estimates between species in which monopolization behavior occurs and species in which this behavior is absent (yes: 1; no: 0). Each model run may contain all data available or part of it (sensitivity analyses). This table presents the estimate of I_f value per type of social mating system and their respective interval of confidence (2.5% CI to 97.5% CI). The number of species and estimates included per social mating system per model is also informed. Marginally significant differences (0.05 < p < 0.10) between social mating systems are indicated with one asterisk (*).There are no statistically significant differences (p < 0.05) between social mating systems.

Model	Monopolization	I_f	2.5% CI	97.5% CI	Estimates	Species
All data; Random variables: phylogeny, effect size identity, mating success meaning, inclusion of zeros, intrasexual competition occurrence, and offspring age	1: yes	-0.057*	-3.242	3.128	101	43
	0: no	0.512*	-2.089	3.112	51	30
All data; Random variables: phylogeny and effect size identity	1: yes	0.448	-2.087	2.983	101	43
	0: no	0.898	-1.034	2.831	51	30
Data: excluding fertilization success as number of fertilization occurrences; Random variables: phylogeny and effect size identity	1: yes	0.453	-2.146	3.052	101	43
	0: no	0.939	-1.044	2.921	49	28
Data: excluding effect sizes that do not include mating success = 0; Random variables: phylogeny and effect size identity	1: yes	0.345*	-2.565	3.255	71	35
	0: no	1.055*	-1.049	3.159	37	21
Data: excluding studies with no intrasexual competition; Random variables: phylogeny and effect size identity	1: yes	0.571	-2.270	3.412	99	41
	0: no	1.002	-1.205	3.209	47	28
Data: excluding lek systems; Random variables: phylogeny and effect size identity	1: yes	0.719	-1.320	2.758	101	43
	0: no	0.748	-0.700	2.197	38	24
Data: excluding older offspring; Random variables: phylogeny and effect size identity	1: yes	0.536	-2.923	3.994	63	41
	0: no	0.684	-2.022	3.390	28	28

Supplementary Material 6 – I (females and targets)

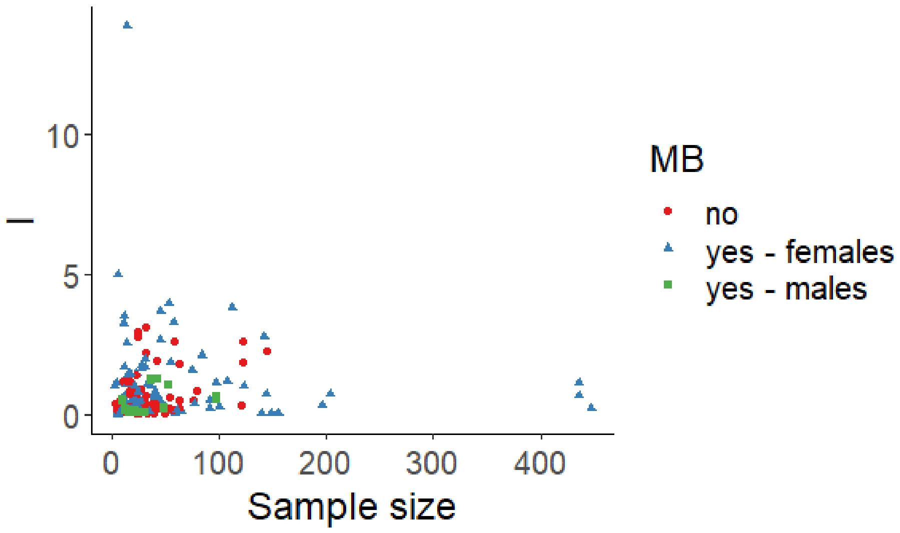

Figure S5. Estimates of the opportunity for selection (I) and the respective sample sizes obtained for targets (females and guarded males) across animals. Estimates are divided in three classes, according to monopolization behavior (MB) occurrence and sex. Estimates of I among females of species that present monopolization behavior (when males try to economically monopolize females) are represented with blue triangles. Estimates of I among guarded males are represented with green squares. Estimates of I among females of species that do not present monopolization behavior are represented with red circles.

Table S7. Results regarding the difference in female I estimates between species in which monopolization behavior occurs and species in which this behavior is absent (yes: 1; no: 0). Each model run may contain all data available or part of it (sensitivity analyses). This table presents the estimate of I value per type of social mating system and their respective interval of confidence (2.5% CI to 97.5% CI). There are no statistically significant differences ($p < 0.05$) or marginally significant differences ($0.05 < p < 0.10$) between social mating systems.

Model	Monopolization	I	2.5% CI	97.5% CI	Estimates	Species
All data; Random variables: phylogeny, effect size id, mating success interference, mating success meaning, inclusion of zeros, intrasexual competition occurrence, and offspring age	1: yes	0.750	-3.800	5.301	88	47
	0: no	1.071	-2.700	4.842	75	38
All data; Random variables: phylogeny and effect size id	1: yes	0.847	-0.487	2.181	88	47
	0: no	0.638	-0.192	1.467	75	38
Data: excluding studies in which authors determined mating success; Random variables: phylogeny and effect size id	1: yes	0.875	-0.612	2.361	87	46
	0: no	0.722	-0.239	1.683	69	35
Data: excluding effect sizes that do not include mating success = 0; Random variables: phylogeny and effect size id	1: yes	1.002	-5.680	7.684	64	35
	0: no	1.267	-3.902	6.436	30	19
Data: excluding studies with no intrasexual competition; Random variables: phylogeny and effect size id	1: yes	0.820	-4.230	5.869	84	44
	0: no	0.872	-3.327	5.070	60	31
Data: excluding lek systems; Random variables: phylogeny and effect size id	1: yes	0.868	-0.492	2.227	88	47
	0: no	0.622	-0.174	1.417	62	32
Data: excluding older offspring; Random variables: phylogeny and effect size id	1: yes	0.917	-0.156	1.990	39	24
	0: no	0.560	0.127	0.993	54	26

Box S3 - The opportunity for selection (I) is not influenced by monopolization behavior among targets (i.e. guarded females and guarded males)

The average I estimate for targets is not different from zero (average I = 0.933, 95% CI = -2.776 to 4.643). Moreover, we found that I estimates among targets do not differ according to the occurrence of monopolization behavior (occurrence of monopolization behavior: I = 0.755, 95% CI = -3.749 to 5.259; no monopolization behavior: I = 1.068, 95% CI = -2.676 to 4.813; contrast: I = 0.313, CI lower end = 1.072, CI upper end = -0.446; for effect sizes, see Figure S5). This pattern is the same across all sensitivity analyses (Supplementary Material 6 - Table S8). Egger's regression revealed no publication bias for I among targets (Egger's regression: $I_{intercept} = 0.067 \pm 0.144$ SE, $t = 0.464$, $p > 0.05$). Finally, the included random variables explained most of the variation in the data (I^2 = 53.29%; I^2 phylogeny: 51.12%; I^2 effect size identity = 0.81%; I^2 mating success interference = 3.41×10^{-8}%; I^2 inclusion of zeros = 0.75%; I^2 intrasexual competition occurrence = 7.35×10^{-9}%; I^2 offspring age: 0.60%).

Table S8. Results regarding the difference in targets' I estimates between species in which monopolization behavior occurs and species in which this behavior is absent (yes: 1; no: 0). Each model run may contain all data available or part of it (sensitivity analyses). This table presents the estimate of I value per type of social mating system and their respective interval of confidence (2.5% CI to 97.5% CI). The number of species and estimates included per social mating system per model is also informed. There are no statistically significant differences ($p < 0.05$) or marginally significant differences ($0.05 < p < 0.10$) between social mating systems.

Model	Monopolization	I	2.5% CI	97.5% CI	Estimates	Species
All data; Random variables: phylogeny, effect size identity, mating success interference, mating success meaning, inclusion of zeros, intrasexual competition occurrence, and offspring age	1: yes	0.755	-3.749	5.259	100	50
	0: no	1.068	-2.676	4.813	75	38
All data; Random variables: phylogeny and effect size identity	1: yes	0.719	-3.630	5.069	100	50
	0: no	0.763	-2.820	4.346	75	38
Data: excluding studies in which authors determined mating success; Random variables: phylogeny and effect size identity	1: yes	0.789	-3.734	5.311	99	49
	0: no	0.852	-2.886	4.590	69	35
Data: excluding effect sizes that do not include mating success = 0; Random variables: phylogeny and effect size identity	1: yes	0.963	-5.568	7.494	72	37
	0: no	1.252	-3.811	6.315	30	19
Data: excluding studies with no intrasexual competition; Random variables: phylogeny and effect size identity	1: yes	0.807	-4.191	5.804	96	47
	0: no	0.870	-3.296	5.035	60	31
Data: excluding lek systems; Random variables: phylogeny and effect size identity	1: yes	0.722	-3.943	5.388	100	50
	0: no	0.793	-3.030	4.617	62	34
Data: excluding older offspring; Random variables: phylogeny and effect size identity	1: yes	0.797	-0.241	1.835	51	27
	0: no	0.549	0.099	0.999	54	26

Supplementary Material 7 – I (males and guardians)

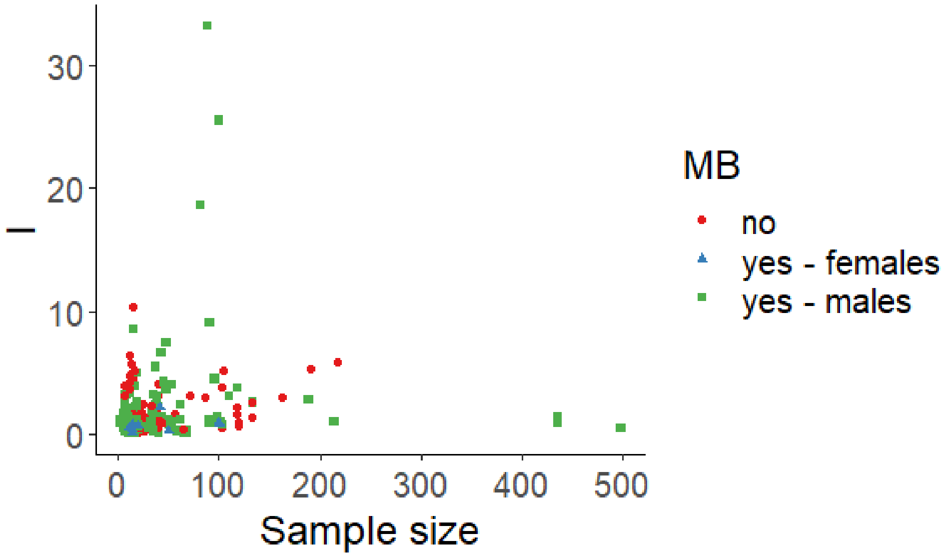

Figure S6. Estimates of the opportunity for selection (I) and the respective sample sizes obtained for guardians (males and females that guard) across animals. Estimates are divided in three classes, according to monopolization behavior (MB) occurrence and sex. Estimates of I among males of species that present monopolization behavior (when males try to economically monopolize females) are represented with green squares. Estimates of I among females that guard are represented with blue triangles. Estimates of I among males of species that do not present monopolization behavior are represented with red circles.

Table S9. Results regarding the difference in male I estimates between species in which monopolization behavior occurs and species in which this behavior is absent (yes: 1; no: 0). Each model run may contain all data available or part of it (sensitivity analyses). This table presents the estimate of I value per type of social mating system and their respective interval of confidence (2.5% CI to 97.5% CI). The number of species and estimates included per social mating system per model is also informed. Marginally significant differences (0.05 < p < 0.10) between social mating systems are indicated with one asterisk (*). There are no statistically significant differences (p < 0.05) between social mating systems.

Model	Monopolization	I	2.5% CI	97.5% CI	Estimates	Species
All data; Random variables: phylogeny, effect size identity, mating success interference, mating success meaning, inclusion of zeros, intrasexual competition occurrence, and offspring age	1: yes	1.178	-7.786	10.142	112	53
	0: no	0.735	-6.726	8.196	72	39
All data; Random variables: phylogeny and effect size identity	1: yes	1.649	-8.103	11.402	112	53
	0: no	1.161	-6.988	9.311	72	39
Data: excluding studies in which authors determined mating success; Random variables: phylogeny and effect size identity	1: yes	1.668	-8.177	11.513	111	52
	0: no	1.124	-7.109	9.358	71	38
Data: excluding effect sizes that do not include mating success = 0; Random variables: phylogeny and effect size identity	1: yes	1.364	-8.210	10.937	82	44
	0: no	1.470	-5.871	8.812	49	28
Data: excluding studies with no intrasexual competition; Random variables: phylogeny and effect size identity	1: yes	1.7874	-9.346	12.434	109	50
	0: no	1.2629	-7.685	10.219	67	36
Data: excluding lek systems; Random variables: phylogeny and effect size identity	1: yes	1.882	-7.970	11.734	112	53
	0: no	0.937	-7.161	9.035	53	32
Data: excluding older offspring; Random variables: phylogeny and effect size identity	1: yes	0.558*	-2.265	3.381	64	32
	0: no	1.239*	-0.835	3.313	44	28

Box S4 - The opportunity for selection (I) is not influenced by monopolization behavior among guardians (i.e. males and females that guard)

The average I estimate for guardians is not different from zero (average I = 0.928, 95% CI = -7.022 to 8.878). Moreover, we found that I estimates among guardians do not differ according to the occurrence of monopolization behavior (occurrence of monopolization behavior: I = 1.211, 95% CI = -8.330 to 10.751; no monopolization behavior: I = 0.789, 95% CI = -7.225 to 8.803; contrast: I = -0.422, CI lower end = 1.105, CI upper end = -1.949; for effect sizes, see Supplementary Material 7 - Figure S6). Again, across almost all sensitivity analyses, the pattern is the same (Supplementary Material 7 - Table S10). Egger's regression revealed publication bias for I among guardians (Egger's regression: $I_{\text{intercept}}$ = 1.599 ± 0.374 SE, $t = 4.272$, $p < 0.05$). Finally, the included random variables explained most of the variation in the data (I^2 = 82.04%; I^2 phylogeny: 76.39%; I^2 effect size identity = 3.78%; I^2 mating success meaning: 6.33×10^{-7}%; I^2 inclusion of zeros = 0.38%; I^2 intrasexual competition occurrence: 1.00%; I^2 offspring age: 0.49%).

Table S10. Results regarding the difference in guardians' I estimates between species in which monopolization behavior occurs and species in which this behavior is absent (yes: 1; no: 0). Each model run may contain all data available or part of it (sensitivity analyses). This table presents the estimate of I value per type of social mating system and their respective interval of confidence (2.5% CI to 97.5% CI). The number of species and estimates included per social mating system per model is also informed. Marginally significant differences (0.05 < p < 0.10) between social mating systems are indicated with one asterisk (*). There are no statistically significant differences (p < 0.05) between social mating systems.

Model	**Monopolization**	**I**	**2.5% CI**	**97.5% CI**	**Estimates**	**Species**
All data; Random variables: phylogeny, effect size identity, mating success interference, mating success meaning, inclusion of zeros, intrasexual competition occurrence, and offspring age	1: yes	1.211	-8.330	10.751	123	54
	0: no	0.789	-7.225	8.803	72	39
All data; Random variables: phylogeny and effect size identity	1: yes	1.564	-8.865	11.993	123	54
	0: no	1.166	-7.631	9.964	72	39
Data: excluding studies in which authors determined mating success; Random variables: phylogeny and effect size identity	1: yes	1.576	-8.971	12.123	122	53
	0: no	1.130	-7.775	10.035	71	38
Data: excluding effect sizes that do not include mating success = 0; Random variables: phylogeny and effect size identity	1: yes	1.657	-8.888	11.441	91	45
	0: no	1.467	-6.407	9.340	49	28
Data: excluding studies with no intrasexual competition; Random variables: phylogeny and effect size identity	1: yes	1.701	-9.559	12.962	120	51
	0: no	1.273	-8.276	10.821	67	36
Data: excluding lek systems; Random variables: phylogeny and effect size identity	1: yes	1.743	-9.156	12.643	123	54
	0: no	0.976	-8.125	10.077	53	32
Data: excluding older offspring; Random variables: phylogeny and effect size identity	1: yes	0.523*	-2.410	3.456	75	33
	0: no	1.213*	-0.979	3.405	44	28

Supplementary Material 8 – Bateman gradient (females and targets)

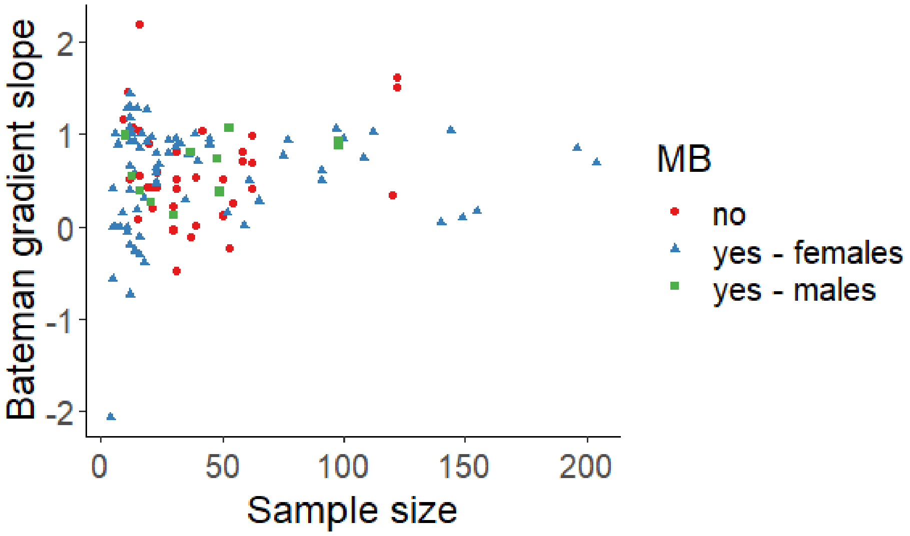

Figure S7. Estimates of the slope of the Bateman gradient and the respective sample sizes obtained for targets (females and guarded males) across animals. Estimates are divided in three classes, according to monopolization behavior (MB) occurrence and sex. Estimates of the Bateman gradient among females of species that present monopolization behavior (when males try to economically monopolize females) are represented with blue triangles. Estimates of the Bateman gradient among guarded males are represented with green squares. Estimates of the Bateman gradient among females of species that do not present monopolization behavior are represented with red circles.

Table S11. Results regarding the difference in female Bateman gradient slopes between species in which monopolization behavior occurs and species in which this behavior is absent (yes: 1; no: 0). Each model run may contain all data available or part of it (sensitivity analyses). This table presents the estimate of I value per type of social mating system and their respective interval of confidence (2.5% CI to 97.5% CI). There are no statistically significant differences ($p < 0.05$) or marginally significant differences ($0.05 < p < 0.10$) between social mating systems.

Model	Monopolization	Slope	2.5% CI	97.5% CI	Estimates	Species
All data; Random variables: phylogeny, effect size identity, mating success interference, inclusion of zeros, intrasexual competition occurrence, and offspring age	1: yes	0.433	-0.102	0.968	79	40
	0: no	0.522	0.182	0.863	38	20
All data; Random variables: phylogeny and effect size identity	1: yes	0.510	0.075	0.945	79	40
	0: no	0.522	0.275	0.769	38	20
Data: excluding mating success as number of mating occurrences; Random variables: phylogeny and effect size identity	1: yes	0.525	0.076	0.973	76	40
	0: no	0.546	0.293	0.799	35	18
Data: excluding studies in which authors determined mating success; Random variables: phylogeny and effect size identity	1: yes	0.547	0.083	1.011	77	39
	0: no	0.594	0.324	0.864	32	17
Data: excluding effect sizes that do not include mating success = 0; Random variables: phylogeny and effect size identity	1: yes	0.544	0.037	1.051	61	30
	0: no	0.518	0.228	0.808	18	12
Data: excluding studies with no intrasexual competition; Random variables: phylogeny and effect size identity	1: yes	0.530	0.056	1.004	73	37
	0: no	0.581	0.300	0.861	30	16
Data: excluding lek systems; Random variables: phylogeny and effect size identity	1: yes	0.465	-0.034	0.964	79	40
	0: no	0.576	0.296	0.856	29	17
Data: excluding older offspring; Random variables: phylogeny and effect size identity	1: yes	0.514	0.080	0.948	33	21
	0: no	0.482	0.276	0.687	25	15

Box S5 - The Bateman gradient is not influenced by monopolization behavior among targets (i.e. guarded females and guarded males)

The average Bateman gradient for targets is positive and different from zero (average slope = 0.478, 95% CI = 0.164 to 0.792). Moreover, we found that Bateman gradient estimates among targets do not differ according to the occurrence of monopolization behavior (occurrence of monopolization behavior: slope = 0.420, 95% CI = -0.133 to 0.972; no monopolization behavior: slope = 0.521, 95% CI = 0.155 to 0.887; contrast: slope = 0.101, CI lower end = 0.288, CI upper end = -0.085; for effect sizes, see Supplementary Material 8 - Figure S7). This pattern is the same across all sensitivity analyses (Supplementary Material 8 - Table S12). Egger's regression revealed publication bias for Bateman gradients among targets (Egger's regression: Bateman gradient $\text{slope}_{\text{intercept}}$ = 0.166 ± 0.045 SE, t = 3.723, $p < 0.05$). Finally, the included random variables explained almost no variation in the data (I^2 = 1.14%; I^2 phylogeny: 0.31%; I^2 effect size identity = 0.61%; I^2 mating success interference = 4.23×10^{-8}%; I^2 inclusion of zeros = 0.22%; I^2 intrasexual competition occurrence = 5.98×10^{-12}%; I^2 offspring age: 0.00%).

Table S12. Results regarding the difference in targets' Bateman gradient slopes between species in which monopolization behavior occurs and species in which this behavior is absent (yes: 1; no: 0). Each model run may contain all data available or part of it (sensitivity analyses). This table presents the estimate of I value per type of social mating system and their respective interval of confidence (2.5% CI to 97.5% CI). The number of species and estimates included per social mating system per model is also informed. There are no statistically significant differences ($p < 0.05$) or marginally significant differences ($0.05 < p < 0.10$) between social mating systems.

Model	Monopolization	Slope	2.5% CI	97.5% CI	Estimates	Species
All data; Random variables: phylogeny, effect size identity, mating success interference, inclusion of zeros, intrasexual competition occurrence, and offspring age	1: yes	0.420	-0.133	0.972	90	43
	0: no	0.521	0.155	0.887	38	20
All data; Random variables: phylogeny and effect size identity	1: yes	0.515	0.094	0.937	90	43
	0: no	0.520	0.280	0.759	38	20
Data: excluding mating success as number of mating occurrences; Random variables: phylogeny and effect size identity	1: yes	0.522	0.085	0.960	86	42
	0: no	0.545	0.298	0.791	35	18
Data: excluding studies in which authors determined mating success; Random variables: phylogeny and effect size identity	1: yes	0.552	0.104	1.001	88	42
	0: no	0.591	0.331	0.852	32	17
Data: excluding effect sizes that do not include mating success = 0; Random variables: phylogeny and effect size identity	1: yes	0.549	0.065	1.031	68	32
	0: no	0.514	0.239	0.789	18	12
Data: excluding studies with no intrasexual competition; Random variables: phylogeny and effect size identity	1: yes	0.535	0.077	0.993	84	40
	0: no	0.577	0.307	0.848	30	16
Data: excluding lek systems; Random variables: phylogeny and effect size identity	1: yes	0.468	-0.019	0.956	90	43
	0: no	0.576	0.302	0.850	29	17
Data: excluding older offspring; Random variables: phylogeny and effect size identity	1: yes	0.550	0.146	0.954	44	24
	0: no	0.486	0.293	0.679	25	15

Supplementary Material 9 – Bateman gradient (males and guardians)

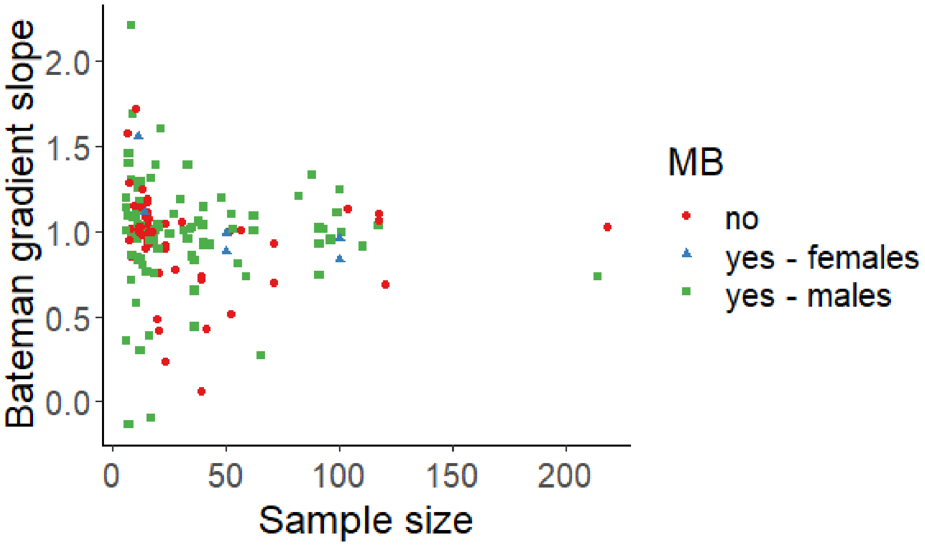

Figure S8. Estimates of the slope of the Bateman gradient and the respective sample sizes obtained for guardians (males and females that guard) across animals. Estimates are divided in three classes, according to monopolization behavior (MB) occurrence and sex. Estimates of the Bateman gradient among males of species that present monopolization behavior (when males try to economically monopolize females) are represented with green squares. Estimates of the Bateman gradient among females that guard are represented with blue triangles. Estimates of the Bateman gradient among females of species that do not present monopolization behavior are represented with red circles.

Table S13. Results regarding the difference in male Bateman gradient slopes between species in which monopolization behavior occurs and species in which this behavior is absent (yes: 1; no: 0). Each model run may contain all data available or part of it (sensitivity analyses). This table presents the estimate of I value per type of social mating system and their respective interval of confidence (2.5% CI to 97.5% CI). There are no statistically significant differences (p < 0.05) or marginally significant differences (0.05 < p < 0.10) between social mating systems.

Model	Monopolization	Slope	2.5% CI	97.5% CI	Estimates	Species
All data; Random variables: phylogeny, effect size identity, mating success interference, inclusion of zeros, intrasexual competition occurrence, and offspring age	1: yes	1.025	0.586	1.465	99	44
	0: no	1.053	0.675	1.432	51	23
All data; Random variables: phylogeny and effect size identity	1: yes	0.921	0.702	1.140	99	44
	0: no	0.942	0.785	1.099	51	23
Data: excluding mating success as number of mating occurrences; Random variables: phylogeny and effect size identity	1: yes	0.936	0.758	1.113	93	43
	0: no	0.968	0.844	1.091	44	18
Data: excluding studies in which authors determined mating success; Random variables: phylogeny and effect size identity	1: yes	0.897	0.677	1.116	99	44
	0: no	0.917	0.758	1.075	50	22
Data: excluding effect sizes that do not include mating success = 0; Random variables: phylogeny and effect size identity	1: yes	0.958	0.742	1.174	76	36
	0: no	0.946	0.799	1.093	39	18
Data: excluding studies with no intrasexual competition; Random variables: phylogeny and effect size identity	1: yes	0.919	0.701	1.138	97	42
	0: no	0.934	0.779	1.090	46	20
Data: excluding lek systems; Random variables: phylogeny and effect size identity	1: yes	0.937	0.733	1.142	99	44
	0: no	0.930	0.798	1.062	36	19
Data: excluding older offspring; Random variables: phylogeny and effect size identity	1: yes	0.909	0.718	1.100	51	24
	0: no	0.926	0.816	1.035	28	17

Box S6 - The Bateman gradient is not influenced by monopolization behavior among guardians (i.e. males and females that guard)

The average Bateman gradient for guardians is positive and different from zero (average slope = 1.055, 95% CI = 0.685 to 1.426). Moreover, we found that Bateman gradient estimates among guardians do not differ according to the occurrence of monopolization behavior (occurrence of monopolization behavior: slope = 1.037, 95% CI = 0.603 to 1.470; no monopolization behavior: slope = 1.062, 95% CI = 0.688 to 1.435; contrast: slope = 0.025, CI lower end = 0.085, CI upper end = -0.035; for effect sizes, see Supplementary Material 9 - Figure S8). This pattern is the same across all sensitivity analyses (Supplementary Material 9 - Table S14). Egger's regression revealed publication bias for Bateman gradients among guardians (Egger's regression: Bateman gradient $\text{slope}_{\text{intercept}}$ = -0.100 ± 0.023 SE, t = -4.416, $p < 0.05$). Finally, the included random variables explained almost no variation in the data (I^2 = 0.31%; I^2 phylogeny: 0.08%; I^2 effect size identity = 0.03%; I^2 mating success interference = 0.19%; I^2 inclusion of zeros = 2.64×10^{-3}%; I^2 intrasexual competition occurrence = 9.12×10^{-11}%; I^2 offspring age: 8.63×10^{-11}%).

Table S14. Results regarding the difference in guardians' Bateman gradient slopes between species in which monopolization behavior occurs and species in which this behavior is absent (yes: 1; no: 0). Each model run may contain all data available or part of it (sensitivity analyses). This table presents the estimate of I value per type of social mating system and their respective interval of confidence (2.5% CI to 97.5% CI). The number of species and estimates included per social mating system per model is also informed. There are no statistically significant differences ($p < 0.05$) or marginally significant differences ($0.05 < p < 0.10$) between social mating systems.

Model	**Monopolization**	**Slope**	**2.5% CI**	**97.5% CI**	**Estimates**	**Species**
All data; Random variables: phylogeny, effect size identity, mating success interference, inclusion of zeros, intrasexual competition occurrence, and offspring age	1: yes	1.037	0.603	1.470	105	45
	0: no	1.062	0.688	1.435	51	23
All data; Random variables: phylogeny and effect size identity	1: yes	0.920	0.708	1.134	105	45
	0: no	0.942	0.790	1.094	51	23
Data: excluding mating success as number of mating occurrences; Random variables: phylogeny and effect size identity	1: yes	0.935	0.761	1.106	99	44
	0: no	0.967	0.847	1.086	44	18
Data: excluding studies in which authors determined mating success; Random variables: phylogeny and effect size identity	1: yes	0.897	0.682	1.111	105	45
	0: no	0.917	0.762	1.071	50	22
Data: excluding effect sizes that do not include mating success = 0; Random variables: phylogeny and effect size identity	1: yes	0.953	0.726	1.180	80	37
	0: no	0.946	0.790	1.103	39	18
Data: excluding studies with no intrasexual competition; Random variables: phylogeny and effect size identity	1: yes	0.919	0.707	1.131	103	43
	0: no	0.934	0.784	1.085	46	20
Data: excluding lek systems; Random variables: phylogeny and effect size identity	1: yes	0.938	0.741	1.136	105	45
	0: no	0.930	0.804	1.057	36	19
Data: excluding older offspring; Random variables: phylogeny and effect size identity	1: yes	0.911	0.731	1.090	57	25
	0: no	0.929	0.826	1.031	28	17

Supplementary Material 10 – Jones index

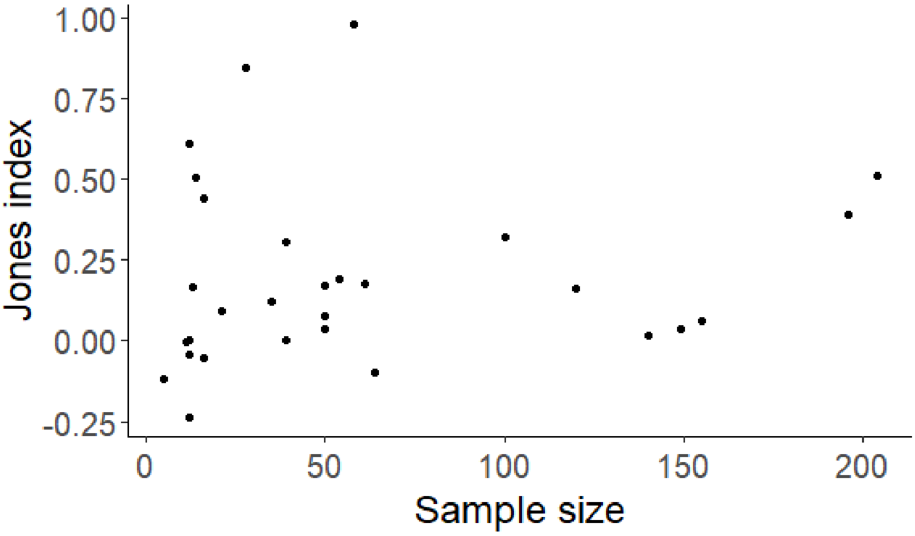

Figure S9. Estimates of the slope of the Jones index (squared root of the opportunity for sexual selection multiplied by the respective slope of the Bateman gradient) and the respective sample sizes obtained for females across animals.

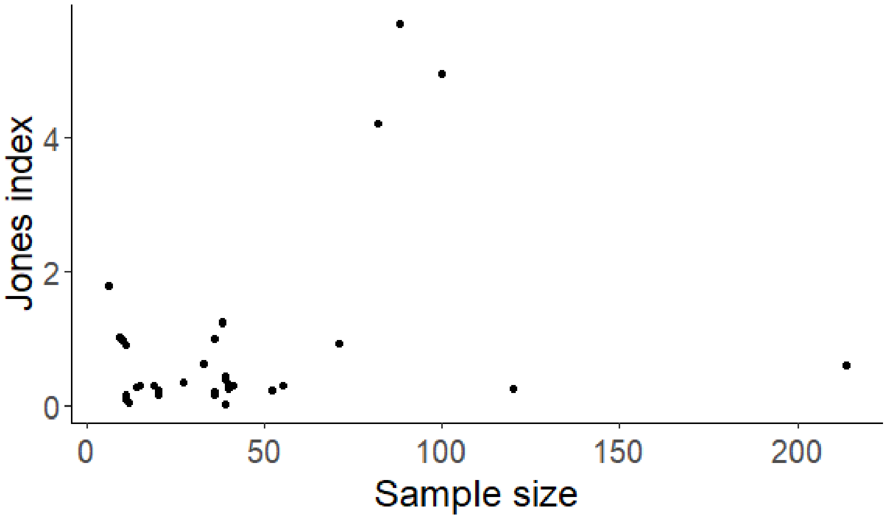

Figure S10. Estimates of the slope of the Jones index (squared root of the opportunity for sexual selection multiplied by the respective slope of the Bateman gradient) and the respective sample sizes obtained for males across animals.

Capítulo 3

Larger females and larger males produce more offspring, regardless of the social mating system: a meta-analyses on animals

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Abstract

In some animal mating systems, males try to economically monopolize females, by defending a resource used by females or by directly guarding females. In other systems, this monopolization behavior does not occur, and males only try to outcompete other males by courting or finding females more efficiently. Larger body size is expected to help males in the attempt to monopolize females. Accordingly, being larger should help females to avoid monopolization attempts. In the present hierarchical meta-analysis, we collected 577 selection gradients, from 188 different species, and tested whether the correlation between body size and reproductive success is higher when monopolization behavior occurs than when it is absent, for both sexes, across animals. Unfortunately, we could not test the same hypothesis on monopolization behavior for traits other than body size, but we could calculate mean effect sizes for courtship and fertilization-related male traits. Against the predictions, for both sexes, the mean slope of the selection gradient based on body size does not differ according to monopolization occurrence/absence. However, regardless of the social mating system, body size is positively correlated with reproductive success, for females and males. Investment in courtship is not correlated with reproductive success, but investment in fertilization-related traits is positively correlated with reproductive success. Here, we demonstrate for the first time that large body size confers higher reproductive success for females and males, across the animal kingdom, corroborating a long-standing Darwinian hypothesis about the evolution of female body size. Monopolization behavior may not modulate the fitness return of being larger because (1) larger females may be more attractive and suffer more sexual harassment than smaller females; and because (2) smaller males may invest more on sperm competition (which we demonstrate that enhances reproductive success), reducing the reproductive success of larger males.

Potential keywords (alphabetical order): armament, cryptic female choice, female defense polygyny, fertilization, harem, lek, male dominance, monopolization, ornament, reproductive alternative tactics, reproductive success, resource defense polygyny, scramble competition, selection gradient, sexual selection, sperm competition, territory defense polygyny, weaponry.

Introduction

The reproductive interactions between females and males vary across animal species, and different social (ecological) mating systems can be identified in nature (Emlen and Oring 1977). In many species, females explore a specific resource (e.g. food, water, territory) and some males defend the access to this resource, preventing rival males from mating and monopolizing females (e.g. Mascolino et al. 2016; LaBarbera et al. 2019). Defensive behaviors also occur in an additional way: the monopolization behavior is not directed to a resource, but to (potential) sexual partners (e.g. Schartl et al. 1993; Ishengoma et al. 2008), the so-called *harems* (see review in Macedo-Rego and Santos 2017). Conversely, in other mating systems, neither females nor males try to economically monopolize sexual partners. For example, in scramble competition, high-quality males may outcompete their competitors by finding females more effectively (e.g. Fincke 1986; Böll and Linsenmair 1998). And in lek mating systems, males have access to females by courting them in display arenas that congregate male contestants and choosy females (e.g. Kraaijeveld-Smit et al. 2003; Krakauer 2008).

As demonstrated in Chapter 2, the behavior of mate monopolization attempt is not only an important feature/component of different social mating systems, but also a relevant factor that modulates the variance in mating success and, potentially, the actual intensity of pre-mating sexual selection across animal species. In this scenario, any trait that enables an individual to better economically/physically monopolize sexual partners tends to be selected. Across all animal *taxa*, it is still not known what kinds of morphological and behavioral traits linked to monopolization behavior influence mate acquisition among males. However, specific evidence provides us potential answers. For example, for many species, evidence shows that larger body size increases male ability to defend a territory (e.g. Kasuya et al. 1997; Johnsson et al. 1999; Ippi et al. 2018), to guard sexual partners (e.g. Modig 1996; Rohwer et al. 1996; Cueva Del Castillo 2003), and to fight other males (e.g. Rowland 1989; Umbers et al. 2012; Tina et al. 2015). And, sometimes, being small means that a male will not be a dominant individual that defends a territory, but that he will behave as a sneaker, who performs sneak mate attempts (e.g. Hutchings and Myers 1988; Shuster and Wade 1991; Hanlon et al. 2002; Buzatto et al. 2014). Charles Darwin himself noted this pattern and hypothesized that male advantage in monopolizing sexual partners could explain sexual size dimorphism when males are larger than females (Darwin 1871). In contrast, social mating systems such as leks and scramble competition are better characterized by non-physical competition among males, which mainly outcompete their rivals by being more attractive or efficient on finding mates (Emlen and Oring 1977; Andersson 1994c). Therefore, it is reasonable to predict that the relevance of male body size on male fitness is higher when monopolization behavior occurs than when it does not.

For females, the scenario is a little bit different. If males try to economically monopolize females, this reduces the opportunity for sexual selection among females (Chapter 2), which probably means that females are mating fewer times (or at least with less partners) than they would if there was no restriction. It is known that females may benefit from mating polyandrously (Jennions and Petrie 2000; Slatyer et al. 2012), and one should not expect that females should remain passive when sexual conflict emerges (Gowaty 1997; Chapter 2), which means that any trait that enables a female to better circumvent monopolizing attempts (and decides to mate or not) tends to be selected. In the mosquitofish *Gambusia holbrooki*, for example, larger males are socially dominant, may defend females in intense intrasexual competition, and have preferential access to females (Bisazza and Marin 1991). Males try to force copulation repeated times (Bisazza and Marin 1991; Wilson 2005) and females respond by evading or attacking males (Iglesias-Carrasco et al. 2019). Recently, an experiment demonstrated that larger females are more prone to avoid male copulation attempts (e.g. Culumber et al. 2020), which allows them to adjust their mating frequency and polyandry degree. Taking this example into account, if female body size is important during sexual conflict contexts, and if male monopolization behavior can impose sexual conflict, we predicted that, among females, the relevance of body size on female fitness is higher when monopolization behavior occurs than when it does not.

Here, by conducting a meta-analysis across animal species, we tested if larger body size confers higher fitness return for both sexes when monopolization behavior occurs than when monopolization behavior is absent. For animals, it is already known that monopolization behavior reduces the opportunity for sexual selection among females and enhances the opportunity for sexual selection among males (Chapter 2). However, while variance-based measures of selection give a perspective on the opportunity and/or strength of sexual selection on a given population, selection manifests itself by non-random changes in traits' expression across generations. Therefore, the use of a trait-based measure of sexual selection (as the selection gradients, here) complements previous research (Chapter 2), focuses on putative targets of selection (Jennions et al. 2012) – mainly body size, here –, and gives the next step in understanding the role played by monopolization behavior in sexual selection events. Complementarily, we tested whether body size increases reproductive success, for both sexes, across animals, regardless of social mating system. We hypothesized that females benefit from being large, because larger females are expected to be more fecund (Darwin 1871; Andersson 1994d; Fairbairn et al. 2007; Monroe et al. 2015). Given that being bigger is expected to be advantageous when males try to economically monopolize territories and/or sexual partners (e.g. Darwin 1871; Székely et al. 2007), but being smaller is expected to be advantageous in scramble competitions (Foellmer and Moya-Laraño 2007; Székely et al. 2007), we also hypothesized that there is no correlation between body size and reproductive success among males.

Methods

Data search

We developed an extensive and systematic literature search on *Scopus* and *Web of Science* (all databases), searching for studies that quantified the correlation between a trait and reproductive success. The search we conducted for this study was the same we used in Chapters 1 and 2, and we updated the search for the last time on 28th May 2017. From the studies found, we first read titles and abstracts, in order to select studies that seemed to measure any trait related to mating and reproductive events, and also seemed to quantify reproductive success of individuals in a given population. We included any trait potentially beneficial for mating and/or reproductive success because there is no standard procedure to choose only the traits that are actually under selection (Klug et al. 2010; Henshaw et al. 2016), and trying to do it would bias the results. At first, our intention was to calculate selection gradients from all sorts of morphological and behavioral traits. However, due to sample size restrictions (see Results), we mainly focus on selection gradients between body size and reproductive success (but see Discussion). We excluded all data coming from studies that were conducted on humans and non-animal organisms, and we also excluded data relating categorical classes of a phenotypic trait and reproductive success (for instance, studies that contrasted reproductive success between males divided into two groups: large males *vs* small males, or armed males *vs* males lacking armaments), because this method prevented us from calculating a selection gradient.

After the first screening, we read all the previously approved studies, checked data availability and extracted the data if it was possible. We included in our meta-analysis data from studies that measured proxies to body size, proxies to courtship behavior, ornaments, armaments and proxies to investment in fertilization. We excluded potential useful effect sizes coming from any experimental treatment that had changed organism's reproductive performance (but, if there was a control group, the effect sizes coming from this group were included). Additionally, following the same procedure of Chapter 2, we excluded studies that were unable to assure maternity and/or paternity. We considered maternity/paternity reliable if the authors performed genetic analyses (e.g. Grunst et al. 2017; Sundin et al. 2017), if the natural conditions of reproduction in the focal species suffice to allow us to identify individual reproductive success and/or the mother/father of each young (e.g. Pitnick and García-González 2002; Rogovin et al. 2015), and if by any other means they succeeded in separating the offspring produced by each individual (e.g. Ribble 1992; Leftwich et al. 2012). As expected, many studies have useful data, but do not report these results in a way that effect sizes and their respective sample sizes can be extracted. To partially circumvent this problem, we actively searched for all the missing data on Dryad© and Figshare repositories. Additionally, for 144 selected studies, we also contacted at least one of its authors to request the data (see Appendix 1 for more information and to see the template of the e-mail sent to the authors).

<u>Data collection – effect sizes</u>

The effect sizes of our multilevel meta-analytic model were the selection gradients (i.e. least square regression between phenotypic trait value and reproductive success) extracted from studies available on the literature. To allow comparison across studies, we standardized the selection gradients following procedure described in Lande and Arnold (1983) and Brodie III et al. (1995). We calculated the reproductive success of each individual by quantifying the number of offspring it produced (e.g. number of embryos in a pouch, number of eggs in a nest, or the number of young produced). Then, we calculated the standard reproductive success per individual by dividing each individual reproductive success by the mean reproductive success in the population, obtaining a new population mean equal one. We calculated the standard phenotypic values per individual by subtracting the mean population value from each individual phenotypic trait value and then dividing by the standard deviation of the same population, obtaining a new population mean equal to zero and a standard deviation equal to one. From the covariance between the standardized trait values and relative fitness, we calculated the standardized selection differential (s’), which represents the strength of the association between a specific trait and reproductive success (Henshaw et al. 2016).

We obtained selection gradients from text or tables of the manuscript, text or tables of the supplementary material, and figures – in the latter case, point values were obtained using the program WebPlotDigitizer (Rohatgi 2015). For each effect size, we recorded the sex of the individuals sampled, the sample size, if the data included individuals with reproductive success equal to 0 (“inclusion of zeros”), if the authors prevented or allowed intrasexual competition to happen among the focal sex (“intrasexual competition occurrence”), the age of the sampled offspring and the type of phenotypic trait measured. We classified offspring in four classes: eggs/embryos, newborn, juveniles, and adults. And we divided phenotypic traits in five classes: avoidance traits, body size traits (the main focus of this Chapter, since this is the class of phenotypic trait whose quantity of effect sizes allowed us to contrast mating systems according to occurrence or absence of monopolization behavior), fight-related traits (any armament/weaponry structure, aggressive display and/or measure of fight ability), ornament traits (any structure that may be potentially used to court/attract sexual partners, excluding body size and armaments), and fertilization traits (any morphological measure assessing investment on gamete quantity and/or quality).

Data collection – moderators

To investigate what modulates the variation in the slope of selection gradients, and test our hypotheses, we included as a moderator variable the monopolization behavior in the species (categorical; coded as absence [0] or occurrence [1] of monopolization behavior). First, we tried to identify the occurrence (or absence) of monopolization behavior, by reading the study that provided the effect sizes. However, in case the main source did not provide enough information on the social mating system of the species, we looked for additional information on the literature. We describe the protocol for monopolization behavior identification in Appendix 3.

As in Chapter 2, we classified a species as presenting monopolization behavior if individuals defend the access to at least one individual of the opposite sex able to reproduce. We also identified the occurrence of monopolization behavior for the cases in which individuals defend a territory or a resource that is used by individuals of the other sex and, consequently, indirectly preclude competitors from accessing individuals of the other sex. We identified absence of monopolization behavior if the authors characterize the mating system as a scramble competition or a lek, and/or if the authors state that individuals do not directly or indirectly guard sexual partners (for more information on monopolization behavior, see Appendix 4). During this procedure, we took note on specific classifications of the mating systems, dividing them into: monogamous defense, female defense polygyny, male defense polyandry, resource defense polyandry/polygyny, lek, scramble competition, and other. We included hermaphrodites in our analysis because monopolization behavior also occurs among hermaphrodites (Oliver 1997; Dillen et al. 2009) and we were able to calculate the reproductive success for individuals acting as females or males (e.g. Cheek 1998; Janssen and Baur 2015; Nakadera et al. 2017).

Statistical analyses

To analyze if monopolization behavior influences the intensity of selection on traits (i.e. body size) involved in mating and reproductive events, we performed multilevel (hierarchical) meta-regression models as this type of model accounts for non-independence of data and allows the inclusion of random effects (Nakagawa et al. 2017). We included the slope of the standardized selection gradient as the response variable and calculated the respective sampling variance by obtaining Pearson's product-moment correlation coefficient (r): $(1 – r^2)^2$ / (sample size – 2) (Lajeunesse et al. 2013). If we succeeded in extracting an effect size, but failed to discover if monopolization behavior occurs or not in the correspondent species, we excluded this effect size from our analysis.

Given that heterogeneity is expected for meta-analyses dealing with biological data and in the attempt to avoid type I error (Senior et al. 2016), we included several random effects in our model. In all models, we included the phylogeny (see phylogeny in Appendix 2). We obtained the phylogeny from the *TimeTree Database* (Hedges et al. 2006) and used *Mesquite* (Maddison and Maddison 2019) and *Phylocon* (Webb et al. 2008) to include in our phylogeny the species not found on the *TimeTree Database*, having times of divergence for all nodes. Next, we pruned the tree according to the species included in each of the models we ran. Another random effect was a correlation matrix containing the correlation between all traits included in the analyses, because some studies measured more than one trait per sampled individual (which means that one study may generate more than one selection gradient per studied group of individuals). When it was possible and useful, we also included the following random effects in our models: inclusion of zeros, intrasexual competition occurrence, and offspring age. To test the robustness of our results, we performed several sensitivity tests (Supplementary Material 1).

During data collection, we also extracted effect sizes from females that try to economically monopolize males and effect sizes from males that are monopolized by females. Therefore, we built additional models, employing the exact same method described above. These additional models were ran combining “guardians” (males and females that try to monopolize sexual partners) or “targets” (females and males that are targets of monopolization attempts). Again, we predicted that, in both scenarios, each increase in body size unity would return a larger increase in fitness when monopolization behavior occurs.

For body size, fertilization related traits, and ornaments, we calculated mean effect sizes, including all data available and all random variables, with no inclusion of monopolization behavior as moderator. These mean effect sizes allow us to evaluate if there is a correlation between a specific trait and reproductive success. For avoidance-related traits and fight-related traits, due to the small sample size, we did not calculate mean effect sizes.

We fit all meta-regression models using the function rma.mv from the *metafor* package (Viechtbauer 2010; R Core Team 2017). We present estimated parameters along with their 95% compatibility intervals (CIs) and discuss our findings interpreting the parameter point estimates, while at the same time acknowledging their uncertainty (Wasserstein et al. 2019).

Results

Data collection

From *Scopus* and *Web of Science*, we found a total of 7,624 studies, after removing duplicates. After reading the titles and abstracts, we selected 1,862 studies to read the full text. From the rejected studies, we also selected 91 studies that seemed to contain citations to potentially useful publications not found by our initial search. These 91 studies led us to 185 new studies whose titles and abstracts indicated they should also be approved. Consequently, we selected 2,138 studies to read in full, and extract effect sizes.

From the 2,138 read studies, we extracted standardized selection gradients from 128 studies. Then, we tried to contact 120 authors, to ask for more data. We received 21 positive answers and 48 negative answers (also, 11 e-mails were not delivered). The positive answers brought us 23 new effect sizes for females and 71 new effect sizes for males, from 16 different studies. So, we extracted 577 standardized selection gradients (females: 173; males: 404; Table 1), from 143 studies, comprising 118 species (of those, we managed to identify if monopolization behavior occurs or not for 108 species). In Table 2, we present the reasons for study rejection after trying to extract the data. In Figure 1, we present all steps of data collection.

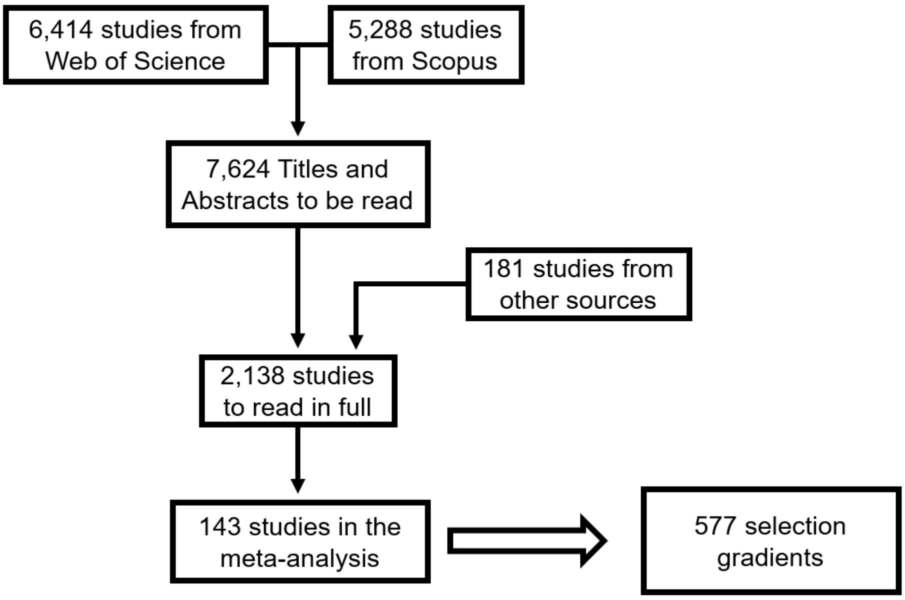

Figure 1. PRISMA diagram of this meta-analysis, presenting the steps developed from data search to data extraction.

Table 1. Number of estimates (i.e. standardized selection gradients) extracted from the selected studies, for females, targets (guarded females and guarded males, combined), males, and guardians (females and males that guard, combined), and the respective number of species. Selection gradients are classified in five main classes: avoidance-related traits, body size, fertilization-related traits, fight-related traits, ornaments, and other. Fertilization-related traits compose the only class of traits directly involved in post-mating episodes of sexual selection. The remaining traits are directly involved in episodes of pre-mating sexual selection. Between parentheses is informed the number of estimates included in each model for models on body size, after exclusion of species for which we could not identify if the monopolization behavior occurs or not. The number of species that provided estimates are also informed, according to a classification based on monopolization behavior (MB). Species are divided in three types: MB occurs ("MB: yes"), MB does not occur ("MB: no"), and we could not identify if MB occurs or not ("MB: ?").

			Species		
Trait class	**Group**	**Estimates**	**MB: yes**	**MB: no**	**MB: ?**
Avoidance	Females	3	1	0	0
Avoidance	Males	0	-	-	-
Body size	Females	155 (141)	33	29	7
Body size	Targets	167 (153)	34	29	7
Body size	Males	235 (219)	36	35	7
Body size	Guardians	244 (228)	37	35	7
Fertilization	Females	0	-	-	-
Fertilization	Males	31	7	6	0
Fight	Females	0	-	-	-
Fight	Males	13	4	1	0
Ornaments	Females	6	4	0	1
Ornaments	Males	111	18	8	0
Other	Females	0	-	-	-
Other	Males	2	1	0	0
Pre-mating episodes	Females	173	35	29	7
Pre-mating episodes	Males	373	43	38	7
Post-mating episodes	Females	0	-	-	-
Post-mating episodes	Males	31	7	6	0

Table 2. List of reasons why studies were rejected during data collection and the number of studies rejected per each listed reason per sex. Bold text indicates rejected studies that contain useful data. A study may be rejected by more than one reason and a study rejected for one sex may have been approved for the other sex.

Reasons for rejection	**Females**	**Males**
there is quantification of reproductive success, but no trait involved in pre- or post-mating sexual selection episodes is measured	506	410
study on sexual selection or animal behavior that does not quantify reproductive success	378	469
study contains useful data, but the data is not available (and we did not contact the authors)	**317**	**300**
study on an unrelated topic	200	200
study contains useful data, but the data is not available. We contacted the authors but received no answer	**102**	**91**
study focus only on males	98	-
study focus only on females	-	90
study is not available online	56	56
study on kinship, heritability, mutation or selection of traits that does not include any measure of reproductive success	54	55
study quantifies reproductive success for a group of individuals but not per individual	47	50
qualitative review on sexual selection	33	33
study (other than reviews) that does not present original data	27	29
mathematical model on sexual selection that does not provide useful data	25	25
meta-analysis, other quantitative reviews or comparative analysis on sexual selection	20	20
study on animal reproduction that does not quantify reproductive success	9	10
reproductive success is calculated but the measured trait is categorical	3	9
study contains useful data, author(s) sent us some data, but the data sent was not useful	**3**	**3**
authors inform that they failed to access maternity/paternity through genetic analyses	3	3
unreliable determination of maternity/paternity	2	11
we thought the study would contain useful data but authors informed us otherwise	0	1
other	84	85

Body size – females (and targets)

Among females, the mean slope of the selection gradient between body size and reproductive success is different from zero and positive (mean slope = 0.224, 95% CI = 0.094 to 0.354). Still on females, the slope of the selection gradient between body size and reproductive success does not differ according to the occurrence (or absence) of monopolization behavior (occurrence of monopolization behavior: slope = 0.245, 95% CI = -0.006 to 0.496; no monopolization behavior: slope = 0.206, 95% CI = 0.064 to 0.348; contrast = -0.039, CI lower end = 0.071, CI upper end = -0.148; Supplementary Material 2 - Figure S1). All sensitivity analyses returned the same result (Supplementary Material 2 - Table S1). The random variables explained little variance among effect sizes (I^2 = 0.15%; I^2 phylogeny = 0.08%; I^2 traits correlation matrix = 0.07%; I^2 inclusion of zeros = 4.08 x 10^{-12}%; I^2 intrasexual competition occurrence = 4.79 x 10^{-11}%; I^2 offspring age: 2.20 x 10^{-14}%). No publication bias was detected after Egger's regression quantification (Egger's regression: $\text{slope}_{\text{intercept}}$ = 0.008 ± 0.023 SE, t = 0.329, p > 0.05).

Among targets, the mean slope of the selection gradient between body size and reproductive success is also positive (mean slope = 0.223, 95% CI = 0.098 to 0.348; p = 0.0005). Once again, the slope of the selection gradient between body size and reproductive success does not differ according to the occurrence (or absence) of monopolization behavior (occurrence of monopolization behavior: slope = 0.242, 95% CI = -0.004 to 0.489; no monopolization behavior: slope = 0.205, 95% CI = 0.067 to 0.343; contrast = -0.037, CI = 0.071, CI upper end = -0.145; Supplementary Material 2 - Figure S1). All sensitivity analyses returned the same result (Supplementary Material 2 - Table S2). The random variables explained little variance among effect size measures (I^2 = 0.14%; I^2 phylogeny = 0.08%; I^2 traits correlation matrix = 0.07%; I^2 inclusion of zeros = 3.93 x 10^{-12}%; I^2 intrasexual competition occurrence = 7.38 x 10^{-12}%; I^2 offspring age: 1.17 x 10^{-14}%). Again, no publication bias was detected (Egger's regression: $\text{slope}_{\text{intercept}}$ = 0.0145 ± 0.022 SE, t = 0.664, p > 0.05).

Body size – males (and guardians)

Among males, the mean slope of the selection gradient between male body size and male reproductive success is different from zero and positive (mean slope = 0.205, 95% CI = 0.015 to 0.396). Still on males, the slope of the selection gradient between body size and reproductive success does not differ according to the occurrence (or absence) of monopolization behavior (occurrence of monopolization behavior: slope = 0.132, 95% CI = -0.217 to 0.480; no monopolization behavior: slope = 0.243, 95% CI = 0.041 to 0.444; contrast: slope = 0.111, CI lower end = 0.258, CI upper end = -0.036; Supplementary Material 3 - Figure S2). For sensitivity analyses, see Supplementary Material 3 - Table S3. The random variables explained little variance among effect sizes (I^2 = 0.53%; I^2 phylogeny = 0.13%; I^2 traits correlation matrix = 0.39%; I^2 inclusion of zeros = 1.37 x 10^{-3}%; I^2 intrasexual competition occurrence = 1.31 x 10^{-8}%; I^2 offspring age: 4.82 x 10^{-9}%). The data we collected present publication bias (Egger's regression: $\text{slope}_{\text{intercept}}$ = 0.124 ± 0.036 SE, t = 3.495, $p < 0.05$).

Among guardians, the mean slope of the selection gradient between body size and reproductive success is also positive (mean slope = 0.200, 95% CI = 0.006 to 0.393; p = 0.043). Once again, the slope of the selection gradient between body size and reproductive success does not differ according to the occurrence (or absence) of monopolization behavior (occurrence of monopolization behavior: slope = 0.119, 95% CI = -0.232 to 0.468; no monopolization behavior: slope = 0.236, 95% CI = 0.028 to 0.443; contrast = 0.117, CI lower end = 0.260, CI upper end = -0.025; Supplementary Material 3 - Figure S2). For sensitivity analyses, see Supplementary Material 3 - Table S4. Once again, the random variables explained little variance among effect sizes (I^2 = 0.52%; I^2 phylogeny = 0.13%; I^2 traits correlation matrix = 0.38%; I^2 inclusion of zeros = 0.01%; I^2 intrasexual competition occurrence = 8.98 x 10^{-10}%; I^2 offspring age: 6.21 x 10^{-11}%). The inclusion of the additional species did not remove the previous reported publication bias (Egger's regression: $\text{slope}_{\text{intercept}}$ = 0.139 ± 0.034 SE, t = 4.031, $p < 0.05$).

Fertilization and ornament-related selection gradients – males only

The mean slope of the selection gradient between male ornaments and male reproductive success is not different from zero (mean slope = 0.120, 95% CI = -0.470 to 0.711; Supplementary Material 4 - Figure S3). The random variables explained little variance among effect sizes (I^2 = 0.95%; I^2 phylogeny = 0.88%; I^2 traits correlation matrix = 0.07%; I^2 inclusion of zeros = 0.00%; I^2 intrasexual competition occurrence = 9.43 x 10^{-10}%; I^2 offspring age: 0.00%). No publication bias was detected after Egger's regression quantification (Egger's regression: $\text{slope}_{\text{intercept}}$ = 0.003 ± 0.030 SE, t = 0.092, p > 0.05).

The mean slope of the selection gradient between fertilization-related traits and male reproductive success is different from zero and positive (mean slope = 0.278, 95% CI = 0.037 to 0.519; Supplementary Material 4 - Figure S4). The random variables explained little variance among effect sizes (I^2 = 0.34%; I^2 phylogeny = 0.05%; I^2 traits correlation matrix = 0.23%; I^2 inclusion of zeros = 9.52 x 10^{-11}%; I^2 intrasexual competition occurrence = 6.55 x 10^{-13}%; I^2 offspring age: 0.05%). No publication bias was detected after Egger's regression quantification (Egger's regression: $\text{slope}_{\text{intercept}}$ = -0.081 ± 0.077 SE, t = -1.048, p > 0.05).

Discussion

General results

We show here that, in animals, for both females and males, individuals with larger body sizes achieve higher reproductive success. As far as we could evaluate, this is the first demonstration of a positive correlation between body size and reproductive success for animal species, regardless of the social mating system. Almost all previous work on the same issue (exception in the following) focused on only one specific animal taxon (e.g. Honěk 1993; Sokolovska et al. 2000; Fairbairn et al. 2007; Bauerfeind and Fischer 2008; Monroe et al. 2015). And, in a meta-analysis, Alissa et al. (2018) showed that, for arthropod, bird, and fish species in which males monopolize reproductive sites, males with larger body size and/or larger armament size achieve higher reproductive success. While our results show that larger body size is positively correlated with reproductive success, our results surprisingly also show that having a larger body size does not translate into having an even higher reproductive success when males attempt to economically monopolize females. It is important to note that our results do not demonstrate that larger body size is fruitless in helping females to avoid male monopolization attempts or in helping males to economically monopolize females (see Alissa et al. 2018). Our results only show that, while comparing social mating system types, when monopolization behavior occurs there is no differential fitness gain for an individual in being larger than its competitors (i.e. monopolization behavior occurrence/absence does not modulate the number of offspring obtained by a unity increase in standardized body size). After we included all targets and all guardians in analyses, the results did not change (in comparison to the analyses including only females and males, respectively). Therefore, in the pursuit of clarity, we focus this discussion mainly on females and males.

Large females have higher reproductive success, regardless of monopolization behavior occurrence

At the very beginning of sexual selection research, Darwin (1871) hypothesized that in fish, females present larger body size than males because a large body size allows females to produce more eggs. Through the years until nowadays, the positive correlation between female body size and female fecundity/reproductive success has been assumed, hypothesized and/or tested in sexual selection studies (see Shine 1988; Andersson 1994c,b; Blanckenhorn et al. 2007; Cox et al. 2007; Fairbairn 2007; Foellmer and Moya-Laraño 2007; Kupfer 2007; Lindenfors et al. 2007; Székely et al. 2007; Monroe et al. 2015). Therefore, the results we present here corroborate a long-standing and ubiquitous hypothesis (but see Shine 1988). This corroboration of Darwin’s fecundity advantage hypothesis may help us to explain why the positive correlation between body size and fitness in females does not differ according to the occurrence of monopolization behavior. If larger females tend to produce more offspring, males will usually directly and indirectly benefit from mating with larger females (directly, by siring more offspring; indirectly, by siring large daughters that will be more attractive than the mean female in the population – which is analogous to the benefits females obtain by mating with high-quality males, see Weatherhead and Robertson 1979). Not surprisingly, males in many *taxa* prefer to mate with larger females (Andersson 1994a; Bonduriansky 2001), which may enhance sexual harassment to larger females. Therefore, even if larger body size confers a higher evading capacity for females, the increase in sexual harassment to larger females may prevent the predicted advantages females have from being larger. If this is common in species presenting the monopolization behavior, there remains a possible explanation for the fact that the correlation between body size and fitness does not differ according to the occurrence of monopolization behavior.

The fact that the correlation between body size and fitness does not differ according to the occurrence/absence of monopolization behavior can be explained by another hypothesis that emerges from our previous work. We already showed that post-mating episodes of sexual selection seem to play a large role in episodes of total selection (Chapter 1) and that monopolization behavior occurrence is effective in restricting females' mating capability (Chapter 2). Therefore, when females are not restricted by monopolization behavior, they mate as many times as they benefit from mating and the potential for cryptic female choice is higher. If larger females tend to be more attractive, large females that faced no monopolization behavior and mated several times may be more prone to exert effective cryptic female choice than large females dealing with monopolization behavior or than any smaller females (that are dealing with monopolization behavior or not). This may be particularly relevant because cryptic female choice allows females to fertilize their eggs with diverse sperm, producing genetically diverse offspring (e.g. Foerster et al. 2003; Garant et al. 2005), and it also allows females to avoid inbreeding and genetic incompatibilities with sexual partners (Slatyer et al. 2012; e.g. Welke and Schneider 2009; Gasparini and Pilastro 2011; Lovlie et al. 2013; Firman and Simmons 2015; Burgess et al. 2019; Pineaux et al. 2019; Speechley et al. 2019). Therefore, it is probable that these large females facing no monopolization behavior are increasing their reproductive success by engaging in cryptic choice. Consequently, we expect an increase in the steepness of the selection gradient between body size and reproductive success when monopolization behavior is absent, preventing monopolization behavior occurrence from modulating the correlation between female body size and fitness when comparing the two classes of social mating systems.

Large males have higher reproductive success, regardless of monopolization behavior occurrence

Similar to females, larger male body size resulted in higher reproductive success for males. However, no differential gain in male fitness resulted from larger body sizes when contrasting mating systems presenting monopolization behavior and mating systems that lack such behavior. This result goes against ubiquitous predictions in sexual selection studies. Mating systems with direct male competition for female monopolization are traditionally expected to illustrate the success of larger males (Darwin 1871; Andersson 1994a,d; Cox et al. 2007; Székely et al. 2007; Monroe et al. 2015) and other mating systems are usually expected to show how smaller males can succeed (Andersson 1994d; Fairbairn 2007; Foellmer and Moya-Laraño 2007; Székely et al. 2007). One possible explanation for our result is that non-dominant males (smaller males) considerably enhance their reproductive success through alternative reproductive tactics such as investment in sperm competition-related traits, consequently reducing the selection gradient between body size and reproductive success when monopolization behavior occurs. This seem to be probable, as the opportunity for post-mating sexual selection is ubiquitous among animals (Chapter 1), post-mating sexual selection seems to alter the outcome of pre-mating sexual selection (Chapter 2), and fertilization-related traits are positively correlated with reproductive success among male animals, as we show here. Therefore, even if body size does modulate mate monopolization and mating success, body size does not confer a differential fitness gain when monopolization behavior occurs. At this point, one might question what is the advantage of large body size and why there is considerable variation in male body size in many species. This is answered by the positive correlation between male body size and male reproductive success we found among animals, regardless of social mating system.

Additional hypotheses may help us to explain why larger body size resulted in no differential gain in male fitness when contrasting mating systems. One possibility is that sexual selection theory underestimates the relevance of large body size in systems such as scramble competitions. Small body size may aid in finding mates faster in scramble competitions (e.g. Vencl and Carlson 1998; Moya-Laraño et al. 2007; Kelly et al. 2008; for opposite pattern, see Barry 2013). However, large individuals may have more energy to perform many searches for females and/or to search longer for females, while small individuals have energy for only a few and/or brief searches for sexual partners. Finally, it is also possible that maybe body size is not the best predictor of male ability to economically monopolize females. Body size is possibly positively correlated with armaments (e.g. Clutton-Brock et al. 1980; Emlen 2008; Yoshino et al. 2011), and armaments may be a better predictor of male ability to perform the monopolization behavior (e.g. Sneddon et al. 1997; Yoshino et al. 2011). Unfortunately, we did not find in our search any studies providing selection gradients between armaments and reproductive success, and all fight-related selection gradients obtained were from measures of aggressiveness (and the correlation between body size and aggressiveness seems to vary from negative to positive - e.g. Rowe et al. 2008; Noble et al. 2013; Rogovin et al. 2015; Devost and Turgeon 2016). Additionally, and not surprisingly, almost all fight-related effect sizes we obtained were from species that present monopolization behavior. Therefore, while it would be interesting to contrast the role played by fight-related traits in different social mating systems, the unequal occurrence of fight-related traits (especially armaments) among social mating systems may preclude researchers from testing the hypothesis presented above.

Missing data and the effect of ornaments and fertilization-related traits on reproductive success

As said above, we had difficulty in finding fight-related selection gradients, which prevented us from contrasting mating systems according to this sort of trait. We also failed to collect enough effect sizes on avoidance, fertilization and ornament-related traits in order to contrast social mating systems for males. More than that, for only two of these trait types, we had enough effect sizes to calculate the mean effect size, regardless of social mating system. We found that among animals there is a positive correlation between male investment in fertilization-related traits and male reproductive success, providing additional evidence of the relevance of post-mating episodes of sexual selection. And we found no correlation between male ornaments and male reproductive success (for similar analysis on birds alone, see Soma and Garamszegi 2011). For ornament-related traits, it seems particularly difficult to identify which structures are related to acquiring mates and/or producing offspring, meaning that it is even more challenging to identify the traits that are targets of selection in the current time (see Klug et al. 2010; Henshaw et al. 2016), which may explain why we found no correlation between ornaments and reproductive success.

For avoidance and fight-related traits, we could not even calculate the mean effect size. And it is important to emphasize that calculating a mean effect size requires even less effect sizes than the models run to contrast social mating systems. Therefore, non-extractable data seems to be a relevant issue in sexual selection research, as studies measuring reproductive success and measuring at least one trait are extremely common in the literature. Therefore, it should be feasible to extract all the necessary data from a sample of more than 7,600 studies (as done here). For example, our search returned more than 600 studies that most certainly contain data useful for the purposes of this project. However, we were able to extract data from only 143 studies. If data were usually made available through supplementary materials or using data repositories (e.g. Dryad© and Figshare) and/or if authors published standardized selection gradients (allowing comparisons among studies and species) instead of publishing selection gradients between absolute trait value and absolute reproductive success, maybe it would be possible to extend the contrast between social mating systems. Additionally, our dataset seems to present a publication bias among males and guardians for body size related selection gradients. Maybe this bias would not exist if more data were made available. Altogether, these results stress out the relevance of good data reporting (for more on good data reporting, see Haddaway 2015; Greenacre 2016).

Future research and conclusions

Thanks to many authors that provided data for this study, we show that larger individuals produce more offspring, but larger body size does not translate into having even more offspring when monopolization behavior occurs. We also show that, among males, investment in fertilization-related traits translates into higher reproductive success. Given this, we recommend that future studies should focus on how cryptic female choice and sperm competition modulate the results found here. Additionally, we also recommend an effort into measuring and studying female traits other than body size (once almost all selection gradients for females we found in the literature are based on the relationship between body size and reproductive success). And we recommend an effort into analyzing whether these other types of trait influence female reproductive success, as females are not passive participants in sexual selection episodes (Thornhill 1983; Gowaty 1997; Chapter 2), and they may court males (Gwynne 1991; and e.g. Kolm 2001; Rillich et al. 2009; Clutton-Brock and Huchard 2013), fight for mates (Gwynne 1991; and e.g. Coddington and Cockburn 1995; Bro-Jørgensen 2002; Papadopoulos et al. 2009; Rillich et al. 2009), and guard males (e.g. Summers 1992; Emlen and Wrege 2004; Aronsen et al. 2013; Hübner et al. 2013). Therefore, this meta-analysis also shows that there is a gender-bias on scientific literature that must be eliminated. All these future studies should take into account what we show here: for both females and males, being larger is beneficial and translates into the acquisition of a higher reproductive success in comparison with smaller competitors. However, being larger is equally relevant in mating systems that mainly differ by the occurrence or absence of monopolization behavior, and, consequently, by the possibility of economically monopolizing sexual partners.

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Supplementary Materials

Supplementary materials are presented according to the order in which they are presented in the main text.

Supplementary Material 1 - Sensitivity tests

To test the robustness of our results, we performed several sensitivity tests. In all sensitivity analyses, we included the correlation matrix and phylogeny as random variables. The sensitivity analyses consisted of excluding effect sizes with some particular nature (we excluded one at a time). We excluded:

i) effect sizes from studies in which individuals with zero reproductive success were not accounted for;
ii) effect sizes from studies in which selection gradient was measured in a context of no intrasexual competition;
iii) effect sizes from leks, because leks are expected to show high sexual selection intensity (Payne 1984; Andersson 1994b; Székely et al. 2007), despite not presenting monopolization behavior as defined here (see Chapter 2);
iv) and effect sizes obtained by sampling older offspring (i.e. juveniles, and adults).

Supplementary Material 2 – Body size (females and targets)

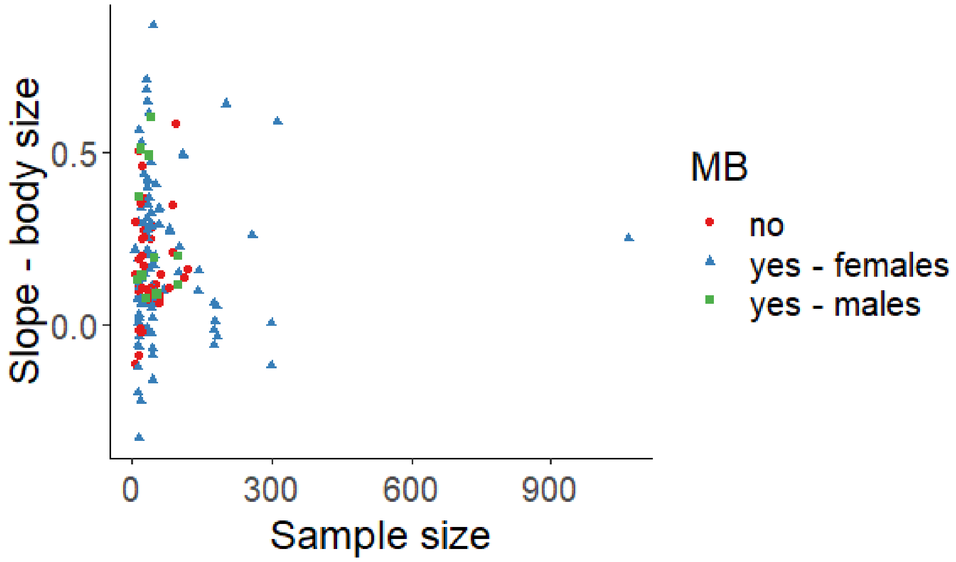

Figure S1. Slopes of the selection gradients between body size and reproductive success and the respective sample sizes for targets (females and guarded males). Estimates are classified according to sex and monopolization behavior (MB) occurrence. In blue triangles, females from species in which males try to economically monopolize females. In green squares, males from species in which females try to economically monopolize males. In red circles, females from species in which males do not try to economically monopolize females.

Table S1. The slope of the selection gradient between female body size and female reproductive success in two scenarios: monopolization behavior occurs (1: yes) or monopolization behavior does not occur (0: no). The estimate of the slope value is presented with the respective confidence interval (2.5% CI to 97.5% CI). The main model is presented in the first line and includes all data and all possible random variables. In sensitivity analyses, part of the data is excluded and the random variables are only the phylogeny and the traits correlation matrix. For all models, the number of estimates and species per social mating system is also informed. No significant ($p < 0.05$) or marginally significant differences ($0.05 < p < 0.10$) between social mating systems were found.

Model	Monopolization	Slope	2.5% CI	97.5% CI	Estimates	Species
All data; Random variables: phylogeny, effect size identity, mating success meaning, inclusion of zeros, and intrasexual competition occurrence	1: yes	0.245	-0.006	0.496	98	33
	0: no	0.206	0.064	0.348	43	29
All data; Random variables: phylogeny and effect size identity	1: yes	0.245	-0.006	0.496	98	33
	0: no	0.206	0.064	0.348	43	29
Data: excluding effect sizes that do not include reproductive success = 0; Random variables: phylogeny and effect size identity	1: yes	0.221	-0.198	0.640	70	20
	0: no	0.193	-0.021	0.408	16	10
Data: excluding studies with no intrasexual competition; Random variables: phylogeny and effect size identity	1: yes	0.232	-0.062	0.527	90	27
	0: no	0.197	0.034	0.359	34	21
Data: excluding lek systems; Random variables: phylogeny and effect size identity	1: yes	0.244	-0.017	0.504	98	33
	0: no	0.208	0.064	0.353	36	25
Data: excluding older offspring; Random variables: phylogeny and effect size identity	1: yes	0.260	-0.007	0.526	64	22
	0: no	0.227	0.068	0.386	41	28

Table S2. The slope of the selection gradient between target body size and target reproductive success in two scenarios: monopolization behavior occurs (1: yes) or monopolization behavior does not occur (0: no). The estimate of the slope value is presented with the respective confidence interval (2.5% CI to 97.5% CI). The main model is presented in the first line and includes all data and all possible random variables. In sensitivity analyses, part of the data is excluded and the random variables are only the phylogeny and the traits correlation matrix. For all models, the number of estimates and species per social mating system is also informed. No significant ($p < 0.05$) or marginally significant differences ($0.05 < p < 0.10$) between social mating systems were found.

Model	Monopolization	Slope	2.5% CI	97.5% CI	Estimates	Species
All data; Random variables: phylogeny, effect size identity, mating success meaning, inclusion of zeros, and intrasexual competition occurrence	1: yes	0.242	-0.004	0.489	110	34
	0: no	0.205	0.067	0.343	43	29
All data; Random variables: phylogeny and effect size identity	1: yes	0.242	-0.004	0.489	110	34
	0: no	0.205	0.067	0.343	43	29
Data: excluding effect sizes that do not include reproductive success = 0; Random variables: phylogeny and effect size identity	1: yes	0.221	-0.181	0.623	79	21
	0: no	0.192	-0.014	0.399	16	10
Data: excluding studies with no intrasexual competition; Random variables: phylogeny and effect size identity	1: yes	0.231	-0.057	0.518	102	28
	0: no	0.196	0.039	0.354	34	21
Data: excluding lek systems; Random variables: phylogeny and effect size identity	1: yes	0.241	-0.014	0.497	110	34
	0: no	0.208	0.066	0.349	36	25
Data: excluding older offspring; Random variables: phylogeny and effect size identity	1: yes	0.273	0.011	0.535	76	23
	0: no	0.222	0.065	0.379	41	28

Supplementary Material 3 – Body size (males and guardians)

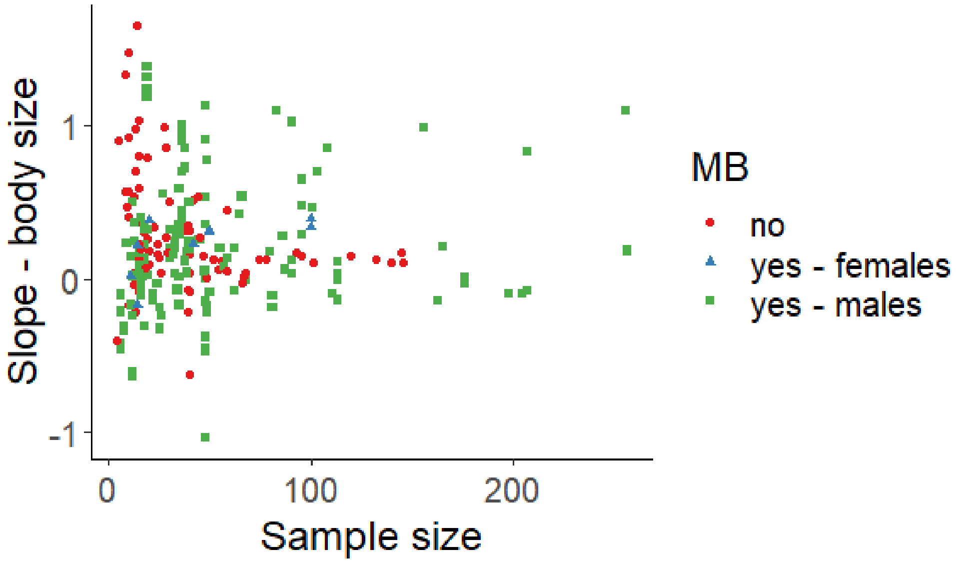

Figure S2. Slopes of the selection gradients between body size and reproductive success and the respective sample sizes for guardians (males and females that guard). Estimates are classified according to sex and monopolization behavior (MB) occurrence. In green squares, males from species in which males try to economically monopolize females. In blue triangles, females from species in which females try to economically monopolize males. In red circles, males from species in which males do not try to economically monopolize females.

Table S3. The slope of the selection gradient between male body size and male reproductive success in two scenarios: monopolization behavior occurs (1: yes) or monopolization behavior does not occur (0: no). The estimate of the slope value is presented with the respective confidence interval (2.5% CI to 97.5% CI). The main model is presented in the first line and includes all data and all possible random variables. In sensitivity analyses, part of the data is excluded and the random variables are only the phylogeny and the traits correlation matrix. For all models, the number of estimates and species per social mating system is also informed. Statistically significant differences ($p < 0.05$) between social mating systems are indicated with two asterisks (**). No marginally significant differences ($0.05 < p < 0.10$) between social mating systems were found.

Model	Monopolization	Slope	2.5% CI	97.5% CI	Estimates	Species
All data; Random variables: phylogeny, effect size identity, mating success meaning, inclusion of zeros, and intrasexual competition occurrence	1: yes	0.132	-0.217	0.480	136	36
	0: no	0.243	0.041	0.444	83	35
All data; Random variables: phylogeny and effect size identity	1: yes	0.134	-0.212	0.481	136	36
	0: no	0.245	0.045	0.444	83	35
Data: excluding effect sizes that do not include reproductive success = 0; Random variables: phylogeny and effect size identity	1: yes	0.152	-0.268	0.571	107	29
	0: no	0.260	0.026	0.494	58	24
Data: excluding studies with no intrasexual competition; Random variables: phylogeny and effect size identity	1: yes	0.176	-0.227	0.580	127	31
	0: no	0.233	0.000	0.466	62	27
Data: excluding lek systems; Random variables: phylogeny and effect size identity	1: yes	0.177	-0.179	0.533	136	36
	0: no	0.213	0.018	0.409	65	30
Data: excluding older offspring; Random variables: phylogeny and effect size identity	1: yes	0.093**	-0.220	0.407	87	22
	0: no	0.273**	0.116	0.431	55	24

Table S4. The slope of the selection gradient between guardian body size and guardian reproductive success in two scenarios: monopolization behavior occurs (1: yes) or monopolization behavior does not occur (0: no). The estimate of the slope value is presented with the respective confidence interval (2.5% CI to 97.5% CI). The main model is presented in the first line and includes all data and all possible random variables. In sensitivity analyses, part of the data is excluded and the random variables are only the phylogeny and the traits correlation matrix. For all models, the number of estimates and species per social mating system is also informed. Statistically significant differences ($p < 0.05$) between social mating systems are indicated with two asterisks (**). No marginally significant differences ($0.05 < p < 0.10$) between social mating systems were found.

Model	Monopolization	Slope	2.5% CI	97.5% CI	Estimates	Species
All data; Random variables: phylogeny, effect size identity, mating success meaning, inclusion of zeros, and intrasexual competition occurrence	1: yes	0.119	-0.232	0.468	145	37
	0: no	0.236	0.028	0.443	83	35
All data; Random variables: phylogeny and effect size identity	1: yes	0.137	-0.209	0.474	145	37
	0: no	0.250	0.046	0.444	83	35
Data: excluding effect sizes that do not include reproductive success = 0; Random variables: phylogeny and effect size identity	1: yes	0.151	-0.258	0.560	114	30
	0: no	0.261	0.029	0.493	58	24
Data: excluding studies with no intrasexual competition; Random variables: phylogeny and effect size identity	1: yes	0.175	-0.223	0.574	136	32
	0: no	0.233	0.001	0.465	62	27
Data: excluding lek systems; Random variables: phylogeny and effect size identity	1: yes	0.180	-0.171	0.530	145	37
	0: no	0.214	0.020	0.407	65	30
Data: excluding older offspring; Random variables: phylogeny and effect size identity	1: yes	0.098**	-0.218	0.415	96	23
	0: no	0.268**	0.102	0.435	55	24

Supplementary Material 4 – Other (males)

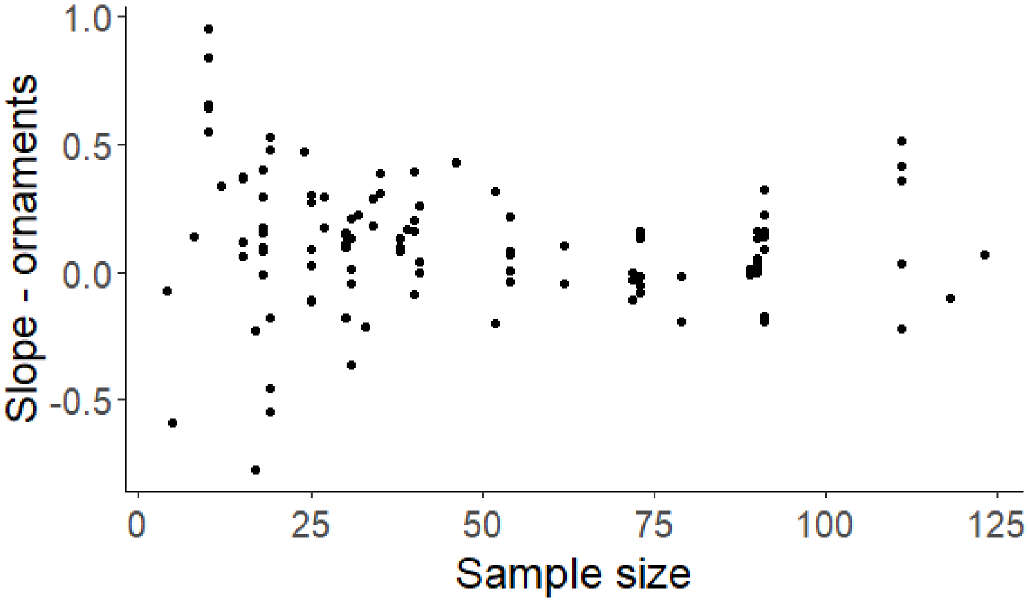

Figure S3. Slopes of the selection gradients between ornament-related traits and reproductive success and the respective sample sizes for males.

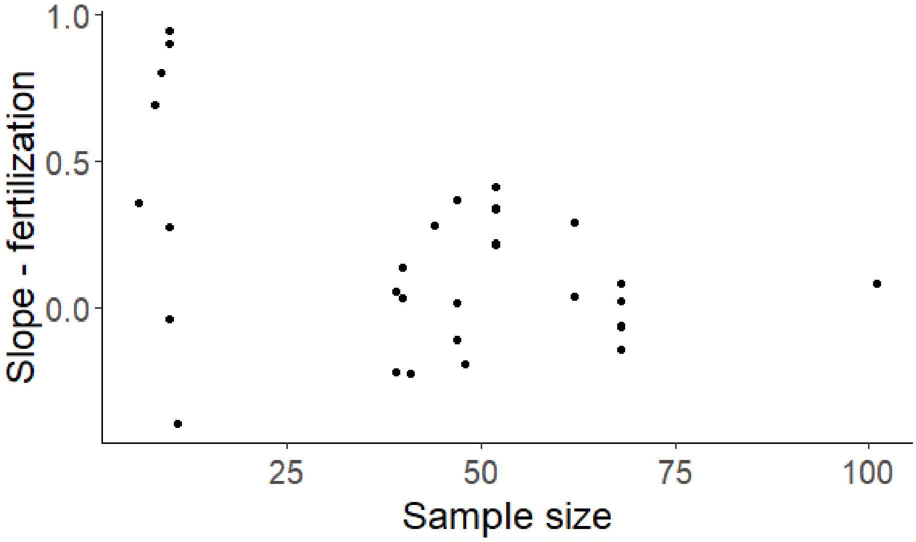

Figure S4. Slopes of the selection gradients between fertilization-related traits and reproductive success and the respective sample sizes for males.

Conclusão geral

Após analisarem os capítulos da tese do autor humano, os membros da banca retornaram e a Dra. Claudinha retomou as atividades:

– Filipinho, acabamos de analisar o estudo selecionado, mas gostaríamos que você expusesse resumidamente os resultados obtidos pelo autor humano e as conclusões a que ele chegou.

– Bom, no Capítulo 1, o autor comparou como diferentes medidas de sucesso de acasalamento influenciam estimativas da intensidade de seleção sexual. O autor viu que acessar sucesso de acasalamento indiretamente, inferindo o número de parceiros sexuais através de testes genéticos de maternidade e paternidade, gera estimativas mais altas da intensidade de seleção sexual do que se a pesquisadora ou pesquisador acessar sucesso de acasalamento diretamente, observando os acasalamentos.

– Isso não é tão simples de entender. O público deve estar com algumas dúvidas. Como alguém consegue inferir sucesso de acasalamento a partir de testes genéticos? E quais os problemas deste método? – perguntou a Dra. Tatianinha.

– Como só dá para ter filhotes com alguém com quem se acasalou, se uma fêmea e um macho são pais de um mesmo filhote, nós sabemos que essa fêmea e esse macho acasalaram. Entendendo-se sucesso de acasalamento como o número de parceiros sexuais que cada indivíduo tem, seria possível inferir o sucesso de acasalamento de cada indivíduo analisando quem teve filhote com quem. Mas esse método tem problemas. O primeiro problema desse método é que dois indivíduos podem acasalar e nenhum filhote ser gerado. Assim, esse acasalamento jamais será detectado pelos testes genéticos. O segundo problema é que, em vez de identificar o número de fêmeas com que cada macho acasalou ou o número de machos com que cada fêmea acasalou, esse processo identifica o número de fêmeas que um macho fertiliza e o número de machos que fertilizam uma fêmea. Assim, os valores obtidos são melhores medidas do sucesso de fertilização do que do sucesso de acasalamento de cada indivíduo. O terceiro problema é que o autor demonstrou que sucesso de acasalamento e sucesso de fertilização geram diferentes estimativas de intensidade de seleção sexual para ambos os sexos.

– E o que o autor propõe a partir desses resultados? – perguntou a Dra. Robertinha.

– Ele destaca que sucesso de acasalamento e sucesso de fertilização não podem ser sinonimizados, pois o primeiro representa o que acontece antes do acasalamento (ou seja, disputa por parceiros sexuais) e o segundo representa o que ocorre depois do acasalamento (ou seja, disputa por fertilização). Como sucesso de fertilização gera uma estimativa maior da intensidade de seleção sexual, o autor demonstra que também ocorre seleção sexual depois que fêmea e macho acasalaram. Nesse sentido, ele propõe um novo índice para se calcular a intensidade de seleção sexual pós-acasalamento.

– E como pode ocorrer essa seleção sexual depois do acasalamento? – perguntou o Dr. Agostinhozinho.

– Segundo a teoria de seleção sexual, há duas formas básicas disso ocorrer. Primeiro, se uma fêmea acasala com mais de um macho, os espermatozoides desses machos competem entre si para fertilizar os óvulos das fêmeas. Alguns machos produzem mais espermatozoides ou apresentam espermatozoides de maior qualidade que, por exemplo, nadam mais rápido e chegam antes aos óvulos das fêmeas. Esses machos serão mais bem sucedidos do que os outros nesse processo chamado competição espermática. Como esse processo pode gerar uma variação não aleatória no sucesso de fertilização e no sucesso reprodutivo dos machos, pode ocorrer seleção sexual pós-acasalamento. Outra forma dessa seleção sexual pós-acasalamento ocorrer é através de escolha críptica da fêmea.

– Por qual razão essa escolha é chamada ‘críptica’? – perguntou a Dra. Tatianinha.

–A escolha é qualificada como críptica porque, nos animais com fertilização interna, ela ocorre dentro do organismo da fêmea, sem que possamos visualizar essa escolha com nossos próprios olhos. É como se fosse uma escolha oculta feita pela fêmea. Após receber os espermatozoides de diferentes machos, fêmeas podem priorizar os espermatozoides de determinados machos para fertilizar seus ovos, o que acarreta em insucesso reprodutivo para os machos cujos espermatozoides são descartados. Por exemplo, em uma espécie de ave chamada *dunnock*, fêmeas acasalam com mais de um macho. Mas elas usam preferencialmente o esperma do macho dominante, e eliminam o esperma dos machos de menor qualidade. Assim, se fêmeas priorizam espermatozoides de determinado machos, elas provocam uma variação não aleatória no sucesso de fertilização e no sucesso reprodutivo de machos. Em outras palavras, a ação das fêmeas promove seleção sexual pós-acasalamento.

– E quanto ao Capítulo 2, Filipinho? – prosseguiu a Dra. Claudinha.

– No segundo capítulo, usando estimativas das intensidades de seleção sexual pré-acasalamento, pós-acasalamento e total (que foca em variação no sucesso reprodutivo), o autor comparou sistemas de acasalamento que apresentam o comportamento de monopolização ou não. O autor viu que quando o comportamento de monopolização ocorre, machos enfrentam maior intensidade de seleção sexual pré-acasalamento e fêmeas enfrentam menor intensidade de seleção sexual pré-acasalamento. Portanto, nesses sistemas, há grande variação no sucesso de acasalamento dos machos e baixa variação entre fêmeas. O que indica que machos são bem sucedidos em dificultar que as suas parceiras sexuais acasalem com mais machos.

– E por que você diz que esses machos ‘dificultam’ que fêmeas acasalem novamente, em vez de dizer que eles ‘evitam’ que elas acasalem novamente? – perguntou o Dr. Agostinhozinho.

– Porque a monopolização é somente aparente. Quando se olha para as estimativas de seleção sexual pós-acasalamento e total, vê-se que não há diferenças entre sistemas de acasalamento com ou sem o comportamento de monopolização. Isso não significa que indivíduos não variam entre si quanto a sucesso de fertilização e sucesso reprodutivo. Tampouco significa que indivíduos bem sucedidos em obter parceiros sexuais não são também bem sucedidos em obter filhotes. O resultado mostra somente que o comportamento de monopolização apresentado por machos de algumas espécies não gera os padrões de intensidade de seleção sexual esperados pela teoria de seleção sexual.

– Eu gostei desse resultado. Não simpatizei muito com esses machos terráqueos – comentou ironicamente a Dra. Tatianinha. – Achei eles inconvenientes.

– Sou obrigada a concordar – comentou a Dra. Robertinha, gerando risadas em boa parte da audiência.

– E o que pode explicar esse resultado? – interrompeu rapidamente o Dr. Hélio.

– Segundo o autor, isso demonstra que fêmeas acasalam com vários machos, abrindo a possibilidade para a ocorrência de competição espermática e escolha críptica da fêmea. E, aparentemente, o efeito dessa seleção sexual pós-acasalamento é suficiente para anular a diferença anteriormente encontrada quando o autor estava comparando diferentes sistemas de acasalamento e olhando somente para a intensidade de seleção sexual pré-acasalamento. Em outras palavras, muita coisa acontece depois que fêmeas e machos acasalam.

– E por que isso é relevante? – perguntou o Dr. Agostinhozinho.

– A teoria de seleção sexual foi formulada há muito tempo por um grande pesquisador humano chamado Charles Darwin[4]. De início, a teoria era baseada somente no que acontece antes do acasalamento e demorou muito tempo para que humanos começassem a teorizar sobre o que ocorre depois do acasalamento[5]. Esse processo histórico resultou em uma maior quantidade de informação disponível para eventos pré-acasalamento do que para eventos pós-acasalamento. O segundo capítulo dessa tese reforça a relevância evolutiva do que ocorre depois do acasalamento e reforça a necessidade já detectada de se integrar eventos pré e pós-acasalamento para se estudar seleção sexual.

– Interessante. E quais os resultados e conclusões do Capítulo 3, Filipinho? – perguntou a Dra. Claudinha.

– No terceiro capítulo, o autor mais uma vez comparou espécies com e sem o comportamento de monopolização. O plano era comparar a correlação entre diferentes tipos de características sexuais e sucesso reprodutivo. Mas o autor só pôde fazer os testes referentes a tamanho corporal, tanto para

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[4] Nota de RCMR: Charles Darwin publicou em 1871 o livro A descendência do homem e seleção em relação ao sexo. Darwin, C. 1871. The Descent of Man and Selection in Relation to Sex. 1st ed. J. Murray, London.

[5] Em 1970, Geoff Parker propôs o conceito de competição espermática. Em 1983, Randy Thornhill propôs o conceito de escolha críptica da fêmea. A: Parker, G. A. 1970. Sperm Competition and Its Evolutionary Consequences in the Insects. Biol. Rev. 45:525–567. B: Thornhill, R. 1983. Cryptic Female Choice and Its Implications in the Scorpionfly *Harpobittacus nigriceps*. Am. Nat. 122:765–788.

fêmeas como para machos. Não havia dados suficientes para comparar sistemas de acasalamento quanto a características envolvidas em luta, cortejo ou fertilização.

– Se o autor só obteve dados para tamanho corporal, por que ele investe espaço no texto para mencionar possíveis testes que ele não pôde fazer? – perguntou a Dra. Claudinha.

– Porque o autor triou um número muito grande de trabalhos. Se mesmo assim ele não obteve dados suficientes para atributos envolvidos em luta, cortejo ou fertilização, isso indica que pesquisadores deveriam investir mais projetos de pesquisa a preencher essa lacuna de conhecimento.

– E o que o autor encontrou em relação a tamanho corporal? – perguntou o Dr. Agostinhozinho. – Se bem entendi, a expectativa do teste aqui é que um maior tamanho corporal é muito importante para machos que tentam monopolizar fêmeas, mas menos ou nada importante quando machos não têm esse comportamento, e se limitam a cortejar fêmeas ou a tentar achar fêmeas de modo mais eficiente. Estou correto?

– Sim.

– Com base nisso, qual era mesmo a hipótese e qual foi o resultado encontrado?

– A hipótese era de que a correlação entre tamanho corporal e sucesso reprodutivo seria maior nas espécies em que machos tentam monopolizar fêmeas. No entanto, ser grande mostrou-se ser algo favorável independentemente do comportamento de monopolização ocorrer ou não. O fato de a expectativa inicial não ter sido corroborada talvez se deva ao fato de que machos pequenos investem muito na quantidade e qualidade de seu esperma, para competir com machos grandes que tentam monopolizar fêmeas. Assim, mesmo acasalando poucas vezes, esses machos pequenos conseguem produzir filhotes, pois investem muito em competição espermática. Já para fêmeas, a expectativa era de que fêmeas maiores seriam mais hábeis em se desvencilhar das tentativas de monopolização de machos e ajustariam assim o seu número de parceiros sexuais. A inexistência desse padrão talvez se deva ao fato de que fêmeas maiores são mais atraentes para machos, dado que elas produzem mais filhotes. Sendo mais atraentes, talvez fêmeas maiores sejam mais defendidas por machos monopolizadores. Se fêmeas grandes e mais atraentes são mais defendidas por machos, a aparente vantagem de ser grande desaparece.

– Mas para que o seu último argumento faça sentido, é necessário que seja verdadeira essa premissa de que fêmeas maiores são mais atraentes. Quão forte é essa premissa? – perguntou a Dra. Tatianinha.

– O autor dessa tese mostra que, independentemente do sistema de acasalamento, fêmeas maiores têm mais filhotes. O que é muito importante, pois corrobora uma hipótese muito antiga, proposta por Charles Darwin, para explicar a evolução de tamanho corporal em fêmeas. A ideia de Darwin é que fêmeas grandes foram selecionadas em muitas espécies uma vez que quanto maior for o corpo da fêmea mais energia ela tem para produzir ovos/óvulos.

– E quanto aos machos? Há alguma correlação entre tamanho corporal e sucesso reprodutivo? – perguntou a Dra. Robertinha.

– Há o mesmo padrão, machos maiores têm mais filhotes. Além disso, ainda para machos, embora não tenha sido possível comparar diferentes sistemas de acasalamento com base em investimento em cortejo ou fertilização, o autor pôde ao menos calcular se há correlação entre investimento em cortejo e sucesso reprodutivo e entre investimento em fertilização e sucesso reprodutivo. Para machos, maior investimento em ornamentos usados em cortejo não resultou em maior sucesso reprodutivo, mas maior investimento em estruturas envolvidas em fertilização de óvulos resultou em maior sucesso reprodutivo.

– Ok. E com base em tudo isso, o que você tem a dizer sobre o método científico adotado por humanos, Filipinho?

– Bom, esse trabalho claramente se utiliza do método hipotético-dedutivo, que é uma das formas de metodologia científica que nós também utilizamos. Assim como nós, os humanos também usam outros métodos científicos eficazes, mas eu simplifico a questão analisando somente um método aqui. O autor fundamentou questões com base no conhecimento científico pré-estabelecido em sua área de pesquisa. A partir dessas questões, ele formulou hipóteses de trabalho e, posteriormente, ele testou essas hipóteses. A partir dos resultados obtidos, ele refutou ou corroborou as hipóteses e discutiu os resultados tendo como base o conhecimento estabelecido na teoria de seleção sexual. Por fim, ele sugeriu passos futuros nessa área de pesquisa. Assim, o procedimento por ele adotado é muito similar ao procedimento que vários de nossos pesquisadores utilizam. E isso claramente se opõe às nossas expectativas em relação aos humanos, tendo em vista a notável e conhecida desigualdade social que a sociedade humana apresenta. Mas essa desigualdade social se deve ao fato de atividades diversas, incluindo a ciência, não serem destinadas ao bem comum. Contudo, constatarmos a existência dessa desigualdade social na espécie humana, no presente momento, não deveria ser suficiente para pressupormos que a ciência humana esteja muito distante da nossa. Na verdade, não está.

– Acho que temos o suficiente para avaliá-lo, Filipinho. Faremos um pequeno intervalo, durante o qual a banca se retirará para debater se você será aprovado ou não. Enquanto isso, o público que está nos assistindo continuará votando. Quando voltarmos, como você bem sabe, revelaremos o resultado da votação popular e o nosso veredicto – anunciou a Dra. Claudinha.

A banca avaliadora se retirou. E Filipinho permaneceu sentado, sozinho com seus pensamentos. As câmeras de toda a estrela voltadas para ele. Enquanto o povo votava se ele deveria ser aprovado ou não. O futuro de Filipinho estava sendo decidido. Seu amigo mais próximo, Zizinho, acabara de se tornar mestre. Seus irmãos todos tinham sido aprovados quando cursaram o mestrado. E se somente Filipinho fosse reprovado?

Enquanto Filipinho e toda a estrela esperavam pela decisão dos membros da banca, a transmissão informava aos espectadores a programação das próximas defesas de mestrado e doutorado. A próxima defesa seria sobre como diferentes sociedades lidam com pandemias. Na sequência, a audiência seria contemplada com algumas outras defesas, até que se chegasse à aguardada defesa de doutorado ‘Viagens no tempo: por que deram tão errado? Uma perspectiva histórica sobre como um torcedor de futebol alterou resultados de partidas do passado'[6]. Terminado o informe, a banca retornou para a sala onde a defesa ocorreu, e a Dra. Claudinha reiniciou os trabalhos:

– Filipinho, sei que você deve estar ansioso para saber a nossa decisão. Por isso mesmo, vou fazer o anúncio o mais rapidamente possível. Eu mesma detesto quando alguém vai anunciar o resultado de uma defesa de mestrado e fica se alongando para dar a resposta, gerando suspense, como se fosse um programa de entretenimento. No caso, até é um programa de entretenimento, mas este não é o nosso foco principal aqui. Outro dia mesmo, eu estava comentando com a Dra. Bianquinha – talvez você conheça a Dra. Bianquinha, é a que tem uma crista dorsal 2D amarela e estuda os vulcões celestes. – Enfim, comentei com a Dra. Bianquinha como ela foi efetivamente direta como chefa de uma banca de doutorado, recentemente. Ela anunciou a reprovação com uma elegância e eficácia invejáveis. Você deve ter assistido essa defesa.

Filipinho sinalizou que sim, sem saber o que estava respondendo.

– Pois bem, vamos então ao resultado – retomou a Dra. Claudinha. – Primeiro, anunciarei o resultado da votação do público que está nos assistindo de casa. Hoje, recebemos mais de 42 bilhões de votos! A audiência está alta. E... para 58,77% dos votantes... aos quais agradeço muito pela participação na votação de hoje, você, Filipinho... deve ser...

Dra. Claudinha então abriu o envelope que estava em suas mãos, e disse:

– Reprovado! Nosso público realmente gosta das execuções. Não canso de me surpreender com isso...

Filipinho se afundou um pouco mais em sua cadeira, completamente tenso. Mas sem razão para isso. Quase sempre o público vota pela reprovação. É como uma forma de piada na estrela de

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[6] Nota do narrador: A espécie de Filipinho não pratica futebol. Mas foi o jeito mais fácil de traduzir. O esporte mais popular na estrela de Filipinho é diferente de tudo o que vocês humanos conhecem. Mas os fãs de lá são tão fanáticos quanto os terráqueos que gostam de futebol.

Filipinho. Todos se divertem, e sabem que não influenciará a decisão da banca avaliadora. Eles têm um humor difícil de explicar.

– Filipinho – retomou a Dra. Claudinha –, nós da banca não tivemos dificuldade para chegar a um consenso. Na verdade, pouco precisamos debater a questão. Filipinho, após avaliação minuciosa de seu trabalho escrito, e da arguição que acabamos de desenvolver, deliberamos que você é o mais novo mestre de nossa estrela. Parabéns.

Nenhuma lágrima foi derramada com o anúncio, pois indivíduos da espécie de Filipinho não produzem lágrimas. E as reprovações são muito mais emocionantes, para ser sincero. Mas todos ficaram felizes por Filipinho.

– Mestre Filipinho, antes de encerrarmos esta sessão, você tem algo a dizer? – perguntou o Dr. Agostinhozinho. – Eventualmente, você gostaria de fazer agradecimentos?

– Sim, claro. Primeiramente, quero agradecer a todas e todos que me acompanharam até aqui, especialmente a quem me ajudou enquanto desenvolvi este projeto. Agradeço minha família, meus orientadores, meus demais amigos do trabalho e de fora do trabalho. Agradeço a vocês da banca, pela dedicação em avaliar minha pesquisa. Agradeço aos órgãos de financiamento que destinaram verba para que eu desenvolvesse o meu projeto. Sem financiamento, não há como fazer ciência, em qualquer lugar do Universo. E ciência é algo imprescindível para uma sociedade próspera, como a nossa. Por fim, agradeço a todas as pesquisadoras e todos os pesquisadores cujos trabalhos passados permitiram que eu realizasse a minha pesquisa. Pois o meu trabalho só foi possível porque muitos antes de mim estudaram o universo e divulgaram as suas descobertas para as próximas gerações de cientistas. Ciência é um trabalho coletivo. E fico feliz por fazer parte dele.

E assim se encerrou o grande dia de Filipinho. Como vocês já sabem, não era exatamente um dia. Mas isso pouco importa.

APPENDIX 1 - E-mail sent to the authors

Below, we present the template of the message sent to contact authors of potentially useful studies. Note that some studies contain data that is useful for all chapters of this thesis. Therefore, we have a single template for all meta-analyses. First, we tried to contact the researcher identified in the study as the corresponding author, and, if necessary or suggested by the corresponding author, we contacted an additional author.

Template

Dear Author,

I'm a PhD student from the University of São Paulo (Brazil) currently working at the Australian National University with Dr. Eduardo Santos & Prof Michael Jennions. I'm working on a meta-analysis asking how opportunities for selection and selection gradients are modulated by monopolization behavior (when an individual tries to physically monopolize sexual partners).

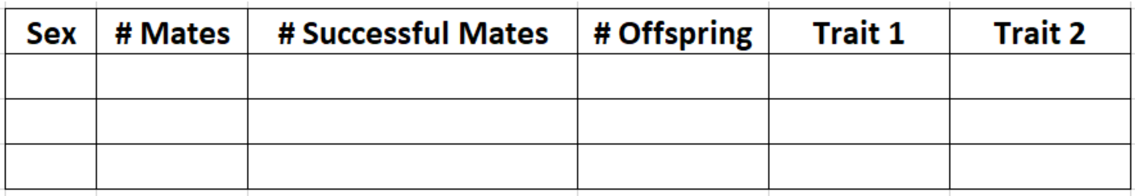
The request: One or more of your publications (see below) may have useful data for this meta-analysis, because you looked at variation in mating and/or reproductive success among a population of individually identifiable adults. I am writing to ask if it would be possible for you to cut and paste the relevant data into the attached Excel spreadsheet.

The data: the sheet has four main columns that each represents one identifiable adult.

1. The sex of each adult (“Sex”)
2. Total number of mating partners (# Mates)
3. Total number of mating partners with whom the individual sired offspring (# Successful Mates)
4. Total number of offspring produced (“# Offspring”)

For 2-4, if possible, please include all cases where the value is zero.

In addition, for any trait or behavior that you measured on these adults, if possible, please include their trait value in the spreadsheet (e.g. body size, tail length, call rate).



Sex	# Mates	# Successful Mates	# Offspring	Trait 1	Trait 2

If you have data from multiple studies, please use a new sheet for each study. We have included a NOTES sheet in the attached Excel file so that you can add any information you think we need (feel free to type everything into the first cell on the sheet).

Of course, if you prefer to send your original datafile (if necessary with irrelevant columns deleted) in a usable form that is equally fine.

What we will do: Please be assured that we do not intend to re-analyse the data you send to compare it to your published estimate of selection gradients, etc. We know that sometimes older data differs slightly from that used in a publication (e.g. maybe you only have a pre-final version of the data). Our sole focus is on the overall patterns across many studies. In return, we will be sure to send you a preprint of the study as soon as it becomes available. If you require any more information, please contact me.

If you are unable to send data, we please ask that you email back and simply say that you cannot assist us. That way we can cross you off the list when it comes to sending out reminder emails in three week's time.

Finally, thank you so much for your assistance. We know it is painful to dig out old data. If only Dryad had been compulsory from the start of our careers!

Best wishes,

Renato Chaves de Macedo Rego

List of publications:

1)

APPENDIX 2 - The phylogeny

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.000000)Node92:9.188141,Eleutherodactylus_coqui:67.188141)Node91:27.011856,Hyalinobatrachium_valerioi:94.199997,((Bufo_americanus:38.299999,Bufo_bufo:38.299999)Node96:26.907902,(Allobates_femoralis:46.900002,(Dendrobates_leucomelas:41.799999,Epipedobates_tricolor:41.799999)Node98:5.100002)Node97:18.307899)Node95:28.992096)Node90:60.514160,((Chiromantis_xerampelina:47.599998,Polypedates_megacephalus:47.599998)Node100:43.598122,Rana_catesbeiana:91.198120)Node99:63.516037)Node89:58.857056,(Alytes_cisternasii:36.703644,Alytes_obstetricans:36.703644)Node101:176.867569)Node88:83.287827,(((Ambystoma_texanum:21.468309,Ambystoma_tigrinum:21.468309)Node104:1.287851,Ambystoma_opacum:22.756161)Node103:128.691376,Taricha_granulosa:151.447540)Node102:145.411499)Node87:54.899445,((((((Agkistrodon_contortrix:42.240414,Vipera_berus:42.240414)Node111:19.497665,((Elaphe_obsoleta:23.799999,Stegonotus_cucullatus:23.799999)Node113:23.799999,Nerodia_sipedon:47.599998)Node112:14.138081)Node110:105.386108,(Barisia_imbricata:165.229095,Crotaphytus_collaris:165.229095)Node114:1.895096)Node109:10.872635,((Podarcis_hispanica:22.770260,Podarcis_melisellensis:22.770260)Node116:22.770260,Lacerta_agilis:45.540520)Node115:132.456299)Node108:6.918411,(Liopholis_whitii:79.199997,Pseudemoia_entrecasteauxii:79.199997,(Eulamprus_heatwolei:9.716383,Eulamprus_quoyii:9.716383)Node118:69.483612)Node117:105.715240)Node107:94.741745,(Chrysemys_picta:253.734207,((Meleagris_gallopavo:37.200001,Pavo_cristatus:37.200001)Node121:60.842869,(Clamator_glandarius:85.199997,(Chiroxiphia_lanceolata:65.691208,(Notiomystis_cincta:61.799999,(Troglodytes_aedon:50.542377,(Pachycephala_pectoralis:44.000000,(((((Agelaius_phoeniceus:6.108348,Molothrus_ater:6.108348)Node131:11.051249,(Geothlypis_trichas:7.783097,Setophaga_ruticilla:7.783097)Node132:9.376500)Node130:17.640402,(Calcarius_pictus:19.200001,Spiza_americana:19.200001)Node133:15.599998,Prunella_collaris:34.799999,Taeniopygia_guttata:34.799999)Node129:3.200001,(((Zonotrichia_albicollis:1.705683,Zonotrichia_leucophrys:1.705683)Node136:3.073124,Junco_hyemalis:4.778807)Node135:14.353638,Volatinia_jacarina:19.132444)Node134:18.867556)Node128:5.700001,((Delichon_urbica:18.730181,Hirundo_rustica:18.730181)Node138:8.606258,Tachycineta_bicolor:27.336439)Node137:16.363562,((((Luscinia_svecica:29.012283,Sialia_currucoides:29.012283)Node142:5.187717,Ficedul a_albicollis:34.200001)Node141:1.248806,Lamprotornis_superbus:35.448807)Node140:7.289822,Acrocephalus_arundinaceus:42.738628,Cyanistes_caeruleus:42.738628)Node139:0.961372)Node127:0.299999)Node126:6.542377)Node125:11.257622)Node124:3.891209)Node123:19.508789)Node122:12.842873)Node120:155.691345)Node119:25.922775)Node106:32.246948,(((((((((Urocitellus_columbianus:2.701175,Urocitellus_parryii:2.701175)Node152:7.347178,Callospermophilus_lateralis:10.048352)Node151:1.279358,Xerospermophilus_tereticaudus:11.327710)Node150:15.472289,(Tamias_amoenus:12.487110,Tamias_striatus:12.487110)Node153:14.312889)Node149:43.744930,((Myodes_glareolus:22.826015,Phodopus_campbelli:22.826015)Node155:5.973984,(Neotoma_cinerea:19.250980,Peromyscus_californicus:19.250980)Node156:9.549019)Node154:41.744930)Node148:2.331779,Ctenodactylus_gundi:72.876709)Node147:16.946480,(((((Macaca_mulatta:6.957132,Macaca_sylvanus:6.957132)Node161:5.442868,Mandrillus_sphinx:12.400000)Node160:17.041548,(Pan_paniscus:2.820060,Pan_troglodytes:2.820060)Node162:26.621489)Node159:13.709747,Alouatta_caraya:43.151295)Node158:30.685596,Microcebus_murinus:73.836891)Node157:15.986298)Node146:6.639198,(((Ovis_aries:27.307281,(Cervus_elaphus:13.600000,Dama_dama:13.600000,Odocoileus_virginanus:13.600000)Node166:13.707281)Node165:50.447678,(Canis_familiaris:45.528351,(Ailuropoda_melanoleuca:39.893414,Mirounga_leonina:39.893414)Node168:5.634937)Node167:32.226608)Node164:11.568863,(Crocidura_russula:33.740665,Sorex_araneus:33.740665)Node169:55.583157)Node163:7.138565)Node145:8.997391,Loxodonta_africana:105.459778)Node144:53.137817,((Antechinus_agilis:8.355157,Antechinus_stuartii:8.355157)Node171:53.273853,Phascolarctos_cinereus:61.629009)Node170:96.968582)Node143:153.306335)Node105:39.854553)Node86:83.565582)Node66:37.981293)Node65:323.250305)Node2:27.444336,Macrostomum_lignano:824.000000)Node1:1.000000;

APPENDIX 3 - Search protocol for moderators

In order to identify if females or males in the populations analyzed try to economically monopolize sexual partners, we used the following protocol:

1) We read the original paper from which we extracted selection indexes and analyzed any description of the ecological/social mating system. If the original paper informed if individuals try or not to monopolize sexual partners, the protocol was finished on this first step. Otherwise, we proceeded to the next step.
2) If the information provided by the original paper did not suffice to identify if there is monopolization of sexual partners, we searched for additional information on *Web of Science*, screening other publications made by the first author of the original paper (Advanced search - TS=("name of the species") AND AU=(surname of the first author of the original paper)). In case these publications did not inform whether individuals try or not to monopolize sexual partners (or if we did not find additional publications), we proceeded to the next step. If the original paper had only one author, we proceeded to Step 5.
3) Same procedure as Step 2, above, but searching for publications by the last author of the original paper from which effect sizes were calculated, instead of the first author (Advanced search - TS=("name of the species") AND AU=(surname of the last author of the original paper)). Once again, in case these publications did not inform whether individuals try or not to monopolize sexual partners (or if we did not find additional publications), we proceeded to the next step. If the original paper had only two authors, we proceeded to Step 5.
4) Same procedure as Step 3, above, but searching for publications by any other authors of the original paper (Advanced search - TS=("name of the species") AND AU=(surname of the 2nd author of the original paper OR surname of the 3rd author of the original paper OR (…) surname of the X^n author of the original paper)). Once again, in case these publications did

not inform whether individuals try or not to monopolize sexual partners (or if we did not find additional publications), we proceeded to the next step.

5) We read only the studies cited in the excerpts from the original paper that describe the social mating system of the studied population. These excerpts may not suffice to characterize the monopolization behavior (or lack of it) in the species at hand, but they can lead to useful studies. In case these cited studies were not useful to identify if individuals try or not to monopolize sexual partners, or if there were no potentially useful cited studies, we proceeded to the next step.
6) Search in the *Web of Science* for any studies about the species analyzed and that focus on sexual contexts (Advanced search - TS=("name of the species") AND TS=(sexual OR mat*)). In case these studies were not useful to identify if individuals try or not to monopolize sexual partners, or if the search did not bring any new studies, we proceeded to the next step.
7) Search in the *Web of Science* for any studies about the species analyzed (Advanced search - TS=("name of the species"). In case these studies were not useful to identify if individuals try or not to monopolize sexual partners, or if the search did not return any new useful studies, we considered that the required information is not available in the literature.

APPENDIX 4 - On monopolization behavior

Why monopolization matters

If an individual, a male, for example, monopolizes a mature individual of the opposite sex, a female (in this example), this male may prevent male conspecifics from mating with the guarded female. Accordingly, this male may also prevent its own sexual partner from mating with additional males. Therefore, this monopolization behavior can influence the intensity of sexual selection in individuals of both sexes. For instance, if only some males are able to monopolize several females and, hence, other males fail to mate, this will produce a high variation in mating success among males. Concomitantly, once monopolized by a male and prevented from mating with other males, females will tend to have similar mating success levels. Altogether, the low variance in mating success among females and the high variance in mating success among males mean that males will face a greater opportunity for sexual selection (I_s) than females. If the sexual monopolization prevents some males from mating, these males will not be able to reproduce, while dominant males will tend to have higher reproductive success. Complementarily, females will tend to present not only similar mating success levels, but will also tend to have similar reproductive success, as the majority of females will mate with a single high-quality male (therefore, females will not differ according to the amount of indirect benefits obtained from mating). This high variance in male reproductive success should produce a higher opportunity for selection among males (I), but the same is not expected for females.

What kind of monopolization are we talking about?

We are interested in characterizing social mating systems. A male may be able to fertilize all of the female's eggs, fathering all or the great majority of a female's offspring, and this could be interpreted as 'monopolization'. However, in this study, we are only interested in the attempt to monopolize mating/pairing/copulating opportunities. These monopolization attempts will interfere in intrasexual post-mating competition, and the monopolization behavior itself may evolve in response to the risk of post-mating competition. However, the focus here is exclusively on the behavior that potentially restrict re-mating ability of a sexual partner, translating into an economical monopolization of this partner. Moreover, we note that we are interested in any monopolization behavior, regardless of the sex exhibiting it, as females are also able to economically monopolize mating/pairing/copulating opportunities with males.

In this study, we are investigating the consequences of monopolization of sexual partners, which translates into the monopolization of mating opportunities. Here, we are not considering the term ‘mating’ to represent a long-term sexual and/or social association between a female and a male. For animals with internal fertilization, we are considering ‘mating’ to represent the occurrence of one copulation event and, for animals with external fertilization, we are considering ‘mating’ to represent the unit of strictly sexual interaction between a female and a male that includes the release of gametes. Therefore, an individual can mate with several sexual partners, but cannot mate with two partners at the exact same time.

Every time an individual of one sex is sexually receptive, this configures a mating opportunity for members of the other sex. As above explained, one individual cannot mate with two different sexual partners at the exact same time (though it is possible that mating events with two sexual partners can occur close together and succeed each other in a very short time period). Moreover, one individual cannot mate continuously, without interruptions, during the whole mating season. So, for example, if a given focal male is mating, recovering from mating activities, engaging in non-sexual activities, or courting a female, and there are other receptive females available at the same time, this focal male is susceptible to lose mating opportunities to competitors. One way to avoid the loss of these mating opportunities is to economically monopolize this resource (i.e. sexually receptive individuals of the opposite sex). And here, we stress out that the situation described by us includes both monogamy and polygamy, given that an individual can try to monopolize mating opportunities with its single sexual partner or to monopolize mating opportunities provided by more than one (potential) sexual partner.

As reported in the main text, individuals can try to monopolize sexual partners directly or indirectly. These forms of monopolization behavior were described by Emlen and Oring (1977) and classified into two mating systems, when it comes to monopolization of females (i.e. female defense polygyny and resource defense polygyny). We considered that monopolization behavior occurs when the population presents defense polyandry/polygyny. Additionally, for populations in which the mating system was described as a lek or scramble competition, we considered that there is no monopolization behavior. For more on the characterization of female defense polygyny, resource defense polygyny, and leks, see Emlen and Oring (1977). For more on the characterization of scramble competition, see Schwagmeyer and Woontner (1986).

In various cases, among the original papers that we analyzed, authors did not explicitly name one of the four classical mating systems described above. In these situations, we read the available descriptions of the social mating system, looking for the description of behaviors that fit one of the previously described mating systems. Therefore, we classified as cases of occurrence of monopolization behavior when the mating system's description portrayed a situation in which an individual defends a resource (including territories), and, by doing that, indirectly restricts the access of other individuals of the same sex to mating opportunities. Accordingly, we classified as cases of occurrence of monopolization behavior when the mating system's description portrayed a situation in which an individual directly defends the access to individuals of the other sex, preventing competitors from achieving mating success.

For the purposes of this study, we did not consider prolonged matings as monopolization behavior. One could argue that an individual can prolong the mating duration in order to monopolize its sexual partner by extending its period out of the mating pool. However, despite the fact that, while a pair mates, female and male are temporarily unavailable for other conspecifics, we did not consider prolonged matings as type of monopolization behavior for three reasons:

(i) It is difficult (if not impossible) to establish which sex is trying to monopolize the other;

(ii) Mate duration can be prolonged in order to extend the time for sperm transfer, to extend the time dedicated to court the sexual partner (which can be advantageous in a context of cryptic female choice, for example), or to minimize the chances of sperm removal by competitors; and

(iii) Every single mating event translates into the removal of two individuals from the mating pool, and, if removing sexual partners from the mating pool was considered as a type of monopolization behavior, any mating event would be considered as an event of the occurrence of monopolization behavior.

The non-occurrence of monopolization behavior is harder to identify. If the literature described a social mating system as being similar to the definitions of lek and scramble competition that we presented above, we classified this mating system as not presenting monopolization. Additionally, if the description did not allow us to establish the occurrence nor the absence of monopolization behavior, we classified the mating system as 'Undefined'.

References

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Schwagmeyer, P. L., and S. J. Woontner. 1986. Scramble competition polygyny in thirteen-lined ground squirrels: the relative contributions of overt conflict and competitive mate searching. Behav. Ecol. Sociobiol. 19:359–364.