1

Does the potential strength of sexual selection differ between mating systems with and without defensive behaviours? A meta-analysis

Renato C. Macedo-Rego[1,2,*] ⓘ, Michael D. Jennions[2,3] ⓘ and Eduardo S. A. Santos[1] ⓘ

[1]*Programa de Pós-graduação em Ecologia, Instituto de Biociências, Universidade de São Paulo, Rua do Matão, trav. 14, no. 321, São Paulo SP 05508-090, Brazil*

[2]*Division of Ecology & Evolution, Research School of Biology, Australian National University, Canberra, ACT, Australia*

[3]*Stellenbosch Institute for Advanced Study (STIAS), Wallenberg Centre, 10 Marais Street, Stellenbosch 7600, South Africa*

ABSTRACT

The Darwin–Bateman paradigm predicts that females enhance their fitness by being choosy and mating with high-quality males, while males should compete to mate with as many females as possible. In many species, males enhance their fitness by defending females and/or resources used by females. That is, males directly defend access to mating opportunities. However, paternity analyses have repeatedly shown that females in most species mate polyandrously, which contradicts traditional expectations that male defensive behaviours lead to monandry. Here, in an extensive meta-analysis, encompassing 109 species and 1026 effect sizes from across the animal kingdom, we tested if the occurrence of defensive behaviours modulates sexual selection on females and males. If so, we can illuminate the extent to which males really succeed in defending access to mating and fertilisation opportunities. We used four different indices of the opportunity for sexual selection that comprise pre-mating and/or post-mating episodes of selection. We found, for both sexes, that the occurrence of defensive behaviours does not modulate the potential strength of sexual selection. This implies that male defensive behaviours do not predict the true intensity of sexual selection. While the most extreme levels of sexual selection on males are in species with male defensive behaviours, which indicates that males do sometimes succeed in restricting females' re-mating ability (e.g. elephant seals, *Mirounga leonina*), estimates of the opportunity for sexual selection vary greatly across species, regardless of whether or not defensive behaviours occur. Indeed, widespread polyandry shows that females are usually not restricted by male defensive behaviours. In addition, our results indicate that post-mating episodes of selection, such as cryptic female choice and sperm competition, might be important factors modulating the opportunity for sexual selection. We discuss: (*i*) why male defensive behaviours fail to lower the opportunity for sexual selection among females or fail to elevate it for males; (*ii*) how post-mating events might influence sexual selection; and (*iii*) the role of females as active participants in sexual selection. We also highlight that inadequate data reporting in the literature prevented us from extracting effect sizes from many studies that had presumably collected the relevant data.

Key words: fertilization success, lek, mate guarding, mating success, opportunity for selection, opportunity for sexual selection, polyandry, polygyny, reproductive success, sperm competition.

CONTENTS

* Author for correspondence (Tel.: +551130917600; E-mail: rcmacedorego@gmail.com).

I. INTRODUCTION

The Darwin–Bateman paradigm predicts that males maximise their reproductive success by mating with as many females as possible because each additional mating increases male fitness (Darwin, 1871; Bateman, 1948; Dewsbury, 2005). Female fitness, on the other hand, is thought to depend more heavily on the quality of her sexual partners, meaning that females should benefit more from being choosy rather than simply seeking out multiple sexual partners (Darwin, 1871; Bateman, 1948; Dewsbury, 2005). This rationale was first introduced by Darwin (1871), and later empirically tested by Bateman (1948) in a series of experiments with fruit flies (*Drosophila melanogaster*). Bateman (1948) showed that multiple mating results in a negligible increase in reproductive success for females, but in a high increase for males, which supported the claim that choosiness will evolve more frequently among females than among males (although Bateman's results were later questioned; Gowaty, Kim & Anderson, 2012). In the following decades, Bateman's approach of relating the number of mates to reproductive success was replicated for numerous species in many taxa: e.g. Actinopterygii (Wacker *et al.*, 2014), Amphibia (Mangold *et al.*, 2015), Coleoptera (Fritzsche & Arnqvist, 2013), *Drosophila melanogaster* (Bjork & Pitnick, 2006), Gastropoda (Johannesson *et al.*, 2016), Hemiptera (Gagnon, Duchesne & Turgeon, 2012), Mammalia (Wells *et al.*, 2017), Passeriformes (Apakupakul & Rubenstein, 2015), Pycnogonida (Barreto & Avise, 2010), and Reptilia (Halliwell *et al.*, 2017). Finally, a comprehensive meta-analysis has shown that the pattern found for fruit flies occurs across the animal kingdom (Janicke *et al.*, 2016), with males having a steeper relationship

between mating and reproductive success than females, giving strong support to the Darwin–Bateman paradigm. It should be noted, however, that the mean relationship is also positive in females, which could be taken to imply that females benefit from mating multiply [Fromonteil *et al.*, 2023; but see Kokko & Jennions (2023) for alternative explanations].

In an effort to understand the uneven distribution of mating opportunities among individuals of a species, Emlen & Oring (1977) presented a classification of ecological mating systems that has guided research in the field ever since. In many species, males try to monopolise access to sexual partners by defending a resource used by females [i.e. resource defence polygyny (e.g. Noble *et al.*, 2013; York & Baird, 2015)] or by directly defending females [i.e. female defence polygyny or harems (Macedo-Rego & Santos, 2021; e.g. Tentelier *et al.*, 2016)]. In other systems, males do not directly defend access to mating opportunities. For instance, males may display ornaments to potential sexual partners and outcompete rivals on leks (Broquet, Jaquiéry & Perrin, 2009; Sardell & DuVal, 2013). In other species, males maximise their reproductive success by investing in finding as many mates as possible and/or finding mates faster than their rivals, under 'scramble competition' (Herberstein, Painting & Holwell, 2017; e.g. Prosser *et al.*, 2002). The theoretical expectation is that the intensity of sexual selection (i.e. non-random variance in mating and/or reproductive success) will be higher among males in species in which male defensive behaviours occur than in species lacking such behaviours (Emlen & Oring, 1977), because these males try directly to prevent competitors from mating. As males directly defend females they reduce mating opportunities for rivals, and the potential for females to mate multiply may be restricted.

This leads to the complementary prediction that the intensity of sexual selection among females will be lower in species in which male defensive behaviours occur than in species without such behaviours (partially following the rationale presented by the constrained female hypothesis: see Gowaty, 2006).

In many species it was traditionally assumed that dominant males fathered the offspring born in their territories and/or harems. However, with genetic parentage analyses, this assumption has been challenged. We now know that males that succeed in securing territories and/or harems frequently lose paternity to subordinate males and/or neighbours (e.g. Dixson, Bossi & Wickings, 1993; Ellis & Bercovitch, 2011). This could be the direct result of female mate choice, because there is increasing evidence that females benefit from multiple matings (Jennions & Petrie, 2000; Slatyer *et al.*, 2012; Kvarnemo & Simmons, 2013; see also Fromonteil *et al.*, 2023; but see Kokko & Jennions, 2023) and that females mate polyandrously in many species (Gowaty, 2006; Taylor, Price & Wedell, 2014). Consequently, if some males try to prevent their rivals from accessing fertile females but (partially) fail, then the social (ecological) mating system can differ from the genetic mating system (Møller & Birkhead, 1994). This means that social mating systems do not tell us the whole story, despite their unquestionable utility. First, for many species, more individuals achieve matings than are documented in the field, which may severely bias our estimates of 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 post-mating than pre-mating episodes of sexual selection, and social mating systems are descriptors of pre-mating events. This is particularly important because sperm competition [i.e. the competition among sperm from different males that mated with the same female (Parker, 1970*a*,*b*)] and cryptic female choice (i.e. female post-mating choice of male sperm; Thornhill, 1983) seem to play a major role in sexual selection (Turnell & Shaw, 2015; Devost & Turgeon, 2016; Firman *et al.*, 2017; Parker, 2020). Consequently, the distribution of matings and offspring in nature may differ from expectations based solely on the described mating system, justifying further investigation of the relative strength of different episodes of sexual selection.

The picture now emerging is that: (*i*) from Darwin (1871) until Parker (1970*a*,*b*), researchers focused on what happens before mating, which distorted our perception of the relative roles played by pre- and post-mating events; (*ii*) sometimes females mate multiply, which increases the opportunity for post-mating sexual selection through sperm competition and cryptic female choice (Kvarnemo & Simmons, 2013); and (*iii*) some non-dominant males that achieve low mating success are effective post-mating competitors, who can therefore still achieve high reproductive success (e.g. Fu, Ne & Gross, 2001; Buzatto, Tomkins & Simmons, 2014). Together these phenomena raise questions about the validity of parsimonious predictions about variation in male reproductive success that are based on

social mating systems. Given this scenario, one may ask how effective dominant males are in defending their access to mating opportunities. How do defensive behaviours influence the intensity of sexual selection on males, and, for that matter, on females?

Defensive behaviours by males should restrict female re-mating potential and thereby reduce the variance in female mating, fertilisation and reproductive success. Here we test the hypothesis that females have a lower opportunity for sexual selection (i.e. an upper limit for sexual selection intensity; Klug *et al.*, 2010*a*) in species in which defensive behaviours occur than in those lacking such behaviours. Complementarily, if defensive behaviours by males increase the variance in male mating, fertilisation and reproductive success, then males have a higher opportunity for sexual selection in species in which defensive behaviours occur than in those lacking such behaviours. To test these hypotheses, we conducted an extensive meta-analysis across the animal kingdom, extracting more than a thousand effect sizes estimates and using four different indices of the opportunity for selection that focus on three different episodes of selection (i.e. mating, fertilisation, and reproduction). In so doing, we use the theoretical bases of sexual selection research established by Darwin (1871), and test if it withstands the new information arising from modern techniques of paternity analysis.

II. METHODS

(1) Literature search

We conducted an extensive and systematic search of the literature for studies that quantified variation in mating, fertilisation and reproductive success among individuals in animal species. We searched for articles using the following combination of key words: '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.

(2) Screening studies

By reading titles and abstracts, we selected articles that seemed to quantify the mating and reproductive success of females and/or males in non-human animals. These included studies that calculated the opportunity for pre-mating sexual selection (I_s), the opportunity for selection (I), and the Bateman gradient. We excluded experimental studies that did not allow mating success to vary (e.g. when individuals could only mate with one partner). We then read all studies selected at this first step to check their eligibility and extract data. Again, we excluded studies that did not allow mating success to vary. Finally, we excluded data from studies with experimental groups in which individuals faced a treatment that changed their reproductive performance. The number of studies retained at each stage is presented in Section III.1.

(3) Effect sizes

We extracted data to calculate effect sizes (i.e. standardized ways of estimating the strength of a phenomenon that can then be compared across studies) that are proxies of the strength of sexual selection. We used five indices of selection as effect sizes because it is important to assess sexual selection at the successive stages between obtaining mates and fertilising eggs [i.e. pre-mating, post-mating and total selection (Fitze & Le Galliard, 2011; Kvarnemo & Simmons, 2013)]. These indices require simple data to be calculated (Henshaw, Kahn & Fritzsche, 2016) and are widely used in sexual selection studies (but see below for more on I_{fss}). The five indices that we used as effect sizes are: I_s, the opportunity for pre-mating sexual selection – the variance in mating success divided by the squared mean mating success (Crow, 1958); I_{fss}, the opportunity for pre-fertilisation sexual selection – the variance in fertilisation success divided by the squared mean fertilisation success (Macedo-Rego, 2020); I, the opportunity for selection – the variance in reproductive success divided by the squared mean reproductive success (Wade, 1979); the Bateman gradient – the slope of the least squares regression of reproductive success on mating success (Bateman, 1948; Arnold & Duvall, 1994); and the Jones index (s_{max}') – the upper limit for the intensity of sexual selection upon a specific trait correlated with mate acquisition [= the square root of I_s multiplied by the respective Bateman gradient (Jones, 2009; Henshaw et al., 2016)].

We estimated these indices for both females and males. For a focal individual, mating success is either the number of times they were observed mating, or the number of different sexual partners. fertilisation success is the number of individuals that fertilised or were fertilised by the focal individual. Reproductive success is the number of offspring produced, which is based on a range of taxon-specific measures (e.g. number of embryos in a pouch, number of eggs in a nest, brood size). Means and variances are calculated among individuals of the same sex in the study population.

Several studies originally calculate I_s by inferring mating success from genetic analyses (i.e. female mating success was the number of males that fertilised her eggs, and male mating success was the number of females fertilised; see Parker & Tang-Martinez, 2005). However, I_s estimates calculated from genetic analyses differ from I_s estimates from observing and recording mating events as genetics underestimates the true number of mating partners (Cramer et al., 2020; Macedo-Rego, 2020). Because genetic analyses reveal fertilisation rather than mating success (not all matings lead to fertilisation and reproduction), we use an additional index of sexual selection, analogous to I_s and I: the opportunity for pre-fertilisation sexual selection, I_{fss}. It equates to the standardized variance in fertilisation success among individuals of the same sex. Although other indices exist to estimate post-mating sexual selection (e.g. Shuster, Briggs & Dennis, 2013), we opted to use I_{fss} as it allows us to compare three indices that are calculated in the same manner, namely I_s, I_{fss}, and I, but provide different information. In summary, I_s reveals the opportunity for sexual selection due to variance in mating success, and is our proxy for pre-mating sexual selection; I_{fss} reveals the opportunity for sexual selection from variance in fertilisation success, and is our proxy for the influence of post-mating sexual selection; and I reflects the opportunity for selection due to variance in reproductive success and is our proxy for total selection (Fig. 1). Being standardized and dimensionless, I_s, I_{fss} and I allow for the comparison of data from different studies (Moura & Peixoto, 2013). A study was only included in our meta-analysis if it provided at least one measure of I and one of I_s or I_{fss} for at least one sex to allow us to investigate different selection episodes (pre-mating, post-mating, and total selection) within a sex. For each effect size, we recorded the sex of the individuals sampled and the sample size. Finally, we excluded potential effect sizes from studies in which the authors somehow influenced the mating success of (some) individuals (e.g. an experimental design where some individuals had fewer potential sexual partners available).

The Bateman gradient is traditionally calculated as the least squares regression of reproductive success on mating success. There can be a positive relationship even when mating success does not *cause* variation in reproductive success. For instance, if some individuals in a population are inherently more fecund/fertile, and thereby more attractive (Parker & Tang-Martinez, 2005; Gerlach et al., 2012; Anthes et al., 2016; Kokko & Jennions, 2023), they might tend to have higher mating success than less-fecund/fertile individuals. Given this, we therefore calculated the Bateman gradient as the r correlation between relative mating success and relative reproductive success (Jones, 2009; Anthes et al., 2016). We calculated relative mating, fertilisation or reproductive success by dividing every individual measure of success by the mean success in the study population. As many studies infer mating success from fertilisation success (i.e. information on actual mating success is lacking), we also calculated the correlation between relative fertilisation success and the relative reproductive success as a proxy for the
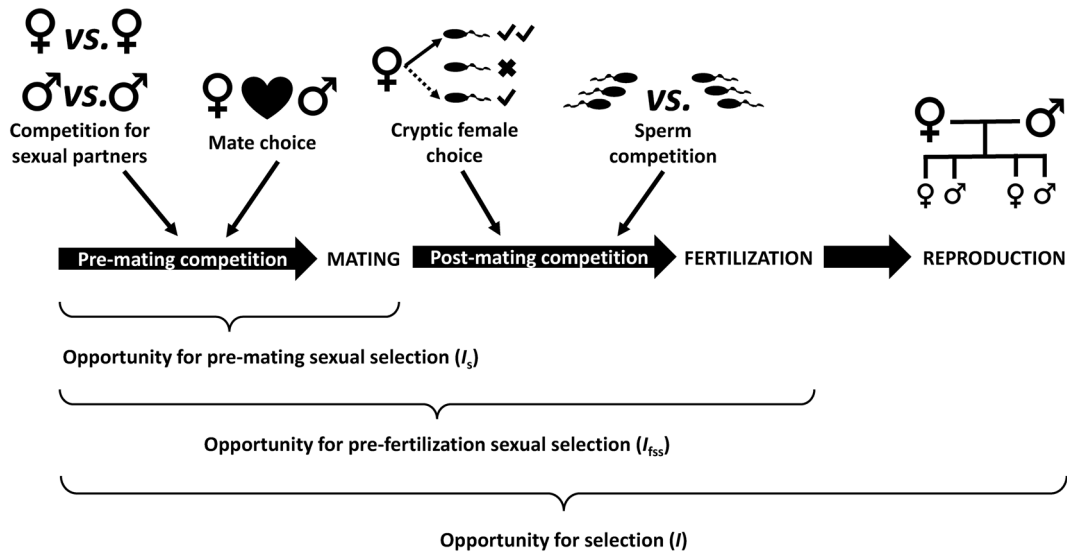
Fig. 1. The standard reproductive sequence in sexually reproducing, dioecious species. Pre-mating competition over mating is followed by post-mating competition for fertilisation. Together they determine reproductive success. Two key processes characterise pre-mating competition: (*i*) direct competition between individuals of one sex for access to mates of the other sex; (*ii*) mate choice. Two key processes also characterise post-mating competition: (*i*) competition between sperm of different males that mated with the same female; (*ii*) post-mating female choice of sperm. We therefore looked at the opportunity for pre-mating sexual selection [standardized variance in mating success (I_s)], the opportunity for pre-fertilisation sexual selection [standardized variance in fertilisation success (I_{fss})], and the opportunity for selection [standardized variance in reproductive success (I)].

Bateman gradient. Our results did not differ for Bateman gradients based on mating or fertilisation success (see Section III.5).

For the Jones index, which defines the upper limit of the intensity of sexual selection upon a specific trait correlated with mate acquisition (Jones, 2009; Henshaw *et al.*, 2016), we calculated the Bateman gradient as the slope of the least squares regression of standardized reproductive success on standardized mating success. Here, we did not calculate the Bateman gradient as a correlation because this selection index is based on the premise that variance in mating success promotes sexual selection because mating success influences reproductive success (see Jones, 2009; Henshaw *et al.*, 2016).

Importantly, for all the selection indices mentioned here, 'population' refers to animal groups for which variance in mating, fertilisation or reproductive success could be measured in each study. Thus, populations may refer to groups of individuals that live in different localities (e.g. LaBarbera, Lovette & Llambías, 2012; Nakadera *et al.*, 2017), but it may also refer to different experimental trials/groups in a field or laboratory experiment (e.g. Gauthey *et al.*, 2016; Morimoto, Pizzari & Wigby, 2016; Sundin *et al.*, 2017). In addition, some studies sampled individuals for more than one year or breeding season (e.g. Kraaijeveld-Smit, Ward & Temple-Smith, 2003; Serbezov *et al.*, 2010) and, because populations may change from one year/season to the next, whenever possible we calculated selection estimates for each season/year. Therefore, some screened studies provided more than one estimate of the same selection index for a given sex.

We calculated as many as possible of the five types of effect size from information provided in the main text or tables of each article and/or their 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. In such cases we searched for the necessary data on two repositories: *Dryad* and *Figshare*. After this step, there were more than 450 studies where the authors appeared to have collected the relevant data, but we could not extract it from the published material. Of these studies, we identified 152 studies where it was feasible to contact the authors to ask for data. We first tried to contact the corresponding author. If necessary, or suggested by the corresponding author, we then contacted an additional author.

(4) The key moderator

To test hypotheses about causes of variation in sexual selection we classified studies based on several moderators. The key moderator we were interested in was the presence or absence of defensive behaviours in each species. We preferentially used information on defensive behaviours from the primary study used to extract the selection indices estimates. If necessary, we used additional information from the literature (for the search protocol, see the online Supporting Information, Appendix S1). As both females and males can display defensive behaviours, we extracted data from species in which females are the sex that mainly shows defensive

behaviours, species in which males are the sex that mainly shows defensive behaviours, and species in which neither sex defends access to mating opportunities. Henceforth, we use 'guardians' to refer to females and males that defend access to mating opportunities. Complementarily, we use 'guarded individuals' to refer to females and males that are targets of defensive attempts. Because male defensive behaviours are far more common than female defensive behaviours (at least in the data set we constructed), most guarded individuals are females and most guardians are males.

We defined individuals as defending access to mating opportunities when: (*i*) they defend access to at least one adult of the opposite sex; and/or (*ii*) they defend access to a resource (including territories) used by the opposite sex, thereby defending access to potential mates. It is possible that defence of sexual partners and resources needed by them co-occur (Emlen & Oring, 1977), and we clump both types of defensive systems together. We defined individuals as not defending access to mating opportunities if: (*i*) the literature reported that neither sex defends access to mature individuals of the opposite sex (either by defending resources/territories or *via* direct defence); (*ii*) the mating system is described as 'scramble competition' or a lek. On leks some males achieve far higher mating success than others (Emlen & Oring, 1977; Mackenzie *et al.*, 1995), but males do not directly defend resources or sexual partners (Emlen & Oring, 1977; Thornhill & Alcock, 1983). Thus, males do not directly preclude competitors from seeking mates. Instead, female choice appears to drive variation in male mating success (see Queller, 1987; Kirkpatrick & Ryan, 1991; Höglund & Alatalo, 1995).

Importantly, categorisation of social mating systems and other social patterns are useful, but they simplify diverse, complex, and often continuous distributions. There is almost certainly a gradient in the intensity of defensive behaviours, ranging from species with no defensive behaviours to those with striking/intense defensive behaviours. Social mating systems are distributed unevenly along this gradient, with some showing more intense/aggressive defensive behaviours than others. So why use a categorical classification? First, we are testing established hypotheses that are based on categorical classifications of mating systems (Emlen & Oring, 1977). Second, there is no universal way to quantify the degree of defensive behaviours across very different species (e.g. bees *versus* elephants). Third, even if there was a way to do this, most studies lack the necessary information on the studied species. In fact, from 153 studies where we extracted effect sizes, only 2.6% directly assessed a behaviour related to intrasexual combats/fights (Noble *et al.*, 2013; Huyghe *et al.*, 2014; York & Baird, 2015; Devost & Turgeon, 2016). We thus compared mating systems according to the presence and absence of defensive behaviours. We provide more details on how we classified mating systems in Appendix S2.

Finally, we included in our data set hermaphroditic species because some of them show defensive behaviours (Oliver, 1997; Dillen, Jordaens & Backeljau, 2009) and it is possible to calculate fitness for individuals acting as females or males (Janicke, David & Chapuis, 2015; Marie-Orleach *et al.*, 2016).

(5) Additional moderators

We recorded additional variables that we felt might influence selection estimates.

(1) 'Mating success measure': authors either counted the number of mating events or the number of mating partners per individual.
(2) 'fertilisation success measure': authors either counted the number of fertilisation events [<0.01% of all cases in our data set (e.g. Nishida, 1987; Böll & Linsenmair, 1998)] or they counted how many individuals the focal individual produced at least one offspring with.
(3) 'Inclusion of zeros': whether the data included individuals with no mating success. Their inclusion or exclusion leads to different estimates of selection (Klug, Lindström & Kokko, 2010*b*; Arnqvist, 2013; Anthes *et al.*, 2016).
(4) 'Intrasexual competition occurrence': if the authors prevented intrasexual competition among individuals of the focal sex, individuals may still vary in their ability to court potential mates successfully and to be fertilised by/fertilise them, which will generate non-random variance in fitness.
(5) Offspring age: when reproductive success was measured. We created four classes: eggs/embryos, newborn, juveniles, and adults. The older the age at sampling the greater the likelihood of natural selection affecting the index of sexual selection intensity/opportunity (Bergeron *et al.*, 2013; Anthes *et al.*, 2016).
(6) Whether or not the mating system is a lek.
(7) Study type. We created three classes of studies: in the field, run under semi-natural conditions (such as mesocosms), and under laboratory conditions.

When possible, these additional variables were included in the statistical analyses (see Section II.7).

(6) Hypotheses and predictions

We tested the following predictions.

(1A) The opportunity for pre-mating sexual selection (I_s) on females is lower when male defensive behaviours occur because it tends to prevent some females from mating multiply.
(1B) The opportunity for pre-mating sexual selection (I_s) on males is higher when male defensive behaviours occur because it tends to prevent some males from mating.
(2A) The opportunity for pre-fertilisation sexual selection (I_{fss}) on females is lower when male defensive behaviours occur because it tends to prevent females from mating multiply, which lowers the probability that they sire offspring from multiple males.
(2B) The opportunity for pre-fertilisation sexual selection (I_{fss}) on males is higher when male defensive behaviours occur

because it tends to prevent some males from mating, and fewer mating opportunities should reduce the number of eggs these males fertilise.

(3A) The opportunity for selection (I) is lower for females when male defensive behaviours occur because it tends to prevent females from mating multiply, and females with more mates often have higher reproductive success (Jennions & Petrie, 2000; Slatyer *et al.*, 2012; Janicke *et al.*, 2016; Fromonteil *et al.*, 2023).

(3B) The opportunity for selection (I) is higher for males when male defensive behaviours occur because it tends to prevent some males from mating which lowers their offspring production.

(4) The Bateman gradient is steeper for males when male defensive behaviours occur if they reduce the number of mating partners per female, which then increases the number of offspring produced by a male per mating event (i.e. there is less shared paternity). It is, however, more difficult to predict how the occurrence of male defensive behaviours will affect the Bateman gradient of females. Multiple mating provides an opportunity for females to bias paternity towards more genetically compatible males (or to avoid only mating with a male who is sterile or sperm depleted), which increases the total number of viable offspring produced. This opportunity does not exist when females mate with a single male (i.e. if male defensive behaviour is highly effective). However, a difference in the distribution of the number of mates per female need not change the relationship between the number of mates and offspring production. For example, it will change the range over which the relationship is measured (e.g. 0 to 2 mates per female *versus* 3 to 6 mates per female), but this will not change the estimated gradient if the relationship is linear. However, as the relationship is likely to be non-linear and decrease with each successive mating, we tentatively predict that it will be steeper when male defensive behaviour leads to fewer matings per female.

For guarded individuals, the predictions are the same as those made for females. For guardians, the predictions are the same as those made for males. Due to the small sample sizes, we did not test any hypotheses for the Jones index. All predictions are summarised in Table 1.

(7) Statistical analysis

To analyse the effect of defensive behaviours on sexual selection, we used multilevel (hierarchical) meta-regression models that allow for the inclusion of random effects and do not assume independence among effect sizes (Nakagawa *et al.*, 2017). Models were run separately for each selection index. In all models, the response variable was the selection index. I_s, I_{fss} and I are all effect sizes based on ratios. While ratios are easy to calculate, they often have challenging statistical properties, such as skewed distributions (Rosenberg, Rothstein & Gurevitch, 2013; Cleophas & Zwinderman, 2017). To circumvent this problem and obtain

Table 1. Predictions about differences in the opportunities for sexual selection between mating systems in which defensive behaviours are present (DB) and mating systems in which defensive behaviours are absent (NDB). Separate predictions are made for females and males for four selection indices: the opportunity for pre-mating sexual selection (I_s), the opportunity for pre-fertilisation sexual selection (I_{fss}), the opportunity for selection (I), and the Bateman gradient.

Selection index	Females	Males
I_s	NDB > DB	DB > NDB
I_{fss}	NDB > DB	DB > NDB
I	NDB > DB	DB > NDB
Bateman gradient	DB > NDB	DB > NDB

a distribution that ranges from $-\infty$ to $+\infty$, with zero as the null value, it is recommended to log-transform estimates based on ratios (Rosenberg *et al.*, 2013; Khan, 2020; Schmid, Stijnen & White, 2021), a method employed in numerous meta-analyses (e.g. Chen *et al.*, 2020; Nessel *et al.*, 2021; Yang *et al.*, 2021), including a meta-analysis on the opportunity for sexual selection (Moura & Peixoto, 2013). We thus log-transformed I_s, I_{fss} and I estimates (Kraaijeveld, Kraaijeveld-Smit & Maan, 2011; Moura & Peixoto, 2013). For the Bateman gradient estimates (which were correlations) we used the Fisher *z*-transformation (following Rosenberg *et al.*, 2013). In all cases, after analyses, results were back-transformed to aid interpretation. The sampling variance used depended on the sexual selection index. Because the Bateman gradient was *z*-transformed, the sampling variance was $1/(N-3)$ (Lajeunesse, Rosenberg & Jennions, 2013). For I_s, I_{fss} and I, we used the sample size (following Kraaijeveld *et al.*, 2011; Moura & Peixoto, 2013). All meta-regression models were fit using the function 'rma.mv' from the *metafor* package (Viechtbauer, 2010; R Core Team, 2017).

Models testing our hypotheses included the occurrence of defensive behaviours as a moderator because our main aim was to evaluate if and how defensive behaviours influence the strength of sexual selection. In these models, the occurrence of defensive behaviours was coded as a categorical variable with two levels (present/absent). For models on females and models on males, occurrence of defensive behaviours only refers to male defensive behaviours. However, we also calculated effect sizes for two pipefish species in which females defend access to mating opportunities. Because these types of species are rare in our data set, we could not run models exclusively focusing on female defensive behaviours. We thus ran additional models that included these effect sizes. Models on guardians included females and males that defend access to mating opportunities, and males from species with no defensive behaviours. Complementarily, models on guarded individuals included females and males that are targets of defensive attempts, and females from species with no defensive behaviours. These two latter types of models also compare presence and absence of defensive behaviours,

but the occurrence of defensive behaviours means that either females or males defend mating opportunities. For all four types of models (i.e. models on females, males, guarded individuals, and guardians), we excluded studies if we could not determine if defensive behaviours were present or absent based on the criteria described above. Additionally, as leks seemed to have higher estimates of I_{fss} and I than other mating systems lacking defensive behaviours, we ran complementary analyses comparing I_{fss} and I estimates for mating systems in which defensive behaviours are absent including a categorical moderator with two levels (lekking/non-lekking).

We took into account non-independence of data (to lower type I error; Nakagawa et al., 2017) by including random effects: the effect size identity (an individual code is assigned for each effect size), species identity, and the phylogeny. We obtained the phylogeny from the *TimeTree Database* (Hedges, Dudley & Kumar, 2006). Using the software *Mesquite* (Maddison & Maddison, 2019) and *Phylocon* (Webb, Ackerly & Kembel, 2008), we then included in the phylogeny species whose times of divergence were not in the *TimeTree Database*. We pruned the phylogeny according to the species included in each model. To explain variation better in the data, when it was feasible, we also included as random variables: mating success measure, fertilisation success measure, inclusion of zeros, intrasexual competition occurrence, and offspring age. We also performed several sensitivity tests to investigate the consistency of the results (Appendix S3). In summary, we tested whether results changed when particular sets of effect sizes were excluded (e.g. when excluding effect sizes based on older offspring).

We assessed heterogeneity among effect sizes using I^2 (note that here I^2 is not the squared version of the metric opportunity for selection, but rather a standard metric of heterogeneity; Higgins & Thompson, 2002). We then calculated the proportion of variance explained by each random variable. Whenever the phylogeny was responsible for moderate or high heterogeneity (50% and 75%, respectively; Nakagawa & Santos, 2012), we ran analyses to test whether animal taxa had different levels of sexual selection based on the indices. These analyses followed the same procedure described above, but with taxon as the moderator. We used six taxa: Amphibia, Aves, Fish, Invertebrates, Mammalia, and Reptilia. Additionally, we used Egger's regression as an indirect measure of publication bias (Rosenthal et al., 2017). It should be noted, however, that asymmetric funnel plots may occur for reasons unrelated to publication bias. This is likely to be the case here as there is no obvious reason to expect publication decisions to depend on the value of the index of selection. Furthermore, there is no P value directly associated with the index in the primary studies, and P values are thought to be the main drivers of publication bias.

Finally, for each sex, we calculated average effect sizes for all selection indices (including here the Jones index). These models included all data available and all relevant random

variables, but without occurrence of defensive behaviours as a moderator.

III. RESULTS

(1) Data collection

After removing duplicates, our initial search resulted in 7624 unique studies (*Web of Science*: 6414 studies; *Scopus*: 5288 studies). After reading their titles and abstracts, we retained 1580 studies to read in full and rejected the remainder (see Table S1 in Appendix S4). From the rejected studies, we identified 79 studies that seemed likely to have cited potentially useful publications not included in our initial list. We read the references of those 79 studies, and thereby located 181 additional studies to read. While contacting authors to ask for more data, we also received suggestions to inspect another four potential useful studies. In total, we read 1844 studies to check for data availability and the possibility of extracting effect sizes (see Fig. S1 in Appendix S4).

We extracted at least one measure of I, and one measure of I_s or I_{fss} for at least one sex from 142 studies. In addition, we contacted 121 authors to ask for additional data that were missing from their paper. We received 20 positive and 55 negative replies. From the positive responses, we extracted 41 effect size estimates for females (I_s: 8, I_{fss}: 8, I: 13, Bateman gradient: 12) and 63 for males (I_s: 7, I_{fss}: 17, I: 19, Bateman gradient: 20) from 11 different studies. In total we extracted effect sizes from 153 of 1844 studies. From the 1691 rejected studies, 454 studies had methods and/or results that implied that the authors had collected data relevant for our meta-analysis, but did not report it in a way that allowed us to extract effect sizes. Details as to why we excluded studies are provided in Table S2 in Appendix S4. Altogether, we extracted 1219 effect sizes from 127 species that provided at least one measure of I, and one measure of I_s or I_{fss} for at least one sex. From the available literature we identified if defensive behaviours occur in 109 species (Fig. 2): 61 with defensive behaviours, 46 with no defensive behaviours, and two with varying defensive behaviours among populations whose effect sizes we classified according to the information in the original study (Murie, 1995; Jones et al., 2001a,b; Jones, Van Zant & Dobson, 2012). Altogether, these species provided 1026 effect sizes (see Appendix S5 for a complete list of effect sizes).

The 1026 effect sizes used in our analyses come from 137 studies. More specifically, we provide data from 89 field studies (e.g. Nishida, 1987; Grunst et al., 2017), 17 studies in mesocosms/seminatural conditions (e.g. Keogh et al., 2013; Turnell & Shaw, 2015), and 31 laboratory studies. Laboratory studies were mainly based on animals difficult to observe and/or sample in field conditions that were kept in cages or aquaria. These include some flying invertebrates (e.g. Pitnick & García-González, 2002; Morimoto et al., 2016), other small

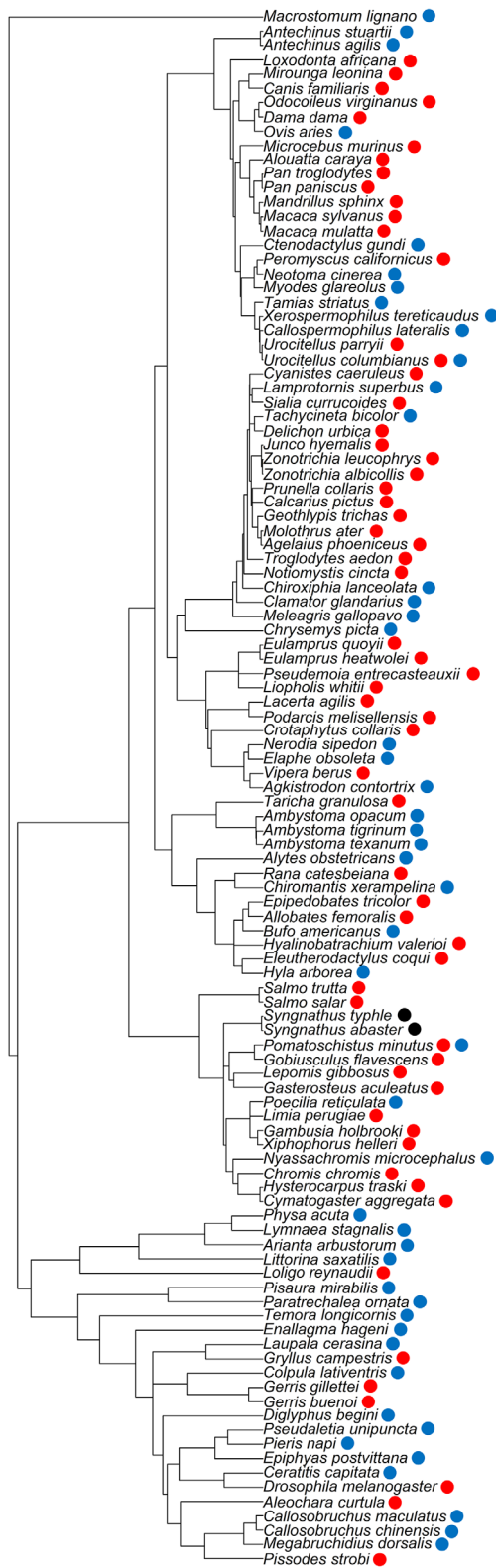**Fig. 2.** Phylogeny for all species included in analyses. Species are labelled according to the presence or absence of defensive behaviours: black = species with female defensive behaviours; blue = species with no defensive behaviours; red = species with male defensive behaviours.

invertebrates (e.g. Fritzsche & Arnqvist, 2013; Marie-Orleach *et al.*, 2016), and aquatic organisms (e.g. Devost & Turgeon, 2016; Vega-Trejo *et al.*, 2017).

(2) Opportunity for pre-mating sexual selection (I_s)

Among females, the opportunity for pre-mating sexual selection was not modulated by the occurrence of male defensive behaviours (present: $I_s = 0.209$, 95% CI = 0.104 to 0.423; absent: $I_s = 0.174$, 95% CI = 0.087 to 0.350; $P = 0.718$). The same result was replicated in all our sensitivity analyses (Fig. 3A; see Table S4 in Appendix S6). The 95% CI for the average I_s estimate for females was 0.117 to 0.311. Publication bias was not detected (Egger's regression: $I_{s\ intercept} = -0.642 \pm 0.335$ SE, $t = -1.913$, $P = 0.062$). Data heterogeneity was high ($I^2 = 98.98\%$), and species identity explained most of the variation (species identity: 96.24%; effect size identity: 2.74%).

Among males, the opportunity for pre-mating sexual selection was also not modulated by the occurrence of male defensive behaviours (present: $I_s = 0.503$, 95% CI = 0.111 to 2.282; absent: $I_s = 0.314$, 95% CI = 0.066 to 1.489; $P = 0.396$). The same result was replicated in all our sensitivity analyses (Fig. 3E; Table S5 in Appendix S6). The 95% CI for the average male I_s estimate was 0.096 to 1.749. There was some evidence for a publication bias (Egger's regression: $I_{s\ intercept} = -1.068 \pm 0.387$ SE, $t = -2.763$, $P = 0.008$), with fewer than expected studies with low precision and high I_s estimates. Data heterogeneity was high ($I^2 = 83.25\%$), and species identity explained most of the variation (species identity: 62.61%; mating success measure: 17.06%; study type: 16.08%; effect size identity: 3.58%).

We did not obtain I_s estimates for species in which females defend access to mates, so we did not run models on guarded individuals or guardians.

(3) Opportunity for pre-fertilisation sexual selection (I_{fss})

Among females, the opportunity for pre-fertilisation sexual selection was not modulated by the occurrence of male defensive behaviours (present: $I_{fss} = 0.280$, 95% CI = 0.054 to 1.461; absent: $I_{fss} = 0.265$, 95% CI = 0.050 to 1.407; $P = 0.854$). The same result was replicated in all our sensitivity analyses (Fig. 3B; Table S6 in Appendix S7). The 95% CI for the average I_{fss} estimate for females was 0.053 to 1.410. Publication bias was not detected (Egger's regression: $I_{fss\ intercept} = -0.004 \pm 0.141$ SE, $t = -0.029$, $P = 0.977$), with fewer than expected studies with low precision and high I_{fss} estimates. Data heterogeneity was high ($I^2 = 99.13\%$), and data variation was moderately explained by species identity (36.53%) and inclusion of zeros (35.56%) while other variables explained some of the remaining variability (effect size identity: 9.70%; study type: 8.93%; offspring age: 8.41%). Models on guarded individuals (i.e. including cases in which females guard males) did not change the findings (Tables S7 and S8 in Appendix S7).
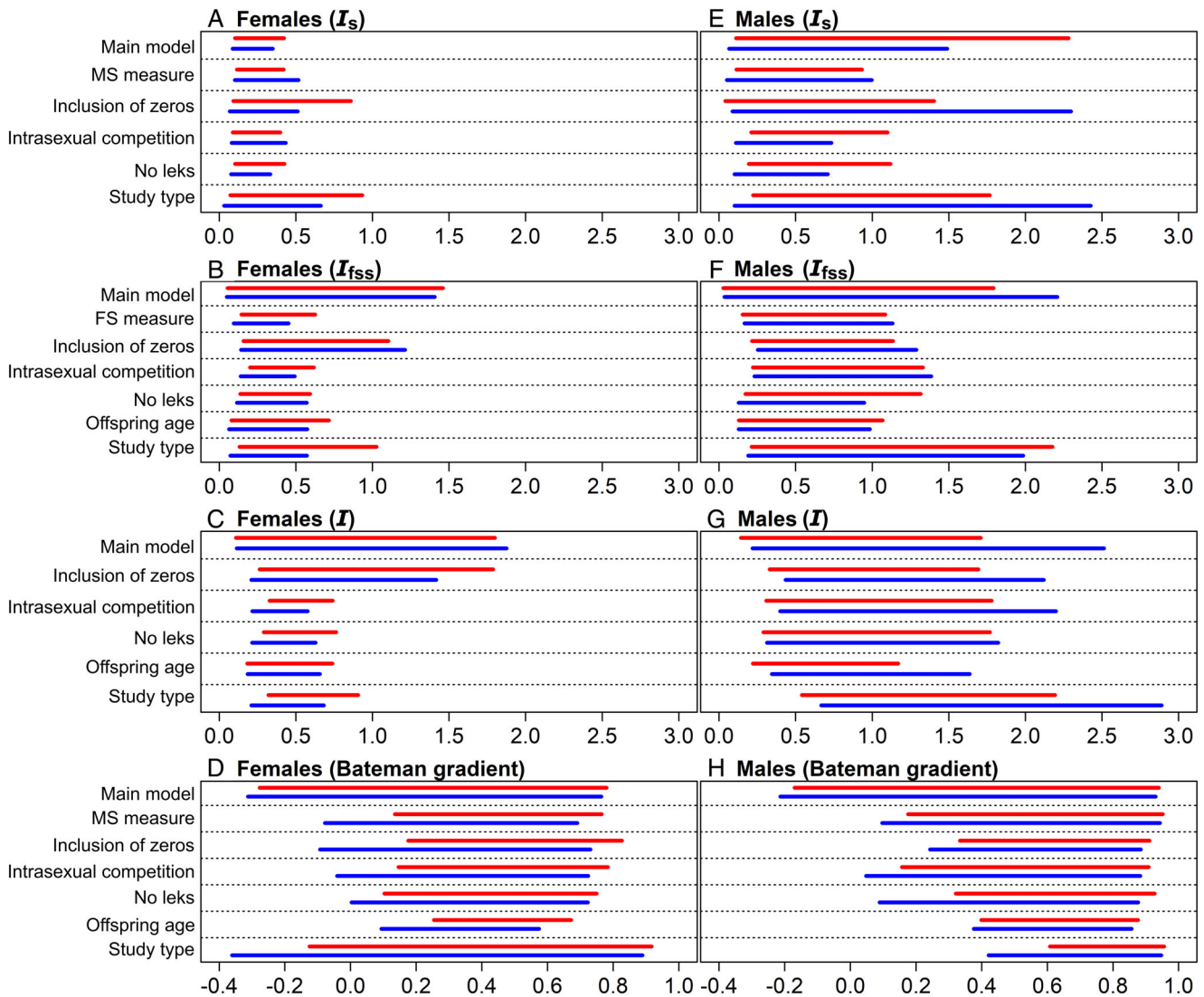
Fig. 3. Estimates of sexual selection (95% confidence intervals) for females (A–D) and males (E–H) based on four indices: opportunity for pre-mating sexual selection (I_s), opportunity for pre-fertilisation sexual selection (I_{fss}), opportunity for selection (I), and the Bateman gradient. Red lines = male defensive behaviours present; blue lines = male defensive behaviours absent. Estimates are based on several models (including sensitivity analyses). Main model: all available data. Model 'MS measure': excluding data in which mating success equates to the number of mating occurrences. Model 'FS measure': excluding data in which fertilisation success equates to the number of fertilisation occurrences. Model 'Inclusion of zeros': excluding effect sizes that (probably) do not include individuals with zero mating success. Model 'Intrasexual competition': excluding data in which the focal sex faced no intrasexual competition. Model 'No leks': excluding data on leks. Model 'Offspring age': excluding data based on juvenile or adult offspring. Model 'Study type': excluding mesocosm or laboratory studies. In all scenarios, confidence intervals overlap for effect sizes when male defensive behaviours are present or absent ($P > 0.05$).

Among males, the opportunity for pre-fertilisation sexual selection was not modulated by the occurrence of male defensive behaviours (present: $I_{fss} = 0.222$, 95% CI = 0.028 to 1.792; absent: $I_{fss} = 0.278$, 95% CI = 0.035 to 2.208; $P = 0.416$). The same result was replicated in all our sensitivity analyses (Fig. 3F; Table S9 in Appendix S7), with a lower upper bound of the confidence interval for mating systems without male defensive behaviours after excluding data from leks (Table S9 in Appendix S7). However, leks do not have significantly higher I_{fss} estimates than other mating systems

that lack male defensive behaviours, although there is a tendency is this direction (leks: $I_{fss} = 0.513$, 95% CI = 0.059 to 4.436; non-leks: $I_{fss} = 0.224$, 95% CI = 0.030 to 1.665; $P = 0.071$). Considering all mating systems, the 95% CI of the average I_{fss} estimate for males was 0.034 to 1.941. There was a possible publication bias (Egger's regression: $I_{fss\ intercept} = 0.919 \pm 0.140$ SE, $t = 6.564$, $P < 0.001$), with fewer than expected studies with low precision that provide low I_{fss} estimates. Data heterogeneity was high ($I^2 = 99.36\%$), inclusion of zeros moderately explained data variation (30.59%) and

other factors contributed to explaining small amounts of the remaining variation (species identity: 16.03%; effect size identity: 15.26%; phylogeny: 14.16%; offspring age: 11.07%; intrasexual competition occurrence: 7.60%; study type: 4.64%). Including cases in which females guard males did not change the findings (Tables S10 and S11 in Appendix S7).

(4) Opportunity for selection (I)

Among females, the opportunity for selection (I) was not modulated by the occurrence of male defensive behaviours (present: $I = 0.443$, 95% CI $= 0.109$ to 1.800; absent: $I = 0.464$, 95% CI $= 0.115$ to 1.876; $P = 0.874$). The same result was replicated in all our sensitivity analyses (Fig. 3C; Table S12 in Appendix S8). The 95% CI of the average I estimate for females was 0.117 to 1.750. No publication bias was detected (Egger's regression: $I_{\text{intercept}} = -0.111 \pm 0.127$ SE, $t = -0.872$, $P = 0.384$). Data heterogeneity was high ($I^2 = 99.21\%$), and species identity moderately explained data variation (species identity: 43.18%), while other factors explained far less (inclusion of zeros: 17.64%; effect size identity: 16.35%; offspring age: 7.46%; intrasexual competition occurrence: 6.12%; phylogeny: 4.74%; study type: 3.71%). Including cases in which females guarded males did not change the findings (Tables S13 and S14 in Appendix S8).

Among males, the opportunity for selection was not modulated by the occurrence of male defensive behaviours (present: $I = 0.494$, 95% CI $= 0.143$ to 1.708; absent: $I = 0.742$, 95% CI $= 0.219$ to 2.513; $P = 0.055$), but there was a tendency for I to be higher when defensive behaviours are absent. In our sensitivity analyses, the opportunity for selection was still not significantly modulated by the occurrence of male defensive behaviours (Fig. 3G; Table S15 in Appendix S8). As for I_{fss}, after excluding leks, there was a lower upper bound of the confidence interval for mating systems without male defensive behaviours (Table S15 in Appendix S8). However, leks do not have significantly higher I estimates than other mating systems lacking male defensive behaviours (leks: $I = 1.091$, 95% CI $= 0.310$ to 3.840; others: $I = 0.689$, 95% CI $= 0.227$ to 2.090; $P = 0.169$). Considering all mating systems, the 95% CI of the average I estimate for males was 0.209 to 1.978. There was some evidence for publication bias (Egger's regression: $I_{\text{intercept}} = 0.563 \pm 0.105$ SE, $t = 5.356$, $P < 0.001$), with fewer than expected studies with low precision and low I estimates. Data heterogeneity was high ($I^2 = 98.87\%$), and no single variable explained more than 30% of the variation (species identity: 28.37%; phylogeny: 26.46%; effect size identity: 15.57%; offspring age: 11.15%; intrasexual competition occurrence: 8.71% inclusion of zeros: 8.62%). Including cases in which females guard males did not change the findings (Tables S16 and S17 in Appendix S8).

(5) Bateman gradients

Among females, Bateman gradients were not modulated by the occurrence of male defensive behaviours (present:

$r = 0.363$, 95% CI $= -0.277$ to 0.780; absent: $r = 0.329$, 95% CI $= -0.312$ to 0.764; $P = 0.783$). The same result was replicated in all our sensitivity analyses (Fig. 3D; Table S18 in Appendix S9). The 95% CI of the average r estimate for females was -0.284 to 0.768. There was some evidence for publication bias (Egger's regression: $Zr_{\text{intercept}} = 0.318 \pm 0.098$ SE, $t = 3.257$, $P = 0.002$), with fewer than expected studies with low precision and negative gradient estimates. Data heterogeneity was high ($I^2 = 94.63\%$), but no single variable explained more than 30% of the variation (phylogeny: 26.13%; inclusion of zeros: 20.62%; mating success measure: 15.93%; effect size identity: 15.91%; species identity: 15.30%). Including cases in which females guard males did not change the main findings (Tables S19 and S20 in Appendix S9).

Among males, Bateman gradients were not modulated by the occurrence of male defensive behaviours (present: $r = 0.654$, 95% CI $= -0.170$ to 0.940; absent: $r = 0.618$, 95% CI $= -0.213$ to 0.930; $P = 0.689$). The same result was replicated in all our sensitivity analyses (Fig. 3H; Table S21 in Appendix S9) and did not change if we included cases in which males are guarded by females (Tables S22 and S23 in Appendix S9). The 95% CI of the average r estimate for males was -0.190 to 0.932. There was some evidence for publication bias (Egger's regression: $Zr_{\text{intercept}} = 0.662 \pm 0.099$ SE, $t = 6.713$, $P < 0.001$), with fewer than expected studies with low precision and negative gradient estimates. Data heterogeneity was high ($I^2 = 96.63\%$), and phylogeny explained almost half the variation (phylogeny: 47.39%; mating success measure: 21.07%; effect size identity: 8.67%; species identity: 7.56%; offspring age: 6.08%; inclusion of zeros: 5.86%). Mammals had steeper Bateman gradients than other taxa (Mammalia: 0.957, 95% CI $= 0.611$ to 0.996; Amphibia: 0.690, 95% CI $= -0.307$ to 0.965, $P = 0.015$; Aves: 0.679, 95% CI $= -0.361$ to 0.966, $P = 0.013$; Fish: 0.605, 95% CI $= -0.438$ to 0.954, $P = 0.014$; Invertebrates: 0.515, 95% CI $= -0.347$ to 0.905, $P = 0.023$; Reptilia: 0.792, 95% CI $= -0.095$ to 0.978, $P = 0.043$; note that these P values refer to a test of the difference between mammals and each of the other taxa; Table S24 in Appendix S10).

(6) Jones index

The 95% CI of the average Jones index was -0.169 to 0.543 for females, and -0.108 to 1.405 for males (Table S25 in Appendix S11).

IV. DISCUSSION

The results of our meta-analysis have important implications for sexual selection theory. Contrary to general expectations, mating systems characterised by male defensive behaviours did not show higher levels of sexual selection (based on indices of selection) than those in which defensive behaviours are absent. This is despite the evidence that male defensive

behaviours are often under sexual selection (Emlen & Oring, 1977; e.g. Gullberg, Olsson & Tegelström, 1997; Halliwell *et al.*, 2017), because socially dominant males usually have higher mating success than subordinates (e.g. Massen *et al.*, 2012; Cafazzo *et al.*, 2014), and that they sometimes restrict females from re-mating (e.g. Fabiani *et al.*, 2004; Mascolino *et al.*, 2016). Our meta-analysis shows, however, that the presence of male defensive behaviours neither suffice to decrease the potential strength of sexual selection among females, nor to increase it among males. This finding appears to be robust. We obtained the same result using four different proxies for selection: the opportunity for pre-mating sexual selection (I_s), the opportunity for pre-fertilisation sexual selection (I_{fss}), the opportunity for selection (I), and the Bateman gradient. The robustness of our findings is strengthened by the fact that we obtained the same results when we ran additional sensitivity analyses. We also ran complementary models that included species in which females perform defensive behaviours and guard males (e.g. Butchart, 2000; Aronsen *et al.*, 2013). Yet again, the results remained the same. We conclude that there is no widespread pattern for the existence of defensive behaviours to modulate estimates of the potential strength of sexual selection. Below, for clarity, we focus on males defending females, or males defending resources that promote access to females, but our arguments generally apply to guarded individuals and guardians, irrespective of which sex is defending the other.

(1) Opportunity for pre-mating sexual selection

As noted, male defensive behaviours neither decrease the opportunity for pre-mating sexual selection on females, nor increase it for males. For both sexes the opportunity for pre-mating sexual selection varies widely, regardless of whether or not defensive behaviours occur (Fig. 3A,E). This result is initially surprising as defensive behaviours seem to elevate the fitness of dominant males (e.g. Paul *et al.*, 1993; Keogh *et al.*, 2013). So why is the opportunity for pre-mating sexual selection similar for species or populations where male defensive behaviours are present or absent? We propose three non-mutually exclusive explanations. First, females play an active role in mating (Hrdy, 1986; Gowaty, Steinichen & Anderson, 2003; Green & Madjidian, 2011; Tang-Martínez, 2016; Orr & Hayssen, 2020). Males try to preclude other males from mating, and, in so doing, sometimes reduce a females' mating success and/or propensity to re-mate (Perry, Sirot & Wigby, 2013; Stockley *et al.*, 2020). However, females are often under selection to circumvent male defensive behaviours if they benefit from mating multiply (Stockley, 1997) – and there are several possible benefits of polyandry (Jennions & Petrie, 2000; Slatyer *et al.*, 2012; Kvarnemo & Simmons, 2013). In short, although males try to monopolise mating opportunities, females are often not monopolised by males, hence the ubiquity of polyandry (e.g. Zeh & Zeh, 1996; Arnqvist & Nilsson, 2000).

Second, dominant males might have higher mating success and sire more offspring *per capita* than subordinates, but this does not mean that they are responsible for most matings

in a population. In many species, dominant males lose mating opportunities to subordinates (Duvall, Bernstein & Gordon, 1976; Sorin, 2004; Stapley & Keogh, 2006; Magalhaes, Smith & Joyce, 2017). If females are active in seeking out matings, males cannot successfully defend access to all their potential mates across an entire breeding season as they have competing demands on their time. For instance, in red-winged blackbirds (*Agelaius phoeniceus*), territorial males that spend more time foraging tend to guard females for shorter periods and lose more paternity to intruders than males that spend most time on their own territory (Westneat, 1994). Similarly, in *Serracutisoma proximum*, a Neotropical harvestman, the more females a male guards, the greater the likelihood that his territory will be invaded by rival males (Munguía-Steyer, Buzatto & Machado, 2012). Across many species, dominant males are outnumbered by subordinates, making it unfeasible to prevent all competitors from mating (e.g. Zamudio & Sinervo, 2000; Fabiani *et al.*, 2004). Indeed, dominant males in a population often fail to guard their partners successfully even when subordinates are in the minority (e.g. Muniz *et al.*, 2015). In sum, inefficient male defensive behaviours that allow females to mate with rivals reduce the difference in the variance in mating success between mating systems with and without male defensive behaviours.

Third, male dominance status often changes as it can be costly to remain dominant for even a single breeding season, let alone several seasons (e.g. Le Boeuf & Reiter, 1988; Dixson *et al.*, 1993; Oklander, Kowalewski & Corach, 2014; Zhu *et al.*, 2016). For instance, in reindeer (*Rangifer tarandus*), guarding females is energetically demanding. One can observe males that: (*i*) only sneak copulations and never guard females; (*ii*) switch between guarding females and sneaking copulations; and (*iii*) guard females over the entire breeding season (Pintus *et al.*, 2015). Males that guard females at any point during the breeding season have higher mating and reproductive success than non-guarders (Pintus *et al.*, 2015). The presence of males that can switch tactics thus reduces the variance in male mating success compared to a population with only guarders and non-guarders. This example illustrates that, even if defensive behaviours are effective and male dominance predicts male mating success, variance in male fitness is reduced, and the potential strength of sexual selection is lower when male status changes over time. From a female perspective, changes in males' status allow guarded females greater access to males, which increases a female's ability to mate multiply, and can also increase their reproductive success. In some species, a newly dominant male may kill the offspring of its vanquished rival (Jindal *et al.*, 2017; Teichroeb & Jack, 2017), but females sometimes mate with the new male, lowering the risk of infanticide (Grinnell & McComb, 1996; Teichroeb & Jack, 2017).

(2) Opportunity for pre-fertilisation sexual selection and net selection

In addition to male defensive behaviours not influencing the opportunity for pre-mating sexual selection, they did not

change the opportunity for pre-fertilisation sexual selection or the opportunity for selection in either sex. This suggests that defensive behaviours are less relevant to determining fitness than is usually assumed, even if they affect mating success, because this does not translate into greater variance in reproductive success, which is a good proxy for Darwinian fitness (Jones, 2009) and critical for directional evolution (see Henshaw *et al.*, 2016). Given that variance in mating success affects variance in fertilisation and reproductive success (as mating precedes fertilisation and reproduction; Fig. 1; see Shuster *et al.*, 2013), the three explanations we offered above to explain why defensive behaviours do not modulate I_s can also explain the lack of modulation of I_{fss} and I. We can, however, gain additional insights by comparing the mean estimates of I_s, I_{fss}, and I from our various models. The confidence intervals always overlap, but the mean I_s estimates for males are almost always higher when male defensive behaviours occur than when they are absent. By contrast, the mean estimates of I_{fss} and I are almost always higher for males when defensive behaviours are absent. This may indicate that deterministic factors and/or stochasticity slightly decrease the opportunities for pre-fertilisation and total selection in species in which defensive behaviours occur. There is no immediately obvious reason for greater stochasticity when defensive behaviours occur, so we focus on two deterministic factors: cryptic female choice (Eberhard, 1996; Firman *et al.*, 2017) and sperm competition (Parker & Pizzari, 2010; Parker, 2020).

Females may circumvent the defensive attempts of socially dominant males by selectively using sperm from rivals with whom they have also mated (Eberhard, 1996; Firman *et al.*, 2017). Females gain from sperm selection if there are genetic benefits for offspring of being sired by certain males (Trivers, 1972; Jennions & Petrie, 2000; Mays & Hill, 2004). In this scenario, subdominant males with low mating success have higher fitness than expected based on their mating success if their sperm is used disproportionate to its availability by females, which reduces the strength of sexual selection on males. A similar reduction in the strength of selection can also be modulated by sperm competition. Mating systems without male defensive behaviours often have a high degree of polyandry, which increases sperm competition (Kappeler, 1997; Holwell *et al.*, 2016). Selection for greater sperm competitiveness when defensive behaviours are absent could increase variance in males' efficiency at fertilising females, thereby increasing the variance in male fertilisation success and the potential strength of selection. Importantly, in many taxa there is a trade-off between investment in pre- and post-mating competition (e.g. Fitzpatrick *et al.*, 2012; Ferrandiz-Rovira *et al.*, 2014; Dines *et al.*, 2015; but see Chung, Jennions & Fox, 2021). In this scenario, dominant males that invest heavily in defensive behaviours subsequently lose paternity to rivals that invest more into post-mating sexual competition (e.g. Fu *et al.*, 2001; Buzzatto *et al.*, 2014). If this trade-off is stronger in species with male defensive behaviours, then I_{fss} and I estimates will be lower due to the greater post-mating investment of subordinate

males compared to species lacking male defensive behaviours.

It is important to note that the higher estimate of male I_{fss} when defensive behaviours are absent seems to be driven by high I_{fss} values in leks. However, this result should be treated with caution as it is based on only six lekking species. We obtained even fewer I_s estimates for males in lekking species, so we cannot determine if the aforementioned result is due to pre- or post-mating events. If pre-mating events are the main cause, our results conform to traditional expectations that there is very high variance in male mating success on leks (Payne, 1984; Andersson, 1994). If, however, post-mating events are the main cause, sperm competition might emerge as being particularly relevant: females on leks can be extremely selective before mating, reducing selection for the ability to exert cryptic female choice (Møller, 1998). Sperm competition is, however, usually considered unimportant in lek mating systems (Sardell & DuVal, 2014), but this might reflect a lack of research. For example, in a lek-forming *Drosophila* species, males with larger testes sire more offspring (Droney, 2001). In a lekking moth, males copulate for longer when pairing with a mated than an unmated female (Engqvist *et al.*, 2014) and transfer more sperm when the risk of sperm competition is higher (Jarrige *et al.*, 2015). In a lekking bird, a manakin, females seem to mate multiply after mating with inexperienced alpha males (Rivers & DuVal, 2019) – which promotes sperm competition. Additionally, older alpha males produce less sperm, which increases the level of multiple paternity (Sardell & DuVal, 2014), as younger individuals fertilise more eggs. Based on these examples and our meta-analytic results, we encourage more studies on sperm competition in lek mating systems.

(3) Bateman gradients

Finally, our results show that the fitness return from each mating does not differ according to the occurrence/absence of male defensive behaviours (i.e. Bateman gradients are equally steep). This is true for both sexes. This finding is perhaps unsurprising as Bateman gradients estimate the benefits of each successive mating, and not the ease with which mating is possible (Kokko, Klug & Jennions, 2012). It is also worth noting that Bateman gradients are almost always based on natural variation in mating rates, and inferring causality is therefore a challenge due to potential confounding factors (for an example, see Fromonteil *et al.*, 2023; Kokko & Jennions, 2023). Besides that, even if causality could be accurately inferred, because females are not monopolised by males (as shown here), there may be no relevant selective pressure driving a steeper Bateman gradient when defensive behaviours occur, regardless of the sex.

Interestingly, Bateman gradients seem to be steeper in mammals than in the other taxa we examined. This probably occurs because mammals usually produce fewer offspring per mating event than the other taxa in our meta-analysis. Producing one or few offspring per successful mating event, the

reproductive success of male mammals can linearly increase as mating and/or fertilisation success increases, which causes a strong, positive correlation between mating and reproductive success. In our data set, this occurred for most mammals: barbary macaques (*Macaca sylvanus*) (Brauch *et al.*, 2008; Modolo & Martin, 2008), black howler monkeys (*Alouatta caraya*) (Oklander *et al.*, 2014), bushy-tailed woodrats (*Neotoma cinerea*) (Topping & Millar, 1998), chimpanzees (*Pan troglodytes*) (Constable *et al.*, 2001; Klinkova *et al.*, 2005; Newton-Fisher *et al.*, 2010), Columbian ground squirrels (*Urocitellus columbianus*) (Jones *et al.*, 2012), elephants (*Loxodonta africana*) (Ishengoma *et al.*, 2008), fallow deer (*Dama dama*) (Say, Naulty & Hayden, 2003), mandrills (*Mandrillus sphinx*) (Dixson *et al.*, 1993), rhesus macaques (*Macaca mulatta*) (Duvall *et al.*, 1976), and white-tailed deer (*Odocoileus virginianus*) (Sorin, 2004). By contrast, for taxa with many offspring per mating event (e.g. Amphibia, fish, and invertebrates), the association between mating success and reproductive success varies more, and we found both negative associations [fish (Jones *et al.*, 2001*b*); invertebrates (Liewlaksaneeyanawin *et al.*, 2003)] and very weak positive ones [fish (Jones *et al.*, 2001*a*); invertebrates (Devost & Turgeon, 2016)].

(4) Publication bias and the scientific literature

Based purely on funnel plot asymmetry there are possible publication biases towards reporting lower values for male I_s and female I_{fss} and higher values for male I_{fss}, male I, and Bateman gradients (females and males). We do not think this is source of concern for our analysis, however, because this pattern is unlikely to affect our comparison of mating systems with and without defensive behaviours. Specifically, the mean sample sizes did not differ between the contrasted mating systems in almost all scenarios in which potential publication bias was detected (Table S26 in Appendix S12). Publication bias with respect to effect sizes has been widely shown to be related to P values, and secondarily to the direction or magnitude of an effect (Møller & Jennions, 2001; Nakagawa *et al.*, 2022). Many of the primary studies we used did not report strength of selection indices, and if they did report them they were not linked to a P value. It is worth noting, however, that it would be easier to test for publication bias if results were reported in a way useable for meta-analysis (see Haddaway, 2015; Anthes *et al.*, 2016; Greenacre, 2016). We found 607 studies containing relevant data, but we succeeded in extracting effect sizes from only 153 studies, which prevented us from testing our hypotheses for the Jones index.

Additionally, we could not find any information to confirm or reject the occurrence of defensive behaviours for >13% of species for which we successfully extracted effect sizes. We recommend that, despite the usefulness of paternity analyses and the relevance of genetic mating systems, authors continue to characterise the social/ecological mating systems of species as those are particularly useful factors to explore as moderators when trying to explain the role of sexual selection in generating species and sex differences in a wide range of traits (Emlen & Oring, 1977; Boulton, Collins & Shuker, 2015; Klug, 2018; Hare & Simmons, 2019; Fritzsche *et al.*, 2021). In addition, we note that there is a gradient in the intensity of defensive behaviours. If the literature provided more information on this variation, we could characterise mating systems at a finer scale than simply the presence or absence of defensive behaviours. A more refined analysis might then be able to identify patterns (effects) that we could not detect in the current study.

Finally, we highlight that our data set contains only three species in which females defend (potential or actual) partners or mating territories. While this is consistent with such species being uncommon in nature (as reviewed by Fritzsche *et al.*, 2021), it might also indicate a research bias that requires attention in future studies.

V. CONCLUSIONS

(1) Using a meta-analytical approach we present evidence that male defensive behaviours do not modulate estimates of the potential strength of sexual selection on females or males in non-human animal species. We also show that this result persists when including species where females guard males and treating individuals of each sex as guarded individuals or guardians.

(2) Our results rely on the efforts of the many researchers whose studies provided over a thousand effect sizes from 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 set and the use of four different indices covering different episodes of sexual selection bolster our findings.

(3) Our results highlight the need to better understand if cryptic female choice and sperm competition operate differently in the presence and absence of male defensive behaviours. Data from lekking species would be especially useful.

(4) It is important to note that non-random variance in fitness relies on it being causally related to behavioural, morphological, and/or physiological attributes of individuals. Thus, the questions we answered here should also be tackled by focusing on specific traits that might affect an individual's mating or reproductive success (R.C. Macedo-Rego, M.D. Jennions & E.S.A. Santos, in preparation). Crucially, variance-based indices that measure the *opportunity* for selection might only be weakly correlated, or even uncorrelated, with the true level of sexual selection (Klug *et al.*, 2010*a*; Jennions, Kokko & Klug, 2012; but see Henshaw *et al.*, 2016).

(5) Finally, our results emphasise the notion that females are active players in sexual selection processes. To avoid gender bias in studies of animal behaviour and sexual selection (Gowaty, 1997; Ah-King & Nylin, 2010; Ah-King, Barron & Herberstein, 2014), it is important that future studies are more attentive to sexual selection on females [see Hare & Simmons (2019) for a review].

VI. ACKNOWLEDGEMENTS

VII. DATA AVAILABILITY STATEMENT

Data and codes can be found at: https://osf.io/8pkcq/?view_only=2015c1fc0ed74d748e48e0400de26099.

VIII. REFERENCES

References identified with an asterisk (*) are cited only within the online supporting information.

Ah-King, M., Barron, A. B. & Herberstein, M. E. (2014). Genital evolution: why are females still understudied? *PLoS Biology* **12**, 1–7.

Ah-King, M. & Nylin, S. (2010). Sex in an evolutionary perspective: just another reaction norm. *Evolutionary Biology* **37**, 234–246.

Andersson, M. (1994). Sexual selection in relation to mating system and parental roles. In *Sexual Selection*, First Edition (ed. M. Andersson), pp. 143–183. Princeton University Press, Princeton, United States.

Anthes, N., Häderer, I. K., Michiels, N. K. & Janicke, T. (2016). Measuring and interpreting sexual selection metrics: evaluation and guidelines. *Methods in Ecology and Evolution* **8**, 918–931.

Apakupakul, K. & Rubenstein, D. R. (2015). Bateman's principle is reversed in a cooperatively breeding bird. *Biology Letters* **11**, 1–4.

Arnold, S. J. & Duvall, D. (1994). Animal mating systems: a synthesis based on selection theory. *The American Naturalist* **143**, 317–348.

Arnqvist, G. (2013). Comment on 'Bateman in nature: predation on offspring reduces the potential for sexual selection'. *Science* **340**, 549.

Arnqvist, G. & Nilsson, T. (2000). The evolution of polyandry: multiple mating and female fitness in insects. *Animal Behaviour* **60**, 145–164.

Aronsen, T., Berglund, A., Mobley, K. B., Ratikainen, I. I. & Rosenqvist, G. (2013). Sex ratio and density affect sexual selection in a sex-role reversed fish. *Evolution* **67**, 3243–3257.

*Balenger, S. L., Scott Johnson, L., Mays, H. L. & Masters, B. S. (2009). Extra-pair paternity in the socially monogamous mountain bluebird *Sialia currucoides* and its effect on the potential for sexual selection. *Journal of Avian Biology* **40**, 173–180.

Barreto, F. S. & Avise, J. C. (2010). Quantitative measures of sexual selection reveal no evidence for sex-role reversal in a sea spider with prolonged paternal care. *Proceedings of the Royal Society B: Biological Sciences* **277**, 2951–2956.

*Barry, F. E., Weatherhead, P. J. & Philipp, D. P. (1992). Multiple paternity in a wild population of northern water snakes, *Nerodia sipedon*. *Behavioral Ecology and Sociobiology* **30**, 193–199.

Bateman, A. J. (1948). Intra-sexual selection in *Drosophila*. *Heredity* **2**, 349–368.

*Becher, S. A. & Magurran, A. E. (2004). Multiple mating and reproductive skew in Trinidadian guppies. *Proceedings of the Royal Society B-Biological Sciences* **271**, 1009–1014.

*Benken, T., Knaak, A., Gack, C., Eberle, M. & Peschke, K. (1999). Variation of sperm precedence in the rove beetle *Aleochara curtula* (Coleoptera: Staphylinidae). *Behaviour* **136**, 1065–1077.

*Berard, J. D., Nurnberg, P., Epplen, J. T. & Schmidtke, J. (1994). Alternative reproductive tactics and reproductive success in male rhesus macaques. *Behaviour* **129**, 177–201.

Bergeron, P., Martin, A. M., Garant, D. & Pelletier, F. (2013). Comment on 'Bateman in nature: predation on offspring reduces the potential for sexual selection'. *Science* **340**, 549.

*Bergeron, P., Montiglio, P. O., Réale, D., Humphries, M. M. & Garant, D. (2012). Bateman gradients in a promiscuous mating system. *Behavioral Ecology and Sociobiology* **66**, 1125–1130.

Bjork, A. & Pitnick, S. (2006). Intensity of sexual selection along the anisogamy-isogamy continuum. *Nature* **441**, 742–745.

*Blouin-Demers, G., Gibbs, H. L. & Weatherhead, P. J. (2005). Genetic evidence for sexual selection in black ratsnakes, *Elaphe obsoleta*. *Animal Behaviour* **69**, 225–234.

Böll, S. & Linsenmair, K. E. (1998). Size-dependent male reproductive success and size-assortative mating in the midwife toad *Alytes obstetricans*. *Amphibia-Reptilia* **19**, 75–89.

*Bolopo, D., Canestrari, D., Martínez, J. G., Roldan, M., Macías-Sanchez, E., Vila, M., Soler, M. & Baglione, V. (2017). Flexible mating patterns in an obligate brood parasite. *Ibis* **159**, 103–112.

Boulton, R. A., Collins, L. A. & Shuker, D. M. (2015). Beyond sex allocation: the role of mating systems in sexual selection in parasitoid wasps. *Biological Reviews* **90**, 599–627.

Brauch, K., Hodges, K., Engelhardt, A., Fuhrmann, K., Shaw, E. & Heistermann, M. (2008). Sex-specific reproductive behaviours and paternity in free-ranging Barbary macaques (*Macaca sylvanus*). *Behavioral Ecology and Sociobiology* **62**, 1453–1466.

*Briskie, J. V. & Boag, P. T. (1998). Paternity and paternal care in the polygynandrous Smith's longspur. *Behavioral Ecology and Sociobiology* **43**, 181–190.

Broquet, T., Jaquiéry, J. & Perrin, N. (2009). Opportunity for sexual selection and effective population size in the lek-breeding European treefrog (*Hyla arborea*). *Evolution* **63**, 674–683.

Butchart, S. H. M. (2000). Population structure and breeding system of the sex-role reversed, polyandrous Bronze-winged Jacana *Metopidius indicus*. *Ibis* **142**, 93–102.

Buzatto, B. A., Tomkins, J. L. & Simmons, L. W. (2014). Alternative phenotypes within mating systems. In *The Evolution of Insect Mating Systems*, First Edition (eds D. M. Shuker and L. W. Simmons), pp. 106–128. Oxford University Press, Oxford, United Kingdom.

*Byrne, P. G. & Whiting, M. J. (2008). Simultaneous polyandry increases fertilization success in an African foam-nesting treefrog. *Animal Behaviour* **76**, 1157–1164.

Cafazzo, S., Bonanni, R., Valsecchi, P. & Natoli, E. (2014). Social variables affecting mate preferences, copulation and reproductive outcome in a pack of free-ranging dogs. *PLoS One* **9**, 1–14.

Chen, X., Chen, H. Y. H., Chen, C., Ma, Z., Searle, E. B., Yu, Z. & Huang, Z. (2020). Effects of plant diversity on soil carbon in diverse ecosystems: a global meta-analysis. *Biological Reviews* **95**, 167–183.

Chung, M.-H. J., Jennions, M. D. & Fox, R. J. (2021). Quantifying the costs of pre- and postcopulatory traits for males: evidence that costs of ejaculation are minor relative to mating effort. *Evolution Letters* **5**, 315–327.

Cleophas, T. J. & Zwinderman, A. H. (2017). *Modern Meta-Analysis – Review and Update of Methodologies*, First Edition. Springer, Cham, Switzerland.

*Coltman, D. W., Bancroft, D. R., Robertson, A., Smith, J. A., Clutton-Brock, T. H. & Pemberton, J. M. (1999). Male reproductive success in a promiscuous mammal: Behavioural estimates compared with genetic paternity. *Molecular Ecology* **8**, 1199–1209.

Constable, J. L., Ashley, M. V., Goodall, J. & Pusey, A. E. (2001). Noninvasive paternity assignment in Gombe chimpanzees. *Molecular Ecology* **10**, 1279–1300.

Cramer, E. R. A., Kaiser, S. A., Webster, M. S. & Ryder, T. B. (2020). Common field data limitations can substantially bias sexual selection metrics. *American Naturalist* **196**, 180–196.

*Croshaw, D. A. (2010). Quantifying sexual selection: a comparison of competing indices with mating system data from a terrestrially breeding salamander. *Biological Journal of the Linnean Society* **99**, 73–83.

Crow, J. F. (1958). Some possibilities for measuring selection intensities in man. *Human Biology* **30**, 1–13.

*Dannewitz, J., Petersson, E., Dahl, J., Prestegaard, T., Löf, A. C. & Järvi, T. (2004). Reproductive success of hatchery-produced and wild-

born brown trout in an experimental stream. *Journal of Applied Ecology* **41**, 355–364.

*Danthanarayana, W. & Gu, H. (1991). Multiple mating and its effect on the reproductive success of female *Epiphyas postvittana* (Lepidoptera: Tortricidae). *Ecological Entomology* **16**, 169–175.

Darwin, C. (1871). *The Descent of Man and Selection in Relation to Sex*, First Edition. J. Murray, London, United Kingdom.

Devost, E. & Turgeon, J. (2016). The combined effects of pre- and post-copulatory processes are masking sexual conflict over mating rate in *Gerris buenoi*. *Journal of Evolutionary Biology* **29**, 167–177.

Dewsbury, D. A. (2005). The Darwin-Bateman paradigm in historical context. *Integrative and Comparative Biology* **45**, 831–837.

Dillen, L., Jordaens, K. & Backeljau, T. (2009). Sperm transfer, sperm storage, and sperm digestion in the hermaphroditic land snail *Succinea putris* (Gastropoda, Pulmonata). *Invertebrate Biology* **128**, 97–106.

Dines, J. P., Mesnick, S. L., Ralls, K., May-Collado, L., Agnarsson, I. & Dean, M. D. (2015). A trade-off between precopulatory and postcopulatory trait investment in male cetaceans. *Evolution* **69**, 1560–1572.

Dixson, A. F., Bossi, T. & Wickings, E. J. (1993). Male dominance and genetically determined reproductive success in the mandrill (*Mandrillus sphinx*). *Primates* **34**, 525–532.

Droney, D. C. (2001). Male lekking duration and mating benefits in a lek-forming Hawaiian Drosophila. *Journal of Insect Behavior* **14**, 621–635.

Duvall, S. W., Bernstein, I. S. & Gordon, T. P. (1976). Paternity and status in a rhesus monkey group. *Journal of Reproduction and Fertility* **47**, 25–31.

Eberhard, W. G. (1996). *Female Control: Sexual Selection by Cryptic Female Choice*, First Edition. Princeton University Press, Princeton, United States.

*Eberle, M., Perret, M. & Kappeler, P. M. (2007). Sperm competition and optimal timing of matings in *Microcebus murinus*. *International Journal of Primatology* **28**, 1267–1278.

Ellis, W. A. H. & Bercovitch, F. B. (2011). Body size and sexual selection in the koala. *Behavioral Ecology and Sociobiology* **65**, 1229–1235.

Emlen, S. T. & Oring, L. W. (1977). Ecology, sexual selection, and the evolution of mating systems. *Science* **197**, 215–223.

Engqvist, L., Cordes, N., Schwenniger, J., Bakhtina, S. & Schmoll, T. (2014). Female remating behavior in a lekking moth. *Ethology* **120**, 662–671.

Fabiani, A., Galimberti, F., Sanvito, S. & Hoelzel, A. R. (2004). Extreme polygyny among southern elephant seals on Sea Lion Island, Falkland Islands. *Behavioral Ecology* **15**, 961–969.

Ferrandiz-Rovira, M., Lemaître, J.-F., Lardy, S., López, B. C. & Cohas, A. (2014). Do pre- and post-copulatory sexually selected traits covary in large herbivores? *BMC Evolutionary Biology* **14**, 1–9.

*Fincke, O. M. (1986). Lifetime reproductive success and the opportunity for selection in a nonterritorial damselfly (Odonata: Coenagrionidae). *Evolution* **40**, 791–803.

Firman, R. C., Gasparini, C., Manier, M. K. & Pizzari, T. (2017). Postmating female control: 20 years of cryptic female choice. *Trends in Ecology and Evolution* **32**, 368–382.

Fitze, P. S. & Le Galliard, J.-F. (2011). Inconsistency between different measures of sexual selection. *The American Naturalist* **178**, 256–268.

Fitzpatrick, J. L., Almbro, M., Gonzalez-Voyer, A., Kolm, N. & Simmons, L. W. (2012). Male contest competition and the coevolution of weaponry and testes in pinnipeds. *Evolution* **66**, 3595–3604.

*Fitzpatrick, S. M. & McNeil, J. N. (1989). Lifetime mating potential and reproductive success in males of the true armyworm, *Pseudaletia unipuncta* (Haw.) (Lepidoptera: Noctuidae). *Functional Ecology* **3**, 37–44.

*Forsman, A. & Hagman, M. (2006). Calling is an honest indicator of paternal genetic quality in poison frogs. *Evolution* **60**, 2148–2157.

Fritzsche, K. & Arnqvist, G. (2013). Homage to Bateman: sex roles predict sex differences in sexual selection. *Evolution* **67**, 1926–1936.

Fritzsche, K., Henshaw, J. M., Johnson, B. D. & Jones, A. G. (2021). The 150th anniversary of the descent of man: Darwin and the impact of sex-role reversal on sexual selection research. *Biological Journal of the Linnean Society* **134**, 525–540.

Fromonteil, S., Marie-Orleach, L., Winkler, L. & Janicke, T. (2023). Sexual selection in females and the evolution of polyandry. *PLoS Biology* **21**, 1–20.

Fu, P., Ne, B. D. & Gross, M. R. (2001). Tactic-specific success in sperm competition. *Proceedings of the Royal Society B-Biological Sciences* **268**, 1105–1112.

Gagnon, M.-C., Duchesne, P. & Turgeon, J. (2012). Sexual conflict in *Gerris gillettei* (Insecta: Hemiptera): influence of effective mating rate and morphology on reproductive success. *Canadian Journal of Zoology* **90**, 1297–1306.

*García-Navas, V., Ferrer, E. S., Bueno-Enciso, J., Barrientos, R., Sanz, J. J. & Ortego, J. (2014). Extrapair paternity in Mediterranean blue tits: socioecological factors and the opportunity for sexual selection. *Behavioral Ecology* **25**, 228–238.

Gauthey, Z., Hendry, A. P., Elosegi, A., Tentelier, C. & Labonne, J. (2016). The context dependence of assortative mating: a demonstration with conspecific salmonid populations. *Journal of Evolutionary Biology* **29**, 1827–1835.

Gerlach, N. M., McGlothlin, J. W., Parker, P. G. & Ketterson, E. D. (2012). Reinterpreting Bateman gradients: multiple mating and selection in both sexes of a songbird species. *Behavioral Ecology* **23**, 1078–1088.

*Gopurenko, D., Williams, R. N. & DeWoody, J. A. (2007). Reproductive and mating success in the small-mouthed salamander (*Ambystoma texanum*) estimated via microsatellite parentage analysis. *Evolutionary Biology* **34**, 130–139.

*Gopurenko, D., Williams, R. N., McCormick, C. R. & DeWoody, J. A. (2006). Insights into the mating habits of the tiger salamander (*Ambystoma tigrinum tigrinum*) as revealed by genetic parentage analyses. *Molecular Ecology* **15**, 1917–1928.

Gowaty, P. A. (1997). *Feminism and Evolutionary Biology: Boundaries, Intersections and Frontiers*, First Edition. Springer, New York, United States.

Gowaty, P. A. (2006). Beyond extra-pair paternity: constraints, fitness components, and social mating systems. In *Essays in Animal Behaviour - Celebrating 50 Years of Animal Behaviour*, First Edition (eds J. R. Lucas and L. W. Simmons), pp. 221–254. Elsevier Academic Press, Burlington, United States.

Gowaty, P. A., Kim, Y.-K. & Anderson, W. W. (2012). No evidence of sexual selection in a repetition of Bateman's classic study of *Drosophila melanogaster*. *Proceedings of the National Academy of Sciences* **109**, 11740–11745.

Gowaty, P. A., Steinichen, R. & Anderson, W. W. (2003). Indiscriminate females and choosy males: within- and between-species variation in Drosophila. *Evolution* **57**, 2037–2045.

Green, K. K. & Madjidian, J. A. (2011). Active males, reactive females: stereotypic sex roles in sexual conflict research? *Animal Behaviour* **81**, 901–907.

Greenacre, M. (2016). Data reporting and visualization in ecology. *Polar Biology* **39**, 2189–2205.

Grinnell, J. & McComb, K. (1996). Maternal grouping as a defense against infanticide by males: evidence from field playback experiments on African lions. *Behavioral Ecology* **7**, 55–59.

Grunst, A. S., Grunst, M. L., Rathbun, N. A., Hubbard, J. K., Safran, R. J., Gonser, R. A. & Tuttle, E. M. (2017). Disruptive selection on plumage coloration across genetically determined morphs. *Animal Behaviour* **124**, 97–108.

Gullberg, A., Olsson, M. & Tegelström, H. (1997). Male mating success, reproductive success and multiple paternity in a natural population of sand lizards: Behavioural and molecular genetics data. *Molecular Ecology* **6**, 105–112.

Haddaway, N. R. (2015). A call for better reporting of conservation research data for use in meta-analyses. *Conservation Biology* **29**, 1242–1245.

Halliwell, B., Uller, T., Wapstra, E. & While, G. M. (2017). Resource distribution mediates social and mating behavior in a family living lizard. *Behavioral Ecology* **28**, 145–153.

Hare, R. M. & Simmons, L. W. (2019). Sexual selection and its evolutionary consequences in female animals. *Biological Reviews* **94**, 929–956.

*Hartley, I. R., Davies, N. B., Hatchwell, B. J., Desrochers, A., Nebel, D. & Burke, T. (1995). The polygynandrous mating system of the alpine accentor, *Prunella collaris*. II. Multiple paternity and parental effort. *Animal Behaviour* **49**, 789–803.

Hedges, S. B., Dudley, J. & Kumar, S. (2006). TimeTree: a public knowledge-base of divergence times among organisms. *Bioinformatics* **22**, 2971–2972.

*Heinz, K. M. (1991). Sex-specific reproductive consequences of body size in the solitary ectoparasitoid, *Diglyphus begini*. *Evolution* **45**, 1511–1515.

Henshaw, J. M., Kahn, A. T. & Fritzsche, K. (2016). A rigorous comparison of sexual selection indexes via simulations of diverse mating systems. *Proceedings of the National Academy of Sciences of the United States of America* **113**, E300–E308.

Herberstein, M. E., Painting, C. J. & Holwell, G. I. (2017). Scramble competition polygyny in terrestrial arthropods. In *Advances in the Study of Behavior* (eds M. Naguib, J. Podos, L. W. Simmons, L. Barrett, S. D. Healy and M. Zuk), pp. 237–295. Elsevier Ltd, Cambridge, United States.

Higgins, J. P. T. & Thompson, S. G. (2002). Quantifying heterogeneity in a meta-analysis. *Statistics in Medicine* **21**, 1539–1558.

Höglund, J. & Alatalo, R. V. (1995). Leks. In *Tetrahedron Letters*, First Edition. Princeton University Press, Princeton, United States.

*Höggren, M. & Tegelström, H. (1996). Does long-term storage of spermatozoa occur in the adder (*Vipera berus*)? *Journal of Zoology* **240**, 501–510.

*Holleley, C. E., Dickman, C. R., Crowther, M. S. & Oldroyd, B. P. (2006). Size breeds success: multiple paternity, multivariate selection and male semelparity in a small marsupial, *Antechinus stuartii*. *Molecular Ecology* **15**, 3439–3448.

Holwell, G. I., Allen, P. J. D., Goudie, F., Duckett, P. E. & Painting, C. J. (2016). Male density influences mate searching speed and copulation duration in millipedes (Polydesmida: *Gigantowales chisholmi*). *Behavioral Ecology and Sociobiology* **70**, 1381–1388.

*Howard, R. D. (1983). Sexual selection and variation in reproductive success in a long-lived organism. *The American Naturalist* **122**, 301–325.

*Howard, R. D. (1988). Sexual selection on male body size and mating behaviour in American toads, *Bufo americanus*. *Animal Behaviour* **36**, 1796–1808.

Hrdy, S. B. (1986). Empathy, polyandry, and the myth of the coy female. In *Feminist Approaches to Science*, First Edition (ed. R. Breed), pp. 119–146. Pergamon Press, New York, United States.

*Hübner, K., Gonzalez-Wanguemert, M., Diekmann, O. E. & Serrao, E. A. (2013). Genetic evidence for polygynandry in the black-striped pipefish *Syngnathus abaster*: a microsatellite-based parentage analysis. *Journal of Heredity* **104**, 791–797.

Huyghe, K., Van Damme, R., Breugelmans, K., Herrel, A., Vanhooydonck, B., Tadič, Z. & Backeljau, T. (2014). Parentage analyses suggest female promiscuity and a disadvantage for athletic males in the colour-polymorphic lizard *Podarcis melisellensis*. *Behavioral Ecology and Sociobiology* **68**, 1357–1366.

Ishengoma, D. R. S., Shedlock, A. M., Foley, C. A. H., Foley, L. J., Wasser, S. K., Balthazary, S. T. & Mutayoba, B. M. (2008). Effects of poaching on bull mating success in a free ranging African elephant (*Loxodonta africana*) population in Tarangire National Park, Tanzania. *Conservation Genetics* **9**, 247–255.

Janicke, T., David, P. & Chapuis, E. (2015). Environment-dependent sexual selection: Bateman's parameters under varying levels of food availability. *The American Naturalist* **185**, 756–768.

Janicke, T., Häderer, I. K., Lajeunesse, M. J. & Anthes, N. (2016). Darwinian sex roles confirmed across the animal kingdom. *Science Advances* **2**, 1–11.

*Janssen, R. & Baur, B. (2015). Seasonal effects on egg production and level of paternity in a natural population of a simultaneous hermaphrodite snail. *Ecology and Evolution* **5**, 2916–2928.

Jarrige, A., Riemann, D., Goubault, M. & Schmoll, T. (2015). Strategic sperm allocation in response to perceived sperm competition risk in a lekking insect. *Animal Behaviour* **109**, 81–87.

Jennions, M. D., Kokko, H. & Klug, H. (2012). The opportunity to be misled in studies of sexual selection. *Journal of Evolutionary Biology* **25**, 591–598.

Jennions, M. D. & Petrie, M. (2000). Why do females mate multiply? A review of the genetic benefits. *Biological Reviews* **75**, 21–64.

Jindal, S., Bose, A. P. H., O'Connor, C. M. & Balshine, S. (2017). A test of male infanticide as a reproductive tactic in a cichlid fish. *Royal Society Open Science* **4**, 1–7.

Johannesson, K., Saltin, S. H., Charrier, G., Ring, A.-K., Kvarnemo, C., André, C. & Panova, M. (2016). Non-random paternity of offspring in a highly promiscuous marine snail suggests postcopulatory sexual selection. *Behavioral Ecology and Sociobiology* **70**, 1357–1366.

Jones, A. G. (2009). On the opportunity for sexual selection, the Bateman gradient and the maximum intensity of sexual selection. *Evolution* **63**, 1673–1684.

*Jones, A. G., Arguello, J. R. & Arnold, S. J. (2002). Validation of Bateman's principles: a genetic study of sexual selection and mating patterns in the rough-skinned newt. *Proceedings of the Royal Society B: Biological Sciences* **269**, 2533–2539.

*Jones, A. G., Arguello, J. R. & Arnold, S. J. (2004). Molecular parentage analysis in experimental newt populations: the response of mating system measures to variation in the operational sex ratio. *The American Naturalist* **164**, 444–456.

*Jones, A. G., Östlund-Nilss, S. & Avise, J. C. (1998). A microsatellite assessment of sneaked fertilizations and egg thievery in the fifteenspine stickleback. *Evolution* **52**, 848–858.

*Jones, A. G., Rosenqvist, G., Berglund, A. & Avise, J. C. (1999). The genetic mating system of a sex-role-reversed pipefish (*Syngnathus typhle*): a molecular inquiry. *Behavioral Ecology and Sociobiology* **46**, 357–365.

*Jones, A. G., Rosenqvist, G., Berglund, A. & Avise, J. C. (2005). The measurement of sexual selection using Bateman's principles: an experimental test in the sex-role-reversed pipefish *Syngnathus typhle*. *Integrative and Comparative Biology* **45**, 874–884.

Jones, A. G., Walker, D., Kvarnemo, C., Lindström, K. & Avise, J. C. (2001*a*). How cuckoldry can decrease the opportunity for sexual selection: data and theory from a genetic parentage analysis of the sand goby, *Pomatoschistus minutus*. *Proceedings of the National Academy of Sciences of the United States of America* **98**, 9151–9156.

Jones, A. G., Walker, D., Lindström, K., Kvarnemo, C. & Avise, J. C. (2001*b*). Surprising similarity of sneaking rates and genetic mating patterns in two populations of sand goby experiencing disparate sexual selection regimes. *Molecular Ecology* **10**, 461–469.

Jones, P. H., Van Zant, J. L. & Dobson, F. S. (2012). Variation in reproductive success of male and female Columbian ground squirrels (*Urocitellus columbianus*). *Canadian Journal of Zoology* **90**, 736–743.

*Kaitala, A. & Wiklund, C. (1994). Polyandrous female butterflies forage for matings. *Behavioral Ecology and Sociobiology* **35**, 385–388.

Kappeler, P. M. (1997). Intrasexual selection in *Mirza coquereli*: evidence for scramble competition polygyny in a solitary primate. *Behavioral Ecology and Sociobiology* **41**, 115–127.

Keogh, J. S., Umbers, K. D. L., Wilson, E., Stapley, J. & Whiting, M. J. (2013). Influence of alternate reproductive tactics and pre- and postcopulatory sexual selection on paternity and offspring performance in a lizard. *Behavioral Ecology and Sociobiology* **67**, 629–638.

*Ketterson, E. D., Parker, P. G., Raouf, S. A., Nolan, V. Jr., Ziegenfus, C. & Chandler, C. R. (1997). The relative impact of extra-pair fertilizations on variation in male and female reproductive success in dark-eyed juncos (*Junco hyemalis*). *Ornithological Monographs* **49**, 81–101.

Khan, S. (2020). *Meta-Analysis – Methods for Health and Experimental Studies*, First Edition. Springer, Singapore, Singapore.

Kirkpatrick, M. & Ryan, M. J. (1991). The evolution of mating preferences and the paradox of the lek. *Nature* **350**, 33–38.

Klinkova, E., Hodges, J. K., Fuhrmann, K., De Jong, T. & Heistermann, M. (2005). Male dominance rank, female mate choice and male mating and reproductive success in captive chimpanzees. *International Journal of Primatology* **26**, 357–484.

Klug, H. (2018). Why monogamy? A review of potential ultimate drivers. *Frontiers in Ecology and Evolution* **6**, 1–6.

Klug, H., Heuschele, J., Jennions, M. D. & Kokko, H. (2010*a*). The mismeasurement of sexual selection. *Journal of Evolutionary Biology* **23**, 447–462.

Klug, H., Lindström, K. & Kokko, H. (2010*b*). Who to include in measures of sexual selection is no trivial matter. *Ecology Letters* **13**, 1094–1102.

Kokko, H. & Jennions, M. D. (2023). Is more always better when it comes to mating? *PLoS Biology* **21**, e3001955.

Kokko, H., Klug, H. & Jennions, M. D. (2012). Unifying cornerstones of sexual selection: operational sex ratio, Bateman gradient and the scope for competitive investment. *Ecology Letters* **15**, 1340–1351.

Kraaijeveld, K., Kraaijeveld-Smit, F. J. L. & Maan, M. E. (2011). Sexual selection and speciation: the comparative evidence revisited. *Biological Reviews* **86**, 367–377.

Kraaijeveld-Smit, F. J. L., Ward, S. J. & Temple-Smith, P. D. (2003). Paternity success and the direction of sexual selection in a field population of a semelparous marsupial, *Antechinus agilis*. *Molecular Ecology* **12**, 475–484.

*Krakauer, A. H. (2008). Sexual selection and the genetic mating system of wild turkeys. *The Condor* **110**, 1–12.

Kvarnemo, C. & Simmons, L. W. (2013). Polyandry as a mediator of sexual selection before and after mating. *Philosophical Transactions of the Royal Society B: Biological Sciences* **368**, 1–16.

*LaBarbera, K., Hayes, K. R. R., Langhans, K. E. & Lacey, E. A. (2019). Elevation affects extra-pair paternity but not a sexually selected plumage trait in dark-eyed juncos. *Behavioral Ecology and Sociobiology* **73**, 1–12.

LaBarbera, K., Lovette, I. J. & Llambías, P. E. (2012). Mating opportunities, paternity, and sexual conflict: paternal care in northern and southern temperate house wrens. *Behavioral Ecology and Sociobiology* **66**, 253–260.

*LaBrecque, J. R., Alva-Campbell, Y. R., Archambeault, S. & Crow, K. D. (2014). Multiple paternity is a shared reproductive strategy in the live-bearing surfperches (Embiotocidae) that may be associated with female fitness. *Ecology and Evolution* **4**, 2316–2329.

*Lacey, E. A., Wieczorek, J. R. & Tucker, P. K. (1997). Male mating behaviour and patterns of sperm precedence in arctic ground squirrels. *Animal Behaviour* **53**, 767–779.

Lajeunesse, M. J., Rosenberg, M. S. & Jennions, M. D. (2013). Phylogenetic nonindependence and meta-analysis. In *Handbook of Meta-Analysis in Ecology and Evolution*, First Edition (eds J. Koricheva, J. Gurevitch and K. Mengersen), pp. 284–299. Princeton University Press, Princeton, United States.

Le Boeuf, B. J. & Reiter, J. (1988). Lifetime reproductive success in northern elephant seals. In *Reproductive Success - Studies of Individual Variation in Contrasting Breeding Systems* (ed. T. H. Clutton-Brock), pp. 344–362. University of Chicago Press, Chicago, United States.

*Leftwich, P. T., Edward, D. A., Alphey, L., Gage, M. J. G. & Chapman, T. (2012). Variation in adult sex ratio alters the association between courtship, mating frequency and paternity in the lek-forming fruitfly *Ceratitis capitata*. *Journal of Evolutionary Biology* **25**, 1732–1740.

*Levine, B. A., Smith, C. F., Schuett, G. W., Douglas, M. R., Davis, M. A. & Douglas, M. E. (2015). Bateman-Trivers in the 21st century: sexual selection in a north American pitviper. *Biological Journal of the Linnean Society* **114**, 436–445.

Liewlaksaneeyanawin, C., Ritland, K., Ritland, C. & El-Kassaby, Y. A. (2003). Experimental analysis of the mating system of the white pine weevil, *Pissodes strobi* (Peck) (Coleoptera: Curculionidae). *Canadian Journal of Zoology* **81**, 424–429.

*Lifjeld, J. T., Dunn, P. O., Robertson, R. J. & Boag, P. T. (1993). Extra-pair paternity in monogamous tree swallows. *Animal Behaviour* **45**, 213–229.

*Liu, J. X., Tatarenkov, A., O'Rear, T. A., Moyle, P. B. & Avise, J. C. (2013). Molecular evidence for multiple paternity in a population of the viviparous tule perch *Hysterocarpus traski*. *Journal of Heredity* **104**, 217–222.

Macedo-Rego, R. C. (2020). *Quando e como ocorrem episódios de seleção sexual em espécies animais? Uma investigação meta-analítica*. Universidade de São Paulo, São Paulo, Brazil.

Macedo-Rego, R. C. & Santos, E. S. A. (2021). Harems. In *Encyclopedia of Evolutionary Psychological Science*. (eds T. K. Shackelford and V. A. Weekes-Schakelford), pp. 3628–3631. Springer International Publishing, Cham, Switzerland. Electronic file available at https://link.springer.com/referenceworkentry/10.1007/978-3-319-19650-3_2722.

MACKENZIE, A., REYNOLDS, J. D., BROWN, V. J. & SUTHERLAND, W. J. (1995). Variation in male mating success on leks. *American Naturalist* **145**, 633–652.

MADDISON, W. P. & MADDISON, D. R. (2019). Mesquite: a modular system for evolutionary analysis. Electronic file available at http://www.mesquiteproject.org.

*MADSEN, T. & SHINE, R. (1994). Components of lifetime reproductive success in adders, *Vipera berus*. *Journal of Animal Ecology* **63**, 561–568.

MAGALHAES, I. S., SMITH, A. M. & JOYCE, D. A. (2017). Quantifying mating success of territorial males and sneakers in a bower-building cichlid fish. *Scientific Reports* **7**, 1–8.

MANGOLD, A., TRENKWALDER, K., RINGLER, M., HÖDL, W. & RINGLER, E. (2015). Low reproductive skew despite high male-biased operational sex ratio in a glass frog with paternal care. *BMC Evolutionary Biology* **15**, 1–13.

MARIE-ORLEACH, L., JANICKE, T., VIZOSO, D. B., DAVID, P. & SCHÄRER, L. (2016). Quantifying episodes of sexual selection: insights from a transparent worm with fluorescent sperm. *Evolution* **70**, 314–328.

*MARVAN, R., STEVENS, J. M. G., ROEDER, A. D., MAZURA, I., BRUFORD, M. W. & DE RUITER, J. R. (2006). Male dominance rank, mating and reproductive success in captive bonobos (*Pan paniscus*). *Folia Primatologica* **77**, 364–376.

MASCOLINO, S., BENVENUTO, C., GUBILI, C., SACCHI, C., BOUFANA, B. & MARIANI, S. (2016). The ART of mating: alternative reproductive tactics and mating success in a nest-guarding fish. *Journal of Fish Biology* **89**, 2643–2657.

MASSEN, J. J. M., OVERDUIN-DE VRIES, A. M., DE VOS-ROUWELER, A. J. M., SPRUIJT, B. M., DOXIADIS, G. G. M. & STERCK, E. H. M. (2012). Male mating tactics in captive rhesus macaques (*Macaca mulatta*): the influence of dominance, markets, and relationship quality. *International Journal of Primatology* **33**, 73–92.

MAYS, H. L. & HILL, G. E. (2004). Choosing mates: good genes versus genes that are a good fit. *Trends in Ecology and Evolution* **19**, 554–559.

*McGUIRE, J. M., CONGDON, J. D., SCRIBNER, K. T. & NAGLE, R. D. (2014). Female reproductive qualities affect male painted turtle (*Chrysemys picta marginata*) reproductive success. *Behavioral Ecology and Sociobiology* **68**, 1589–1602.

*MILLS, S. C., GRAPPUTO, A., KOSKELA, E. & MAPPES, T. (2007). Quantitative measure of sexual selection with respect to the operational sex ratio: a comparison of selection indices. *Proceedings of the Royal Society B: Biological Sciences* **274**, 143–150.

*MINORETTI, N., SCHMERA, D., KUPFERNAGEL, S., ZSCHOKKE, S., ARMBRUSTER, G. F. J., BEESE, K., BAUR, A. & BAUR, B. (2011). Determinants of female and male reproductive success in a simultaneous hermaphrodite land snail. *Animal Behaviour* **82**, 707–715.

*MJOLNEROD, I. B., FLEMING, I. A., REFSETH, U. H. & HINDAR, K. (1998). Mate and sperm competition during multiple-male spawnings of Atlantic salmon. *Canadian Journal of Zoology* **76**, 70–75.

*MOBLEY, K. B., ABOU CHAKRA, M. & JONES, A. G. (2014). No evidence for size-assortative mating in the wild despite mutual mate choice in sex-role-reversed pipefishes. *Ecology and Evolution* **4**, 67–78.

*MOBLEY, K. B., AMUNDSEN, T., FORSGREN, E., SVENSSON, P. A. & JONES, A. G. (2009). Multiple mating and a low incidence of cuckoldry for nest-holding males in the two-spotted goby, *Gobiusculus flavescens*. *BMC Evolutionary Biology* **9**, 1–10.

MODOLO, L. & MARTIN, R. D. (2008). Reproductive success in relation to dominance rank in the absence of prime-age males in barbary macaques. *American Journal of Primatology* **70**, 26–34.

MØLLER, A. P. (1998). Sperm competition and sexual selection. In *Sperm Competition and Sexual Selection*, First Edition (eds T. R. BIRKHEAD and A. PAPE MØLLER), pp. 55–90. Academic Press, San Diego, United States.

MØLLER, A. P. & BIRKHEAD, T. R. (1994). The evolution of plumage brightness in birds is related to extrapair paternity. *Evolution* **48**, 1089–1100.

MØLLER, A. P. & JENNIONS, M. D. (2001). Testing and adjusting for publication bias. *Trends in Ecology and Evolution* **16**, 580–586.

*MONROE, M. J., AMUNDSEN, T., UTNE-PALM, A. C. & MOBLEY, K. B. (2016). Seasonal variation in male alternative reproductive tactics. *Journal of Evolutionary Biology* **29**, 2362–2372.

MORIMOTO, J., PIZZARI, T. & WIGBY, S. (2016). Developmental environment effects on sexual selection in male and female *Drosophila melanogaster*. *PLoS One* **11**, 1–27.

MOURA, R. R. & PEIXOTO, P. E. C. (2013). The effect of operational sex ratio on the opportunity for sexual selection: a meta-analysis. *Animal Behaviour* **86**, 675–683.

MUNGUÍA-STEYER, R., BUZATTO, B. A. & MACHADO, G. (2012). Male dimorphism of a neotropical arachnid: harem size, sneaker opportunities, and gonadal investment. *Behavioral Ecology* **23**, 827–835.

MUNIZ, D. G., GUIMARAES, P. R., BUZATTO, B. A. & MACHADO, G. (2015). A sexual network approach to sperm competition in a species with alternative mating tactics. *Behavioral Ecology* **26**, 121–129.

*MUNROE, K. E. & KOPROWSKI, J. L. (2011). Sociality, Bateman's gradients, and the polygynandrous genetic mating system of round-tailed ground squirrels (*Xerospermophilus tereticaudus*). *Behavioral Ecology and Sociobiology* **65**, 1811–1824.

MURIE, J. O. (1995). Mating behavior of Columbian ground squirrels. I. Multiple mating by females and multiple paternity. *Canadian Journal of Zoology* **73**, 1819–1826.

NAKADERA, Y., MARIËN, J., VAN STRAALEN, N. M. & KOENE, J. M. (2017). Multiple mating in natural populations of a simultaneous hermaphrodite, *Lymnaea stagnalis*. *Journal of Molluscan Studies* **83**, 56–62.

NAKAGAWA, S., LAGISZ, M., JENNIONS, M. D., KORICHEVA, J., NOBLE, D. W. A., PARKER, T. H., SÁNCHEZ-TÓJAR, A., YANG, Y. & O'DEA, R. E. (2022). Methods for testing publication bias in ecological and evolutionary meta-analyses. *Methods in Ecology and Evolution* **13**, 4–21.

NAKAGAWA, S., NOBLE, D. W. A., SENIOR, A. M. & LAGISZ, M. (2017). Meta-evaluation of meta-analysis: ten appraisal questions for biologists. *BMC Biology* **15**, 1–14.

NAKAGAWA, S. & SANTOS, E. S. A. (2012). Methodological issues and advances in biological meta-analysis. *Evolutionary Ecology* **26**, 1253–1274.

*NAUD, M. J., SAUER, W. H. H., McKEOWN, N. J. & SHAW, P. W. (2016). Multiple mating, paternity and complex fertilisation patterns in the chokka squid *Loligo reynaudii*. *PLoS One* **11**, 1–11.

NESSEL, M. P., KONNOVITCH, T., ROMERO, G. Q. & GONZÁLEZ, A. L. (2021). Nitrogen and phosphorus enrichment cause declines in invertebrate populations: a global meta-analysis. *Biological Reviews* **96**, 2617–2637.

NEWTON-FISHER, N. E., THOMPSON, M. E., REYNOLDS, V., BOESCH, C. & VIGILANT, L. (2010). Paternity and social rank in wild chimpanzees (*Pan troglodytes*) from the Budongo Forest, Uganda. *American Journal of Physical Anthropology* **142**, 417–428.

NISHIDA, T. (1987). Measurement of the opportunity for natural and sexual selection in a breeding population of the coreid bug (*Colpula lativentris*). *Researches on Population Ecology* **29**, 271–289.

NOBLE, D. W. A., WECHMANN, K., KEOGH, J. S. & WHITING, M. J. (2013). Behavioral and morphological traits interact to promote the evolution of alternative reproductive tactics in a lizard. *American Naturalist* **182**, 726–742.

*NUTT, K. J. (2007). Genetic reconstruction of breeding patterns in gundis (Rodentia: Ctenodactylidae). *Behavioral Ecology and Sociobiology* **61**, 1651–1663.

OKLANDER, L. I., KOWALEWSKI, M. & CORACH, D. (2014). Male reproductive strategies in black and gold howler monkeys (*Alouatta caraya*). *American Journal of Primatology* **76**, 43–55.

OLIVER, A. S. (1997). Size and density dependent mating tactics in the simultaneously hermaphroditic seabass *Serranus subligarius* (Cope, 1870). *Behaviour* **134**, 563–594.

ORR, T. J. & HAYSSEN, V. (2020). The female snark is still a boojum: looking toward the future of studying female reproductive biology. *Integrative and Comparative Biology* **60**, 782–795.

*PANDULLI-ALONSO, I., QUAGLIA, A. & ALBO, M. J. (2017). Females of a gift-giving spider do not trade sex for food gifts: a consequence of male deception? *BMC Evolutionary Biology* **17**, 1–8.

PARKER, G. A. (1970a). Sperm competition and its evolutionary consequences in the insects. *Biological Reviews* **45**, 525–567.

PARKER, G. A. (1970b). Sperm competition and its evolutionary effect on copula duration in the fly *Scatophaga stercoraria*. *Journal of Insect Physiology* **16**, 1301–1328.

PARKER, G. A. (2020). Conceptual developments in sperm competition: a very brief synopsis. *Philosophical Transactions of the Royal Society B* **375**, 1–10.

PARKER, G. A. & PIZZARI, T. (2010). Sperm competition and ejaculate economics. *Biological Reviews* **85**, 897–934.

PARKER, P. G. & TANG-MARTINEZ, Z. (2005). Bateman gradients in field and laboratory studies: a cautionary tale. *Integrative and Comparative Biology* **45**, 895–902.

PAUL, A., KUESTER, J., TIMME, A. & ARNEMANN, J. (1993). The association between rank, mating effort, and reproductive success in male Barbary macaques (*Macaca sylvanus*). *Primates* **34**, 491–502.

PAYNE, R. B. (1984). Sexual selection, lek and arena behavior, and sexual size dimorphism in birds. *Ornithological Monographs* **33**, 1–52.

*PÉLISSIÉ, B., JARNE, P. & DAVID, P. (2012). Sexual selection without sexual dimorphism: Bateman gradients in a simultaneous hermaphrodite. *Evolution* **66**, 66–81.

PERRY, J. C., SIROT, L. & WIGBY, S. (2013). The seminal symphony: how to compose an ejaculate. *Trends in Ecology and Evolution* **28**, 414–422.

PINTUS, E., UCCHEDDU, S., RØED, K. H., GONZALÉZ, J. P., CARRANZA, J., NIEMINEN, M. & HOLAND, Ø. (2015). Flexible mating tactics and associated reproductive effort during the rutting season in male reindeer (*Rangifer tarandus*, L. 1758). *Current Zoology* **61**, 802–810.

PITNICK, S. & GARCÍA-GONZÁLEZ, F. (2002). Harm to females increases with male body size in *Drosophila melanogaster*. *Proceedings of the Royal Society B: Biological Sciences* **269**, 1821–1828.

*POESEL, A., GIBBS, H. L. & NELSON, D. A. (2011). Extrapair fertilizations and the potential for sexual selection in a socially monogamous songbird. *The Auk* **128**, 770–776.

PROSSER, M. R., WEATHERHEAD, P. J., GIBBS, H. L. & BROWN, G. P. (2002). Genetic analysis of the mating system and opportunity for sexual selection in northern water snakes (*Nerodia sipedon*). *Behavioral Ecology* **13**, 800–807.

QUELLER, D. C. (1987). The evolution of leks through female choice. *Animal Behaviour* **35**, 1424–1432.

R Core Team (2017). *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna. Electronic file available at https://www.r-project.org/.

*Ribble, D. O. (1992). Lifetime reproductive success and its correlates in the monogamous rodent, *Peromyscus californicus*. *Journal of Animal Ecology* **61**, 457–468.

*Richard, A., Dionne, M., Wang, J. & Bernatchez, L. (2013). Does catch and release affect the mating system and individual reproductive success of wild Atlantic salmon (*Salmo salar* L.)? *Molecular Ecology* **22**, 187–200.

*Rios-Cardenas, O. (2005). Patterns of parental investment and sexual selection in teleost fishes: do they support Bateman's principles? *Integrative and Comparative Biology* **45**, 885–894.

Rivers, P. R. & DuVal, E. H. (2019). Multiple paternity in a lek mating system: females mate multiply when they choose inexperienced sires. *Journal of Animal Ecology* **89**, 1–11.

*Rodríguez-Muñoz, R., Bretman, A., Slate, J., Walling, C. A. & Tregenza, T. (2010). Natural and sexual selection in a wild insect population. *Science* **328**, 1269–1272.

Rohatgi, A. (2015). *WebPlotDigitizer*. WebPlotDigitizer, Austin. Electronic file available at https://automeris.io/WebPlotDigitizer.html.

Rosenberg, M. S., Rothstein, H. R. & Gurevitch, J. (2013). Effect sizes: conventional choices and calculations. In *Handbook of Meta-Analysis in Ecology and Evolution*, First Edition (eds J. Koricheva, J. Gurevitch and K. Mengersen), pp. 61–71. Princeton University Press, Princeton, United States.

Rosenthal, M. F., Gertler, M., Hamilton, A. D., Prasad, S. & Andrade, M. C. B. (2017). Taxonomic bias in animal behaviour publications. *Animal Behaviour* **127**, 83–89.

Sardell, R. J. & DuVal, E. H. (2013). Differential allocation in a lekking bird: females lay larger eggs and are more likely to have male chicks when they mate with less related males. *Proceedings of the Royal Society B: Biological Sciences* **281**, 1–7.

Sardell, R. J. & DuVal, E. H. (2014). Small and variable sperm sizes suggest low sperm competition despite multiple paternity in a lekking suboscine bird. *The Auk* **131**, 660–671.

Say, L., Naulty, F. & Hayden, T. J. (2003). Genetic and behavioural estimates of reproductive skew in male fallow deer. *Molecular Ecology* **12**, 2793–2800.

*Schartl, M., Erbelding-Denk, C., Hölter, S., Nanda, I., Schmid, M., Schröder, J. H. & Epplen, J. T. (1993). Reproductive failure of dominant males in the poeciliid fish *Limia perugiae* determined by DNA fingerprinting. *Proceedings of the National Academy of Sciences of the United States of America* **90**, 7064–7068.

*Schlicht, E. & Kempenaers, B. (2013). Effects of social and extra-pair mating on sexual selection in blue tits (*Cyanistes caeruleus*). *Evolution* **67**, 1420–1434.

Schmid, C. H., Stijnen, T. & White, I. R. (2021). *Handbook of Meta-Analysis*, First Edition. CRC Press, Boca Raton, United States.

*Schwagmeyer, P. L. & Woontner, S. J. (1986). Scramble competition polygyny in thirteen-lined ground squirrels: the relative contributions of overt conflict and competitive mate searching. *Behavioural Ecology and Sociobiology* **19**, 359–364.

Serbezov, D., Bernatchez, L., Olsen, E. M. & Vøllestad, L. A. (2010). Mating patterns and determinants of individual reproductive success in brown trout (*Salmo trutta*) revealed by parentage analysis of an entire stream living population. *Molecular Ecology* **19**, 3193–3205.

Shuster, S. M., Briggs, W. R. & Dennis, P. A. (2013). How multiple mating by females affects sexual selection. *Proceedings of the Royal Society B-Biological Sciences* **368**, 1–27.

*Sichlau, M. H. & Kiørboe, T. (2011). Age- and size-dependent mating performance and fertility in a pelagic copepod, *Temora longicornis*. *Marine Ecology Progress Series* **442**, 123–132.

*Simmons, L. W., Beveridge, M. & Evans, J. P. (2008). Molecular evidence for multiple paternity in a feral population of green swordtails. *Journal of Heredity* **99**, 610–615.

Slatyer, R. A., Mautz, B. S., Backwell, P. R. Y. & Jennions, M. D. (2012). Estimating genetic benefits of polyandry from experimental studies: a meta-analysis. *Biological Reviews* **87**, 1–33.

Sorin, A. B. (2004). Paternity assignment for white-tailed deer (*Odocoileus virginianus*): mating across age classes and multiple paternity. *Journal of Mammalogy* **85**, 356–362.

Stapley, J. & Keogh, J. S. (2006). Experimental and molecular evidence that body size and ventral colour interact to influence male reproductive success in a lizard. *Ethology Ecology and Evolution* **18**, 275–288.

Stockley, P. (1997). Sexual conflict resulting from adaptations to sperm competition. *Trends in Ecology and Evolution* **12**, 154–159.

Stockley, P., Franco, C., Claydon, A. J., Davidson, A., Hammond, D. E., Brownridge, P. J., Hurst, J. L. & Beynon, R. J. (2020). Revealing mechanisms of mating plug function under sexual selection. *Proceedings of the National Academy of Sciences of the United States of America* **117**, 27465–27473.

Sundin, J., Aronsen, T., Rosenqvist, G. & Berglund, A. (2017). Sex in murky waters: algal-induced turbidity increases sexual selection in pipefish. *Behavioral Ecology and Sociobiology* **71**, 1–8.

*Székely, T., Lislevand, T. & Figuerola, J. (2007). Sexual size dimorphism in birds. In *Sex, Size and Gender Roles: Evolutionary Studies of Sexual Size Dimorphism*, First Edition (eds D. J. Fairbairn, W. U. Blanckenhorn and T. Székely), pp. 27–37. Oxford University Press, Oxford.

*Taff, C. C., Freeman-Gallant, C. R., Dunn, P. O. & Whittingham, L. A. (2013). Spatial distribution of nests constrains the strength of sexual selection in a warbler. *Journal of Evolutionary Biology* **26**, 1392–1405.

Tang-Martínez, Z. (2016). Rethinking Bateman's principles: challenging persistent myths of sexually reluctant females and promiscuous males. *Journal of Sex Research* **53**, 532–559.

*Tatarenkov, A., Healey, C. I. M., Grether, G. F. & Avise, J. C. (2008). Pronounced reproductive skew in a natural population of green swordtails, *Xiphophorus helleri*. *Molecular Ecology* **17**, 4522–4534.

Taylor, M. L., Price, T. A. R. & Wedell, N. (2014). Polyandry in nature: a global analysis. *Trends in Ecology and Evolution* **29**, 376–383.

Teichroeb, J. A. & Jack, K. M. (2017). Alpha male replacements in nonhuman primates: variability in processes, outcomes, and terminology. *American Journal of Primatology* **79**, 1–10.

Tentelier, C., Lepais, O., Larranaga, N., Manicki, A., Lange, F. & Rives, J. (2016). Sexual selection leads to a tenfold difference in reproductive success of alternative reproductive tactics in male atlantic salmon. *Science of Nature* **103**, 1–13.

Thornhill, R. (1983). Cryptic female choice and its implications in the scorpionfly *Harpobittacus nigriceps*. *The American Naturalist* **122**, 765–788.

Thornhill, R. & Alcock, J. (1983). Male mating systems. In *The Evolution of Insect Mating Systems* (eds R. Thornhill and J. Alcock), pp. 230–268. Harvard University Press, Harvard, United States.

*Toft, S. & Albo, M. J. (2015). Optimal numbers of matings: the conditional balance between benefits and costs of mating for females of a nuptial gift-giving spider. *Journal of Evolutionary Biology* **28**, 457–467.

Topping, M. G. & Millar, J. S. (1998). Mating patterns and reproductive success in the bushy-tailed wood rat (*Neotoma cinerea*), as revealed by DNA fingerprinting. *Behavioral Ecology and Sociobiology* **43**, 115–124.

*Townsend, D. S. (1989). Sexual selection, natural selection, and a fitness trade-off in a tropical frog with male parental care. *The American Naturalist* **133**, 266–272.

Trivers, R. L. (1972). Parental investment and sexual selection introduction. In *Sexual Selection and the Descent of Man 1871–1971*, First Edition (ed. B. Campbell), pp. 136–207. Aldine Publishing Company, Chicago, United States.

Turnell, B. R. & Shaw, K. L. (2015). High opportunity for postcopulatory sexual selection under field conditions. *Evolution* **69**, 2094–2104.

*Ursprung, E., Ringler, M., Jehle, R. & Hödl, W. (2011). Strong male/male competition allows for nonchoosy females: high levels of polygynandry in a territorial frog with paternal care. *Molecular Ecology* **20**, 1759–1771.

Vega-Trejo, R., Head, M. L., Keogh, J. S. & Jennions, M. D. (2017). Experimental evidence for sexual selection against inbred males. *Journal of Animal Ecology* **86**, 394–404.

Viechtbauer, W. (2010). Conducting meta-analyses in R with the metafor package. *Journal of Statistical Software* **36**, 1–48.

Wacker, S., Amundsen, T., Forsgren, E. & Mobley, K. B. (2014). Within-season variation in sexual selection in a fish with dynamic sex roles. *Molecular Ecology* **23**, 3587–3599.

Wade, M. J. (1979). Sexual selection and variance in reproductive success. *The American Naturalist* **114**, 742–747.

*Walker, L. K., Ewen, J. G., Brekke, P. & Kilner, R. M. (2014). Sexually selected dichromatism in the hihi *Notiomystis cincta*: multiple colours for multiple receivers. *Journal of Evolutionary Biology* **27**, 1522–1535.

*Weatherhead, P. J. & Boag, P. T. (1997). Genetic estimates of annual and lifetime reproductive success in male red-winged blackbirds. *Ecology* **78**, 884–896.

Webb, C. O., Ackerly, D. D. & Kembel, S. W. (2008). Phylocom: software for the analysis of phylogenetic community structure and trait evolution. *Bioinformatics* **24**, 2098–2100.

Wells, C. P., Tomalty, K. M., Floyd, C. H., McElreath, M. B., May, B. P. & Van Vuren, D. H. (2017). Determinants of multiple paternity in a fluctuating population of ground squirrels. *Behavioral Ecology and Sociobiology* **71**, 1–13.

Westneat, D. F. (1994). To guard mates or go forage - conflicting demands affect the paternity of male red-winged blackbirds. *American Naturalist* **144**, 343–354.

*Whittingham, L. A. & Lifjeld, J. T. (1995). Extra-pair fertilizations increase the opportunity for sexual selection in the monogamous house martin *Delichon urbica*. *Journal of Avian Biology* **26**, 283–288.

*Williams, R. N. & DeWoody, J. A. (2009). Reproductive success and sexual selection in wild eastern tiger salamanders (*Ambystoma t. tigrinum*). *Evolutionary Biology* **36**, 201–213.

*Woolfenden, B. E., Lisle Gibbs, H. & Sealy, S. G. (2002). High opportunity for sexual selection in both sexes of an obligate brood parasitic bird, the brown-headed cowbird (*Molothrus ater*). *Behavioral Ecology and Sociobiology* **52**, 417–425.

Yang, Y., Lagisz, M., Foo, Y. Z., Noble, D. W. A., Anwer, H. & Nakagawa, S. (2021). Beneficial intergenerational effects of exercise on brain and cognition: a multilevel meta-analysis of mean and variance. *Biological Reviews* **96**, 1504–1527.

York, J. R. & Baird, T. A. (2015). Testing the adaptive significance of sex-specific mating tactics in collared lizards (*Crotaphytus collaris*). *Biological Journal of the Linnean Society* **115**, 423–436.

Zamudio, K. R. & Sinervo, B. (2000). Polygyny, mate-guarding, and posthumous fertilization as alternative male mating strategies. *Proceedings of the National Academy of Sciences of the United States of America* **97**, 14427–14432.

Zeh, J. A. & Zeh, D. W. (1996). The evolution of polyandry I: intragenomic conflict and genetic incompatibility. *Proceedings of the Royal Society B-Biological Sciences* **263**, 1711–1717.

Zhu, P., Ren, B., Garber, P. A., Xia, F., Grueter, C. C. & Li, M. (2016). Aiming low: a resident male's rank predicts takeover success by challenging males in Yunnan snub-nosed monkeys. *American Journal of Primatology* **78**, 974–982.

IX. SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Appendix S1. Search protocol (moderators).
Appendix S2. On defensive behaviours.
Appendix S3. Sensitivity tests.
Appendix S4. Rejected studies.
Appendix S5. Quantities of effect sizes.
Appendix S6. Opportunity for pre-mating sexual selection (I_s).
Appendix S7. Opportunity for pre-fertilisation sexual selection (I_{fss}).
Appendix S8. Opportunity for selection (I).
Appendix S9. The Bateman gradient.
Appendix S10. Bateman gradient across the phylogeny.
Appendix S11. The Jones index.
Appendix S12. Mean sample sizes.