Temperature as a modulator of sexual selection and sexual conflict

García-Roa, R.[1], Garcia-Gonzalez, F.[2, 3], Noble, D.W.A.[4,5] & Carazo, P.[1]*

[1]Behaviour and Evolution, Ethology lab, Cavanilles Institute of Biodiversity and Evolutionary Biology, University of Valencia.
[2]Doñana Biological Station (CSIC).
[3]Centre for Evolutionary Biology, School of Biological Sciences, The University of Western Australia.
[4] Ecology and Evolution Research Centre, School of Biological, Earth and Environmental Sciences, University of New South Wales, Sydney, NSW 2052, Australia
[5] Division of Ecology and Evolution, Research School of Biology, The Australian National University, Canberra, ACT 2061, Australia

***Correspondence and address of corresponding author**: Pau Carazo, Cavanilles Institute of Biodiversity and Evolutionary Biology, C/Catedrático José Beltrán 2, 46980, Paterna, Valencia, Spain (e-mail: pau.carazo@uv.es).

Co-author emails and adresses: Roberto García-Roa, Cavanilles Institute of Biodiversity and Evolutionary Biology, C/Catedrático José Beltrán 2, 46980, Paterna, Valencia, Spain (email: Roberto.Garcia-Roa@uv.es); Francisco Garcia-Gonzalez, Doñana Biological Station, Spanish Research Council CSIC, c/ Americo Vespucio, 26, Isla de la Cartuja, 41092 Sevilla, Spain (email: paco.garcia@ebd.csic.es); Daniel WA Noble, Division of Ecology and Evolution, Research School of Biology, The Australian National University, Canberra, ACT 2061, Australia (email: daniel.wa.noble@gmail.com).

Running title: Temperature and sexual selection.

Statement of authorship: PC conceived this paper; PC, RG-R and FG-G discussed and developed the ideas and conceptual framework presented; PC, RG-R and DWAN conducted the systematic search; DWAN conducted the meta-analysis; PC wrote the paper with close feedback from RG-R, FG-G and DWAN.

Keywords: Sexual selection, temperature, sexual conflict, rapid environmental change, population viability, meta-analysis.

Word count: 6,924.

Abstract

A central question in ecology and evolution is to understand why sexual selection varies so much in strength across taxa. Here, we contend that temperature, a critical abiotic ecological factor at a global taxonomic scale, can be a critical modulator of sexual selection. We outline the main pathways by which temperature can affect the strength of sexual selection and related phenomena (e.g. sexual conflict). This framework suggests that temperature may modulate sexual selection in ways that, depending on species-specific underlying mechanisms, can both exacerbate or buffer its intensity. We then tested this general prediction by conducting a meta-analysis of available studies experimentally manipulating temperature and reporting effects on the variance of male/female fitness components and/or traits under sexual selection. Our results show that temperature can have a large net impact on sexual selection in both sexes. Current studies focus on the direct effects that environmental temperature has on traits linked with individual fitness and population viability, ignoring eco-evolutionary feedbacks. Here, we show that studying the feedback between temperature and sexual selection processes can be vital to better understand variation in the strength of sexual selection in nature, and its consequences for population viability.

Introduction

Through the ages, our planet has witnessed an unimaginable array of lifeforms, of sounds, colours, smells, and behaviours, of *"endless forms most beautiful and most wonderful",* in Darwin's own words (Darwin 1859). Many of these biological phenomena have been shaped by sexual selection, one of the main engines of evolution. Driven by competition for reproduction (Andersson 1994; Jennions & Kokko 2010), since Darwin's first formulation in 1871 (Darwin 1871) sexual selection has become a cornerstone to understand the evolution of male and female adaptations and life-histories (Andersson 1994), speciation (Janicke *et al.* 2018), and the maintenance of sexual reproduction itself (Agrawal 2001). Precisely due to its central role in evolutionary theory, we have also come to understand that sexual selection is an equally important determinant of population viability and evolvability, and thus of its capacity to withstand environmental change (Pomiankowski & Moller 1995). Indeed, sexual selection is a potent mechanism by which the genome can be purged of deleterious mutations (Radwan 2004; Whitlock & Agrawal 2009) and, in so doing, effectively protect populations against extinction (Jarzebowska & Radwan 2010; Lumley *et al.* 2015). Sexual selection has also been shown to increase the rate of adaptation in traits under both sexual and natural selection via "genic capture"(Rowe & Houle 1996; Lorch *et al.* 2003), which is presumed to be particularly effective in response to directional environmental change (Long *et al.* 2012; Martinez-Ruiz & Knell 2017; Parrett & Knell 2018), allowing populations where sexual selection is present or intense to adapt faster and hence be more effective in tracking the environment.

Strong sexual selection can also lead to sexual conflict (including sexually antagonistic coevolution), which can have complex direct and indirect repercussions on different sexual selection mechanisms and population viability. On the one hand, sexually antagonistic co-evolution can lead to and/or reinforce reproductive isolation and speciation (Parker & Partridge 1998; Rice 1998) or promote increased intraspecific genetic variation without speciation (Gavrilets 2014), thereby functioning as an engine of biodiversity. On the other hand, sexual conflict frequently entails detrimental effects on male, and in particular female, fitness. Sexual conflict decreases male and female fitness by displacing the sexes from their respective evolutionary optima (i.e. gender load; (Rice & Chippindale 2002)), and can further decrease female fitness if it leads to male adaptations that harm females (i.e. male harm; e.g. (Pitnick & Garcia-Gonzalez 2002)). This, in turn, leads to a decrease in population productivity (i.e. by depressing net female productivity (Holland & Rice 1999; Arnqvist & Tuda 2010; Berger *et al.* 2016)), which can even lead to population extinction (Le Galliard *et al.* 2005). Whether sexual conflict leads to one or the other outcome will depend, among other things, on population size (Gay *et al.* 2010), the potential for gender load (Berger *et al.* 2016), and the degree and form of associated male harm adaptations and female counter-adaptations (Arnqvist & Rowe 2005). In addition, sexually antagonistic co-evolution can feedback to affect the opportunity, form and/or intensity of sexual selection. For example, avoiding male harassment (a common source of harm to females) in crickets leads to a larger opportunity for (and stronger) sexual selection (Hall *et al.* 2008). To summarize, there is now ample theoretical and empirical evidence that sexual selection (and sexual conflict) is a fundamental engine of biodiversity, a driving force of male and female adaptations and life-histories, and a keystone determinant of population viability and extinction risk.

Given the undisputed relevance of sexual selection for individual phenotypes and population fates, a central question in evolutionary biology is to disentangle why sexual selection and sexual conflict vary so much in their form, strength and outcomes across taxa. Selection does not operate in a void, and we have long realized that abiotic ecological factors are crucial to understand the operation of sexual selection (Emlen & Oring 1977; Maan & Seehausen 2011), and more recently of sexual conflict (Arbuthnott *et al.* 2014; Berger *et al.* 2014; Perry *et al.* 2017; García-Roa *et al.* 2018; Perry & Rowe 2018). Actually, and despite the fact that studies on the factors governing underlying eco-evolutionary interactions are still scarce (Svensson 2018), there is increasing evidence that sexual selection very frequently fluctuates with changing environmental conditions (Cornwallis & Uller 2010; Miller & Svensson 2014; Evans & Garcia-Gonzalez 2016). For example, the strength and direction of sexual selection vary with resource quality and availability (Gwynne & Simmons 1990; Gillespie *et al.* 2014), population density (Kokko & Rankin 2006), or sex ratio (Punzalan *et al.* 2010), amongst others (Miller & Svensson 2014).

Surprisingly, however, the role of temperature has received very little attention in relation to sexual selection and sexual conflict. While there is good evidence that sexual selection can influence the capacity of a population to withstand environmental change in the form of rising temperatures (Plesnar-Bielak *et al.* 2012b; Miller & Svensson 2014; Parrett & Knell 2018), the opposite causal relationship, that is, whether temperature fluctuations can drive eco-evolutionary feedbacks affecting sexual selection, has received surprisingly little attention. Only a handful of studies so far have directly addressed this issue. In cold-water pipefish sexual selection seems to be stronger in warmer waters (Monteiro & Lyons 2012), and significant co-variation between water temperature and several potential indicators of sexual selection intensity (e.g. sexual size dimorphism) has been documented across populations along a thermal cline (Monteiro *et al.* 2017). Temperature has also been shown to disrupt mating patterns in Artemia (*Artemia franciscana*), ultimately modulating sexual selection intensity (Santos *et al.* 2018). In grey-seals (*Halichoerus grypus*), changes in local weather conditions affect the degree of polygyny and hence the opportunity for selection (Twiss *et al.* 2007). Similarly, a decade-long study in a population of free-ranging sand lizards (*Lacerta agilis*) reported that elevated temperatures correlated with an increase in the degree of polygyny, number of sires per clutch, and opportunity for post-copulatory sexual selection (Olsson *et al.* 2011). In the cigarette beetle (*Lasioderma serricorne*), thermal conditions affect post-copulatory but not pre-copulatory traits, which suggests that temperature variation moderates the relative weight of (as well as the covariances between) the two episodes of sexual selection which, in turn, would determine the total opportunity for sexual selection (Suzaki *et al.* 2018). Finally, in an elegant study in another beetle species, the seed beetle *Callosobruchus maculatus*, Berger and colleagues recently reported an increase in the opportunity for selection under conditions of exposure to a stressful thermal environment (Berger *et al.* 2014), with very similar results being subsequently reported in a more recent study in the same species (Martinossi-Allibert *et al.* 2017).

A framework for the study of temperature and sexual selection

In conjunction, the handful of studies above provides preliminary evidence in support of the idea that temperature can be a fundamental abiotic factor modulating sexual selection, but evidence so far is scant and mostly indirect. This is striking given that temperature is a keystone determinant affecting the physiology and ecology of most animal and plant species, along with many reproductive parameters that are key modulators of sexual selection (e.g. timing of reproduction, duration of the reproductive season, resource availability and quality, population density, sex ratio etc.). Furthermore, beyond such a limited body of evidence we also seem to lack a conceptual framework to explore how and why temperature effects on organisms may feedback to modulate the action of sexual selection, and when we might expect such modulation to be important. A main objective of this paper is to fill this gap by outlining pathways by which temperature can directly or indirectly affect the opportunity for, and strength of, sexual selection, and by extension, a population's viability and evolvability (Fig. 1). We also discuss the most likely avenues of future research in this area, and briefly explore how understanding the link between sexual selection, sexual conflict (Box 1) and temperature may provide crucial insights into the effects of rapid temperature changes on populations (Fig. 2 & Box 2).

Direct temperature effects on the ecology of sexual selection

It has been long recognized that temperature can affect sexual selection through its effects on population dynamics (Gavrilets 2000; Gay *et al.* 2010). To the extent that temperature variation can underlie population growth (e.g. through the availability of nutrients), pose limits to population size, determine the spatial-temporal distribution of populations and individuals (e.g. driving population subdivision and consequently altering population sizes and the probabilities of encountering the opposite sex; (Yasui & Garcia-Gonzalez 2016)), population viscosity and/or mating patch size (McDonald *et al.* 2013; Pizzari *et al.* 2015; McDonald & Pizzari 2018), temperature can moderate sexual selection at large. Beyond these obvious effects, however, the strength and form of sexual selection ultimately depends on the mating system of any given population, and hence on the "ecology of sexual selection" (Emlen & Oring 1977; Schuster & Wade 2003). As we review below, temperature can have direct effects on many of the key parameters in the ecology of sexual selection (Fig. 1A).

Environmental potential for polygyny

There are multiple ways in which temperature may affect the environmental potential for polygyny/polyandry, mainly by affecting male and female spatial-temporal distribution. For example by prolonging/shortening the reproductive season (Sheriff *et al.* 2011), temperature shifts may make female reproduction more or less synchronous and/or shorten/spread out the breeding population in time, hence increasing/decreasing male opportunities to monopolize females and ultimately the environmental potential for polygyny/polyandry (Olsson *et al.* 2011). Similarly, in the Barn swallow (*Hirundo rustica*), warming temperatures have been reported to result in increased protandry, and this has been associated to an increase in the size of a secondary sexual character suggestive of stronger sexual selection

(Moller 2004). Female diapause is also controlled by temperature in many insect species, while males usually either lack reproductive diapause or have a less intense diapause than females (Pener 1992). As such, temperature effects on the onset of female reproductive diapause can, in theory, drastically affect the synchrony of female receptivity within the reproductive season, with potentially important consequences for polygyny and polygamy levels. In essence, temperature is bound to affect male and female timing in entering the mating pool, as well as the amount of time they spend there, which ultimately affect operational sex ratios and sexual selection (Kokko *et al.* 2012).

Sex-specific reproduction costs/benefits

Changes in environmental temperatures and associated environmental stress can alter the costs/benefits of reproduction in a sex-specific way (e.g. costs of investment in offspring, sex-specific mortality linked to reproduction, costs of parental care, offspring survival etc.), affecting sex-specific selection pressures and the opportunity for sexual selection (Fig. 1). For example, Grazer and Martin (Grazer & Martin 2012) showed that the survival costs of reproduction for female *Tribolium castaneum* decrease at higher temperatures. Similarly, in seed beetles thermal stress has been shown to affect selective pressures in a sex-specific way, whereby thermal stress increased the opportunity for selection in adult males, but not females (Martinossi-Allibert *et al.* 2017). Studies looking at this link are still very scarce (Grazer & Martin 2012; Martinossi-Allibert *et al.* 2017), and focus on the short-term plastic consequences of thermal stress, but they provide good preliminary evidence that such effects are not only possible, but theoretically expected (Martinossi-Allibert *et al.* 2017).

Potential reproductive rate (PRR), the operational sex ratio (OSR) and density

Second, several studies have shown that temperature can drastically modulate the potential reproductive rate (PRR) of males and females, and in a sex-specific manner (Kvarnemo 1994). For example, environmental temperature has frequently been found to affect the availability of nutritional resources during reproduction (Vatka *et al.* 2011), which is generally expected to affect female more than male PRR because egg production is particularly dependent on food intake in many animals (Warner *et al.* 2007). Much in the same way, temperature shifts are likely to affect oviposition site availability in many species (e.g.(Fogleman 1979; Berger *et al.* 2008)), which could also differentially affect the PRR of females. On the other hand, temperature may differentially increase male (vs. female) PRR if male reproductive rates are particularly dependent on activity levels, as is frequently the case in species with resource-defence polygynous systems. Temperature also drastically influences incubation time, particularly in species where egg development depends almost exclusively on environmental temperature (most ectotherms), thus greatly determining the PRR of the sex in charge of incubation and brood care (Kokko & Jennions 2008; Kokko *et al.* 2012). This is the case in sand gobies (*Pomatoschistus minutus*), where males build a nest and care for the eggs until hatching. Increased temperatures accelerate egg developmental rates and ultimately male PRR (Kvarnemo 1994). Sex-specific temperature effects on PRR are expected to modulate the operational sex ratio (OSR), and hence the strength of sexual selection (Kvarnemo 1996; Schuster & Wade 2003). Temperature can also directly affect the OSR, a phenomenon bound to be particularly common in species with temperature-dependent sex-determination (Cunningham *et al.* 2017). Finally, population density has been shown to be a crucial determinant of mating systems, and hence sexual selection processes, in many taxa. Density can strongly affect mating skew or mate encounter rates, for example, with cascading effects on mate choice, mate guarding, re-mating rates or female resistance (Kokko & Rankin 2006). In turn, population density (and population dynamics at large) is frequently bound to be under the strong influence of temperature (Gamelon *et al.* 2017). Through its effects on population density, temperature could thus also be an important determinant of sexual selection (Fig. 1).

Indirect temperature effects on the ecology of sexual selection

Temperature effects on the ecology of sexual selection can be mediated not only by direct effects of temperature on the ecology of sexual selection (Fig. 1A), but indirectly by temperature influences on phenotypic traits that subsequently modulate important parameters in the ecology of sexual selection (Fig. 1B).

Behaviour, physiology and life-history traits

Temperature has been shown to drive changes in many facets of reproductive behaviour, including underlying (e.g. physiological) mechanisms, which can in turn be important determinants of sexual selection intensity. For example, temperature is a key determinant of metabolism and activity levels in most species of animals (Kearney *et al.* 2010; Gunderson & Leal 2015), which can directly affect mate searching, the number of male-male and male-female interactions, and general patterns of male and female spatio-temporal distribution. Much in the same way, temperature has been shown to modulate male-male competition intensity (e.g. aggressiveness (Kvarnemo 1998)), courtship rates, mating latency and duration (Jiao *et al.* 2009), female choice (Conrad *et al.* 2017), re-mating rates (Katsuki & Miyatake 2009), and female fecundity (Nunney & Cheung 1997). There are also studies showing that temperature affects sexual signals and/or sexual signalling behaviour (Llusia *et al.* 2013; Sentis *et al.* 2015; Conrad *et al.* 2017), with potential impact on the mate choice and intrasexual competition. Actually, any effect of temperature on the phenotypic mean and variance of sexually selected characters is likely to influence selection on the trait (the covariance between trait magnitude and fitness). Given that the expression of many traits, including secondary sexual traits, can be dependent on temperature (West & Packer 2002; House *et al.* 2013; Reinhardt *et al.* 2015), the significance of this environmental factor on the evolution of mate preferences, and on sexual selection generally, will be evident. Post-copulatory processes have also been reported to be under the influence of temperature. It is well known that the sperm phenotype is in many species contingent on temperature (Reinhardt *et al.* 2015; Sales *et al.* 2018). Most notably sperm competition ability (i.e. in terms of both sperm offence and defence) has been shown to be profoundly influenced by temperature, via effects on the amount and quality of sperm transferred (Katsuki & Miyatake 2009; Lieshout *et al.* 2013; Vasudeva *et al.* 2014). Sperm competitiveness determines siring success, which together with mating success is the main component of male reproductive success in polyandrous species. Critically, then, the action of temperature on sperm competitiveness has the potential to directly affect the opportunity for sexual selection, either through its effects on the variance across males in post-copulatory reproductive success, or on the covariance between the pre-mating and post-mating episodes of sexual selection (Evans & Garcia-Gonzalez 2016).

Finally, temperature has been shown to exert significant changes in life-history traits across different species and populations (Jensen *et al.* 2008; Isaac 2009), some of which are sex-specific (Rogell *et al.* 2014). Many of these changes (e.g. in lifespan, the onset of reproduction, survival, age or size at maturity) have great potential to affect important parameters modulating intra- or inter-sexual competition, such as the OSR, PRR or the environmental potential for polygyny. The broad influence of temperature on key reproductive behaviours and life-history traits highlights its potential importance as a modulator of sexual selection, but makes it all the more surprising that this link has received such little attention so far.

Body size, sexual size dimorphism and condition

Body size, a primary determinant of both inter- and intra-sexual competition, is under the strong influence of environmental temperature via both plastic and evolutionary responses (Lindmark *et al.* 2018). In the seed beetle *Stator limbatus* temperature has been shown to affect scramble competition, whereby smaller males are more successful at finding mates than large males when at cool temperatures (Moya-Laraño *et al.* 2007). Similarly, sexual size dimorphism is a frequent proxy of sexual selection intensity, and also likely to be affected by temperature (Fox *et al.* 2007). For example, via changes in the time and size at emergence, temperature has been shown to reduce sexual dimorphism in some insects (De Block & Stoks 2003), which is predicted to affect the capacity of males to monopolize females and in turn decrease the opportunity for selection (Vanpa *et al.* 2008). Shifts in temperature during development have also been shown to directly influence sexual dimorphism (Ketola *et al.* 2012). Indeed, sexual differences in the sensitivity to rearing temperatures, which would lead to variation in sexual size dimorphism, may be widespread (Fox *et al.* 2007). More generally, temperature changes may, at least in the short-term, affect sexual selection due to sex-biased effects on metabolic rate and/or PRR in species exhibiting strong sexual size dimorphism. In species with strong sexual size dimorphism, and controlling for other potential effects discussed above, temperature will tend to affect the metabolic rate of the smaller sex more than that of the larger sex, simply due to the surface/volume relationship (i.e. surface scales bi-dimensionally with size, while volume scales tri-dimensionally with size). In particular, increasing temperatures will tend to increase the relative PRR of the smaller sex (e.g. males in species with strong fecundity selection –such as *D. melanogaster*– and females in most species with strong sexual selection), which would result in modifications in the strength of sexual selection.

Constraints and trade-offs

Temperature may also modulate sexual selection by its effects on existing trade-offs. For example, environmental temperatures can affect pathogen abundance and virulence, as well as hosts' susceptibility and immune response (Elliot *et al.* 2002). To the extent that immunity is related to body condition and that it trades-off with reproductive effort and primary and secondary sexual traits (Simmons & Roberts 2005; Cotter *et al.* 2010; Mills *et al.* 2010), studying the interplay between thermal ecology and immune ecology, and their combined effects on sexual selection, may inform on other avenues via which temperature can affect processes underlying sexual selection.

Finally, some studies have established links between temperature variation and changes in the levels of genetic variance (measured as additive genetic variances, heritability, or evolvability) and in morphological or life-history traits (Bubliy & Loeschcke 2002; Sgro & Hoffmann 2002; Husby *et al.* 2011; Martinez-Padilla *et al.* 2017). These results show that the evolutionary potential of populations to adapt to changing environments is constrained by genetic architectures that can be temperature-dependent. They also raise the intriguing possibility that temperature can significantly affect the genetic variances of sexually selected traits, or traits that mediate the benefits of sexual selection. For instance, in Martinez-Padilla et al.'s (Martinez-Padilla *et al.* 2017) study on data from 20 European wild bird populations belonging to 12 species, the evolutionary potential of traits that were related to body size and body mass (relevant for sexual selection in general), were seen to be associated with environmental favourability, which was greatly influenced by temperature.

Temperature effects through correlated abiotic factors

It is important to note that many of the effects described above may be driven by abiotic factors that are correlated with temperature, and not by temperature itself (Fig. 1). For example, increases in environmental temperature may facilitate eutrophication and consequently lead to elevated water turbidity (Paerl & Paul 2012), which may have obvious consequences for the action of sexual selection in aquatic animals in which mate choice is based on visual signals, and/or increase the importance of scramble competition vs. mate choice. Human activities leading to higher turbidity have been identified as important threats to the biological diversity of one of the most notable examples of explosive evolution known, the highly diverse species flocks of cichlid fish from the Great Lakes of Africa. In these fish, water turbidity is known to interfere with mate choice and to relax sexual selection (Seehausen *et al.* 1997; Maan & Seehausen 2011), and similar findings have been reported in other systems (Engstrom & Candolin 2007; Candolin *et al.* 2016). In contrast, in the broad-nosed pipefish, *Syngnathus typhle*, a species with male pregnancy, turbidity strengthens sexual selection (Sundin *et al.* 2017). What seems clear, although largely overlooked, is that temperature may be an important mediator in these effects.

Meta-analysis: experimental evidence that temperature impacts on sexual selection

To test whether available data support the idea that temperature can significantly modulate sexual selection, we conducted a systematic review and meta-analysis of the existing literature focusing on studies that experimentally manipulated temperature and measured its impact on either: 1) mating or reproductive success of males and/or females or 2) its effect on traits known to be under sexual selection. Our focus in this review is to explore temperature effects *per se*, beyond any effects that temperature may have due to subjecting individuals/populations to a new environment to which they are maladapted. Environmental duress can modulate the strength of sexual selection in a variety of ways (Arbuthnott & Whitlock 2018), for example increasing sexual selection if the variability in fitness is inflated when populations are pushed off their fitness peak (Martinossi-Allibert *et al.* 2017; Martinossi-Allibert *et al.* 2018a). As such, drastic temperature changes can modulate sexual selection not due to specific effects of temperature but by imposing a stressful environment, much in the same way as a pollutant or a sharp change in another abiotic factors would. To avoid conflating this type of effects, here we explicitly avoided studies implementing heat/cold shock treatments and also assessed the potential influence of using extreme temperature treatments (see below).

It is also important to note that there are no clear theoretical expectations regarding the directionality of temperature effects on sexual selection processes. As laid out in the proposed framework above, increases/decreases in temperature are not necessarily expected to impact sexual selection parameters in the same direction across different species. Some biological processes will tend to exhibit monotonic relationships temperature that are relevant to selection. For example, given that temperature constraints certain fundamental biochemical properties such as protein folding and enzymic reactions, it has recently been proposed that mutations will have increasing fitness effects, and hence lead to stronger selection, with increasing temperatures (Berger *et al.* 2018). However, the net relationship between temperature and sexual selection across taxa is likely to rest largely on the physiology, morphology, behaviour and mating system of each species. Thus, our main aim was not so much to explore the directionality of the relationship between temperature and sexual selection, but to test the more general prediction that temperature has the potential to affect sexual selection in different species, irrespective of direction.

1- Literature Search and Data Collection

We conducted a systematic review and meta-analysis of the existing literature following the PRISMA protocol (Liberati *et al.* 2009) as closely as possible. More specifically, we looked for studies that experimentally manipulated temperature and measured its impact on either: 1) mating or reproductive success of males and/or females or 2) its effect on traits known to be under sexual selection. We only extracted trait values when it was clear from the reported paper, or the raw data, that the trait directly impacted reproductive success. If traits had a tenuous link with reproductive fitness they were not included. We conducted a first literature search on 11/09/18 using the Scopus, PubMed and Web of Science (WoS) databases with the search terms "sexual selection" AND "selecti* intensity" AND "temperature" or "sexual selection" AND "selecti* strength" AND "temperature" for animal taxa. Overall, very few papers were found with these search strings (21 total: Scopus = 5, PubMed = 11 and WoS = 5). After removing duplicates only 15 papers were relevant and 2 more were added through forward and backward searches of citations and references in the 15 papers. Given the small number of hits, we conducted a second search on 17/09/18 across the same databases (i.e., Scopus, PubMed and WoS), using a more general search query: "sexual selection" AND "fitness" AND "temperature" OR "mating success" AND "fitness" AND "temperature" OR "reproductive success" AND "fitness" AND "temperature". This search string was able to capture a broader set of studies for screening. In total, we found 747 studies (Scopus = 291; PubMed = 98; WoS = 358) and after removing 249 duplicates, we were left with 498 unique studies for more detailed screening. Based on the title and abstract we excluded studies that were not on animals (n = 38), had no measure of sexual selection or traits under sexual selection (n = 354), did not do a temperature manipulation (n = 145), and where the effects of temperature could not be isolated because they were confounded by other abiotic or biotic variables (n = 46). We also excluded n = 12 review and theoretical model papers. Note that many studies met more than one of the above criteria, and after this search we were left with a total of 61 papers across both searches as being potentially relevant. We carefully screened these papers to identify articles that met all our above inclusion criteria, and at this stage we also excluded all papers reporting heat/cold shock treatments), which left us with a final set of 19 studies.

We extracted mean fitness or trait value from each temperature treatment along with the standard deviation and sample size for each group from tables and figures [using the R package *metaDigitise* to extract from figures – (Pick *et al.* 2018)]. Experimental designs were highly variable across studies and there were designs that exhibited some level of non-independence in replicate measurements within temperature treatments (e.g., measurements of replicate individuals from isofemale lines). Given that this can affect the sampling variance of the effect size we used conservative sample sizes (i.e., the number of independent lines, or number of mating cages) (Noble *et al.* 2017a). However, when raw data were available, and could be clearly interpreted, we calculated an intraclass correlation coefficient for the clusters (e.g., lines) and computed an 'effective sample size' for the treatment and used this for calculating the sampling variance (Noble *et al.* 2017a). Fitness was often reported on a proportion scale (e.g., the average proportion of mating's/offspring sired). While these are not normally distributed, they were often treated as so in the paper, and given that we required ratio-scale data for our effect sizes (see below) we assumed that these were approximately normally distributed in accordance with the study. Nonetheless, we conducted a sensitivity analysis to determine if effect sizes calculated with proportion data were different than non-proportion data and included this as a covariate to assess their impact on inferences. This has little impact on our major conclusions and so we assumed proportion data was similar to effect sizes derived from other measurement types (See *Supplementary Materials Section 6.2*). A few studies conducted experimental manipulations under fluctuating conditions, but for comparison across studies we focused on constant temperature treatments. In addition, several studies used more than two temperature treatments, in which cases we extracted only the extreme temperatures provided within the most "natural" range for each population (i.e. within the range of minimum-maximum mean monthly temperatures in spring-summer). We acknowledge that some studies included were on populations that were part of experimental evolution experiments reared in the lab at specific constant temperatures. It is not entirely clear the impact this may have on variance if the temperature manipulation was conducted using conditions population were reared at (see *Supplementary Materials* section 6.2 for a more thorough discussion of this problem), however, we dealt with this issue to some extent by analysing magnitudes of variance difference (see below). Finally, we were conservative and only used data from treatments where there was potential for sexual selection to occur (e.g., multiple males and / or females competing) and excluded data from treatments of single pair mating experiments.

2- Effect size statistics– Comparing variance in fitness

We compared how temperature impacted both the mean and variance across experimental groups using the log response ratio (lnRR), the log variance ratio (lnVR) and the log coefficient of variation ratio (lnCVR) (for effect size equations see Nakagawa et al. 2015). We were most interested in how variance in reproductive success, or traits known to be directly related to reproductive success, change as a function of temperature as this directly tests temperature effects on sexual selection, and so, we focus mainly on lnVR and lnCVR in our meta-analysis, but we report the results from lnRR in the *Supplementary Materials*. We used lnVR as a direct estimate of the variance, however, lnVR does not account for mean-variance relationships that existed in our data (See *Supplementary Materials*), and so, we used lnCVR to estimate how variance in reproductive success change independent of changes in average fitness / trait between temperature treatments (Nakagawa et al. 2015). In all cases, when using directional effect sizes (i.e., not absolute magnitude) positive effect sizes indicated higher temperature treatments had a larger variance compared to lower temperature treatments, whereas negative effect sizes indicated the opposite.

3- Moderator Variables

We collected a number of variables we, *a priori*, predicted would moderate the impact of temperature on sexual selection within and across studies. These included: 1) the temperature difference between experimental treatments (continuous variable) – larger temperature differences between treatments are likely to lead to greater effect sizes; 2) the sex of the sample – we predict stronger sexual selection and effects of temperature in males compared to females (Janicke *et al.* 2016); 3) life-history stage at which the temperature manipulation took place (i.e., 'lifetime', 'juvenile/early', 'adults') – given that temperature can impact development that subsequently affects reproductive traits and success; and 4) whether the trait in question was a 'direct' or 'indirect' proxy for sexual selection, where 'direct' estimates were those measuring some aspect of mating or reproductive success and 'indirect' were those estimated with traits that were linked to mating or reproductive success. In some cases, "hot" or "cold" temperature treatments were necessarily outside of this range, so we also classified all effects sizes depending on whether the temperature treatment was "natural" or "stressful". Briefly, if experimental individuals came from a natural population, treatments were categorized as “natural” vs. “stressful” depending on whether they were within the aforementioned max-min temperature range for that population. If experimental individuals came from populations adapted to the lab (i.e. kept for more than 100 generations under a constant temperature regime), we considered temperature treatments > 4ºC away from their normal rearing temperature as stressful. In two cases, experimental individuals came from long-term lab populations reared at a given temperature that were then subject to a short-term (< 20 generations; (Plesnar-Bielak *et al.* 2012a; Plesnar-Bielak *et al.* 2018)) experimental evolution study at a different temperature; in these two cases we considered the long-term rearing temperature as the “adapted” temperature.

4- Meta-analysis

We used multi-level meta-analytic (MLMA) and multi-level meta-regression models (MLMR) to test temperature effects on sexual selection and to explore drivers of effect size variation (Hadfield & Nakagawa 2010; Nakagawa & Santos 2012). In all models we included a random effect of study and species and also included an observation-level random effect to estimate a residual variance given *metaphor* (Viechtbauer 2010) does not estimate one by default. While we had a diversity of species in our dataset, these were taxonomically biased towards insects and we had difficulty resolving the phylogenetic position of most of the taxa in our dataset (tested with TimeTree.org – only 5 / 15 species were identified) – we therefore were limited in our ability to control for phylogeny in our analyses (Chamberlain *et al.* 2012; Noble *et al.* 2017a). However, we generated tree topology and assessed the impact of including phylogenetic correlation matrices in our models. In many cases, including phylogenetic correlation matrices or not including them did not impact our results (See *Supplementary Materials*) and so we just controlled for species in our models. We also assessed publication bias by looking at funnel plots (See Fig. S1 – Section 5, *Supplementary Materials*).

In addition to estimating the overall directional mean effect across studies from our MLMA models, we estimated measures of effect size heterogeneity using I^2 (Higgins & Thompson 2002; Nakagawa & Santos 2012). We estimated the between study heterogeneity (I^2_{stdy} – proportion of variation in effects from shared studies), species heterogeneity (I^2_{sp} – proportion of variation in effects from shared species) and total sampling heterogeneity (I^2_{err} – proportion of variation in effects resulting from sampling variance). However, as discussed above, directional predictions regarding temperatures role on sexual selection processes depends on many factors which make clear directional predictions on how variance is expected to change challenging. As such, we estimated the overall magnitude of variance difference across temperature treatments. To avoid bias in these estimates, we modelled the directional effect sizes assuming a normal distribution and then subsequently transformed this mean estimate using the folded normal distribution, to get the mean absolute magnitude (sensu (Morrissey 2016). To estimate uncertainty around this estimate, we used a Bayesian approach with *MCMCglmm* (Hadfield 2010), and applied the entire posterior distribution of mean estimates to the folded normal to generate 95% credible intervals.

We tested whether our hypothesized moderators explained heterogeneity in effects using our MLMR models. Given our limited sample size (Males: n = 31 effects from k = 14 studies; Females: n = 18 effects from 9 studies), we limited the number of moderators fit to each model to two, and modelled the sexes separately as subset analyses. We ended up not modelling developmental stage given that most of the studies manipulated temperature over the lifetime of the animals. A full presentation on the results and models run can be found in the *Supplementary Materials Sections 2, 3 and 6.*

5- Meta-analysis results and discussion

Experimental studies assessing the effects of temperature on sexual selection are currently biased towards insects (16/19 studies), with only one on arachnids and two on fish. Between study heterogeneity was moderate to high for males (I^2_{stdy}: lnVR = 0.77, lnCVR = 0.34) and small to non-existent for females (I^2_{stdy}: lnVR = 0.13, lnCVR = 0), however, differences between males and females likely reflect the different number of effects reported for each sex. Nonetheless, there was still a high degree of heterogeneity beyond simple sampling variance (I^2_{err} - Males: lnVR = 0.16, lnCVR = 0.31; females: lnVR = 0.33, lnCVR = 0.31).

The overall directional mean effect on variance in all cases did not differ from zero (although there does seem to be a trend whereby higher temperatures are associated with increased variance), so there was no clear directional impact of temperature on sexual selection (Fig. 3). In contrast, the magnitude of effects was moderate, suggesting that temperature does indeed influence direct and indirect measures of sexual selection (Fig. 3). At an average temperature difference between treatments of 7.5 degrees Celsius, male variance decreased at the higher temperature relative to the lower temperature if the temperature manipulation was stressful or if it was a direct measure of reproductive fitness

(Fig. 3A – lnVR). However, this effect was driven by changes in the mean phenotype and when controlling for the mean there was no significant change in variance resulting from stressed or natural conditions and as well as direct fitness measure (Fig. 3B). In contrast, when controlling for the mean, traits indirectly associated with reproductive success showed an increased variance relative to lower temperatures (Fig. 3B). Results from females generally mirrored results from males, excepted it was not possible to robustly compare direct and indirect fitness measures given that indirect measures came from one study. An interesting difference with males is that, accounting for changes in the mean, stressful temperatures seemed to explain the observed increase in the variance of reproductive success in females (Fig. 3C & D). This may indicate that temperature effects on the variance of female reproductive success, and hence potentially sexual selection, are largely mediated by environmental duress. In contrast, temperature effects on males were not dependent on whether temperature treatments were natural or stressful, suggesting temperature *per se* impacts sexual selection in males.

In conjunction, our meta-analysis offers suggestive evidence in support of the idea that temperature may be an important modulator of sexual selection. As evidenced by our systematic search, available data are scant and come mostly from studies that did not aim to measure the relationship between temperature and sexual selection. We did find a few other observational studies reporting correlations between temperature and sexual selection in wild populations (the most relevant ones are discussed above), but interpretation in these cases is problematic due to the large number of confounding co-variables (e.g. humidity, precipitation). In addition, we failed to include Santos et al.'s (Santos *et al.* 2018) relevant study where they clearly show that temperatures disrupt mating patterns, which impacts sexual selection intensity, in *Artemia*. In this study, the authors measured selection differentials based on size differences between mated and unmated individuals. Body size has been shown to be under sexual selection in this species, but we opted to conservatively eliminate this from our meta-analysis because body size is also under strong natural selection and directly influenced by temperature. For the reasons stated above, available studies were altogether surprisingly scarce. This difficulted proper evaluation of interesting arising questions, such as the existence of sex-specific temperature effects on sexual selection and a general trend in the directionality of such effects (Berger *et al.* 2018).

Concluding remarks

To conclude, there is now ample theoretical and empirical evidence that sexual selection (and sexual conflict) is key to understand male and female adaptations and life-histories, and can be a critical determinant of population viability. Given the relevance of sexual selection for individual phenotypes and population fates, a central question in evolutionary biology is therefore to disentangle why sexual selection and sexual conflict vary so much in their form, strength and outcomes across taxa. The role of ecology in explaining sexual selection has been considered prominent so far; albeit less so in the case of sexual conflict. Surprisingly, though, the specific role of temperature, perhaps the most important abiotic ecological factor at a global taxonomic scale, has been relatively ignored. Here, we provide preliminary evidence that temperature can indeed modulate sexual selection in a biologically meaningful way, and develop a framework that will hopefully foster much needed research in this area. We contend a priority for the immediate future is to explore fundamental questions about the interplay between temperature and sexual selection, with respect to short-term plastic changes (i.e. behavioural plasticity; Box 3), intergenerational and transgenerational effects, evolutionary responses, and the consequences such processes have for population viability. For example, upcoming studies will need to consider the effects of adult vs. developmental thermal environments, constant vs. fluctuating temperature regimes (or heat/cold shocks), or the role of behaviour in buffering temperature effects on reproductive parameters and mating systems in natural populations (and thus sexual selection processes).

Specifically, there is much need for experimental studies, ideally on individuals from wild populations, that manipulate temperature within their natural range and ask how such manipulation affects their mating system, ensuing sexual selection and/or sexual conflict intensity, and if possible population viability. Similarly useful will be comprehensive field studies that seek to: a) Identify differences in traits between populations (e.g. secondary sexual traits), b) document whether such differences can be explained by variation in the strength and/or form of sexual selection (e.g. strength of male-male competition, relative importance of inter- vs. intra-sexual selection), c) document the causes and underlying mechanisms of sexual selection (e.g., social interactions, OSR etc.), d) show that temperature changes causal interactions in ways that modify selection (e.g., weaker social interactions in hot climates) and e) study the consequences of temperature’s impact on sexual selection in terms of population viability. In addition to advancing our understanding of sexual selection (and sexual conflict) we suggest studies along these lines can be fundamental for a comprehensive understanding of the impact that rapid environmental changes in temperature (e.g. due to global warming) may have in terms of population extinction. While current studies focus mainly on the direct effects that rising temperatures have on traits linked with population viability, this approach ignores the potentially important feedbacks on processes mediating sexual selection (Fig. 2). Beyond directly affecting population viability, rising temperatures may modulate sexual selection in ways that can both exacerbate (e.g. if rising temperatures slow sexual selection and, with it, the ability to purge mutations and/or viability of populations) or buffer (e.g. if rising temperatures decrease sexual conflict, and with it gender load) its impact on populations.

Acknowledgments

We thank Tobias Uller and Manuel Serra for insightful comments on an earlier draft of this manuscript. PC was supported by a "Plan Nacional I+D+i Excelencia" grant (CGL2017-89052-P), co-funded by the European Regional Development Fund, a Generalitat Valenciana "Excellence of Young Researchers" SEJI grant (SEJI/2018/037), and by a 2018 Leonardo Grant for Researchers and Cultural Creators, from the BBVA Foundation. FGG was supported by a MINECO "Plan Nacional I+D+i Excelencia" grant (CGL2016-76173-P) co-funded by the European Regional Development Fund, and a CSIC start-up grant (201730I034). DWAN was supported by an ARC Discovery Early Career Research Award (DE150101774) and UNSW VC Fellowship.

Supplementary material: https://osf.io/5eqfu/

References

1. Agrawal, A.F. (2001). Sexual selection and the maintenance of sexual reproduction. *Nature*, 411, 692-695.

2. Andersson, M. (1994). *Sexual Selection*. Princeton Univ. Press, Princeton, NJ.

3. Arbuthnott, D., Dutton, E.M., Agrawal, A.F. & Rundle, H.D. (2014). The ecology of sexual conflict: ecologically dependent parallel evolution of male harm and female resistance in Drosophila melanogaster. *Ecol Lett*, 17, 221-228.

4. Arbuthnott, D. & Whitlock, M.C. (2018). Environmental stress does not increase the mean strength of selection. *J Evol Biol*, 31, 1599-1606.

5. Arnqvist, G. & Rowe, C. (2005). *Sexual Conflict*. Princeton University Press, Princeton.

6. Arnqvist, G. & Tuda, M. (2010). Sexual conflict and the gender load: correlated evolution between population fitness and sexual dimorphism in seed beetles. *Proceedings of the Royal Society B: Biological Sciences*, 277, 1345.

7. Berger, D., Grieshop, K., Lind, M.I., Goenaga, J., Maklakov, A.A. & Arnqvist, G. (2014). INTRALOCUS SEXUAL CONFLICT AND ENVIRONMENTAL STRESS. *Evolution*, 68, 2184-2196.

8. Berger, D., Martinossi-Allibert, I., Grieshop, K., Lind, M.I., Maklakov, A.A. & Arnqvist, G. (2016). Intralocus Sexual Conflict and the Tragedy of the Commons in Seed Beetles. *Am Nat*, 188, E98-E112.

9. Berger, D., Stangberg, J. & Walters, R.J. (2018). A Universal Temperature-Dependence of Mutational Fitness Effects. *bioRxiv*.

10. Berger, D., Walters, R. & Gotthard, K. (2008). What limits insect fecundity? Body size- and temperature-dependent egg maturation and oviposition in a butterfly. *Functional Ecology*, 22, 523-529.

11. Bonduriansky, R., Maklakov, A., Zajitschek, F. & Brooks, R. (2008). Sexual selection, sexual conflict and the evolution of ageing and life span. *Functional Ecology*, 22, 443-453.

12. Bubliy, O.A. & Loeschcke, V. (2002). Effect of low stressful temperature on genetic variation of five quantitative traits in Drosophila melanogaster. *Heredity*, 89, 70.

13. Candolin, U. & Heuschele, J. (2008). Is sexual selection beneficial during adaptation to environmental change? *Trends in Ecology & Evolution*, 23, 446-452.

14. Candolin, U., Tukiainen, I. & Bertell, E. (2016). Environmental change disrupts communication and sexual selection in a stickleback population. *Ecology*, 97, 969-979.

15. Chamberlain, S.A., Hovick, S.M., Dibble, C.J., Rasmussen, N.L., Van Allen, B.G., Maitner, B.S. *et al.* (2012). Does phylogeny matter? Assessing the impact of phylogenetic information in ecological meta-analysis. *Ecology Letters*, 15, 627-636.

16. Conrad, T., Stocker, C. & Ayasse, M. (2017). The effect of temperature on male mating signals and female choice in the red mason bee, Osmia bicornis (L.). *Ecology and evolution*, 7, 8966-8975.

17. Cornwallis, C.K. & Uller, T. (2010). Towards an evolutionary ecology of sexual traits. *Trends Ecol Evol*, 25, 145-152.

18. Cotter, S.C., Simpson Stephen, J., Raubenheimer, D. & Wilson, K. (2010). Macronutrient balance mediates tradeâoffs between immune function and life history traits. *Functional Ecology*, 25, 186-198.

19. Coyne, J.A. & Orr, A.H. (2004). *Speciation*. Sinauer, Sunderland, MA.

20. Cunningham, G.D., While, G.M. & Wapstra, E. (2017). Climate and sex ratio variation in a viviparous lizard. *Biol Lett*, 13.

21. Darwin, C. (1859). *On the Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life*. John Murray, London.

22. Darwin, C. (1871). *The descent of Man and Selection in Relation to Sex*. John Murray, London, UK.

23. De Block, M. & Stoks, R. (2003). Adaptive sex-specific life history plasticity to temperature and photoperiod in a damselfly. *Journal of Evolutionary Biology*, 16, 986-995.

24. De Lisle, S.P., Goedert, D., Reedy, A.M. & Svensson, E.I. (2018). Climatic factors and species range position predict sexually antagonistic selection across taxa. *Philosophical transactions of the Royal Society of London. Series B, Biological sciences*, 373.

25. Donkin, I. & Barres, R. (2018). Sperm epigenetics and influence of environmental factors. *Molecular Metabolism*.

26. Dowling, D.K., Williams, B.R. & Garcia-Gonzalez, F. (2014). Maternal sexual interactions affect offspring survival and ageing. *J Evol Biol*.

27. Du, W.G. & Shine, R. (2015). The behavioural and physiological strategies of bird and reptile embryos in response to unpredictable variation in nest temperature. *Biol Rev Camb Philos Soc*, 90, 19-30.

28. Elliot, S.L., Blanford, S. & Thomas, M.B. (2002). Host-pathogen interactions in a varying environment: temperature, behavioural fever and fitness. *Proceedings of the Royal Society B: Biological Sciences*, 269, 1599-1607.

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

30. Engstrom, J. & Candolin, U. (2007). Human-induced water turbidity alters selection on sexual displays in sticklebacks. *Behavioral Ecology*, 18, 393-398.

31. Evans, J.P. & Garcia-Gonzalez, F. (2016). The total opportunity for sexual selection and the integration of pre- and post-mating episodes of sexual selection in a complex world. *J Evol Biol*, 29, 2338-2361.

32. Fogleman, J.C. (1979). Oviposition site preference for substrate temperature in Drosophila melanogaster. *Behavior Genetics*, 9, 407-412.

33. Fox, C.R., Stillwell, R.C. & Moya-Larano, J. (2007). Variation in selection, phenotypic plasticity, and the ecology of sexual size dimorphism in two seed-feeding beetles. . In: *Sex,*

size and gender roles: evolutionary studies of sexual size dimorphism. (eds. Fairbairn, DJ, Blackenhorn, WU & Szekely, T). Oxford University Press Oxford.

34. Gamelon, M., Grotan, V., Nilsson, A.L.K., Engen, S., Hurrell, J.W., Jerstad, K. *et al.* (2017). Interactions between demography and environmental effects are important determinants of population dynamics. *Science Advances*, 3.

35. Garcia-Gonzalez, F. & Simmons, L.W. (2007). Paternal Indirect Genetic Effects on Offspring Viability and the Benefits of Polyandry. *Current Biology*, 17, 32-36.

36. García-Roa, R., Chirinos, V. & Carazo, P. (2018). The ecology of sexual conflict: behaviorally plastic responses to temperature variation in the social environment can drastically modulate male harm to females. *bioRxiv*.

37. Gavrilets, S. (2000). Rapid evolution of reproductive barriers driven by sexual conflict. *Nature*, 403, 886-889.

38. Gavrilets, S. (2014). Is Sexual Conflict an "Engine of Speciation"? *Cold Spring Harbor perspectives in biology*, 6.

39. Gay, L., Hosken, D.J., Eady, P., Vasudev, R. & Tregenza, T. (2010). The evolution of harm--effect of sexual conflicts and population size. *Evolution*, 65, 725-737.

40. Gilbert, S.F., Bosch, T.C. & Ledon-Rettig, C. (2015). Eco-Evo-Devo: developmental symbiosis and developmental plasticity as evolutionary agents. *Nat Rev Genet*, 16, 611-622.

41. Gillespie, S.R., Scarlett Tudor, M., Moore, A.J. & Miller, C.W. (2014). Sexual selection is influenced by both developmental and adult environments. *Evolution*, 68, 3421-3432.

42. Gomez-Llano, M.A., Bensch, H.M. & Svensson, E.I. (2018). Sexual conflict and ecology: Species composition and male density interact to reduce male mating harassment and increase female survival. *Evolution*, 72, 906-915.

43. Grazer, V.M. & Martin, O.Y. (2012). Elevated temperature changes female costs and benefits of reproduction. *Evolutionary Ecology*, 26, 625-637.

44. Gunderson, A.R. & Leal, M. (2015). Patterns of thermal constraint on ectotherm activity. *Am Nat*, 185, 653-664.

45. Gwynne, D.T. & Simmons, L.W. (1990). Experimental reversal of courtship roles in an insect. *Nature*, 346, 172.

46. Hadfield, J.D. (2010). MCMC methods for milti-response Generalized Linear Mixed Models: The MCMCglmm R Package. *Journal of Statistical Software*, 33, 1-22.

47. Hadfield, J.D. & Nakagawa, S. (2010). General quantitative genetic methods for comparative biology: phylogenies, taxonomies and multi-trait models for continuous and categorical characters. *J Evol Biol*, 23, 494-508.

48. Hall, M.D., Bussiere, L.F., Hunt, J. & Brooks, R. (2008). Experimental evidence that sexual conflict influences the opportunity, form and intensity of sexual selection. *Evolution*, 62, 2305-2315.

49. Higgins, J.P. & Thompson, S.G. (2002). Quantifying heterogeneity in a meta-analysis. *Stat Med*, 21, 1539-1558.

50. Hoffmann, A.A. & Sgro, C.M. (2011). Climate change and evolutionary adaptation. *Nature*, 470, 479.

51. Holland, B. & Rice, W.R. (1999). Experimental removal of sexual selection reverses intersexual antagonistic coevolution and removes a reproductive load. *PNAS*, 96, 5083-5088.

52. House, C.M., Lewis, Z., Hodgson, D.J., Wedell, N., Sharma, M.D., Hunt, J. *et al.* (2013). Sexual and natural selection both influence male genital evolution. *PLoS One*, 8, e63807.

53. Husby, A., Visser, M.E. & Kruuk, L.E. (2011). Speeding up microevolution: the effects of increasing temperature on selection and genetic variance in a wild bird population. *PLoS Biol*, 9, e1000585.

54. Isaac, J.L. (2009). Effects of climate change on life history: implications for extinction risk in mammals. *Endangered Species Research*, 7, 115-123.

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

56. Janicke, T., Ritchie, M.G., Morrow, E.H. & Marie-Orleach, L. (2018). Sexual selection predicts species richness across the animal kingdom. *Proc Biol Sci*, 285.

57. Jarzebowska, M. & Radwan, J. (2010). Sexual selection counteracts extinction in small populations of bulb mites. *Evolution*, 64, 1283-1289.

58. Jenkins, T.G., Aston, K.I., James, E.R. & Carrell, D.T. (2017). Sperm epigenetics in the study of male fertility, offspring health, and potential clinical applications. *Systems Biology in Reproductive Medicine*, 63, 69-76.

59. Jennions, M. & Kokko, H. (2010). Sexual selection. In: *Evolutionary Behavioral Ecology* (eds. Westneat, DF & Fox, C). OUP Oxford, pp. 343-364.

60. Jensen, L.F., Hansen, M.M., Pertoldi, C., Holdensgaard, G., Mensberg, K.-L.D. & Loeschcke, V. (2008). Local adaptation in brown trout early life-history traits: implications for climate change adaptability. *Proceedings of the Royal Society B: Biological Sciences*, 275, 2859.

61. Jiao, X., Wu, J., Chen, Z., Chen, J. & Liu, F. (2009). Effects of temperature on courtship and copulatory behaviours of a wolf spider Pardosa astrigera (Araneae: Lycosidae). *Journal of Thermal Biology*, 34, 348-352.

62. Katsuki, M. & Miyatake, T. (2009). Effects of temperature on mating duration, sperm transfer and remating frequency in Callosobruchus chinensis. *J Insect Physiol*, 55, 112-115.

63. Kearney, M., Simpson, S.J., Raubenheimer, D. & Helmuth, B. (2010). Modelling the ecological niche from functional traits. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 365, 3469.

64. Ketola, T., Kristensen, T.N., Kellermann, V.M. & Loeschcke, V. (2012). Can evolution of sexual dimorphism be triggered by developmental temperatures? *Journal of Evolutionary Biology*, 25, 847-855.

65. Kingsolver, J.G. & Buckley, L.B. (2017). Evolution of plasticity and adaptive responses to climate change along climate gradients. *Proceedings of the Royal Society B: Biological Sciences*, 284.

66. Klosin, A., Casas, E., Hidalgo-Carcedo, C., Vavouri, T. & Lehner, B. (2017). Transgenerational transmission of environmental information in C. elegans. *Science*, 356, 320.

67. Kokko, H. & Jennions, M.D. (2008). Parental investment, sexual selection and sex ratios. *Journal of Evolutionary Biology*, 21, 919-948.

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

69. Kokko, H. & Rankin, D.J. (2006). Lonely hearts or sex in the city? Density-dependent effects in mating systems. *Philosophical transactions of the Royal Society of London. Series B, Biological sciences*, 361, 319-334.

70. Kvarnemo, C. (1994). Temperature differentially affects male and female reproductive rates in the sand goby: consequences for operational sex ratio. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, 256, 151.

71. Kvarnemo, C. (1996). Temperature affects operational sex ratio and intensity of male-male competition: an experimental study of sand gobies, Pomatoschistus minutus. *Behavioral Ecology*, 7, 208-212.

72. Kvarnemo, C. (1998). Temperature modulates competitive behaviour: why sand goby males fight more in warmer water. *Ethology Ecology & Evolution*, 10, 105-114.

73. Le Galliard, J.F., Fitze, P.S., Ferriäre, R. & Clobert, J. (2005). Sex ratio bias, male aggression, and population collapse in lizards. *Proc.Natl.Acad.Sci.USA*, 102, 18231-18236.

74. Liberati, A., Altman, D.G., Tetzlaff, J., Mulrow, C., GÃ¸tzsche, P.C., Ioannidis, J.P.A. *et al.* (2009). The PRISMA Statement for Reporting Systematic Reviews and Meta-Analyses of Studies That Evaluate Health Care Interventions: Explanation and Elaboration. *PLOS Medicine*, 6, e1000100.

75. Lieshout, E., Tomkins Joseph, L. & Simmons Leigh, W. (2013). Heat stress but not inbreeding affects offensive sperm competitiveness in Callosobruchus maculatus. *Ecology and evolution*, 3, 2859-2866.

76. Lindmark, M., Huss, M., Ohlberger, J. & Gardmark, A. (2018). Temperature-dependent body size effects determine population responses to climate warming. *Ecol Lett*, 21, 181-189.

77. Llusia, D., Marquez, R., Beltran, J.F., Benitez, M. & do Amaral, J.P. (2013). Calling behaviour under climate change: geographical and seasonal variation of calling temperatures in ectotherms. *Glob Chang Biol*, 19, 2655-2674.

78. Long, T.A.F., Agrawal, A.F. & Rowe, L. (2012). The Effect of Sexual Selection on Offspring Fitness Depends on the Nature of Genetic Variation. *Current Biology*, 22, 204-208.

79. Lorch, P.D., Proulx, S., Rowe, L. & Day, T. (2003). Condition-dependent sexual selection can accelerate adaptation. *Evolutionary Ecology Research*, 5, 867-881.

80. Lumley, A.J., Michalczyk, L., Kitson, J.J., Spurgin, L.G., Morrison, C.A., Godwin, J.L. *et al.* (2015). Sexual selection protects against extinction. *Nature*.

81. Maan, M.E. & Seehausen, O. (2011). Ecology, sexual selection and speciation. *Ecology Letters*, 14, 591-602.

82. Martinez-Padilla, J., Estrada, A., Early, R. & Garcia-Gonzalez, F. (2017). Evolvability meets biogeography: evolutionary potential decreases at high and low environmental favourability. *Proc Biol Sci*, 284.

83. Martinez-Ruiz, C. & Knell, R.J. (2017). Sexual selection can both increase and decrease extinction probability: reconciling demographic and evolutionary factors. *J Anim Ecol*, 86, 117-127.

84. Martinossi-Allibert, I., Arnqvist, G. & Berger, D. (2017). Sex-specific selection under environmental stress in seed beetles. *J Evol Biol*, 30, 161-173.

85. Martinossi-Allibert, I., Savkovic, U., Dordevic, M., Arnqvist, G., Stojkovic, B. & Berger, D. (2018a). The consequences of sexual selection in well-adapted and maladapted populations of bean beetles. *Evolution*, 72, 518-530.

86. Martinossi-Allibert, I., Thilliez, E., Arnqvist, G. & Berger, D. (2018b). Sexual selection, environmental robustness and evolutionary demography of maladapted populations: a test using experimental evolution in seed beetles. *bioRxiv*.

87. McDonald, G.C., James, R., Krause, J. & Pizzari, T. (2013). Sexual networks: measuring sexual selection in structured, polyandrous populations. *Philosophical transactions of the Royal Society of London. Series B, Biological sciences*, 368, 20120356.

88. McDonald, G.C. & Pizzari, T. (2018). Structure of sexual networks determines the operation of sexual selection. *Proc Natl Acad Sci U S A*, 115, E53-E61.

89. Miller, C.W. & Svensson, E.I. (2014). Sexual selection in complex environments. *Annu Rev Entomol*, 59, 427-445.

90. Miller, D., Brinkworth, M. & Iles, D. (2010). Paternal DNA packaging in spermatozoa: more than the sum of its parts? DNA, histones, protamines and epigenetics. *Reproduction*, 139, 287-301.

91. Mills, S.C., Grapputo, A., Jokinen, I., Koskela, E., Mappes, T. & Poikonen, T. (2010). Fitness trade-offs mediated by immunosuppression costs in a small mammal. *Evolution*, 64, 166-179.

92. Moller, A.P. (2004). Protandry, sexual selection and climate change. *Global Change Biology*, 10, 2028-2035.

93. Monteiro, N., Cunha, M., Ferreira, L., Vieira, N., Antunes, A., Lyons, D. *et al.* (2017). Parabolic variation in sexual selection intensity across the range of a cold-water pipefish: implications for susceptibility to climate change. *Global Change Biology*, 23, 3600-3609.

94. Monteiro, N.M. & Lyons, D.O. (2012). Stronger sexual selection in warmer waters: the case of a sex role reversed pipefish. *PLoS One*, 7, e44251.

95. Morrissey, M.B. (2016). Meta-analysis of magnitudes, differences and variation in evolutionary parameters. *Journal of Evolutionary Biology*, 29, 1882-1904.

96. Moya-Laraño, J., El-Sayyid, M.E.T. & Fox, C.W. (2007). Smaller beetles are better scramble competitors at cooler temperatures. *Biology Letters*, 3, 475.

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

98. Noble, D.W.A., Lagisz, M., O'Dea, R.E. & Nakagawa, S. (2017a). Nonindependence and sensitivity analyses in ecological and evolutionary meta-analyses. *Molecular Ecology*, 26, 2410-2425.

99. Noble, D.W.A., Stenhouse, V. & Schwanz, L.E. (2017b). Developmental temperatures and phenotypic plasticity in reptiles: a systematic review and meta-analysis. *Biological Reviews*, 93, 72-97.

100. Nunney, L. & Cheung, W. (1997). THE EFFECT OF TEMPERATURE ON BODY SIZE AND FECUNDITY IN FEMALE DROSOPHILA MELANOGASTER: EVIDENCE FOR ADAPTIVE PLASTICITY. *Evolution*, 51, 1529-1535.

101. Olsson, M., Wapstra, E., Schwartz, T., Madsen, T., Ujvari, B. & Uller, T. (2011). IN HOT PURSUIT: FLUCTUATING MATING SYSTEM AND SEXUAL SELECTION IN SAND LIZARDS. *Evolution*, 65, 574-583.

102. Paerl, H.W. & Paul, V.J. (2012). Climate change: Links to global expansion of harmful cyanobacteria. *Water Research*, 46, 1349-1363.

103. Parker, G.A. (2006). Sexual conflict over mating and fertilization: an overview. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 361, 235-259.

104. Parker, G.A. & Partridge, L. (1998). Sexual conflict and speciation. *Philosophical transactions of the Royal Society of London. Series B, Biological sciences*, 353, 261-274.

105. Parmesan, C. (2006). Ecological and Evolutionary Responses to Recent Climate Change. *Annual Review of Ecology, Evolution, and Systematics*, 37, 637-669.

106. Parrett, J.M. & Knell, R.J. (2018). The effect of sexual selection on adaptation and extinction under increasing temperatures. *Proc Biol Sci*, 285.

107. Pener, M.P. (1992). Environmental Cues, Endocrine Factors, and Reproductive Diapause in Male Insects. *Chronobiology International*, 9, 102-113.

108. Perry, J.C., Garroway, C.J. & Rowe, L. (2017). The role of ecology, neutral processes and antagonistic coevolution in an apparent sexual arms race. *Ecol Lett*, 20, 1107-1117.

109. Perry, J.C. & Rowe, L. (2018). Sexual conflict in its ecological setting. *Philosophical transactions of the Royal Society of London. Series B, Biological sciences*, 373.

110. Pick, J.L., Nakagawa, S. & Noble, D.W.A. (2018). Reproducible, flexible and high‐throughput data extraction from primary literature: The metaDigitise R package. *Methods in Ecology & Evolution*, In Press.

111. Pitnick, S. & Garcia-Gonzalez, F. (2002). Harm to females increases with male body size in Drosophila melanogaster. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, 269, 1821.

112. Pizzari, T., Biernaskie, J.M. & Carazo, P. (2015). Inclusive fitness and sexual conflict: How population structure might modulate the battle of the sexes. *BioEssays*, 37, 155-166.

113. Plesnar-Bielak, A., Skrzynecka, A.M., Prokop, Z.M. & Radwan, J. (2012a). Mating system affects population performance and extinction risk under environmental challenge. *Proceedings of the Royal Society B-Biological Sciences*, 279, 4661-4667.

114. Plesnar-Bielak, A., Skrzynecka, A.M., Prokop, Z.M. & Radwan, J. (2012b). Mating system affects population performance and extinction risk under environmental challenge. *Proceedings of the Royal Society B: Biological Sciences*, 279, 4661.

115. Plesnar-Bielak, A., Skwierzynska, A.M., Hlebowicz, K. & Radwan, J. (2018). Relative costs and benefits of alternative reproductive phenotypes at different temperatures - genotype-by-environment interactions in a sexually selected trait. *Bmc Evolutionary Biology*, 18.

116. Pomiankowski, A. & Moller, A. (1995). A resolution of the lek paradox. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, 260, 21.

117. Punzalan, D., Rodd, F.H. & Rowe, L. (2010). Temporally variable multivariate sexual selection on sexually dimorphic traits in a wild insect population. *Am Nat*, 175, 401-414.

118. Radwan, J. (2004). Effectiveness of sexual selection in removing mutations induced with ionizing radiation. *Ecology Letters*, 7, 1149-1154.

119. Rankin, D.J., Dieckmann, U. & Kokko, H. (2011). Sexual conflict and the tragedy of the commons. *Am Nat*, 177, 780-791.

120. Rankin, D.J. & Kokko, H. (2006). Sex, death and tragedy. *Trends in Ecology & Evolution*, 21, 225-226.

121. Reinhardt, K., Dobler, R. & Abbott, J. (2015). An Ecology of Sperm: Sperm Diversification by Natural Selection. *Annual Review of Ecology, Evolution, and Systematics*, 46, 435-459.

122. Rice, W.R. (1996). Sexually antagonistic male adaptation triggered by experimental arrest of female evolution. *Nature*, 381, 232-234.

123. Rice, W.R. (1998). Intergenomic conflict, interlocus antagonistic coevolution, and the evolution of reproductive isolation. In: *Endless forms: Species and speciation* (ed. Howard, DJ). Oxford University Press New York.

124. Rice, W.R. & Chippindale, A.K. (2002). The Evolution of Hybrid Infertility: Perpetual Coevolution between Gender-Specific and Sexually Antagonistic Genes. *Genetica*, 116, 179-188.

125. Rogell, B., Widegren, W., Hallsson, L.R., Berger, D., Björklund, M., Maklakov, A.A. *et al.* (2014). Sex-dependent evolution of life-history traits following adaptation to climate warming. *Functional Ecology*, 28, 469-478.

126. Rowe, L. & Houle, D. (1996). The lek paradox and the capture of genetic variance by condition dependent traits. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, 263, 1415.

127. Sales, K., Vasudeva, R., Dickinson, M.E., Godwin, J.L., Lumley, A.J., Michalczyk, Å.u. *et al.* (2018). Experimental heatwaves compromise sperm function and cause transgenerational damage in a model insect. *Nature Communications*, 9, 4771.

128. Santos, M.R., Vieira, N. & Monteiro, N.M. (2018). High temperatures disrupt Artemia franciscana mating patterns and impact sexual selection intensity. *Estuarine, Coastal and Shelf Science*, 207, 209-214.

129. Schuster, S.M. & Wade, M.J. (2003). *Mating systems and strategies*.

130. Seebacher, F., White, C.R. & Franklin, C.E. (2014). Physiological plasticity increases resilience of ectothermic animals to climate change. *Nature Climate Change*, 5, 61.

131. Seehausen, O., Alphen, J.J.M.v. & Witte, F. (1997). Cichlid Fish Diversity Threatened by Eutrophication That Curbs Sexual Selection. *Science*, 277, 1808.

132. Sentis, A., Ramon�-Portugal, F., Brodeur, J. & Hemptinne, J.L. (2015). The smell of change: warming affects species interactions mediated by chemical information. *Global Change Biology*, 21, 3586-3594.

133. Sgro, C., M. & Hoffmann, A.A. (2002). Effects of temperature extremes on genetic variances for life history traits in Drosophila melanogaster as determined from parentâ��offspring comparisons. *Journal of Evolutionary Biology*, 11, 1-20.

134. Sheriff, M.J., Kenagy, G.J., Richter, M., Lee, T., Toien, O., Kohl, F. *et al.* (2011). Phenological variation in annual timing of hibernation and breeding in nearby populations of Arctic ground squirrels. *Proc Biol Sci*, 278, 2369-2375.

135. Simmons, L.W. & Roberts, B. (2005). Bacterial Immunity Traded for Sperm Viability in Male Crickets. *Science*, 309, 2031.

136. Snell-Rood, E.C., Van Dyken, J.D., Cruickshank, T., Wade, M.J. & Moczek, A.P. (2010). Toward a population genetic framework of developmental evolution: the costs, limits, and consequences of phenotypic plasticity. *BioEssays : news and reviews in molecular, cellular and developmental biology*, 32, 71-81.

137. Stuppia, L., Franzago, M., Ballerini, P., Gatta, V. & Antonucci, I. (2015). Epigenetics and male reproduction: the consequences of paternal lifestyle on fertility, embryo development, and children lifetime health. *Clinical Epigenetics*, 7, 120.

138. 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, 78.

139. Suzaki, Y., Kodera, S., Fujiwara, H., Sasaki, R., Okada, K. & Katsuki, M. (2018). Temperature variations affect postcopulatory but not precopulatory sexual selection in the cigarette beetle. *Animal Behaviour*, 144, 115-123.

140. Svensson, E.I. (2018). Eco-evolutionary dynamics of sexual selection and sexual conflict. *Functional Ecology*, In press.

141. Twiss, S.D., Thomas, C., Poland, V., Graves, J.A. & Pomeroy, P. (2007). The impact of climatic variation on the opportunity for sexual selection. *Biology Letters*, 3, 12.

142. Vanpa, C., Kjellander, P., Galan, M., Cosson, J.-F., Aulagnier, S., Liberg, O. *et al.* (2008). Mating system, sexual dimorphism, and the opportunity for sexual selection in a territorial ungulate. *Behavioral Ecology*, 19, 309-316.

143. Vasudeva, R., Deeming, D.C. & Eady, P.E. (2014). Developmental temperature affects the expression of ejaculatory traits and the outcome of sperm competition in Callosobruchus maculatus. *J Evol Biol*, 27, 1811-1818.

144. Vatka, E., Orell, M. & RytkÖNen, S. (2011). Warming climate advances breeding and improves synchrony of food demand and food availability in a boreal passerine. *Global Change Biology*, 17, 3002-3009.

145. Viechtbauer, W. (2010). Conducting Meta-Analyses in R with the metafor Package. *Journal of Statistical Software; Vol 1, Issue 3 (2010)*.

146. Wang, Y., Liu, H. & Sun, Z. (2017). Lamarck rises from his grave: parental environmentâ��induced epigenetic inheritance in model organisms and humans. *Biological Reviews*, 92, 2084-2111.

147. Warner, D.A., Lovern, M.B. & Shine, R. (2007). Maternal nutrition affects reproductive output and sex allocation in a lizard with environmental sex determination. *Proc Biol Sci*, 274, 883-890.

148. West, P.M. & Packer, C. (2002). Sexual selection, temperature and the Lion's mane. *Science*, 297, 1339-1343.

149. West-Eberhard, M.J. (2003). *Developmental Plasticity and Evolution*. Oxford University Press, New York.

150. Whitlock, M.C. & Agrawal, A.F. (2009). Purging the genome with sexual selection: Reducing mutation load though selection on males. *Evolution*, 63, 569-582.

151. Wigby, S. & Chapman, T. (2004). Female resistance to male harm evolves in response to manipulation of sexual conflict. *Evolution*, 58, 1028-1037.

152. Yasui, Y. & Garcia-Gonzalez, F. (2016). Bet-hedging as a mechanism for the evolution of polyandry, revisited. *Evolution*, 70, 385-397.

153. Zajitschek, S.R.K., Dowling, D.K., Head, M.L., Rodriguez-Exposito, E. & Garcia-Gonzalez, F. (2018). Transgenerational effects of maternal sexual interactions in seed beetles. *Heredity (Edinb)*.

Figure 1.

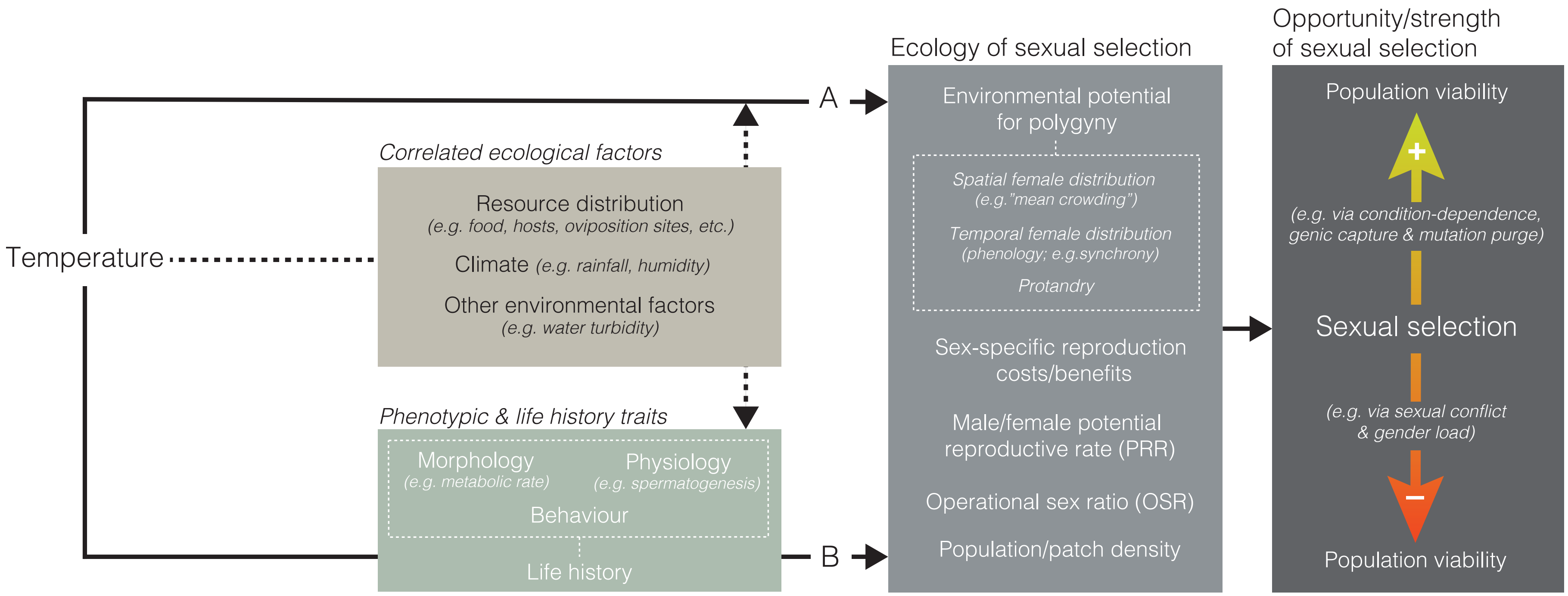

Temperature
A
B
Correlated ecological factors
Resource distribution
(e.g. food, hosts, oviposition sites, etc.)
Climate (e.g. rainfall, humidity)
Other environmental factors
(e.g. water turbidity)
Phenotypic & life history traits
Morphology
(e.g. metabolic rate)
Physiology
(e.g. spermatogenesis)
Behaviour
Life history
Ecology of sexual selection
Environmental potential for polygyny
Spatial female distribution
(e.g."mean crowding")
Temporal female distribution
(phenology; e.g.synchrony)
Protandry
Sex-specific reproduction costs/benefits
Male/female potential reproductive rate (PRR)
Operational sex ratio (OSR)
Population/patch density
Opportunity/strength of sexual selection
Population viability
+
(e.g. via condition-dependence, genic capture & mutation purge)
Sexual selection
(e.g. via sexual conflict & gender load)
−
Population viability

Figure 2.

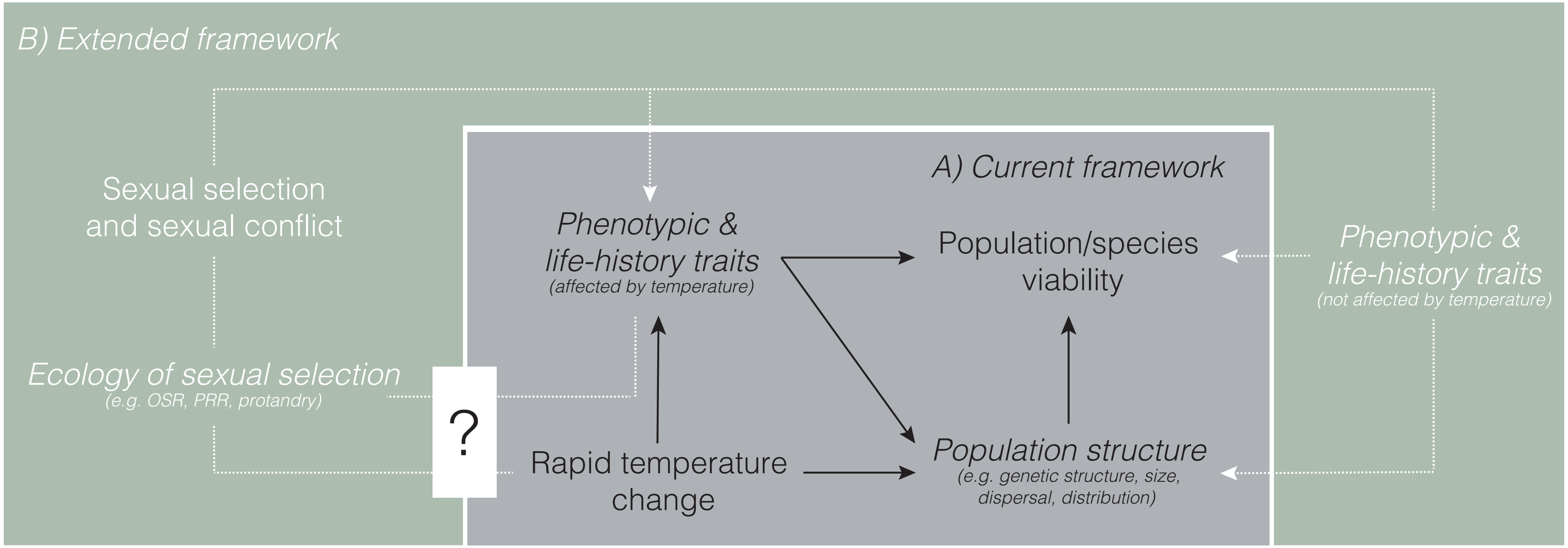
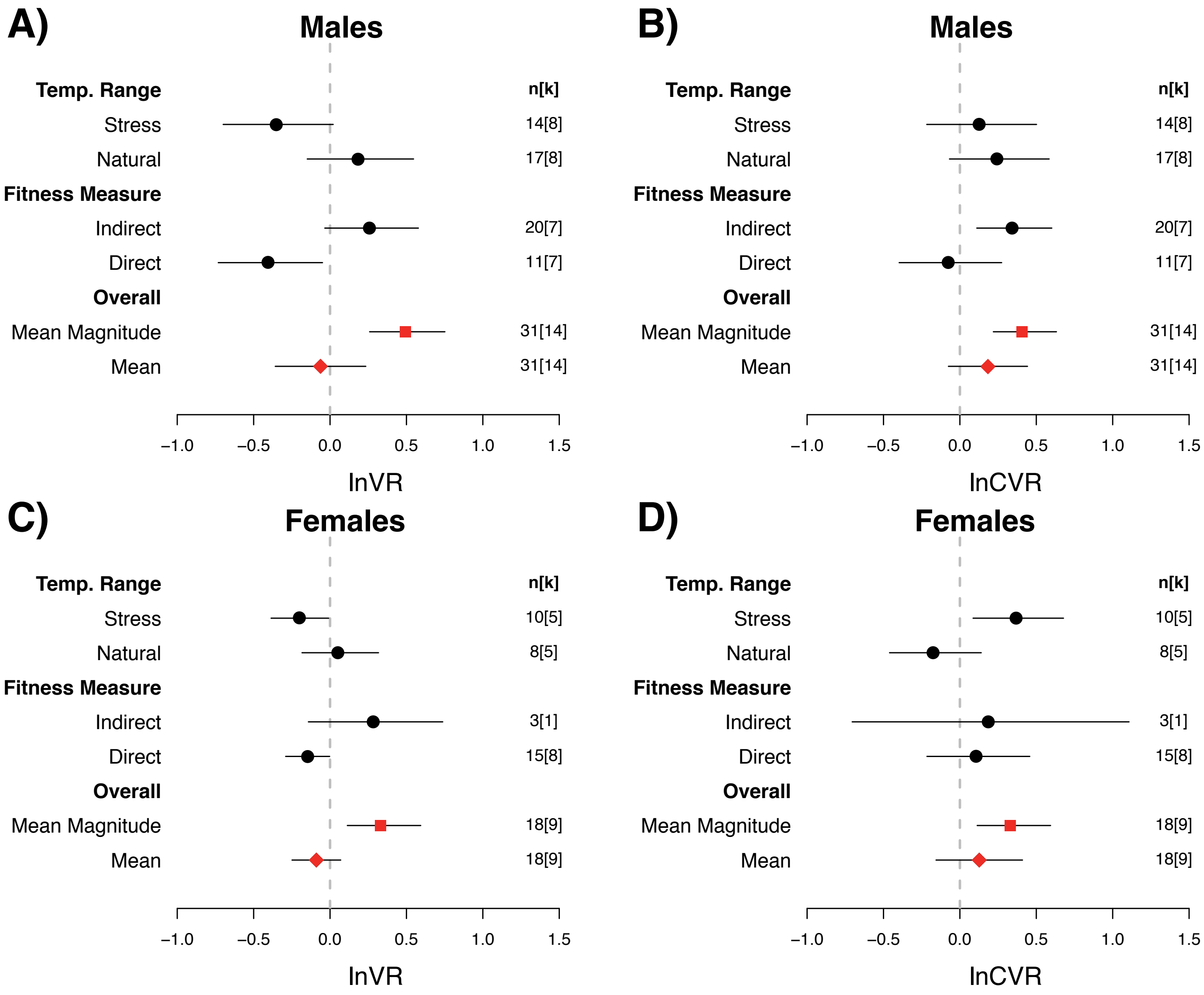

B) Extended framework
A) Current framework
Sexual selection and sexual conflict
Ecology of sexual selection
(e.g. OSR, PRR, protandry)
?
Phenotypic & life-history traits
(affected by temperature)
Rapid temperature change
Population/species viability
Population structure
(e.g. genetic structure, size, dispersal, distribution)
Phenotypic & life-history traits
(not affected by temperature)

Figure 3.



A)
Males
Temp. Range
Stress
Natural
Fitness Measure
Indirect
Direct
Overall
Mean Magnitude
Mean
n[k]
14[8]
17[8]
20[7]
11[7]
31[14]
31[14]
−1.0
−0.5
0.0
0.5
1.0
1.5
lnVR
B)
Males
Temp. Range
Stress
Natural
Fitness Measure
Indirect
Direct
Overall
Mean Magnitude
Mean
n[k]
14[8]
17[8]
20[7]
11[7]
31[14]
31[14]
−1.0
−0.5
0.0
0.5
1.0
1.5
lnCVR
C)
Females
Temp. Range
Stress
Natural
Fitness Measure
Indirect
Direct
Overall
Mean Magnitude
Mean
n[k]
10[5]
8[5]
3[1]
15[8]
18[9]
18[9]
−1.0
−0.5
0.0
0.5
1.0
1.5
lnVR
D)
Females
Temp. Range
Stress
Natural
Fitness Measure
Indirect
Direct
Overall
Mean Magnitude
Mean
n[k]
10[5]
8[5]
3[1]
15[8]
18[9]
18[9]
−1.0
−0.5
0.0
0.5
1.0
1.5
lnCVR

Figure 1. A schematic outline of some of the pathways by which temperature can affect sexual selection, and ultimately population viability. Temperature can have direct effects on parameters of the ecology of sexual selection (A), such as in density or female spatiotemporal distribution (e.g. by affecting the availability of food resources), which will in turn modulate the strength of sexual selection and its likely effects on population viability. In addition, temperature can have direct effects on phenotypic traits (B), such as body size or metabolic rate, that in turn condition the ecology of sexual selection, impacting how sexual selection operates. Finally, temperature usually co-varies with other abiotic factors that can have similar direct and indirect effects on parameters in the ecology of sexual selection.

Figure 2. The current framework (A; text in black over grey background) focuses on the direct effects that rapid temperature changes have on populations, through its effects on the phenotype of individuals in a population and/or population structure. We suggest an extended framework (B; text in white over green background) would need to consider the feedback that such direct temperature effects can have on sexual selection processes, along with other direct effects of temperature on the ecology of sexual selection (Fig. 1). Through both these routes, rapid temperature changes can ultimately impact population viability.

Figure 3. Meta-analytic means for a temperature treatment difference of 7.5 degrees Celsius across MLMA and MLMR models for the log variance ratio (lnVR) and the log coefficient of variation ratio (lnCVR) for males and females. n = total number of effect sizes, whereas k = the total number of studies. Mean estimates and 95% credible/confidence intervals are provided. Subset analyses exploring the impact of various moderators on lnVR and lnCVR are provided ('circles'), along with the overall meta-analytic mean ('red diamond') and the mean magnitude of log variance ratio differences between treatments ('red square').

Box 1- Temperature, sexual selection and rapid environmental change

From an eco-evolutionary point of view, a rapid environmental change results in a mismatch between an organism's optimal and current environment, potentially leading to population decline and extinction. Whether a population is able to withstand such environmental changes and avoid extinction will depend essentially on whether it is capable of adapting quickly enough to track these changes (Parmesan 2006; Hoffmann & Sgro 2011; Kingsolver & Buckley 2017; Martinez-Padilla *et al.* 2017). Most studies that try to predict the consequences of rapid environmental change for natural populations focus on studying the direct effects of, for example, temperature shifts on certain phenotypic and life-history traits that are likely to be causally influenced by temperature, and then examine how these changes affect population viability. Above we have reviewed how these effects can also affect the strength and opportunity of sexual selection through a variety of pathways (Figure 1). In doing so, the initial effects of a sustained temperature shift can feedback to impact a much wider diversity of phenotypic traits irrespective of whether they are under the direct causal influence of temperature. Furthermore, temperature can affect the capacity of individuals in a population/species to purge deleterious mutations and fix beneficial alleles (Lorch *et al.* 2003; Radwan 2004; Whitlock & Agrawal 2009; Jarzebowska & Radwan 2010; Lumley *et al.* 2015), adapt against environmental stress (Lorch *et al.* 2003; Plesnar-Bielak *et al.* 2012b; Martinez-Ruiz & Knell 2017; Parrett & Knell 2018), and generate sexual conflict (Berger *et al.* 2016). Therefore, sexual selection has great potential to influence the fate of populations/species facing directional environmental changes (Candolin & Heuschele 2008), such as for example those imposed by global warming. In particular, recent evidence has shown that strong sexual selection can help buffer against warming temperatures, with experimental populations facing rising temperatures having higher fecundity and offspring survival when under a strong sexual selection regime (Parrett & Knell 2018). This means that any effects of temperature on sexual selection and/or sexual conflict are likely to feedback and impact a wide range of phenotypic traits linked with population extinction (Figure 2).

Box 2- Temperature and sexual conflict

Sexual conflict has received much attention in recent years (Rice 1996; Holland & Rice 1999; Wigby & Chapman 2004), and is currently recognized as a key mechanism shaping male/female adaptations and life-history traits (Bonduriansky *et al.* 2008). Importantly, sexual conflict can also decrease male and female fitness by displacing the sexes off their respective evolutionary optima (i.e. gender load; (Rice & Chippindale 2002), and via male adaptations that harm females (i.e. male harm; e.g. (Pitnick & Garcia-Gonzalez 2002)). Sexual selection will frequently favour males that outcompete each other by means of traits that harm females and reduce their fitness (Parker 2006). Such male harm is a widespread consequence (and cause) of sexual conflict that not only impacts female fitness, but can have pronounced repercussions for female productivity and the population as a whole, reducing population growth and even leading to local extinction (Le Galliard *et al.* 2005; Rankin & Kokko 2006; Rankin *et al.* 2011; Berger *et al.* 2016).

Despite impressive advances in the field of sexual conflict, we are still far from being able to explain the overwhelming diversity of adaptations to deal with sexual conflict, and particularly for male harm, or the net consequences that such adaptations have for population viability. The apparently arbitrary nature of the co-evolutionary trajectories that often result from strong sexual conflict has been sometimes interpreted to mean that ecology occupies a rear seat in such processes, or is altogether irrelevant (Coyne & Orr 2004; Arbuthnott *et al.* 2014). This, however, seems highly unlikely given that sexual conflict critically depends on the intensity of male-male competition, and sexual selection is profoundly affected by ecological factors. In fact, there is good evidence to show that the opportunity of sexual conflict does depend on the ecological context (Arbuthnott *et al.* 2014; Perry *et al.* 2017; De Lisle *et al.* 2018; Gomez-Llano *et al.* 2018; Perry & Rowe 2018). In particular, three recent studies suggest that temperature can modulate sexual conflict. First, Berger et al. showed that gender load via intralocus sexual conflict is reduced in a natural population of *C. maculatus* beetles subject to a stressful thermal environment ((Berger *et al.* 2014); see also (Martinossi-Allibert *et al.* 2018b)). This is in line with theoretical expectations that intralocus sexual conflict will decrease in novel environments, for example due to concordant (in both sexes) natural selection of previously neutral alleles (Long *et al.* 2012). Second, Perry et al. showed that different ecological parameters, among them being temperature, contributed to explain inter-population differences in a sexually antagonistic arms-race in natural populations of water striders (*Gerris incognitus* (Perry *et al.* 2017)). This can be due to, for example, inter-population differences in ecological forces acting on mating system variation and ensuing sexual conflict (Perry & Rowe 2018). Finally, García-Roa *et al.*

manipulated sexual conflict levels in *D. melanogaster* and showed that the resulting increase in female harm levels (with increasing sexual conflict) decreases sharply in both colder (21ºC) and hotter (29ºC) social environments to those to which the population had adapted (García-Roa et al. unpublished). In this species, therefore, temperature shifts are likely modulators of male harm mechanisms (e.g. production of sperm and/or toxic components in the ejaculate), which is perhaps to be expected whenever male harm adaptations are expressed in a sub-optimal environment.

More generally, these studies show that temperature does indeed have the potential to modulate sexual conflict, pinpoint some of the main ways in which this may happen, and generally suggest that the negative impact of sexual conflict on population viability, due both to gender load and female harm, may be ameliorated when populations face rapid temperature changes (e.g. global warming), which would ultimately increase the ability of populations to avoid extinction.

Box 3- Processes involved in sexual selection responses to temperature

Transversal to the links we have described so far is the question of what type of responses (adaptive and non-adaptive) may result from temperature shifts in the environment. Adaptive population-level responses in the face of environmental change can ensue via both natural selection (including sexual selection), by exploiting existing genetic variation, and via phenotypic plasticity, by exploiting the ability of individuals to adjust their development/behaviour to the environment and/or by revealing cryptic genetic variation that can later be the target of selection, via genetic assimilation (West-Eberhard 2003; Snell-Rood *et al.* 2010; Gilbert *et al.* 2015). Phenotypic plasticity, whether adaptive or maladaptive, is likely to be of particular importance in understanding temperature-mediated effects on sexual selection for the obvious reason that development is critically affected by environmental temperature in most species, and particularly so in ectotherms. For example, meta-analyses have identified strong effects of temperature during development on suites of traits, such as growth rate, physiology, performance and morphology, with these effects having long-lasting consequences on traits and moulding underlying physiology (Seebacher *et al.* 2014; Noble *et al.* 2017b). Behavioural plasticity, including paternal effects, might also be very important because it is a way in which parents can buffer the developmental temperature of their offspring, mitigating the consequences of environmental temperature shifts (Du & Shine 2015).

Similarly, temperature is perhaps also particularly likely to impact sexual selection via intergenerational and transgenerational effects, both because temperature is frequently a cue of many other environmental changes (e.g. food availability, onset of reproductive/breeding period etc.) and because temperature affects a host of physiological mechanisms that may spill over to the next/s generation/s via paternal effects or the transmission of epigenetic marks. Paternal germline epigenetic changes that are environmentally triggered are increasingly recognised as modulators of sperm function (Stuppia *et al.* 2015; Jenkins *et al.* 2017) but also, remarkably, as sources of variance in offspring phenotype (Miller *et al.* 2010; Stuppia *et al.* 2015; Jenkins *et al.* 2017; Wang *et al.* 2017; Donkin & Barres 2018). In *Caenorhabditis elegans,* for instance, it has been documented that temperature variation induces multigenerational inheritance of gene expression through both oocytes and sperm (Klosin *et al.* 2017). Demonstrating such long-lasting epigenetic memory of parental temperature experiences and at the same time unravelling the underlying mechanisms is challenging and has been seldom achieved (Klosin *et al.* 2017), but there are reasons to suspect that temperature-induced transmission of epigenetic marks affecting sperm and offspring phenotypes may be common (Evans et al., unpublished). Whether these cross-generational effects stemming from paternal experiences are driven by epigenetic mechanisms or are mediated by other factors (e.g. direct or female-moderated paternal effects arising from variation in the non-sperm fraction of the ejaculate (Garcia-Gonzalez & Simmons 2007)) is not known, but any intergenerational or transgenerational effect has the capacity to significantly alter the economics of sexual interactions (Dowling *et al.* 2014; Zajitschek *et al.* 2018), leading to unknown but presumably significant effects on sexual selection. We anticipate that investigations on the transmission of parental temperature environments across generations, and on their effects on sexual selection, will yield important insight.