

# 1 **Temperature as a modulator of sexual selection**

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19 **Running title:** Temperature and sexual selection

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## 22 23 **ABSTRACT**

24 A central question in ecology and evolution is to understand why sexual selection varies so  
25 much in strength across taxa; it has long been known that ecological factors are crucial to  
26 this. Temperature is a particularly salient abiotic ecological factor that modulates a wide  
27 range of physiological, morphological and behavioural traits, impacting individuals and  
28 populations at a global taxonomic scale. Furthermore, temperature exhibits substantial  
29 temporal variation (e.g. daily, seasonally and inter-seasonally), and hence for most species in  
30 the wild sexual selection will regularly unfold in a dynamic thermal environment.  
31 Unfortunately, studies have so far almost completely neglected the role of temperature as a  
32 modulator of sexual selection. Here, we outline the main pathways via which temperature can  
33 affect the intensity and form (i.e. mechanisms) of sexual selection, *via*: (a) direct effects on

34 secondary sexual traits and preferences (i.e. trait variance, opportunity for selection and trait–  
35 fitness covariance), and (b) indirect effects on key mating parameters, sex-specific  
36 reproductive costs/benefits, trade-offs, demography and correlated abiotic factors. Building  
37 upon this framework, we show that, by focusing exclusively on the first-order effects that  
38 environmental temperature has on traits linked with individual fitness and population  
39 viability, current global warming studies may be ignoring eco-evolutionary feedbacks  
40 mediated by sexual selection. Finally, we tested the general prediction that temperature  
41 modulates sexual selection by conducting a meta-analysis of available studies experimentally  
42 manipulating temperature and reporting effects on the variance of male/female reproductive  
43 success and/or traits under sexual selection. Our results show a clear association between  
44 temperature and sexual selection measures in both sexes. In short, we suggest that studying  
45 the feedback between temperature and sexual selection processes may be vital to developing  
46 a better understanding of variation in the strength of sexual selection in nature, and its  
47 consequences for population viability in response to environmental change (e.g. global  
48 warming).

49

50 *Key words:* sexual selection, temperature, sexual conflict, rapid environmental change,  
51 population viability, meta-analysis.

52

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88

## 89 **I. INTRODUCTION**

90 Sexual selection is the process whereby organisms evolve to be better competitors in their  
91 struggle for reproductive opportunities. Since Darwin’s formulation (Darwin, 1871), it has  
92 become a cornerstone to understand the evolution of male and female adaptations and life  
93 histories (Andersson, 1994), speciation (Janicke *et al.*, 2018), and the maintenance of sexual  
94 reproduction itself (Agrawal, 2001). Precisely due to its central role in evolutionary theory,  
95 we have also come to understand that sexual selection is an equally important determinant of  
96 population viability and evolvability, and thus of a population’s capacity to withstand  
97 environmental change (Pomiankowski & Moller, 1995; Cally, Stuart-Fox & Holman, 2019).  
98 Indeed, sexual selection is a potent mechanism by which the genome can be purged of  
99 deleterious mutations (Whitlock & Agrawal, 2009; Radwan, 2004) and, in so doing,  
100 effectively protect populations against extinction (Lumley *et al.*, 2015; Jarzebowska &  
101 Radwan, 2010). Sexual selection has been shown to increase the rate of adaptation in traits

102 under both sexual and natural selection *via* ‘genetic capture’ (Rowe & Houle, 1996; Lorch *et*  
103 *al.*, 2003), a process presumed to be particularly effective in response to directional  
104 environmental change (Martinez-Ruiz & Knell, 2017; Long, Agrawal & Rowe, 2012; Parrett  
105 & Knell, 2018). Given the relevance of sexual selection for individual phenotypes and the  
106 fate of populations (Cally *et al.*, 2019), a central question in evolutionary biology is to  
107 disentangle why sexual selection varies so much in its form, strength and outcomes across  
108 taxa.

109         We have long realised that ecological factors are relevant to understanding the  
110 operation of sexual selection (Emlen & Oring, 1977; Maan & Seehausen, 2011) and sexual  
111 conflict (Rowe *et al.*, 1994; Arbuthnott *et al.*, 2014; Perry, Garroway & Rowe, 2017; Berger  
112 *et al.*, 2014; Perry & Rowe, 2018; García-Roa, Chirinos & Carazo, 2019). Despite the fact  
113 that studies on the factors governing eco-evolutionary interactions are still scarce (Svensson,  
114 2019), there is increasing evidence that sexual selection frequently fluctuates with changing  
115 environmental conditions (Evans & Garcia-Gonzalez, 2016; Miller & Svensson, 2014;  
116 Cornwallis & Uller, 2010). For example, the strength and direction of sexual selection can  
117 vary with resource quality and availability (Gillespie *et al.*, 2014; Gwynne & Simmons,  
118 1990), population density (Kokko & Rankin, 2006), or sex ratio (Punzalan, Rodd & Rowe,  
119 2010), amongst others (Miller & Svensson, 2014). Surprisingly, however, while there is  
120 ample evidence that temperature strongly impacts organism physiology, metabolism,  
121 morphology and behaviour, its role in relation to sexual selection and sexual conflict has  
122 mostly been neglected. There is good evidence that sexual selection can influence the  
123 capacity of a population to withstand environmental change in the form of rising  
124 temperatures (Plesnar-Bielak *et al.*, 2012; Parrett & Knell, 2018; Miller & Svensson, 2014),  
125 but we know very little about how temperature affects sexual selection.

126         In particular, only a handful of studies have tackled the role of temperature  
127 fluctuations at an ecologically relevant temporal (i.e. circadian, seasonal, or inter-seasonal)  
128 and/or spatial (i.e. micro- and macrogeographic) scale. In the worm pipefish (*Nerophis*  
129 *lumbriciformis*) sexual selection seems to be stronger in warm waters (Monteiro & Lyons,  
130 2012), and there is significant co-variation between water temperature and several potential  
131 indicators of sexual selection intensity (e.g. sexual size dimorphism) across populations along  
132 a thermal cline (Monteiro *et al.*, 2017). Temperature has also been shown to disrupt mating  
133 patterns in artemia (*Artemia franciscana*), ultimately modulating sexual selection intensity  
134 (Santos, Vieira & Monteiro, 2018). In grey seals (*Halichoerus grypus*), changes in local  
135 weather conditions affect the degree of polygyny and hence the opportunity for selection

136 (Twiss *et al.*, 2007). Similarly, a decade-long study in a population of free-ranging sand  
137 lizards (*Lacerta agilis*) reported that elevated temperatures correlated with an increase in the  
138 degree of polygyny, number of sires per clutch, and the opportunity for post-copulatory  
139 sexual selection (Olsson *et al.*, 2011). In the cigarette beetle (*Lasioderma serricornis*),  
140 thermal conditions affect post-copulatory, but not pre-copulatory, traits. This is bound to  
141 change the relative weight of (and covariance between) these two episodes of sexual selection  
142 which, in turn, will determine the nature and total opportunity for sexual selection (Suzaki *et*  
143 *al.*, 2018). While tantalising results, studies so far have provided preliminary and mostly  
144 indirect support for the idea that temperature can modulate sexual selection across taxa.  
145 Much of the attention has focused on understanding the direct consequences of abrupt  
146 temperature shifts (e.g. stressful/extreme events) on organism fitness and population viability.  
147 However, most organisms are reproductively active across a relatively wide range of  
148 temperatures in the wild, which means intra- and inter-sexual selection will normally unfold  
149 in a constantly fluctuating thermal environment. This contrasts starkly with the constant  
150 temperature conditions under which most sexual selection research has been (and still is)  
151 currently conducted in the laboratory. To conclude, we know surprisingly little about: (a)  
152 whether and how temperature fluctuations might modulate the form and strength of sexual  
153 selection, and (b) whether and how this may lead to eco-evolutionary feedback, and hence  
154 affect population viability. The overarching aim of this review is to knit together existing  
155 theory to provide a comprehensive conceptual framework for how and why temperature  
156 effects on organisms may modulate sexual selection (Fig. 1), and hopefully stimulate further  
157 study on this area of research.

158

## 159 **II. FRAMEWORK FOR THE STUDY OF TEMPERATURE AND SEXUAL** 160 **SELECTION**

161 There is a fundamental reason why temperature may be a particularly salient ecological  
162 determinant of sexual selection. The laws of thermodynamics pose constraints on  
163 biochemical processes inherent to metabolism and development, with cascading effects on  
164 organism physiology, morphology, phenology and behaviour. Temperature is a measure of  
165 the amount of kinetic energy in a system, and kinetic energy determines the rate of  
166 conformational changes in proteins (e.g. enzymes), the activation energy of reactants in  
167 biochemical reactions (Fields, 2001) and the fluidity of cell membranes, which in turn  
168 determines the transport of materials in and out of cells (Hazel & Williams, 1990). In this  
169 way, kinetic effects ultimately impact performance of cell, organ and systemic (e.g. muscular,

170 nervous, digestive) processes over a wide temporal scale that spans short-term effects (e.g.  
171 rapid metabolic changes measured in minutes/seconds), medium-term effects (i.e. within an  
172 ontogenetic phase, measured in hours/days) and long-term changes across different  
173 ontogenetic phases and – potentially – generations (reviewed in Abram *et al.*, 2017). In the  
174 wild, temperature can vary significantly at all these time scales, setting the scene for its  
175 widespread effects on organism phenotypes. Precisely due to these effects, organisms have  
176 evolved behavioural and physiological responses to environmental temperature variation at  
177 all these time scales, arguably in a distinct way to other abiotic environmental variables  
178 (Abram *et al.*, 2017). Ultimately, the scaling up of all these temperature effects can impact  
179 ecosystem-level processes such as population growth rates, trophic interactions or biomass  
180 production (Brown *et al.*, 2004; Gillooly *et al.*, 2001). Unsurprisingly, there is ample  
181 evidence that temperature strongly impacts all aspects of an animal’s phenotype, including its  
182 physiology, morphology, phenology and behaviour (e.g. Noble, Stenhouse & Schwanz,  
183 2017b; Abram *et al.*, 2017; Hetem *et al.*, 2014). For example, the metabolic theory of ecology  
184 poses that temperature is the main determinant of metabolic rate along with body size, which  
185 has itself partly evolved in response to environmental temperature (Brown *et al.*, 2004;  
186 Gillooly *et al.*, 2001).

187        Obviously, traits involved in sexual selection are no exception and thus temperature  
188 has the potential to modulate secondary sexual traits and how they co-vary with fitness,  
189 impacting both the intensity and the relative importance of sexual selection mechanisms.  
190 Conceptually, we suggest it is useful to distinguish between direct and indirect effects of  
191 temperature on sexual selection (Fig. 1). By direct effects we mean that temperature variation  
192 will translate into immediate changes in the selection and/or response to selection of  
193 secondary sexual traits, by affecting either the opportunity for selection, trait–fitness  
194 covariance or trait heritability. By indirect effects, we mean that temperature variation will  
195 affect the overall phenotypes, demography, trade-offs and/or sex-specific reproductive  
196 costs/benefits of organisms in a way that can change sexual selection pressures (i.e. sexual  
197 selection optima). While this classification does not reflect a true dichotomy, and we actually  
198 discuss both types of effects together in Section III, we do believe it can be conceptually  
199 useful to think generally about the different processes involved. A similar distinction can be  
200 made regarding the type of temperature variation faced by organisms. More specifically, we  
201 believe it can be useful to distinguish between the effects of temperature variation within the  
202 range of temperatures under which organisms have adapted to reproduce in their recent  
203 evolutionary past *versus* maladaptive temperature variations (e.g. climate change) that will

204 trigger stress responses (Fig. 1). Again, we note this distinction is not absolute, both because  
205 stress responses are adaptive in themselves and because the limits of ‘natural’ *versus*  
206 maladaptive temperatures is in most cases unclear. However, the type of evolutionary  
207 responses and underlying theory at play are likely to be qualitatively different in these two  
208 cases (Sections II.1 and II.2 below), and this distinction is useful in disentangling  
209 evolutionary responses to stressful stimuli that are not specific to temperature from responses  
210 that will be specific to temperature.

211

### 212 **(1) Direct effects of temperature on sexual selection**

213 First, maladaptive environmental variation, including temperature, can directly affect sexual  
214 selection. Fitness landscape theory predicts that the variability of secondary sexual traits  
215 under strong stabilising selection will be particularly affected by stressful temperature  
216 fluctuations, leading to pronounced genotype-by-environment interactions (Martinossi-  
217 Allibert, Arnqvist & Berger, 2017). Given that males are typically under stronger sexual  
218 selection than females (Janicke *et al.*, 2016), this may lead to sex-specific environmental  
219 sensitivity and a concomitant change in the net opportunity for sexual selection (Martinossi-  
220 Allibert *et al.*, 2017). In addition, Martinossi-Allibert *et al.* (2019a) recently showed that  
221 rapid environmental change can in principle result in less-effective good-genes sexual  
222 selection, at least in species where sexual selection takes place in small- to medium-size  
223 organisms (i.e. applicable to most animal species in the wild). This happens because stress  
224 increases selection on both sexes (by increasing the variance in fitness), but selection on  
225 females is ‘harder’ than on males so that the ratio of  $I_M$  (variance in male fitness) to  $I_F$   
226 (variance in female fitness) decreases drastically (e.g. Martinossi-Allibert *et al.*, 2018).  
227 Briefly, because female fitness depends on fecundity selection while male fitness depends on  
228 their ability to monopolise fertilizations within a mating patch, group size poses an upper  
229 limit for male (but not female) variance (Martinossi-Allibert *et al.*, 2019a). By contrast, there  
230 is substantial theoretical and empirical work showing that genomic conflict between the sexes  
231 should be ameliorated in populations facing environments to which they are not adapted,  
232 hence increasing population adaptation (e.g. Long *et al.*, 2012; Punzalan, Delcourt & Rundle,  
233 2014; Berger *et al.*, 2014). This happens, essentially, because natural selection under a  
234 maladaptive environment tends to align male and female interests. It is worth noting that the  
235 effects described above, however, are predicted in response to variations in any abiotic factor  
236 that places organisms in a maladaptive environment. In this sense, temperature may well be a

237 particularly pervasive stressful abiotic factor, but the theoretical underpinnings of its effects  
238 are no different to other abiotic factors.

239 Maladaptive temperature changes have also been shown to have specific and  
240 widespread effects on essential features of reproduction (e.g. spermatogenesis) that may  
241 directly translate into changes in the opportunity for selection (e.g. Walsh *et al.*, 2019; Sales  
242 *et al.*, 2018). More importantly, inasmuch as the expression of many phenotypic traits is  
243 governed by temperature-dependent processes, both their mean and their variance can be  
244 affected by temperature variation regardless of whether such variation is maladaptive or not.  
245 Several studies have established links between temperature variation and changes in the  
246 levels of genetic variance (measured as additive genetic variances, heritability, or  
247 evolvability) of morphological or life-history traits (Bubliy & Loeschcke, 2002; Husby,  
248 Visser & Kruuk, 2011; Martinez-Padilla *et al.*, 2017; Sgro & Hoffmann, 2002). Similarly,  
249 recent work suggests that, due to kinetic effects on protein functionality, elevated  
250 temperatures can cause a dramatic increase in the fitness effects of *de novo* mutations over a  
251 biologically relevant temperature range (D. Berger, J. Stanberg & R. J. Walters in  
252 preparation). Temperature variation can hence affect the variance in the reproductive success  
253 of males and females ( $I_M/I_F$ ), and with it the opportunity for selection. In short, temperature  
254 variation within both adaptive and maladaptive ranges can directly modulate the variance in  
255 reproductive traits, in fitness (i.e. opportunity for selection), and the co-variance between the  
256 two, thus directly affecting sexual selection (Fig. 1).

257

## 258 **(2) Indirect effects of temperature on sexual selection**

259 There are numerous ways in which temperature variation, both within and outside the range  
260 of temperatures organisms have adapted to, can indirectly affect sexual selection. First and  
261 foremost, there are several pathways by which temperature can affect key parameters of the  
262 mating system (i.e. the ecology of sexual selection) that will end up modulating the  
263 opportunity for selection (e.g. sex-specific potential reproductive rates, operational sex ratios,  
264 density, etc.). Sex-specific reproductive costs and benefits are, in many cases, largely  
265 dependent on the environment (e.g. costs of investment in offspring, sex-specific mortality  
266 linked to reproduction, costs of parental care, etc.), and are also amenable to be modulated by  
267 temperature, hence potentially impacting sex-specific selection pressures and the opportunity  
268 for sexual selection (e.g. Grazer & Martin, 2012). The same rationale holds for trade-offs  
269 (e.g. those depending on physiological constraints) and population demography (e.g.  
270 population growth rate mediated by nutrient availability), which we also discuss in Section



271 III below. Finally, indirect effects will also include the influence of temperature on other  
272 abiotic factors that can directly (e.g. oxygen concentration in air/water) or indirectly (e.g.  
273 humidity, water turbidity etc.) affect animal phenotypes, and ultimately shape sexual  
274 selection processes.

275

### 276 **III. SPECIFIC PATHWAYS FOR TEMPERATURE EFFECTS ON SEXUAL** 277 **SELECTION**

#### 278 **(1) Temperature effects on secondary sexual traits and associated preferences**

##### 279 *(a) Behaviour, physiology and life-history traits related to sexual selection*

280 Temperature has been shown to drive changes in many facets of reproductive behaviour that  
281 can determine sexual selection, including underlying physiological mechanisms. For  
282 example, temperature is a key determinant of metabolism and activity levels in most species  
283 of animals (Gunderson & Leal, 2015; Kearney *et al.*, 2010), which can directly affect mate  
284 searching, the number of male–male and male–female interactions, and general patterns of  
285 male and female spatio-temporal distribution. In the ambush bug (*Phymata americana*),  
286 sexual dimorphism in colour has been shaped by sexual selection on thermoregulatory  
287 performance, whereby dark males have higher mate-searching success at cool ambient  
288 temperatures (Punzalan, Rodd & Rowe, 2008). Similarly, temperature can modulate male–  
289 male competition intensity (e.g. aggressiveness; Kvarnemo, 1998), courtship rates, mating  
290 latency and duration (Jiao *et al.*, 2009), female choice (Conrad, Stocker & Ayasse, 2017), re-  
291 mating rates (Katsuki & Miyatake, 2009), and female fecundity (Nunney & Cheung, 1997).  
292 There are also studies showing that temperature affects sexual signals and/or sexual  
293 signalling behaviour or perception (Conrad *et al.*, 2017; Sentis *et al.*, 2015; Llusia *et al.*,  
294 2013; Linn, Campbell & Roelofs, 1988; Groot & Zizzari, 2019), with potential impacts on  
295 mate choice and intra-sexual competition. Actually, any effect of temperature on the  
296 phenotypic mean and variance of sexually selected characters is likely to influence selection  
297 on a secondary sexual trait (i.e. the covariance between trait value and relative fitness). Given  
298 that the expression of many traits (including secondary sexual traits) can be dependent on  
299 temperature (House *et al.*, 2013; Reinhardt, Dobler & Abbott, 2015; West & Packer, 2002),  
300 its significance to understand mate preferences and sexual selection at large is evident.

301 Post-copulatory processes have also been reported to be under the influence of  
302 temperature. It is well known that the sperm phenotype is in many species contingent on  
303 temperature (Reinhardt *et al.*, 2015; Sales *et al.*, 2018; Walsh *et al.*, 2019). Most notably,  
304 sperm competition ability (i.e. in terms of both sperm offence and defence) is affected

305 through the amount and quality of sperm transferred (Katsuki & Miyatake, 2009; Vasudeva,  
306 Deeming & Eady, 2014; Lieshout, Tomkins & Simmons, 2013). For example, a recent study  
307 in the Mediterranean field cricket (*Grillus bimaculatus*) showed that 4°C temperature  
308 differences (within the natural range of variation of the study population in the wild)  
309 significantly affected sperm production and quality. Males had higher sperm production and  
310 quality when they were exposed to hotter temperatures throughout development, but the  
311 opposite was true if they were exposed to hotter temperatures as adults (Gasparini *et al.*,  
312 2018). In addition, temperature also impacted offspring fitness *via* effects on male sperm (i.e.  
313 non-adaptive paternal effects). These results show that temperature effects on sperm traits  
314 and overall competitiveness may depend on the temporal scale of temperature fluctuations  
315 with respect to ontogeny, highlighting the potential for trans-generational effects. Sperm  
316 competitiveness determines siring success, which together with mating success is the main  
317 component of male reproductive success in polyandrous species. Critically, then, the action  
318 of temperature on sperm competitiveness has the potential to directly affect the opportunity  
319 for sexual selection, either through its effects on male variance in post-copulatory  
320 reproductive success or on the covariance between the pre-mating and post-mating episodes  
321 of sexual selection (Evans & Garcia-Gonzalez, 2016).

322 Finally, temperature can exert significant changes in life-history traits across different  
323 species and populations (Isaac, 2009; Jensen *et al.*, 2008), some of which are sex-specific  
324 (Rogell *et al.*, 2014). Many of these changes (e.g. in lifespan, the onset of reproduction,  
325 survival, age or size at maturity) have great potential to affect parameters modulating intra- or  
326 inter-sexual selection, such as the operational sex ratio (OSR), the potential reproductive rate  
327 or the environmental potential for polygyny/polyandry.

328

### 329 (b) *Body size and sexual size dimorphism*

330 Body size, a primary determinant of both inter- and intra-sexual competition, is under the  
331 influence of environmental temperature through both plastic and evolutionary responses  
332 (Lindmark *et al.*, 2018; Fox, Stillwell & Moya-Larano, 2007). For example, temperature has  
333 been shown to reduce sexual dimorphism in some insects by modifying emergence times and  
334 developmental rates (De Block & Stoks, 2003; Ketola *et al.*, 2012). This is predicted to  
335 decrease the capacity of males to monopolise females, and with it the opportunity for  
336 selection (Vanpa *et al.*, 2008; Fox *et al.*, 2007). In the leaf beetle *Stator limbatus* temperature  
337 can affect scramble competition, whereby smaller males are more successful at finding mates  
338 than large males when at cool temperatures (Moya-Laraño, El-Sayyid & Fox, 2007).

339 Similarly, temperature is one of the main environmental factors underlying phenotypic  
340 plasticity in body size, and the sexes commonly show marked difference in their degree of  
341 phenotypic plasticity to body size (Stillwell *et al.*, 2010). For example, males of the seed  
342 beetle (*Callosobruchus maculatus*) exhibit greater plasticity in body size than females in  
343 response to temperature manipulations (Stillwell & Fox, 2007), and existing evidence shows  
344 that, in insects, male body size varies more with latitude and altitude than does female body  
345 size (Blackenhorn *et al.*, 2006). Some of these differences in sexual size dimorphism may be  
346 explained by the ‘condition-dependence hypothesis’, which predicts that traits under stronger  
347 directional selection will be more condition dependent, and hence more responsive to  
348 environmental cues (Bonduriansky, 2007). It would be interesting to explore whether the  
349 larger sex is generally more affected by stressful temperature changes than the smaller sex,  
350 and how this may affect sexual selection.

351

### 352 (c) *Mate choice preferences*

353 We have long known that temperature can affect mate choice preferences in both vertebrates  
354 and invertebrates. For example, classic studies by Walker (1957), in crickets, and by Gerhardt  
355 (1978), in anurans, described thermal coupling, whereby female preferences shift to track  
356 temperature-dependent changes in male sexual signals. Thermal coupling may reflect  
357 adaptive phenotypic plasticity or non-functional physiological responses to temperature  
358 (Greenfield & Medlock, 2007; Ritchie *et al.*, 2001), but at least in some cases it will act to  
359 buffer mate choice against disruption by temperature fluctuations (Beckers & Schul, 2008).  
360 In other cases, however, temperature effects on preferences can disrupt mate choice  
361 processes. For example, in the American green tree frog (*Hyla cinerea*) temperature effects  
362 on female preferences are not matched by changes in male signals, potentially hampering  
363 species recognition at low temperatures (Gerhardt & Mudry, 1980). Similarly, in the pipefish  
364 *Sygnathus abaster* warm temperatures seem to affect female preferences towards males  
365 (Silva *et al.*, 2007). More generally, temperature may also indirectly affect female  
366 preferences *via* its effects on body condition. In some species, females in good condition  
367 have been shown to exert stronger preferences and/or invest more in mate assessment  
368 (Hebets, Wesson & Shamble, 2008; Cotton, Small & Pomiankowski, 2006).

369

## 370 (2) **Temperature effects on mating systems**

371 The strength and form of sexual selection ultimately depend on the mating system, and hence  
372 on the ‘ecology of sexual selection’ (Emlen & Oring, 1977; Schuster & Wade, 2003). First,

373 there are multiple ways in which temperature can affect the environmental potential for  
374 polygyny/polyandry, i.e. the potential for the environment (e.g. clumped resources) to allow  
375 for the monopolisation of multiple males (Emlen & Oring, 1977). For example, by  
376 prolonging/shortening the reproductive season (Sheriff *et al.*, 2011), temperature shifts may  
377 make female reproduction more or less synchronous and/or clump/spread out the breeding  
378 population in time. This may increase/decrease male opportunities to monopolise females  
379 and, ultimately, the environmental potential for polygyny/polyandry (Olsson *et al.*, 2011). In  
380 the barn swallow (*Hirundo rustica*), warming temperatures have been reported to increase  
381 protandry, and this has been associated with an increase in the size of a secondary sexual  
382 character, which is suggestive of stronger sexual selection (Moller, 2004). Female  
383 reproductive diapause (i.e. period of reproductive arrestment in response to adverse  
384 environmental conditions, such as low temperatures in winter) is also at least partially  
385 controlled by temperature in many insect species. By contrast, males usually either lack  
386 reproductive diapause or it is less intense than in females (Pener, 1992). As such, temperature  
387 effects on the onset/outset of female reproductive diapause can, in theory, affect the  
388 synchrony of female receptivity within the reproductive season, with potential consequences  
389 for levels of polygyny and polygamy.

390 Second, several studies have shown that temperature can drastically modulate the  
391 potential reproductive rate (PRR) of males and females in a sex-specific manner (Kvarnemo,  
392 1994). For example, environmental temperature has frequently been found to affect the  
393 availability of nutritional resources during reproduction (Vatka, Orell & Rytönen, 2011),  
394 which is generally expected to affect female PRR more than male PRR because egg  
395 production is particularly dependent on food intake in many animals (Warner, Lovorn &  
396 Shine, 2007). Much in the same way, temperature shifts are likely to affect oviposition site  
397 availability in many species (e.g. Fogleman, 1979; Berger, Walters & Gotthard, 2008), which  
398 could also differentially affect the PRR of females. On the other hand, high temperature may  
399 differentially increase male (*versus* female) PRR if male reproductive rates are particularly  
400 dependent on activity levels, as is frequently the case in species with resource-defence  
401 polygynous systems. Temperature also drastically influences incubation time, particularly in  
402 species where egg development depends almost exclusively on environmental temperature  
403 (most ectotherms), thus greatly determining the PRR of the sex in charge of incubation and  
404 brood care (Kokko, Klug & Jennions, 2012; Kokko & Jennions, 2008). This is the case in  
405 sand gobies (*Pomatoschistus minutus*), where males build a nest and care for the eggs until

406 hatching. Increased temperature accelerates egg developmental rates and ultimately male  
407 PRR, as they can be alleviated from egg guarding sooner (Kvarnemo, 1994).

408 Sex-specific temperature effects on polygyny/polyandry levels and PRR are  
409 ultimately expected indirectly to modulate the OSR by modulating how and when males and  
410 females enter and exit the mating pool, and hence the strength of sexual selection (Schuster &  
411 Wade, 2003; Kvarnemo, 1996; Kokko *et al.*, 2012). Temperature can also directly affect the  
412 OSR in species with temperature-dependent sex determination (Cunningham, While &  
413 Wapstra, 2017; Grayson *et al.*, 2014), or if the sexes have different reproductive operational  
414 temperature ranges. The latter will be particularly likely in species with strong sexual size  
415 dimorphism. For example, in species where females are larger than males, females may  
416 exhibit a greater acclimation capacity in response to temperature fluctuations and extremes  
417 (Rohr *et al.*, 2018) and, hence, be reproductively active over a wider range of temperatures  
418 (Stone, 1994). The implication is that the OSR will be progressively more female-biased as  
419 temperatures approach the thresholds of the male reproductive operational thermal range.

420 Finally, population density can influence mating systems, and hence sexual selection  
421 processes, in many taxa. Population density (and population dynamics at large) is frequently  
422 under the influence of temperature (Gamelon *et al.*, 2017), and can strongly affect mating  
423 skew or mate encounter rates, for example, with cascading effects on mate choice, mate  
424 guarding, re-mating rates or female resistance (Kokko & Rankin, 2006). Through its effects  
425 on population density, temperature could thus also influence sexual selection (Fig. 1).

426

### 427 **(3) Temperature effects on sex-specific costs/benefits of reproduction**

428 Changes in environmental temperatures can alter the costs/benefits of reproduction in a sex-  
429 specific way (e.g. costs of investment in offspring, sex-specific mortality linked to  
430 reproduction, costs of parental care, offspring survival, etc.), impacting sex-specific selection  
431 pressures and the opportunity for sexual selection. For example, Grazer & Martin (2012)  
432 showed that the survival costs of reproduction for females of the flour beetle *Tribolium*  
433 *castaneum* decrease at higher temperatures. Studies looking at how temperature may affect  
434 sex-specific reproductive costs and benefits are still very scarce and focus on the short-term  
435 plastic consequences of thermal stress, yet provide good preliminary evidence that such  
436 effects are not only possible, but may be theoretically expected (Martinossi-Allibert *et al.*,  
437 2017). More generally, the relative importance of intra- and inter-sexual selection can also  
438 vary with environmental conditions (Miller & Svensson, 2014). For example, in collared  
439 flycatchers (*Ficedula albicollis*) mate choice has a heritable component, and selection on

440 mate choice varies annually according to climatic conditions: females choosing highly  
441 ornamented males have increased reproductive success in dry breeding seasons but low  
442 relative reproductive success in wet breeding seasons (Robinson *et al.*, 2012). To our  
443 knowledge, however, there is no evidence thus far of similar effects mediated by temperature.  
444

#### 445 **(4) Temperature effects on constraints and trade-offs**

446 Temperature may also modulate sexual selection through its effects on physiological trade-  
447 offs. For example, environmental temperatures can affect pathogen abundance and virulence,  
448 as well as host susceptibility and immune responses (Elliot, Blanford & Thomas, 2002).  
449 Several studies have also shown that immunity is related to body condition, and that it trades  
450 off with reproductive effort and primary and secondary sexual traits (Simmons & Roberts,  
451 2005; Mills *et al.*, 2010; Cotter *et al.*, 2010). Therefore, studying the interplay between  
452 thermal ecology and immune ecology, and their combined effects on sexual selection, may  
453 inform on other avenues thorough which temperature can affect sexual selection. Similarly,  
454 temperature can shape the costs and benefits of secondary sexual traits, for example of visual  
455 signals that may also play a role in thermoregulation. This seems to be the case for the  
456 sexually selected male wing colouration in the dragonfly *Pachydiplax longipennis*. In this  
457 species, greater wing colouration improves flight performance under cool conditions (leading  
458 to greater territory acquisition), but dramatically reduces it under warm conditions, which  
459 seems to constrain the evolution of sexual colouration in the hottest portions of the species'  
460 range (Moore *et al.*, 2019). As stated above, some studies have also established links between  
461 temperature variation and changes in the levels of genetic variance (measured as additive  
462 genetic variances, heritability, or evolvability) and in morphological or life-history traits  
463 (Bubliy & Loeschke, 2002; Husby *et al.*, 2011; Martinez-Padilla *et al.*, 2017; Sgro &  
464 Hoffmann, 2002). These results show that the evolutionary potential of populations to adapt  
465 to changing environments is constrained by genetic architectures that can be temperature  
466 dependent. For instance, Martinez-Padilla *et al.* (2017) used data from 20 European wild bird  
467 populations belonging to 12 species, and found the evolutionary potential of traits relating to  
468 body size and body mass (relevant to sexual selection in general) were associated with  
469 environmental favourability, which was greatly influenced by temperature.  
470

#### 471 **(5) Temperature effects on population dynamics/demographics**

472 Temperature can affect sexual selection through its impact on population  
473 demography/dynamics (Gavrilets, 2000; Gay *et al.*, 2010). Temperature variation can

474 underlie changes in population growth (e.g. through the availability of nutrients; Clark *et al.*,  
475 2003), pose limits to population size (e.g. modify population carrying capacity; Newman,  
476 2003), determine the spatial-temporal distribution of populations and individuals (e.g. driving  
477 population subdivision and consequently altering population sizes and the probabilities of  
478 encountering the opposite sex; Yasui & Garcia-Gonzalez, 2016), and affect population  
479 viscosity (i.e. limit dispersal), mating patch size and sexual networks (Pizzari, Biernaskie &  
480 Carazo, 2015; McDonald *et al.*, 2013; McDonald & Pizzari, 2018; McDonald *et al.*, 2019).  
481 As such, temperature may modulate sexual selection at a large taxonomic scale. Importantly,  
482 while some of the temperature effects on population dynamics are predicted to be  
483 temperature-specific, *via* the scaling of integrated effects (Brown *et al.*, 2004; Gillooly, 2001;  
484 Abram *et al.*, 2017), others will simply be due to correlated effects *via* other abiotic factors.

485

#### 486 **(6) Abiotic factors correlated with temperature**

487 Some of the effects described above may be at least partly driven in nature by abiotic factors  
488 that are correlated with temperature, and not necessarily by temperature *per se*, such as  
489 temperature effects *via* the availability of nutrients (Clark *et al.*, 2003). For example,  
490 increases in environmental temperature may facilitate eutrophication and consequently lead  
491 to elevated water turbidity (Paerl & Paul, 2012), with obvious consequences for the action of  
492 sexual selection in aquatic animals in which mate choice is based on visual signals. Human  
493 activities leading to higher turbidity have been shown to threaten the biological diversity of  
494 one of the most notable examples of explosive evolution known, the highly diverse species  
495 flocks of cichlid fish from the Great Lakes of Africa. In these fish, water turbidity is known  
496 to interfere with mate choice and to relax sexual selection (Maan & Seehausen, 2011;  
497 Seehausen, Alphen & Witte, 1997), and similar findings have been reported in other systems  
498 (Engstrom & Candolin, 2007; Candolin, Tukiainen & Bertell, 2016). By contrast, in the  
499 broad-nosed pipefish (*Syngnathus typhle*; a species with male pregnancy), turbidity  
500 strengthens sexual selection (Sundin *et al.*, 2017). Humidity is an abiotic factor that is also  
501 closely linked to temperature, and there is some evidence that it could also affect sexual  
502 selection. In the common lizard (*Zootoca vivipara*), for example, post-natal humidity  
503 differentially affects female *versus* male growth, thereby influencing adult SSD and,  
504 potentially, sexual selection (Le Galliard *et al.*, 2006). Nonetheless, due to the widespread  
505 thermodynamic constraints on enzymatic activity, the resulting physiological, morphological,  
506 behavioural and life-history traits of organisms are inherently temperature dependent (Clarke,  
507 2004; Brown *et al.*, 2004). Hence, temperature is likely to be generally more central for

508 sexual selection processes than other abiotic factors.

509

#### 510 **IV. TEMPERATURE AND SEXUAL CONFLICT**

511 A particularly direct link between sexual selection and population viability emerges due to  
512 the consequences of sexual conflict. Strong sexual selection frequently leads to sexual  
513 conflict, where male and female evolutionary interests do not coincide. While classic theory  
514 of sexual selection often assumed that male/female coevolution is largely mutualistic, an  
515 increasing appreciation of sexual conflict has led to the realisation that genes that confer a  
516 reproductive advantage to males may have the opposite effect in females, and *vice versa*.  
517 According to the genetic underpinnings of the traits under sexual selection, sexual conflict  
518 can take two qualitatively distinct forms: inter-locus or intra-locus sexual conflict. Inter-locus  
519 sexual conflict (IRSC) occurs in relation to traits governed by genes that are at different loci  
520 in males and females, and where expression benefits one sex at the cost of the other. IRSC  
521 frequently gives rise to an antagonistic process of inter-sexual coevolution (Arnqvist &  
522 Rowe, 2005), particularly in polygamous species where males and females often show  
523 different optima for mating frequencies and reproductive schedules (Chapman *et al.*, 1995;  
524 Rice, 1996; Holland & Rice, 1999; Arnqvist & Rowe, 2005). Sexually antagonistic  
525 coevolution has received much attention in recent years (Rice, 1996; Holland & Rice, 1999;  
526 Wigby & Chapman, 2004), and is currently recognised as one of the key evolutionary  
527 processes shaping male and female adaptations and life-history traits (Bonduriansky *et al.*,  
528 2008), but also population viability and diversification. Intra-locus sexual conflict (IASC)  
529 arises when there is sex-specific selection on a trait expressed in both sexes and the shared  
530 genetic architecture underlying the expression of the trait impedes optimal expression levels  
531 in each sex (Arnqvist & Rowe, 2005). The theoretical basis of IASC was developed long ago  
532 (Lande, 1980; Rice, 1984) and, although its effects have proved to be more subtle than IRSC,  
533 it is receiving increasing empirical attention (Bonduriansky & Chenoweth, 2009).

534 Sexual conflict can, *via* IRSC and IASC, act both as an engine of biodiversity and to  
535 decrease population viability. On the one hand, sexually antagonistic coevolution can  
536 function as an engine of biodiversity, both by leading to and/or reinforcing reproductive  
537 isolation and speciation (Parker & Partridge, 1998; Rice, 1998) and by promoting increased  
538 intra-specific genetic variation without speciation (Gavrilets, 2014). On the other hand,  
539 sexually antagonistic coevolution can lead to adaptations in one sex (most frequently males)  
540 that harm members of the other sex (most frequently females; Pitnick & Garcia-Gonzalez,  
541 2002). As a matter of fact, male adaptations that cause harm to females, and female



542 adaptations to resist such harm, are indeed paradigmatic examples of IRSC (Arnqvist &  
543 Rowe, 2005). Male harm to females generally leads to a decrease in population productivity  
544 [i.e. by depressing net female productivity (Berger *et al.*, 2016; Arnqvist & Tuda, 2010;  
545 Holland & Rice, 1999)] that can facilitate population extinction (Le Galliard *et al.*, 2005).  
546 Furthermore, sexual conflict can also decrease male and female fitness by displacing the  
547 sexes from their respective evolutionary optima (normally referred to as ‘gender load’ but  
548 hereafter referred to as ‘sex load’; Rice & Chippindale, 2002), normally *via* IASC.  
549 Ultimately, whether sexual conflict fosters biodiversity or reduces population productivity  
550 and facilitates extinction will depend, among other things, on population size (Gay *et al.*,  
551 2010), the potential for sex load (Berger *et al.*, 2016), and the degree and form of associated  
552 male harm adaptations and female counter-adaptations (Arnqvist & Rowe, 2005). In addition,  
553 sexual conflict can feed back to affect the opportunity, form and/or intensity of sexual  
554 selection. For example, avoiding male harassment (a common source of harm to females) in  
555 crickets leads to a larger opportunity for (and stronger) sexual selection (Hall *et al.*, 2008). To  
556 summarise, there is now ample theoretical and empirical evidence that sexual conflict is a  
557 fundamental engine of biodiversity, a driving force of male and female adaptations and life  
558 histories, and a keystone determinant of population viability and extinction risk.

559         Despite the impressive advances in the field of sexual conflict, we are still far from  
560 being able to explain the overwhelming diversity of related adaptations or their net impact on  
561 population viability. The apparently arbitrary nature of the coevolutionary trajectories that  
562 often result from strong sexual conflict has been sometimes interpreted to mean that ecology  
563 occupies a rear seat in such processes, or is altogether irrelevant (Arbuthnott *et al.*, 2014;  
564 Coyne & Orr, 2004). This, however, seems highly unlikely given that sexual conflict depends  
565 on the intensity of male–male competition, and sexual selection is profoundly affected by  
566 ecological factors. In fact, there is now good evidence to show that the opportunity for sexual  
567 conflict does depend on the ecological context (Perry *et al.*, 2017; Arbuthnott *et al.*, 2014;  
568 Gomez-Llano, Bensch & Svensson, 2018; De Lisle *et al.*, 2018; Perry & Rowe, 2018),  
569 including maladaptive environmental changes (Connallon & Clark, 2014) and environmental  
570 fluctuation *per se* (Connallon & Hall, 2018)

571         Temperature can in principle modulate both adaptations for sexual conflict (e.g. by  
572 affecting the expression of adaptations leading to male harm *via* behavioural plasticity) and  
573 sexual conflict itself, *via* its effects on the degree to which male and female interests overlap.  
574 A few studies have shown that stressful temperature environments (and stressful  
575 environments at large) can relax sexual conflict, because in a maladaptive environment male

576 and female interests may tend to overlap more due to strong concordant selection in new  
577 environmental conditions (Long *et al.*, 2012; Berger *et al.*, 2014; Connallon & Hall, 2018,  
578 but see Delcourt, Blows & Rundle, 2009; Punzalan *et al.*, 2014; Connallon & Hall, 2016;  
579 Holman & Jacomb, 2017; Martinossi-Allibert *et al.*, 2018). However, there is scarcely any  
580 information on whether non-extreme temperature fluctuations at an ecologically relevant  
581 temporal (i.e. circadian, seasonal, or inter-seasonal) and/or spatial (i.e. micro- and  
582 macrogeographic) scale modulate sexual conflict.

583

### 584 **(1) Temperature effects on inter-locus sexual conflict**

585 Temperature can be expected to modulate IRSC in two ways. First, by constraining or  
586 conditioning the expression of male/female traits evolved via IRSC. For example, García-Roa  
587 *et al.* (2019) manipulated sexual conflict levels in *Drosophila melanogaster* and showed that  
588 resulting male harm to females decreased sharply in both colder (21°C) and hotter (29°C)  
589 social environments than at the average temperature to which the population was adapted  
590 (25°C). In this species, therefore, temperature shifts are likely modulators of male harm  
591 mechanisms [e.g. production of sperm and/or toxic components in the ejaculate (Chapman *et al.*,  
592 1995; Perry, Sirot & Wigby, 2013)], which is perhaps to be expected whenever male  
593 harm adaptations cannot be optimally expressed across the whole range of temperatures at  
594 which reproduction ensues. *D. melanogaster* exhibits both pre-copulatory (i.e. sexual  
595 harassment) and post-copulatory (i.e. toxic ejaculates) mechanisms of male harm and,  
596 interestingly, preliminary evidence suggests these are affected differently by warm *versus*  
597 cold temperatures (García-Roa *et al.*, 2019). Investment in pre- *versus* post-copulatory male–  
598 male competition traits/mechanisms can be traded-off *via* resource allocation (e.g. (Simmons  
599 & Emlen, 2006), and male ejaculates have been shown to manipulate female mating  
600 frequency and affect the balance between pre-copulatory and post-copulatory sexual selection  
601 in *D. melanogaster* (Morimoto *et al.*, 2019). Hence, such temperature effects are likely to  
602 modulate both the total opportunity for sexual selection and the integration between pre- and  
603 post-mating processes (Evans & Garcia-Gonzalez, 2016). Recent work on seed beetles  
604 (*Callosobruchus maculatus*) has also reported evidence that a stressful increase in  
605 temperature can reduce IRSC in populations evolved under polygamous/monogamous  
606 conditions and then tested under different levels of sexual conflict (single pairs *versus* groups  
607 of 10 beetles); interestingly, this is not the case in populations with male-limited evolution  
608 (Martinossi-Allibert *et al.*, 2019b).

609 Second, variation in temperature, such as consistent spatial inter-population  
610 differences or long-term intra-population fluctuations, can vary the degree to which male and  
611 female reproductive interests diverge. This type of effect may modulate the intensity and/or  
612 direction of sexually antagonistic coevolution. For example, Perry *et al.* (2017) showed that  
613 different ecological parameters, among them temperature, contributed to explaining inter-  
614 population differences in a sexually antagonistic arms race in natural populations of water  
615 striders (*Gerris incognitus*); likely due to inter-population differences in ecological forces  
616 acting on mating system variation and ensuing sexual conflict (Perry & Rowe, 2018).

617

## 618 **(2) Temperature effects on intra-locus sexual conflict**

619 As in the case of IRSC, spatio-temporal variation in temperature can modulate IASC by  
620 changing the degree to which male and female interests overlap. IASC is generally expected  
621 to decrease in novel environments, for example due to concordant natural selection of  
622 previously neutral alleles in both sexes (Long *et al.*, 2012). In accordance with theory, Berger  
623 *et al.* (2014) showed that sex load *via* intra-locus sexual conflict is reduced in a natural  
624 population of seed beetles (*Callosobruchus maculatus*) subject to a stressful thermal  
625 environment (but see Martinossi-Allibert *et al.*, 2019b). To conclude, there is now theoretical  
626 and empirical evidence to show that temperature does indeed have the potential to modulate  
627 both IASC and IRSC. Interestingly, data so far seem to suggest that the negative impact of  
628 sexual conflict on population viability, due both to sex load and female harm, may be  
629 ameliorated when populations face temperature changes. We suggest that exploring this idea  
630 should be a priority in the near future, not only because it will further our understanding of  
631 sexual conflict but also because, in species with high sexual conflict, this type of effect can  
632 ultimately increase the ability of populations to avoid extinction in the face of persistent  
633 anthropogenic temperature changes (e.g. global warming).

634

## 635 **V. TEMPERATURE, SEXUAL SELECTION AND RAPID ENVIRONMENTAL** 636 **CHANGE**

637 From an eco-evolutionary point of view, rapid environmental change results in a mismatch  
638 between an organism's optimal and current environment, potentially leading to population  
639 decline and extinction. Whether a population is able to withstand such environmental change  
640 and avoid extinction over the long term will depend essentially on whether it is capable of  
641 adapting quickly enough to track these changes (Hoffmann & Sgro, 2011; Parmesan, 2006;  
642 Kingsolver & Buckley, 2017; Martinez-Padilla *et al.*, 2017). Most studies that try to predict

643 the consequences of rapid environmental change for natural populations focus on studying  
644 the direct effects of temperature shifts on phenotypic traits that respond plastically to  
645 temperature, and then examine how these changes affect population viability, and the  
646 potential for subsequent evolutionary rescue. Above we have reviewed how these effects can  
647 affect sexual selection through a variety of pathways (Fig. 1). In doing so, the initial impact  
648 of a sustained temperature shift can feed back to influence a wide diversity of phenotypic  
649 traits that are not directly affected by temperature. Furthermore, as mentioned above sexual  
650 selection has great potential to influence the fate of populations/species (Cally *et al.*, 2019),  
651 especially those facing directional environmental changes such as for example those imposed  
652 by global warming (Candolin & Heuschele, 2008). In particular, recent evidence has shown  
653 that strong sexual selection can help buffer against warming temperatures, with experimental  
654 populations facing rising temperatures having higher fecundity and offspring survival when  
655 under a strong sexual selection regime (Parrett & Knell, 2018; Plesnar-Bielak *et al.*, 2012).  
656 This means that any effects of temperature on sexual selection are likely to feed back and  
657 impact a wide range of phenotypic traits linked with population viability and extinction *via*  
658 genic capture of sexually selected traits. In addition, current projections predict global  
659 warming to result not only in an increase in mean and modal temperatures, but also in  
660 temperature fluctuations at any given spatial scale (IPCC, 2014). This makes it all the more  
661 important to understand how such fluctuations may impact sexual selection *via* both short-  
662 term plastic changes and long-term evolutionary responses.

663

## 664 **VI. PROCESSES INVOLVED IN EFFECTS OF TEMPERATURE ON SEXUAL** 665 **SELECTION**

666 An overarching question to the links we have described so far is what type of responses  
667 (adaptive and non-adaptive) may result from temperature shifts in the environment. Adaptive  
668 population-level responses in the face of environmental change can ensue *via* both natural  
669 selection (including sexual selection), by exploiting existing genetic variation, and *via*  
670 phenotypic plasticity, by exploiting the ability of individuals to adjust their phenotype to the  
671 environment and/or by revealing cryptic genetic variation that can later be the target of  
672 selection, *via* genetic assimilation (West-Eberhard, 2003; Gilbert, Bosch & Ledon-Rettig,  
673 2015; Snell-Rood *et al.*, 2010). For example, high developmental temperatures have been  
674 shown to reveal cryptic genetic variation in female sperm compartments of the yellow dung  
675 fly (*Scathopaga stercoraria*), which play a key role in cryptic female choice in this species  
676 (Berger *et al.*, 2011). Phenotypic plasticity (whether adaptive or maladaptive) is likely to be

677 of particular importance in understanding temperature-mediated effects on sexual selection  
678 for the obvious reason that development is critically affected by environmental temperature  
679 in most species, and particularly so in ectotherms. Accordingly, meta-analyses have  
680 identified strong long-lasting effects of developmental temperature on suites of traits, such as  
681 growth rate, physiology, performance and morphology (Seebacher, White & Franklin, 2014;  
682 Noble *et al.*, 2017b). Behavioural plasticity, including paternal effects, might also be very  
683 important because it is a way in which parents can buffer the developmental temperature of  
684 their offspring, mitigating the consequences of environmental temperature shifts (Du &  
685 Shine, 2015; Huey, Hertz & Sinervo, 2003).

686 As in any selective process, evolutionary responses to changes in temperature will  
687 depend on the amount of additive genetic variation underlying the trait or traits affected.  
688 Interestingly, temperature fluctuations may actually play a role in the maintenance of genetic  
689 variation underlying sexually selected traits and mate preferences through genotype-by  
690 (temperature-determined) environment interactions. Evidence for such role of temperature  
691 variation has been found across study systems (Miller & Svensson, 2014; Jia, Greenfield &  
692 Collins, 2000; Narraway *et al.*, 2010; Hunt & Hosken, 2014), and it has been shown that  
693 plastic responses to novel environments more generally tend to align with underlying additive  
694 genetic variation in traits (Noble, Radersma & Uller, 2019).

695 Finally, temperature is also likely to impact sexual selection *via* inter-generational and  
696 trans-generational effects. First, because temperature is frequently a cue for many other  
697 sources of environmental variation (e.g. food availability, onset of reproductive/breeding  
698 period, etc.). Second, because temperature affects a host of physiological mechanisms with  
699 consequences that may spill over to subsequent generations *via* paternal effects or the  
700 transmission of epigenetic marks. Paternal germline epigenetic changes that are  
701 environmentally triggered are increasingly recognised as modulators of sperm function  
702 (Jenkins *et al.*, 2017; Stuppia *et al.*, 2015) but also, remarkably, as sources of variance in the  
703 offspring phenotype (Miller, Brinkworth & Iles, 2010; Wang, Liu & Sun, 2017; Jenkins *et*  
704 *al.*, 2017; Stuppia *et al.*, 2015; Donkin & Barres, 2018; Evans *et al.*, 2019). In the nematode  
705 *Caenorhabditis elegans*, for instance, temperature variation induces multigenerational  
706 inheritance of gene expression through both oocytes and sperm (Klosin *et al.*, 2017).  
707 Demonstrating such long-lasting epigenetic memory of parental temperature experiences, and  
708 at the same time unravelling the underlying mechanisms, is challenging and has been seldom  
709 achieved (Klosin *et al.*, 2017). Nonetheless, there are reasons to suspect that temperature-  
710 induced transmission of epigenetic marks affecting sperm and offspring phenotypes may be

711 common (Evans *et al.*, 2019). In most systems, we ignore whether cross-generational effects  
712 driven by paternal environment are driven by epigenetic mechanisms or mediated by other  
713 factors [e.g. direct or female-moderated paternal effects arising from variation in the non-  
714 sperm fraction of the ejaculate (Garcia-Gonzalez & Simmons, 2007; Gasparini *et al.*, 2018)].  
715 However, any inter-generational or trans-generational effect has the capacity significantly to  
716 alter the economics of sexual interactions (Dowling, Williams & Garcia-Gonzalez, 2014;  
717 Zajitschek *et al.*, 2018), leading to unknown but presumably significant effects on sexual  
718 selection. We anticipate that investigations focusing on how temperature-driven maternal and  
719 paternal effects impact sexual selection will yield important insights.

720

## 721 **VII. META-ANALYSIS: EXPERIMENTAL EVIDENCE THAT TEMPERATURE** 722 **IMPACTS SEXUAL SELECTION**

723 To test whether available data support the idea that temperature can significantly modulate  
724 sexual selection, we conducted a systematic review and meta-analysis of the existing  
725 literature focusing on studies that experimentally manipulated temperature and measured its  
726 impact on either: (1) mating or reproductive success of males and/or females, or (2) its effect  
727 on traits known to be under sexual selection. While excellent observational studies exist,  
728 given that temperature can be correlated with a host of other environmental changes, we  
729 avoided including correlative studies in our meta-analysis. Our focus in this meta-analysis is  
730 to explore temperature effects *per se*, beyond any effects that temperature may have due to  
731 subjecting individuals/populations to a new environment to which they are maladapted.  
732 Environmental stress can modulate the strength of sexual selection in a variety of ways  
733 (Arbuthnott & Whitlock, 2018), for example increasing sexual selection if the variability in  
734 fitness is inflated when populations are pushed off their fitness peak (Martinossi-Allibert *et*  
735 *al.*, 2017, 2018). As such, drastic temperature changes can modulate sexual selection not due  
736 to specific effects of temperature but by imposing a stressful environment, much in the same  
737 way as a pollutant or a sharp change in another abiotic factor would. To avoid conflating this  
738 type of effects, here we also explicitly avoided studies implementing heat/cold shock  
739 treatments and also assessed the potential influence of using extreme temperature treatments  
740 (Section VII.3).

741 It is also important to note that there are no clear theoretical expectations regarding  
742 the directionality of temperature effects on sexual selection processes. As laid out above,  
743 increases/decreases in temperature are not necessarily expected to impact sexual selection  
744 parameters in the same direction across different species. Some biological processes will tend

745 to exhibit monotonic relationships in temperature that are relevant to selection. For example,  
746 given that temperature constrains certain fundamental biochemical properties such enzymic  
747 reactions, it has recently been proposed that mutations will have increasing fitness effects,  
748 and hence lead to stronger selection, with increasing temperatures (D. Berger, J. Stanberg &  
749 R. J. Walters in preparation). However, the net relationship between temperature and sexual  
750 selection across taxa is likely to rest largely on the physiology, morphology, behaviour and  
751 mating system of each species. Thus, our main aim was not so much to explore the  
752 directionality of the relationship between temperature and sexual selection, but to test the  
753 more general prediction that temperature has the potential to affect sexual selection in  
754 different species, irrespective of direction.

755

### 756 **(1) Literature search and data collection**

757 We conducted a systematic review and meta-analysis of the existing literature following the  
758 PRISMA protocol (Liberati *et al.*, 2009) as closely as possible. More specifically, we looked  
759 for studies that experimentally manipulated temperature and measured its impact on either:  
760 (1) mating or reproductive success of males and/or females, or (2) traits known to be under  
761 sexual selection. We only extracted phenotypic trait values when it was clear from the  
762 reported paper, or the raw data, that the trait directly impacted reproductive success. If traits  
763 had a tenuous link with reproductive success they were not included. We conducted a first  
764 literature search on 11/09/18 using the *Scopus*, *PubMed* and *Web of Science* (WoS) databases  
765 with the search terms “sexual selection” AND “selecti\* intensity” AND “temperature” or  
766 “sexual selection” AND “selecti\* strength” AND “temperature” for animal taxa. Overall,  
767 very few papers were found with these search strings (21 total: *Scopus* = 5, *PubMed* = 11 and  
768 *WoS* = 5). After removing duplicates only 15 papers were relevant and two more were added  
769 through forward and backward searches of citations and references in the 15 papers. Given  
770 the small number of hits, we conducted a second search on 17/09/18 across the same  
771 databases (i.e. *Scopus*, *PubMed* and *WoS*), using a more general search query: “sexual  
772 selection” AND “fitness” AND “temperature” OR “mating success” AND “fitness” AND  
773 “temperature” OR “reproductive success” AND “fitness” AND “temperature”. This search  
774 string was able to capture a broader set of studies for screening. In total, we found 747 studies  
775 (*Scopus* = 291; *PubMed* = 98; *WoS* = 358) and after removing 249 duplicates, we were left  
776 with 498 unique studies for more detailed screening. Based on the title and abstract we  
777 excluded studies that were not on animals ( $N = 38$ ), had no measure of sexual selection or  
778 traits under sexual selection ( $N = 354$ ), did not involve a temperature manipulation ( $N = 145$ ),

779 and where the effects of temperature could not be isolated because they were confounded by  
780 other abiotic or biotic variables ( $N = 46$ ). We also excluded  $N = 12$  review and theoretical  
781 model papers. Note that many studies met more than one of the above criteria, and after this  
782 search we were left with a total of 61 papers across both searches as being potentially  
783 relevant. We carefully screened these papers to identify articles that met all our above  
784 inclusion criteria, and at this stage we also excluded all papers reporting heat/cold shock  
785 treatments), which left us with a final set of 19 studies (see online Supporting information,  
786 Table S1).

787 We extracted mean fitness or trait value from each temperature treatment along with  
788 the standard deviation and sample size for each group from tables and figures using the R  
789 package *metaDigitise* to extract from figures (Pick, Nakagawa & Noble, 2018). Experimental  
790 designs were highly variable across studies and there were designs that exhibited some level  
791 of non-independence in replicate measurements within temperature treatments (e.g.  
792 measurements of replicate individuals from isofemale lines). Given that this can affect the  
793 sampling variance of the effect size we used conservative sample sizes (i.e. the number of  
794 independent lines, or number of mating cages; Noble *et al.*, 2017a). However, when raw data  
795 were available, and could be clearly interpreted, we calculated an intraclass correlation  
796 coefficient for the clusters (e.g. lines) and computed an ‘effective sample size’ for the  
797 treatment and used this for calculating the sampling variance (Noble *et al.*, 2017a). Fitness  
798 was often reported on a proportion scale (e.g. the average proportion of mating’s/offspring  
799 sired). While these are not normally distributed, they were often treated as so in the paper,  
800 and given that we required ratio-scale data for our effect sizes (see Section VII.2) we  
801 assumed that these were approximately normally distributed in accordance with the study.  
802 Nonetheless, we conducted a sensitivity analysis to determine if effect sizes calculated with  
803 proportion data were different than non-proportion data and included this as a covariate to  
804 assess their impact on inferences. This had little impact on our major conclusions and so we  
805 assumed proportion data were similar to effect sizes derived from other measurement types  
806 (see Appendix S1, Section 6.2). A few studies conducted experimental manipulations under  
807 fluctuating conditions, but for comparison across studies we focused on constant temperature  
808 treatments. In addition, several studies used more than two temperature treatments, in which  
809 case we extracted only the extreme temperatures provided within the range of minimum–  
810 maximum mean monthly temperatures in spring–summer. We did this to avoid introducing a  
811 form of non-independence in our data through the use of shared temperature treatments when  
812 calculating effect sizes (Noble *et al.*, 2017a). We acknowledge that some studies included



813 were on populations that were part of experimental evolution experiments reared in the  
814 laboratory at specific constant temperatures. The impact of this on phenotypic variance is not  
815 entirely clear if the temperature manipulation was conducted using the conditions the  
816 population were reared at previous to experimental evolution (see Appendix S1, Section 6.3  
817 for a more thorough discussion of this problem). However, we dealt with this issue to some  
818 extent by analysing magnitudes of variance difference (see Section VII.2). Finally, we were  
819 conservative by only using data from treatments where there was potential for sexual  
820 selection to occur (e.g. multiple males and/or females competing) and excluded data from  
821 treatments of single-pair mating experiments.

822

### 823 **(2) Effect size statistics – comparing variance in fitness**

824 We compared how temperature impacted both the mean and variance across experimental  
825 groups using the log response ratio (lnRR), the log variance ratio (lnVR) and the log  
826 coefficient of variation ratio (lnCVR) (for effect size equations see Nakagawa *et al.*, 2015).  
827 We were most interested in how variance in reproductive success, or traits known to be  
828 directly related to reproductive success, change as a function of temperature as this is a more  
829 direct test of temperature effects on sexual selection, given it is a measure of the opportunity  
830 for sexual selection. Hence, we focus mainly on lnVR and lnCVR in our meta-analysis, but  
831 we report the results from lnRR in Appendix S1. We used lnVR as a direct estimate of the  
832 difference in trait variance. However, given that lnVR does not account for mean variance  
833 relationships that existed in our data, we used lnCVR to estimate how variance in  
834 reproductive success changes independent of changes in average fitness/trait between  
835 temperature treatments (Nakagawa *et al.*, 2015). In all cases, when using directional effect  
836 sizes (i.e. not absolute magnitude) positive effect sizes indicated that higher temperature  
837 treatments had a larger variance compared to lower temperature treatments, whereas negative  
838 effect sizes indicated the opposite.

839

### 840 **(3) Moderator variables**

841 We collected a number of variables that we, *a priori*, predicted would moderate the impact of  
842 temperature on sexual selection within and across studies. These included: (1) the  
843 temperature difference between experimental treatments (continuous variable) – larger  
844 temperature differences between treatments are likely to lead to greater effect sizes; (2) the  
845 sex of the sample – we predict stronger sexual selection and effects of temperature in males  
846 compared to females (Janicke *et al.*, 2016); (3) life-history stage at which the temperature

847 manipulation took place (i.e. ‘lifetime’, ‘juvenile/early’, ‘adults’) – given that temperature  
848 can impact development that subsequently affects reproductive traits and success; and (4)  
849 whether the trait in question was a ‘direct’ or ‘indirect’ proxy for sexual selection, where  
850 ‘direct’ estimates were those measuring some aspect of mating or reproductive success and  
851 ‘indirect’ estimates were those traits linked to mating or reproductive success. Finally, in  
852 some cases, ‘hot’ or ‘cold’ temperature treatments were outside of the natural range (see  
853 Section VII.1), so we also classified all effect sizes depending on whether the temperature  
854 treatment was ‘natural’ or ‘stressful’. Briefly, if experimental individuals came from a natural  
855 population, treatments were categorised as ‘natural’ *versus* ‘stressful’ depending on whether  
856 they were within the maximum–minimum temperature range for that population. Given that  
857 studies varied in terms of whether temperatures were stressful or not, and the types of traits  
858 were different across studies (not all were direct measures of fitness), we could not calculate  
859 more direct measures of environmental stress (e.g. change in reproductive output across  
860 temperature). If experimental individuals came from populations adapted to laboratory  
861 conditions (i.e. kept for more than 100 generations under a constant temperature regime), we  
862 considered temperature treatments  $> 4^{\circ}\text{C}$  away from their normal rearing temperature as  
863 stressful. In two cases, experimental individuals came from long-term laboratory populations  
864 reared at a given temperature that were then subject to a short-term ( $< 20$  generations;  
865 Plesnar-Bielak *et al.*, 2012, 2018) experimental evolution study at a different temperature; in  
866 these two cases we considered the long-term rearing temperature as the ‘ancestral’  
867 temperature.

868

#### 869 **(4) Meta-analysis**

870 We used multi-level meta-analytic (MLMA) and multi-level meta-regression (MLMR)  
871 models in the R package *metafor* (Viechtbauer, 2010) to test temperature effects on sexual  
872 selection and to explore drivers of effect size variation (Nakagawa & Santos, 2012; Hadfield  
873 & Nakagawa, 2010). In all models we included a random effect of study and species and also  
874 included an observation-level random effect to estimate residual variance, given that *metafor*  
875 does not estimate one by default. While we had a diversity of species in our data set, these  
876 were taxonomically biased towards insects and we had difficulty resolving the phylogenetic  
877 position of most of the taxa in our data set (tested with TimeTree.org – only 5/15 species  
878 were identified) – we therefore were limited in our ability to control for phylogeny in our  
879 analyses (Noble *et al.*, 2017a; Chamberlain *et al.*, 2012). Instead, we used a phylogeny that  
880 was based only on topological relationships between taxa. We used Grafen’s method (Grafen,

881 1989) to create phylogenetic correlation matrices and included these matrices in our models  
882 as a sensitivity analysis. Including phylogenetic correlation matrices or not did not impact our  
883 results (see Appendix S1, Section 6.1) and so we just controlled for species in our models by  
884 including a random effect of species. We also assessed publication bias by looking at funnel  
885 plots and found little evidence for bias that may impact our results (see Fig. S1 in Appendix  
886 S1, Section 5).

887 In addition to estimating the overall directional mean effect across studies from our  
888 MLMA models, we estimated measures of effect size heterogeneity (Higgins & Thompson,  
889 2002; Nakagawa & Santos, 2012). We estimated the between-study heterogeneity ( $Het_{\text{study}}$ :  
890 proportion of variation in effects from shared studies), species heterogeneity ( $Het_{\text{sp}}$ :  
891 proportion of variation in effects from shared species) and total sampling heterogeneity  
892 ( $Het_{\text{err}}$ : the proportion of variation in effects resulting from sampling variance).  $Het_{\text{err}}$   
893 describes how much variation in effects can simply be explained by changes in sample sizes  
894 (i.e. related to sampling variance) across studies as opposed to real biological variation.  
895 Directional predictions regarding the role of temperature on sexual selection processes  
896 depends on many factors, which make clear directional predictions on how variance is  
897 expected to change challenging. As such, we estimated the overall magnitude of variance  
898 difference across temperature treatments. To avoid bias in these estimates, we modelled the  
899 directional effect sizes assuming a normal distribution and then subsequently transformed this  
900 mean estimate using the folded normal distribution, to get the mean absolute magnitude  
901 (*sensu* Morrissey, 2016). To estimate uncertainty around this estimate, we used a Bayesian  
902 approach with MCMCglmm (Hadfield, 2010), and applied the entire posterior distribution of  
903 mean estimates to the folded normal.

904 We tested whether our hypothesised moderators explained heterogeneity in effects  
905 using our MLMR models. Given our limited sample size (males:  $N = 31$  effects from 14  
906 studies; females:  $N = 18$  effects from 9 studies), we limited the number of moderators fit to  
907 each model to two, and modelled the sexes separately as subset analyses. We ended up not  
908 modelling developmental stage given that most of the studies manipulated temperature over  
909 the lifetime of the animals. A full presentation on the results and models run can be found in  
910 Appendix S1, sections 2, 3 and 6. In all cases we present 95% credible/confidence intervals  
911 around our mean effect sizes. Intervals not overlapping each other and zero are considered  
912 significant.

913

## 914 (5) Meta-analysis results and discussion

915 Experimental studies assessing the effects of temperature on sexual selection are currently  
916 biased towards insects (16/19 studies), with only one on arachnids and two on fish. Between-  
917 study heterogeneity was moderate to high for males ( $Het_{\text{stdy}}$ :  $\ln VR = 0.77$ ,  $\ln CVR = 0.34$ ) and  
918 small to non-existent for females ( $Het_{\text{stdy}}$ :  $\ln VR = 0.13$ ,  $\ln CVR = 0$ ). Nonetheless, there was  
919 still a moderate amount of heterogeneity beyond simple sampling variance ( $Het_{\text{err}}$ : males –  
920  $\ln VR = 0.16$ ,  $\ln CVR = 0.31$ ; females –  $\ln VR = 0.33$ ,  $\ln CVR = 0.31$ ).

921 The magnitude of effects (i.e. non-directional effect of temperature on variance) was  
922 moderate, suggesting that temperature does indeed influence direct and indirect measures of  
923 sexual selection (Fig. 2). By contrast, the overall directional mean effect on variance in all  
924 cases did not differ from zero (although there does seem to be a trend whereby higher  
925 temperatures are associated with increased variance). Therefore, there was no clear  
926 directional impact of temperature on sexual selection (Fig. 2). At an average temperature  
927 difference between treatments of 7.5 °C, male variance ( $\ln VR$ ) decreased at the higher  
928 temperature relative to the lower temperature if the temperature manipulation was stressful or  
929 if it was a direct measure of reproductive fitness (Fig. 2A). However, this effect was driven  
930 by changes in the mean phenotype and when controlling for the mean there was no  
931 significant change in variance resulting from stressed or natural conditions (Fig. 2B). By  
932 contrast, when controlling for the mean, traits indirectly associated with reproductive success  
933 showed an increased variance relative to lower temperatures (Fig. 2B). Results from females  
934 generally mirrored results from males, except it was not possible robustly to compare direct  
935 and indirect fitness measures given that indirect measures came from only one study. An  
936 interesting difference from males is that, accounting for changes in the mean, stressful  
937 temperatures seemed to explain the observed increase in the variance of reproductive success  
938 in females (Fig. 2D). This may indicate that temperature effects on the variance of female  
939 reproductive success are largely mediated by environmental stress. A recent model predicts  
940 exactly this outcome, due to the fact that fecundity selection on females is relatively ‘hard’,  
941 so that an increase in female variability in fitness is expected with greater environmental  
942 stress (Martinossi-Allibert *et al.*, 2019a). By contrast, selection on males is relatively ‘soft’  
943 because they compete against other ‘maladapted’ males and their fitness is mainly  
944 constrained by limited access to females and overall female productivity (Martinossi-Allibert  
945 *et al.*, 2019a). In accordance with this idea, we found that temperature effects on males did  
946 not seem to be driven by stressful temperature treatments.

947 Our meta-analysis offers suggestive evidence in support of the idea that temperature  
948 may modulate sexual selection. As evidenced by our systematic search, available data are  
949 scant and come mostly from studies that did not aim to measure the relationship between  
950 temperature and sexual selection. We did find a few other observational studies reporting  
951 correlations between temperature and sexual selection in wild populations (the most relevant  
952 are discussed in Section I), but interpretation in these cases is problematic due to the large  
953 number of confounding variables (e.g. humidity, precipitation). In addition, we failed to  
954 include one relevant study (Santos *et al.*, 2018) which clearly showed that temperature  
955 disrupts mating patterns, which impacts sexual selection intensity in *Artemia franciscana*. In  
956 this study, the authors measured selection differentials based on size differences between  
957 mated and unmated individuals. Body size has been shown to be under sexual selection in  
958 this species, but we decided to act conservatively by eliminating this from our meta-analysis  
959 because body size is also under strong natural selection and is directly influenced by  
960 temperature. As stressed herein, and for the reasons stated, available studies were surprisingly  
961 scarce. This made it difficult for our meta-analysis to evaluate properly the interesting  
962 questions arising from our review, such as the existence of sex-specific temperature effects  
963 on sexual selection and a general trend in the directionality of such effects (D. Berger, J.  
964 Stanberg & R. J. Walters in preparation). We hope that our work spurs further studies into the  
965 connections between temperature and sexual selection, which will allow for more powerful  
966 meta-analyses.

967

## 968 **VIII. THE PATH AHEAD: STUDYING THE INTERPLAY BETWEEN** 969 **TEMPERATURE, SEXUAL SELECTION AND POPULATION VIABILITY**

### 970 **(1) Considering temperature effects on sexual selection**

971 We suggest that studies aimed at understanding the link between sexual selection and  
972 temperature should focus not only on fluctuations in mean temperature, but also on the role  
973 of maximum/minimum temperatures and temperature variability. Spermatogenesis seems to  
974 be generally vulnerable to peak temperatures across different taxa (Walsh *et al.*, 2019),  
975 suggesting that considering maximum/minimum temperatures may be particularly important  
976 when studying temperature effects on post-copulatory processes. For example, a recent study  
977 in the flour beetle (*Tribolium castaneum*) found that experimental heat-waves compromise  
978 sperm function even if they occur after sperm is stored in the female spermatheca, and that  
979 successive heat-waves can render males infertile (Sales *et al.*, 2018). Sales *et al.* (2018) also

980 found temperature-induced trans-generational effects in line with those reported in other  
981 species (Gasparini *et al.*, 2018).

982         Studying the role of temperature fluctuations may also provide insight into the  
983 maintenance of additive and cryptic genetic variation, and generally on how sexual selection  
984 operates in complex environments (Miller & Svensson, 2014). Due to circadian, intra-  
985 seasonal and inter-seasonal temperature variation, many (if not most) organisms will be  
986 reproductively active under a range of environmental temperatures in the wild (i.e.  
987 reproductive operational thermal range). This means that sexual selection will unfold in a  
988 constantly varying thermal environment which, as long as there are inter-individual  
989 differences in genotype-by-environment interactions, can both increase or decrease the  
990 opportunity for sexual selection, as well as change the relative importance and integration  
991 between pre- and post-copulatory processes. In a constantly fluctuating environment, males  
992 that are particularly successful at competing for reproduction at the mean temperature within  
993 its operational range may also happen to be better competitors at other temperatures (e.g.  
994 high phenotypic plasticity; Gilchrist, 1995). That is, good males may tend to be even better in  
995 fluctuating scenarios, perhaps due to being in a generally better condition and/or having a  
996 higher degree of adaptive phenotypic plasticity. Hence, the variability in net male  
997 mating/reproductive success will be higher when considering intra- and inter-sexual selection  
998 across the whole reproductive operational thermal range (and not just the mean temperature,  
999 as is commonly done in laboratory experiments) leading to higher opportunity for sexual  
1000 selection/selection ( $I_s/I$ ; Fig. 3A). For example, in the red mason bee (*Osmia bicornis*) female  
1001 choice is partly based on male vibrational signals, which are affected by the marked  
1002 temperature changes that this species experiences during reproduction in the wild. In contrast  
1003 to males that are rejected by females, vibrational signals by male bees that are accepted by  
1004 females are far less influenced by temperature changes (Conrad *et al.*, 2017). An added  
1005 consequence of this type of scenario is that sexual selection traits that are particularly  
1006 resilient to temperature will likely experience consistent selection across mating patches  
1007 representing different thermal conditions, and hence steeper net selection gradients at the  
1008 population level. By contrast, selection on more labile traits may vary in intensity and  
1009 direction across mating patches that vary in their thermal conditions, and hence experience  
1010 weaker selection pressures. Alternatively, due to temperature-dependent constraints and/or  
1011 trade-offs in underlying mechanisms, males good at competing at a given temperature may be  
1012 relatively less competitive at other temperatures (e.g. ‘thermal specialists’; Gilchrist, 1995),  
1013 leading to the opposite scenario (Fig. 3B). Yet another alternative is the coexistence of both

1014 thermal generalists and specialists in the same population, with frequency-dependent effects  
1015 that will necessarily rest largely on prevailing temperature conditions. This type of  
1016 evolutionary scenario can favour diverging strategies across the operational thermal range,  
1017 and hence contribute to the maintenance of genetic variability (see Fig. 3B). As a case in  
1018 point, Svensson *et al.* (2020) recently showed that temperature drives pre-reproductive  
1019 selection in the female-colour-polymorphic damselfly *Ischnura elegans*, such that the  
1020 frequency of female morphs varies geographically due to differential temperature sensitivity  
1021 and maturation rates across morphs.

1022         In the above cases, sexual selection will ultimately maximise mating/reproductive  
1023 success over the whole range of reproductive operational temperatures, which underscores  
1024 the need to integrate different episodes/mechanisms of sexual selection to consider the total  
1025 opportunity for sexual selection (Evans & Garcia-Gonzalez, 2016; Miller & Svensson, 2014).  
1026 Competition across fluctuating environments is also bound to affect covariation between  
1027 pre/post and/or intra/inter-sexual mechanisms (Evans & Garcia-Gonzalez, 2016) if different  
1028 mechanisms are affected differently by temperature; e.g. spermatogenesis and sperm-  
1029 competition processes may be more vulnerable to high temperatures (see above).  
1030 Understanding how temperature affects different sexual selection mechanisms (i.e. inter-  
1031 *versus* intra-sexual and pre- *versus* post-copulatory), and in particular genotype-by-  
1032 environment interactions, may thus further our understanding of sexual selection in wild  
1033 populations.

1034         Importantly, coarse-grained temperature fluctuations may have different  
1035 consequences for sexual selection, as they may lead to maximisation of geometric (rather  
1036 than arithmetic) mean fitness. Fine-grained temperature variation (as discussed so far)  
1037 reflects fluctuations in temperature that individual organisms experience across their  
1038 reproductive lifespan, whereas coarse-grained temperature variation reflects fluctuations that  
1039 are only experienced across generations (e.g. inter-seasonal variation in non-iteroparous  
1040 species). In the latter case, temperature variation poses the classic problem of dealing with  
1041 unpredictable future environments (Levins, 1968). Knowing whether such environmental  
1042 fluctuations lead to different bet-hedging strategies (Slatkin, 1974) in the context of sexual  
1043 selection would be key to understanding the causes and consequences of sexual selection in  
1044 complex environments. For example, some sexual selection mechanisms are bound to be  
1045 more vulnerable to temperature changes than others (e.g. post-copulatory processes  
1046 dependent on ejaculate size or quality at high temperatures). As a consequence, in a coarse-  
1047 grained temporal scale, sexual selection may give rise to conservative bet-hedging strategies

1048 by favouring investment in sexual selection traits that are more robust to temperature  
1049 changes. Thus, strategies that may appear suboptimal when considering intra- and inter-  
1050 sexual selection within the lifetime of individuals (i.e. lower mean arithmetic fitness) may  
1051 actually be advantageous when considering selection acting across multiple generations (i.e.  
1052 higher mean geometric fitness; e.g. Yasui & Garcia-Gonzalez, 2016).

1053         An interesting feature of ectotherms that should be taken into account when studying  
1054 responses to temperature is that thermal fitness curves of ectotherms are highly asymmetric,  
1055 such that fitness drops faster with increasing than decreasing temperatures away from the  
1056 optimum (Martin & Huey, 2008). This can have biologically relevant consequences. For  
1057 example, the predicted optimal behaviour when fitness functions are non-linear will depend  
1058 drastically on the variance and skewness of the fitness-temperature curve (Martin & Huey,  
1059 2008). Finally, an interesting question that we have already touched upon is whether we may  
1060 expect directional effects of temperature on sexual selection. Generally speaking, we have  
1061 argued above that we may expect the relationship between temperature and sexual selection  
1062 to rest largely on the physiology, morphology, behaviour and mating system of each species.  
1063 However, some biological processes will tend to exhibit monotonic relationships with  
1064 temperature that are relevant to sexual selection, potentially driving directional effects. Given  
1065 that temperature constrains certain fundamental biochemical properties it has recently been  
1066 proposed that mutations will have increasing fitness effects, and hence lead to stronger  
1067 selection, with increasing temperatures (D. Berger, J. Stanberg & R. J. Walters in  
1068 preparation). Similarly, some of the effects of temperature on mating systems may be  
1069 expected to modulate sexual selection consistently in the same direction. For example,  
1070 temperature increases may lead to longer reproductive seasons, which in some species may  
1071 relax sexual selection by spreading competition over a longer time frame (Monteiro & Lyons,  
1072 2012). Detecting directional effects of temperature on sexual selection is an exciting  
1073 prospect, as it may allow us to identify previously unrecognised taxonomic (e.g. ectotherms  
1074 *versus* endotherms) and/or macro-evolutionary (e.g. tropics *versus* temperate zones) patterns  
1075 in sexual selection processes/traits. In other species, however, longer reproductive seasons  
1076 could intensify and/or change the form of sexual selection. For example, in harvestmen  
1077 (Opiliones) the length of the breeding season is mainly affected by the number of warm  
1078 months, and longer breeding seasons increase the probability of resource defence polygyny  
1079 and the magnitude of sexual dimorphism (Machado *et al.*, 2016).

1080



1081 **(2) Considering eco-evolutionary feedback**

1082 As we have pointed out above, temperature effects on sexual selection may feed back to  
1083 impact population viability and evolvability. The evidence that populations where sexual  
1084 selection is present or intense adapt faster and are more effective in tracking the environment  
1085 keeps accumulating (Parrett *et al.*, 2019). A step forward would be to provide evidence that  
1086 temperature effects on sexual selection can be strong enough to impact population viability  
1087 and/or evolvability in a meaningful way. As far as we know, direct evidence for this is almost  
1088 completely absent except for a few studies drawing indirect connections between  
1089 temperature, sexual conflict intensity and population productivity (Berger *et al.*, 2014;  
1090 García-Roa *et al.*, 2019; Martinossi-Allibert *et al.*, 2019b). To bridge this gap, we suggest  
1091 that future studies looking at the relationship between sexual selection and temperature  
1092 should try to incorporate population measures of viability/evolvability, or at least attempt to  
1093 extrapolate fitness consequences at the level of individuals to populations, ideally under  
1094 different population demography scenarios (Edward *et al.*, 2010).

1095

1096 **(3) Where and how to study temperature effects on sexual selection**

1097 While the ideas described so far are in principle generally applicable to a wide range of  
1098 animals, it is obvious that some taxa, such as ectotherms, will be more vulnerable to  
1099 temperature effects on sexual selection. In consequence, we would generally predict much  
1100 stronger temperature effects on insects, reptiles, amphibians and fish than on, say, mammals  
1101 or birds. For this reason, future work on ectotherms is bound to bring a sharper focus on the  
1102 links between temperature and sexual selection. However, we stress the need to explore as  
1103 wide a variety of taxa as possible if the aim is to understand what mechanisms of sexual  
1104 selection are impacted by temperature and how.

1105 Sexual selection in plants, too, is likely to be affected by temperature both directly  
1106 (e.g. physiology; Hedhly, Hormaza & Herrero, 2009) and indirectly, *via* its effect on  
1107 pollinators through any of the pathways described above. More specifically, temperature may  
1108 affect intra-sexual selection in plants at different levels: during competition for pollination,  
1109 *via* its effects on pollen receipt and removal (Murcia, 1990), the successful transfer of pollen  
1110 to stigmas (e.g. if temperature affects insect activity and/or spatial range; Nielsen *et al.*,  
1111 2017), and more generally by affecting plant–insect interactions (DeLucia *et al.*, 2012). After  
1112 pollination, temperature is one of the main determinants of pollen performance, potentially  
1113 affecting the opportunity for sperm competition (i.e. post-pollination intra-sexual selection;  
1114 Mazer *et al.*, 2018). In addition, temperature can affect the amount of time outcrossing

1115 flowers stay fresh and receptive (Arroyo *et al.*, 2013), modulating the possibility of receiving  
1116 pollen from multiple donors and hence the potential for post-pollination intra-sexual  
1117 competition. Flower size and morphology has also been shown to be dependent on  
1118 temperature in some species (Murcia, 1990), and stigma size and style length can intensify  
1119 gametophytic competition (Travers & Shea, 2001; Mazer *et al.*, 2018).

1120         Regardless of the specific taxa targeted, we suggest studies will need to consider the  
1121 effects of adult *versus* developmental thermal environments, constant *versus* fluctuating  
1122 temperature regimes (or heat/cold shocks), and the role of behaviour in buffering temperature  
1123 effects on reproductive parameters and mating systems in natural populations (and thus  
1124 sexual selection processes). More specifically, there is much need for realistic experimental  
1125 studies, ideally on individuals from wild populations, that manipulate temperature within  
1126 their natural range (i.e. daily, intra-seasonal and inter-seasonal fluctuations) and ask how such  
1127 manipulation affects their mating system, ensuing sexual selection and/or sexual conflict  
1128 intensity, and if possible population viability. Similarly useful will be comprehensive field  
1129 studies that seek to: (a) identify differences in traits among populations (e.g. secondary  
1130 sexual traits); (b) document whether such differences can be explained by variation in the  
1131 strength and/or form of sexual selection, the relative importance of inter- *versus* intra-sexual  
1132 selection, and the relative weight of pre-copulatory *versus* post-copulatory episodes of  
1133 selection; (c) document the causes and underlying mechanisms of sexual selection (e.g. social  
1134 interactions, OSR, etc.); (d) show that temperature changes causal interactions in ways that  
1135 modify selection (e.g. weaker social interactions in hot climates); and (e) study the broad  
1136 consequences of the impact of temperature on sexual selection (e.g. in terms of the  
1137 opportunity for selection/sexual selection) and, when possible, on population viability. Given  
1138 that temperature effects are best tested using carefully controlled experimental manipulations  
1139 at the population level it will likely mean that suitable invertebrate, plant and a sample of  
1140 small-vertebrate systems will contribute most to our understanding of how temperature  
1141 impacts sexual selection. This taxonomic bias may be challenging to deviate from without  
1142 creative ways to manipulate and isolate temperature in certain systems.

1143

## 1144 **IX. CONCLUSIONS**

1145 (1) Given the relevance of sexual selection for individual phenotypes and population fates, a  
1146 central question in evolutionary biology is to disentangle why sexual selection and sexual  
1147 conflict vary so much in their form, strength and outcomes across taxa. The role of ecology in  
1148 explaining sexual selection has been considered prominent so far; albeit less so in the case of

1149 sexual conflict. Surprisingly, though, the specific role of temperature, perhaps the most  
1150 salient abiotic ecological factor at a global taxonomic scale, has been relatively ignored.

1151 (2) Temperature is a fundamental abiotic factor with a strong impact on organism physiology,  
1152 morphology and behaviour. In the wild, environmental temperature exhibits frequent and  
1153 significant variation at both the spatial scale (i.e. micro- and macro ecological) and temporal  
1154 scale (i.e. circadian, seasonal and inter-seasonal). However, the question whether temperature  
1155 can modulate sexual selection and sexual conflict, and the consequences in terms of potential  
1156 eco-evolutionary feedback on population viability, has been largely neglected.

1157 (3) We currently lack the empirical data necessary to understand: (a) the degree to which  
1158 temperature may affect sexual selection and sexual conflict in nature; (b) the mechanisms  
1159 underlying such effects, in terms of how temperature modulates secondary sexual traits,  
1160 male/female reproductive success and mating systems; (c) how such effects unfold in the  
1161 short (phenotypic plasticity) and the long (evolutionary) term; and (d) the degree to which  
1162 such effects may impact population viability/extinction risk.

1163 (4) Here, we knit together existing theory and empirical data to weave a framework on how  
1164 temperature may modulate sexual selection *via* direct and indirect effects on sexually selected  
1165 traits and preferences, population dynamics, mating systems, constraints and trade-offs and  
1166 correlated abiotic factors. *Via* these same pathways, temperature may also be a fundamental  
1167 modulator of sexual conflict, which is not only an increasingly appreciated evolutionary  
1168 mechanism to understand the evolution of male and female adaptations and life-histories, but  
1169 a particularly direct link between sexual selection and population viability.

1170 (5) While current studies on the impact of rapid environmental changes in temperature (e.g.  
1171 due to global warming) on population extinction focus mainly on first-order effects of rising  
1172 temperatures on population viability, this approach ignores potential feedbacks on processes  
1173 mediating sexual selection. Beyond directly affecting population viability, we suggest that  
1174 rising temperatures may modulate sexual selection in ways that can both negatively (e.g. if  
1175 rising temperatures slow sexual selection and, with it, the ability to purge mutations and/or  
1176 viability of populations) or positively (e.g. if rising temperatures decrease sexual conflict, and  
1177 with it, gender load) affect population fitness.

1178 (6) To evaluate the general idea that sexual selection may be modulated by temperature, we  
1179 performed a meta-analysis of existing evidence (mostly from studies not directly aimed at  
1180 studying this link) and thereby provide preliminary evidence that temperature can indeed  
1181 modulate sexual selection within a biologically relevant range.

1182 (7) We conclude that a priority for the immediate future is to explore fundamental questions  
1183 about the interplay between temperature and sexual selection, with respect to both short-term  
1184 plastic changes (i.e. behavioural plasticity), inter-generational and trans-generational effects,  
1185 evolutionary responses, and the consequences that such processes have for population  
1186 viability. We highlight ways in which future studies may bridge these gaps in knowledge.

1187

## 1188 **X. ACKNOWLEDGMENTS**

1189 We thank Tobias Uller, Manuel Serra, three anonymous reviewers and in particular David  
1190 Berger for insightful comments on previous drafts of this manuscript. P.C. was supported by  
1191 a “Plan Nacional I+D+i Excelencia” grant (CGL2017-89052-P), co-funded by the Agencia  
1192 Estatal de Investigacion and the European Regional Development Fund, a Generalitat  
1193 Valenciana “Excellence of Young Researchers” SEJI grant (SEJI/2018/037), and by a 2018  
1194 Leonardo Grant for Researchers and Cultural Creators, from the BBVA Foundation. F.G.-G.  
1195 was supported by a MINECO “Plan Nacional I+D+i Excelencia” grant (CGL2016-76173-P)  
1196 co-funded by the Agencia Estatal de Investigacion and the European Regional Development  
1197 Fund, and a CSIC start-up grant (201730I034). D.W.A.N. was supported by an ARC  
1198 Discovery Early Career Research Award (DE150101774) and UNSW VC Fellowship.

1199 **Author contributions:** P.C. conceived this paper; P.C., R.G.-R. and F.G.-G. discussed and  
1200 developed its conceptual framework; P.C., R.G.-R. and D.W.A.N. conducted the systematic  
1201 search; D.W.A.N. conducted the meta-analysis; P.C., R.G.-R., F.G.-G. and D.W.A.N. wrote  
1202 the paper.

1203

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1819

## 1820 **XII. SUPPORTING INFORMATION**

1821 Additional supporting information may be found online in the Supporting information section  
1822 at the end of this article.

1823 **Table S1.** Final sample of studies (and extracted effect sizes) used in the meta-analysis.

1824 **Appendix S1.** Meta-analysis on the effects of temperature on sexual selection.

1825

## Figure legends

**Fig. 1.** A schematic outline of pathways by which temperature can affect sexual selection, and ultimately population viability.  $I_M/I_F$  stand for opportunity for selection in males and females (respectively),  $w$  stands for fitness and  $SST$  stands for sexually selected trait.

**Fig. 2.** Meta-analytic means for a temperature treatment difference of approximately 7.5 °C 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;  $k$  = 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 (black circles), along with the overall meta-analytic mean (red diamond) and the mean magnitude of log variance ratio differences between treatments (red square).

**Fig. 3.** Depending on the shape of reaction norms to temperature fluctuations during the reproductively active period of the day/season, temperature effects on mating success may increase (A) or decrease (B) the opportunity for selection. For simplicity, here we consider an equiprobable distribution of temperatures across this range. In A, high-quality competitors at the mean temperature ( $t_{opt}$ ) also adjust better to temperature fluctuations (higher adaptive phenotypic plasticity) and maintain a more stable mating success and/or reproductive success across this thermal range. As a consequence, male variability in fitness ( $\sigma$ ) is higher in fluctuating ( $\sigma_A$  and solid black line) *versus* stable ( $\sigma_{stable}$  and dotted gold line) thermal environments, and temperature effects increase the opportunity for sexual selection ( $I_s$ ) and/or the opportunity for selection at large ( $I$ ). In B, individuals with high mating and/or reproductive success at the mean temperature fare worse at other temperatures (e.g. due to the existence of trade-offs and/or constraints in underlying mechanisms across temperatures). The variability in mean male fitness is hence reduced when considering intra- and inter-sexual selection across the whole thermal environment ( $\sigma_B$  and solid black line) *versus* the mean ( $\sigma_{stable}$  and dotted gold line) thermal environment, and so are  $I_s$  and/or  $I$ .

Figure 1.

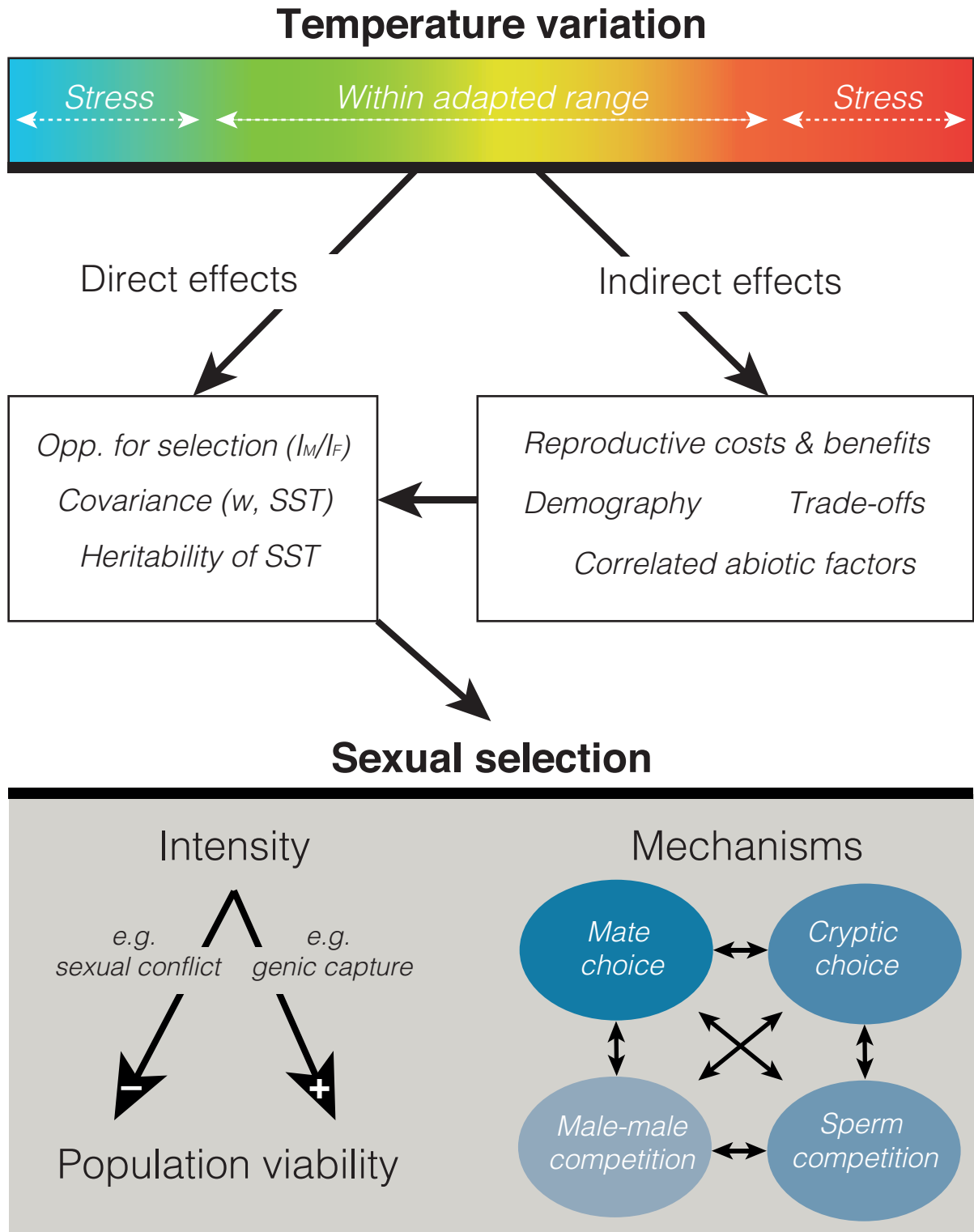


Figure 2.

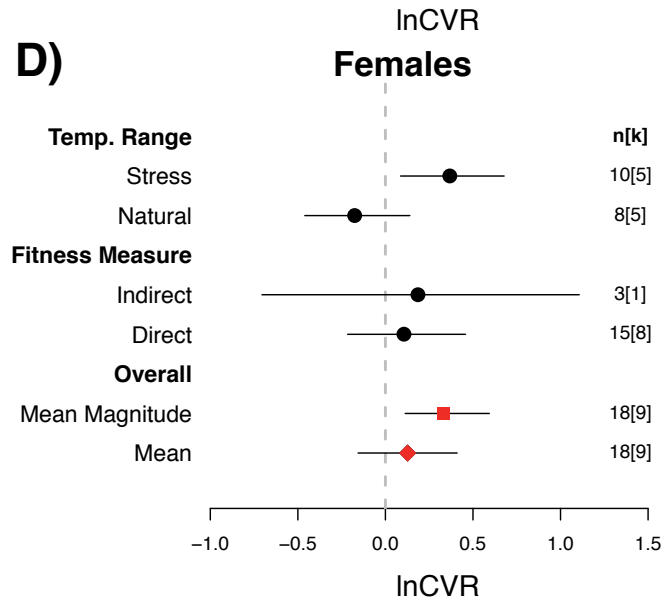
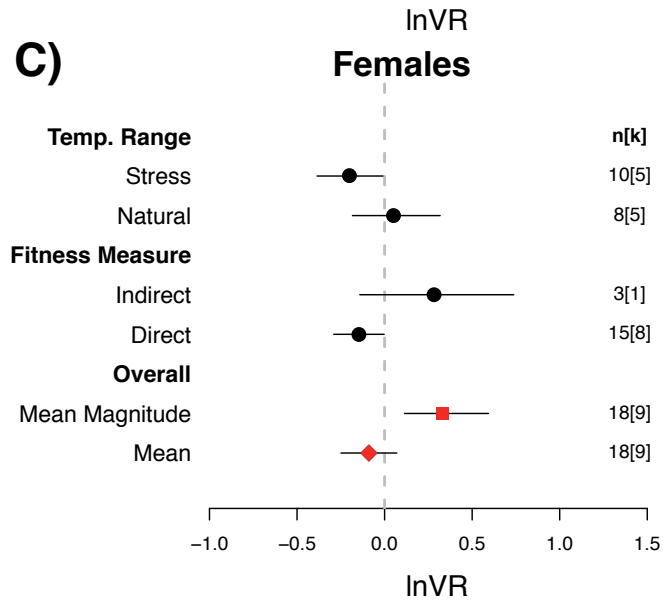
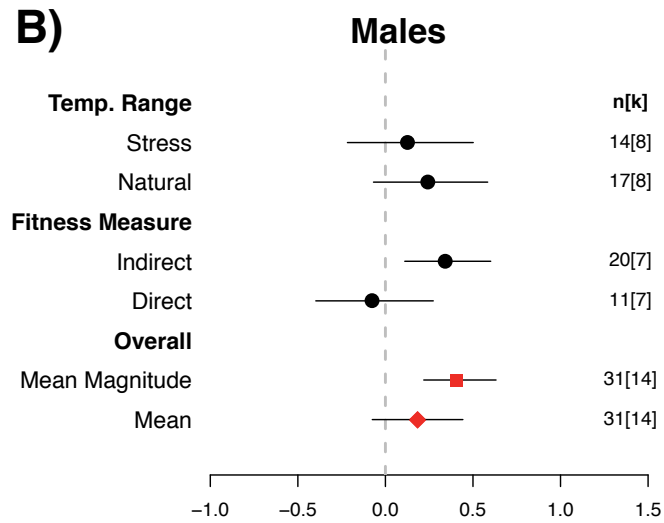
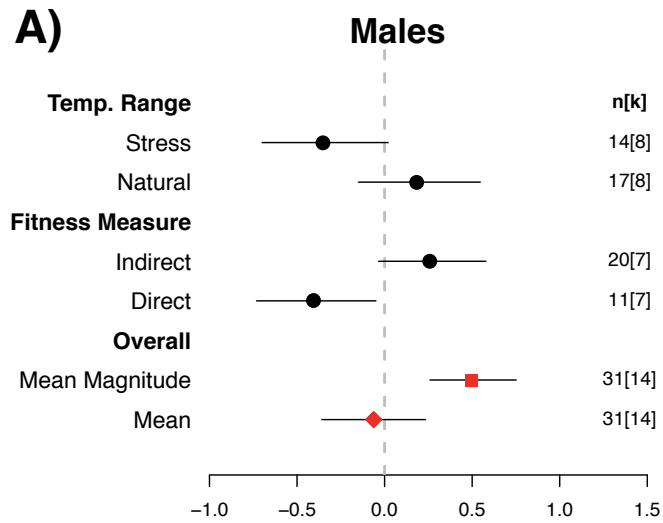


Figure 3.

