

14 **ABSTRACT**

- 15 1. In light of global climate change, there is a pressing need to understand how populations
16 will respond to rising temperatures. Understanding the effects of temperature changes on
17 mating behaviour is particularly important, given its implications for population viability.
- 18 2. To this end, we performed a meta-analysis of 53 studies to examine how temperature
19 changes influence mating latency, choosiness, and mating success. We hypothesized that
20 if higher temperatures make mate searching and mate assessment more costly due to an
21 elevated metabolism, this may lead to a reduction in mating latency and choosiness,
22 thereby increasing overall mating success.
- 23 3. We found no evidence for a global effect of temperature on mating latency, choosiness,
24 or mating success. There was an increase in mating success when animals were exposed
25 to higher temperatures during mating, but not when they were exposed before mating.
- 26 4. Interestingly, in a subset of studies that measured both mating latency and mating
27 success, there was a strong negative relationship between the effect sizes for these traits.
28 This suggests that a decrease in mating latency at higher temperatures was associated
29 with an increase in mating success and vice versa.
- 30 5. In sum, our meta-analysis provides new insights into the effects of temperature on mating
31 patterns. The absence of a consistent directional effect of temperature on mating
32 behaviours and mating success suggests it may be difficult to predict changes in the
33 strength of sexual selection in natural populations in a warming world. Nevertheless,
34 there is some evidence that (*i*) higher temperatures during mating may lead to an increase
35 in mating success and that (*ii*) an increase in mating success is associated with a decrease
36 in mating latency.

37 INTRODUCTION

38 In light of global climate change, there is a pressing need to understand how populations
39 will respond and adapt to rising temperatures (Crozier & Hutchings 2014). Because animal
40 behaviour is particularly labile, there is a growing body of literature investigating the effects
41 of temperature on a wide range of behavioural traits (Abram et al. 2017). Understanding
42 how temperature changes might affect mating behaviour and mating success is particularly
43 important, given its link to population viability and performance (Candolin & Heuschele
44 2008).

45 A number of studies have already shown that strong sexual selection can increase
46 population fitness and reduce the risk of extinction (Moller and Alatalo 1999, Lorch et al.
47 2003, Price et al. 2010, Lumley et al. 2015, Cally et al. 2019; but see Tanaka 1996). Sexual
48 selection could therefore play a major role in the capacity of populations to cope with
49 climate change if stronger mate preferences for ‘good genes’ can lead to higher-quality
50 offspring (Candolin & Heuschele 2008, Martinossi-Alliberti et al. 2019, Godwin et al. 2020).
51 In order to better understand the link between temperature and the strength and direction of
52 sexual selection, we need to focus on reproductive traits involved in precopulatory and
53 postcopulatory processes to identify the specific underlying mechanisms influenced by
54 temperature variation (García-Roa et al. 2020).

55 Here, we performed a meta-analysis examining how an increase in temperature
56 influences mating latency, choosiness, and mating success. We focused on plastic, rather
57 than evolutionary, responses to changes in temperature because there are far fewer studies
58 on the latter. Temperature can have both direct and indirect effects on mating behaviour and
59 mating success (reviewed in Garcia-Roa et al. 2020). For example, temperature is a key

60 determinant of metabolic rate and locomotor performance, particularly in ectotherms
61 (Gibert et al. 2007, Lachenicht et al. 2010). In turn, metabolic rate is closely linked to
62 activity levels (Kearney et al. 2010, Gunderson & Leal 2015) and can thus influence mate
63 searching and spatio-temporal distributions of the two sexes (Garcia-Roa et al. 2020). As a
64 result, temperature has been shown to modulate a wide range of precopulatory mating
65 behaviours, including mating latency, mate choice, courtship behaviour, remating rate, and
66 the intensity of intrasexual competition (e.g., Kvarnemo 1998, Jiao et al. 2009, Katsuki &
67 Miyatake 2009, Conrad et al. 2017, Gudka & Santos 2019).

68 Two possible outcomes for our meta-analysis were as follows: (i) if higher
69 temperatures make mate searching and mate assessment more energetically costly due to an
70 elevated metabolic rate, this might lead to a reduction in mating latency and cause females
71 to be less choosy, thereby indirectly increasing overall mating success; (ii) alternatively, if
72 the benefits of mate choice are higher under warmer conditions, we might expect an
73 increase in mating latency and choosiness, along with a decrease in mating success at the
74 population level. In the former scenario, a reduction in mating latency and choosiness
75 would lead to weaker sexual selection, whereas in the latter scenario an increase in mating
76 latency and choosiness would lead to stronger sexual selection. Stronger sexual selection
77 may in turn improve population viability by purging deleterious alleles in males that are also
78 deleterious in females (Whitlock & Agrawal 2009, McGuigan et al. 2011).

79 Our meta-analysis also examined whether the relationship between temperature and
80 mating behaviour or mating success depends on the magnitude of the temperature change,
81 the life stage during which the temperature change occurred, and whether there was a short-
82 term or long-term change in temperature. We expected stronger effects of temperature on

83 mating behaviour and mating success when the change in temperature was larger and when
84 it represented a long-term change in thermal conditions. We might also expect stronger
85 effects when the change in temperature occurred during mating than before mating, because
86 it would directly affect metabolism, activity levels, and locomotor performance during mate
87 searching and assessment (Garcia-Roa et al. 2020). On the other hand, temperature changes
88 in early development may have a more pronounced effect on mating behaviour than
89 temperature changes in adulthood, since ‘critical windows’ in early life can affect brain
90 development with long-term consequences for behaviour (e.g., Adewale et al. 2011,
91 O’Connor et al. 2021).

92 The ability to generate general predictions for how populations will respond to
93 climate change is crucial for management and conservation efforts, but it is difficult for
94 individual empirical studies to address this issue, as they generally focus on a single species
95 (Crozier & Hutchings 2014). We suggest that meta-analytical approaches present a powerful
96 tool for better understanding and predicting the effects of rising temperatures on natural
97 populations. By synthesizing data from published studies, meta-analyses can detect
98 common patterns across species (Harrison 2011). Thus, in the context of predicting
99 population responses to climate change, if a meta-analysis reveals consistent directional
100 effects of temperature on a particular trait across a wide range of taxonomic groups, it may
101 allow us to generate some general predictions.

102

103 **METHODS**

104 **Search protocol and data collection**

105 This meta-analysis was conducted following the preferred reporting items for systematic
106 reviews (PRISMA) approach (Moher et al. 2009; Supplementary Figure 1). Database
107 searches were conducted using Web of Science and Scopus on the 20th and 21st of February
108 2020, respectively. We used search terms that would identify studies focusing on
109 temperature variation and mating latency, choosiness, or mating success: (“temperature”
110 OR “thermal” OR “warm*” OR “cold*”) AND (“latency” OR “mate” or “mating” OR
111 “mate choice” OR “choosy” OR “choosiness” OR “mat* preference” OR “copulat*” or
112 “mating success”). All papers identified through these searches were checked for relevance
113 based on the title and abstract (Supplementary Figure 1). After removing papers that were
114 clearly not relevant to our question, we screened the full text of the remaining papers to find
115 studies that contained information on mating latency, choosiness, and/or mating success
116 under two or more temperature conditions. We considered mating latency to be a measure
117 of individuals’ propensity to mate, which was described using different terms across papers
118 (e.g., time to copulation, time to mating, premating period, precopulation period). We
119 defined choosiness as “the change in mating propensity in response to alternative stimuli”
120 (Reinhold & Schielzeth 2015). Choosiness thus referred to the strength of the mating
121 preference when individuals were choosing between two potential mates (e.g., small vs
122 large) or sexual signals (e.g., mating calls). Mating success referred to the proportion of
123 experimental pairs that engaged in copulation during the mating trial.

124 We included experimental studies with either short-term or long-term exposure to
125 different constant temperatures within a generation. Because our aim was to examine
126 plastic, rather than evolutionary, responses to temperature, we excluded experimental
127 evolution studies where organisms were exposed to contrasting thermal environments over

128 multiple generations. We also excluded studies where there were confounding variables, for
129 example when the temperature treatments were coupled with other factors (e.g.,
130 comparisons between a warm and dry environment versus a cold and wet environment).
131 We excluded studies where animals were exposed to fluctuating temperatures. For studies
132 on mating latency and choosiness, we only included those where the choosing sex (usually
133 the female) was subjected to a temperature treatment (Supplementary Table 1). For studies
134 on mating success, we included studies where the male, female, or both were subjected to a
135 temperature treatment (Supplementary Table 1).

136 Our full-text screening also included a small number of additional references that
137 were not identified through our literature search and were instead obtained from other
138 sources, such as a request for relevant papers from colleagues on Twitter ($n = 10$). Data from
139 two of these papers were deemed relevant and included in the final analysis. Overall, full-
140 text screening identified 62 studies that met the experimental design criteria for inclusion in
141 our meta-analysis (Supplementary Figure 1).

142

143 **Effect size calculation**

144 To calculate effect sizes, we extracted data from the main text, tables, or figures using the
145 image analysis software WebPlotDigitizer (Rohatgi 2019). We were unable to extract
146 appropriate effect sizes from 13 studies due to missing test statistics or sample sizes. In these
147 cases, we contacted the corresponding authors of these studies using a standardized email
148 asking for the missing information. Seven of these authors responded to our email, and of
149 those, four were able to provide the information needed to calculate effect sizes.

150 For each of the studies included in our meta-analysis ($n = 53$), we calculated r effect
151 sizes (correlation coefficient). In our analysis, a positive r effect size indicates that
152 temperature and the trait of interest are positively correlated (e.g., higher temperatures are
153 associated with increased mating success). Some studies included multiple effect sizes for
154 the same or different species; to control for this, we included “study” as a random factor in
155 our analysis (see *Data analysis* for details). Overall, we collected 29 effect sizes for mating
156 latency, 29 effect sizes for choosiness, and 58 effect sizes for mating success (Table 1). These
157 data comprised both vertebrates (amphibians, birds, fishes, reptiles) and invertebrates
158 (arachnids, crustaceans, insects, molluscs) with insects being the most common taxonomic
159 group studied (Table 1).

160

161 **Data analysis**

162 All statistical analyses were performed in R version 3.6.1 (R Core Team 2019), and figures
163 were generated using *ggplot2* (Wickham 2016). Meta-analyses were performed using
164 Fisher’s z transform of the correlation coefficient (Zr). We then converted mean effect size
165 estimates derived from our statistical models back to r for presentation in figures.

166 Assumptions of linear mixed models (i.e., normality of residuals) were met for all models
167 reported below.

168

169 *Main effects models*—Using the function ‘*rma.mv*’ from the R package ‘*metafor*’ (Viechtbauer
170 2010), we run a multilevel intercept-only meta-analytic model for each of our three traits of
171 interest (mating latency, choosiness, and mating success) to test for an overall effect of
172 temperature. We ran both phylogenetic and non-phylogenetic models to examine whether

173 the evolutionary relationships between species influenced this overall effect. For the
174 phylogenetic models, we first used the R package ‘rotl’ (Michonneau et al. 2016, OpenTree
175 et al. 2021) to generate phylogenetic trees of the species included in our meta-analysis
176 (Supplementary Figure 2). This tree was then imported into the ‘ape’ package (Paradis et al.
177 2004), and a correlation matrix obtained using the ‘vcv’ function. The resulting correlation
178 matrix was then included in our multivariate meta-analytic models as a random factor. We
179 included additional random effects in our phylogenetic and non-phylogenetic models to
180 account for non-independence due to the extraction of multiple effect sizes from the same
181 study (study ID) and included a unit level random effect (effect size ID) as a measure of
182 residual heterogeneity (Santos et al. 2011). In non-phylogenetic models, we also included a
183 random effect to account for the use of the same species across studies (species ID).

184
185 *Moderator effects models*—Because phylogeny failed to resolve any of the heterogeneity, we did
186 not include it in our moderator effects models (Santos et al. 2011; but see Supplementary
187 Table 2). Moderators were tested using non-phylogenetic multilevel meta-regression models
188 with study ID, species ID, and effect size ID as random effects (Santos et al. 2011). We first
189 included a continuous moderator (“intensity of temperature treatment”) to test whether
190 variation in effect sizes could be explained by the extent of the temperature differences (°C)
191 between treatments within each study. A second categorical moderator (“time of
192 temperature treatment”) tested for differences between studies that exposed animals in early
193 development, in adulthood before the mating trial, or during the mating trial. A third
194 categorical moderator (“type of temperature treatment”) tested for differences between
195 studies that exposed animals to a short-term versus a long-term temperature treatment (i.e.,

196 acute exposure versus acclimation). We defined long-term temperature treatment as any
197 exposure to a different temperature that lasted more than 24 hr. Lastly, for mating success,
198 we included an additional categorical moderator (“sex exposed to temperature treatment”)
199 to test for differences between studies that exposed males, females, or both sexes to the
200 temperature treatment. For each of these models, we calculated R^2_{marginal} , which describes the
201 percentage of heterogeneity that was explained by the inclusion of a moderator (i.e., the
202 estimated percentage decrease in heterogeneity between the main effects model and
203 moderator model).

204
205 *Relationship between $Zr_{\text{mating latency}}$ and $Zr_{\text{mating success}}$* —We also examined the relationship between
206 effect sizes (Zr) for mating latency and mating success from studies that measured both
207 traits. This was the case for 14 effect sizes from 10 studies on 9 different species. We
208 analysed this reduced dataset using (i) a Pearson’s correlation test between $Zr_{\text{mating latency}}$ and
209 $Zr_{\text{mating success}}$, as well as (ii) a meta-regression with $Zr_{\text{mating success}}$ as the response variable,
210 $Zr_{\text{mating latency}}$ as the moderator, and study ID, species ID, and effect size ID as random effects.

211
212 *Publication bias tests*—To examine the potential for underreporting of non-significant results,
213 we used the function ‘regrest’ to test for funnel plot asymmetry in our meta-regression
214 models (Nakagawa et al. 2017). We also tested for time-lag bias using (i) a rank correlation
215 test between effect size and publication year for each study and (ii) a meta-regression with
216 publication year as a continuous moderator (Jennions & Møller 2002).

217

218 **RESULTS**

219 We present mean effect size estimates derived from the statistical models with 95%
220 confidence intervals in square brackets.

221

222 **Publication bias tests**

223 There was evidence for funnel asymmetry for mating success ($z = -2.48$, $P = 0.013$) but not
224 for mating latency ($z = 1.21$, $P = 0.23$) or choosiness ($z = 1.01$, $P = 0.31$). This suggests a
225 potential for publication bias in the mating success dataset (Supplementary Figure 3). In
226 addition, our models with publication year as a continuous moderator showed a time-lag
227 bias in the mating latency dataset ($Zr = 0.03$ [0.003, 0.05], $P = 0.026$) and the choosiness
228 dataset ($Zr = -0.04$ [-0.06, -0.01], $P = 0.004$) but not the mating success dataset ($Zr = -0.001$
229 [-0.02, 0.02], $P = 0.86$; Supplementary Figure 4). Similarly, the rank correlation test
230 indicated significant variation in effect size over time for mating latency ($\rho = 0.53$, $P =$
231 0.003) and choosiness ($\rho = -0.59$, $P < 0.001$), but no overall trend for mating success ($\rho =$
232 0.03 , $P = 0.81$).

233

234 **Main effects models**

235 Phylogeny failed to resolve any heterogeneity in our main effects models; the estimates from
236 phylogenetic and non-phylogenetic models were very similar or identical. Our intercept-
237 only models for mating latency (non-phylogenetic method: $Zr = -0.13$ [-0.32, 0.05],
238 phylogenetic method: $Zr = -0.13$ [-0.31, 0.05]), choosiness (non-phylogenetic method: $Zr =$
239 0.001 [-0.17, 0.18], phylogenetic method: $Zr = 0.001$ [-0.17, 0.18]), and mating success (non-
240 phylogenetic method: $Zr = 0.06$ [-0.11, 0.22], phylogenetic method: $Zr = 0.06$ [-0.11, 0.22])
241 showed no overall effect of temperature (Figure 1; Supplementary Figures 5 & 6).

242

243 **Moderator models**

244 As in the main effects models, the estimates from the phylogenetic and non-phylogenetic
245 moderator models were similar or identical in all analyses. Statistical results reported below
246 are based on the non-phylogenetic models (see Supplementary Table 2 for phylogenetic
247 models).

248 There was some variation in the effect of temperature on mating latency depending
249 on whether the animals were exposed to a temperature treatment during early development
250 ($Zr = 0.19 [-0.21, 0.59]$), in adulthood before mating ($Zr = -0.10 [-0.39, 0.19]$), or during
251 mating ($Zr = -0.30 [-0.57, -0.03]$), but this moderator (“time of temperature treatment”) was
252 not statistically significant overall ($QM=4.05$, $P=0.13$, $R^2_{\text{marginal}}=0.075$; Figure 2). The effects
253 of temperature on mating latency also did not vary in response to the type of temperature
254 treatment (acute exposure: $Zr = -0.17 [-0.40, -0.06]$; acclimation: $Zr = -0.06 [-0.41, 0.28]$;
255 $QM=2.23$, $P=0.33$) or the intensity of the treatment ($Zr = -0.01 [-0.04, 0.01]$, $QM=1.50$,
256 $P=0.22$).

257 The relationship between temperature and choosiness was not influenced by the time
258 of the temperature treatment (early development: $Zr = 0.05 [-0.15, 0.26]$; during mating
259 trial: $Zr = -0.04 [-0.23, 0.14]$; $QM=1.32$, $P=0.25$). Similarly, this relationship did not vary
260 based on the type of temperature treatment (acute exposure: $Zr = -0.05 [-0.26, 0.15]$;
261 acclimation: $Zr = 0.02 [-0.17, 0.21]$; $QM=0.84$, $P=0.66$) or the intensity of the temperature
262 treatment ($Zr = -0.03 [-0.06, 0.01]$; $QM=2.59$, $P=0.11$).

263 The effect of temperature on mating success varied depending on whether the
264 animals were exposed to a temperature treatment during early development ($Zr = -0.07 [-$

265 0.30, 0.17]), in adulthood before mating ($Zr = -0.17 [-0.38, 0.04]$), or during mating ($Zr =$
266 $0.17 [0.01, 0.34]$). Higher temperatures during the mating trial were associated with a higher
267 mating success (QM=15.6, $P < 0.001$; Figure 2). This moderator (“time of temperature
268 treatment”) explained about 5% of the heterogeneity among effect sizes ($R^2_{\text{marginal}} = 0.048$). In
269 contrast, the effects of temperature on mating latency did not vary in response to the type of
270 temperature treatment (acute exposure: $Zr = 0.09 [-0.11, 0.29]$; acclimation: $Zr = -0.09 [-$
271 $0.29, 0.11]$; QM=0.89, $P = 0.64$) or the intensity of the treatment ($Zr = 0.01 [-0.02, 0.03]$,
272 QM=0.36, $P = 0.55$). Lastly, there were no substantial differences in effect sizes between
273 studies that exposed males ($Zr = -0.21 [-0.59, 0.17]$), females ($Zr = -0.19 [-0.70, 0.33]$), or
274 both sexes ($Zr = 0.09 [-0.10, 0.27]$) to the temperature treatment (QM=3.14, $P = 0.37$).

275

276 **Relationship between $Zr_{\text{mating latency}}$ and $Zr_{\text{mating success}}$**

277 We found a strong negative correlation between the effect sizes (Zr) for mating latency and
278 mating success from studies that measured both traits ($r = -0.77$, $t_{12} = -4.13$, $P = 0.001$; Figure
279 3). Similarly, our meta-regression showed that $Zr_{\text{mating latency}}$ explained 75% of the
280 heterogeneity in $Zr_{\text{mating latency}}$ (QM=18.6, $P < 0.0001$, $R^2_{\text{marginal}} = 0.745$). This negative
281 relationship indicates that in studies where a higher temperature led to an increase in mating
282 latency, this was associated with a decrease in mating success, and vice versa (Figure 3).

283

284 **DISCUSSION**

285 Our meta-analysis of 53 studies found no evidence for a global effect of temperature on
286 mating latency, choosiness, or mating success. There was an increase in mating success
287 when animals were exposed to higher temperatures during mating, but not when they were

288 exposed before mating. Interestingly, in a subset of studies that measured both mating
289 latency and mating success, we found a strong negative relationship between the effect sizes
290 for these traits. This suggests that a decrease in mating latency at higher temperatures was
291 associated with an increase in mating success.

292 These temperature-induced changes in mating behaviour may be mediated through
293 physiological changes (Abram et al. 2017). The body temperature and metabolic rate of
294 ectothermic animals is directly influenced by changes in ambient temperature, which can
295 affect their activity levels (Kearney et al. 2010, Gunderson & Leal 2015). This also means
296 that higher temperatures might lead to increased costs of mate searching and mate
297 assessment (Punzalan et al. 2008, García-Roa et al. 2020). For example, ambush bugs
298 (*Phymata americana*) have reduced mate-searching success at higher ambient temperatures
299 (Punzalan et al. 2008), which might result in a higher propensity to mate with a potential
300 partner under these conditions.

301 Previous work has suggested that temperature may also affect mating behaviour
302 through changes in communication between mates (Martin & Lopez 2013). Both mating
303 latency and mating success are dependent of the ability of a male to stimulate the female for
304 mating. When mate communication involves chemical signals over large areas, such as
305 femoral secretions to mark territories, females may take longer to detect them due to faster
306 evaporation at higher temperatures (Martin & Lopez 2013). Such a disruption in mate
307 communication may lead to a higher mating latency and lower mating success in warmer
308 environments. On the other hand, when mate communication involves chemical signals at a
309 small spatial scale, a higher temperature may increase the volatility of these chemicals and
310 improve mate recognition and assessment. This may lead to a shorter mating latency and

311 higher mating success in warmer environments. In line with this latter scenario, our meta-
312 analysis found evidence for an increase in mating success when animals were exposed to
313 higher temperatures during mating, but it is unclear whether the underlying mechanism for
314 this pattern was a change in mate communication through chemical signals.

315 Contrary to our expectation, we found no evidence that temperature-induced
316 changes in mating success were accompanied with changes in mating latency or choosiness.
317 This was somewhat surprising, given that mating latency, choosiness, and mating success
318 are closely linked (Lindström & Lehtonen 2013, Breedveld & Fitze 2015). For example, a
319 choosier individual may require more time for mate assessment, leading to an increase in
320 mating latency, which can then result in lower mating success (Hegde & Krishna 1997).
321 Similarly, a choosier individual may be less likely to mate with low-quality partners,
322 resulting in lower mating success. The absence of a directional effect of temperature on
323 mating latency and choosiness, despite its effects on mating success, may be partly due to
324 the use of different datasets for each of these traits (Table 1). In fact, only one of the studies
325 in our meta-analysis included data on all three traits (Supplementary Table 2). In a subset of
326 studies that measured both mating latency and mating success, there was a strong negative
327 relationship between the effect sizes for these traits, as we had expected (Figure 3). This
328 supports our interpretation that the different patterns we observed in mating latency,
329 choosiness, and mating success may be due to differences in the species used across the
330 three datasets. A recent review argued that the relationship between temperature and sexual
331 selection is likely to vary across species in relation to their mating system, physiology, and
332 behaviour (García-Roa et al. 2020). The absence of global directional effects in mating
333 behaviour in our meta-analysis provides support for this prediction. Importantly, our

334 findings suggest that due to substantial among-species variation, it may be difficult to
335 generate predictions for how the strength of sexual selection in natural populations will
336 change in a warming world.

337 Phylogeny did not seem to influence the effects of temperature on mating behaviour
338 across the range of species included in our analysis (mating latency: $n = 14$, choosiness: $n =$
339 14 , choosiness: $n = 28$). This may be because certain features of our datasets make the
340 detection of a phylogenetic signal unlikely. For example, mating behaviour has the capacity
341 to evolve rapidly and is thus evolutionarily labile (Blomberg et al. 2003, Dougherty &
342 Shuker 2015). Our analysis also includes measures of mating preference (choosiness) for a
343 wide range of traits, such as body size, colouration, and mating calls, which might make it
344 more difficult to find a phylogenetic signal. Lastly, it is worth noting that a large majority of
345 studies included in our analysis were on insects (Table 1), limiting our ability to draw
346 conclusions about general patterns across taxa. For example, we initially intended for our
347 meta-analysis to include a comparison between endotherms and ectotherms. We expected
348 that temperature changes would have a stronger effect on mating behaviour and mating
349 success in ectotherms, given that ambient temperature can directly affect their body
350 temperature, metabolic rate, locomotor performance, and activity levels (Gibert et al. 2007,
351 Kearney et al. 2010, Lachenicht et al. 2010, Gunderson & Leal 2015). However, it was not
352 possible to carry out this comparison due to the relevant studies available in published
353 literature. Out of 53 studies included in our meta-analysis, only two were on endotherms
354 (birds). We therefore strongly encourage future research on the effects of temperature on
355 mating behaviour and mating success in endotherms, as well as ectotherms other than
356 insects.

357 Our publication bias tests suggest there may be some influence on the overall results.
358 Firstly, there was evidence for funnel asymmetry for mating success, suggesting a potential
359 for publication bias in this dataset. The observed bias may have also been caused by
360 unexplained heterogeneity among studies due to other moderators that we did not consider
361 in our analysis. Secondly, we found evidence for a time-lag bias in the mating latency and
362 choosiness datasets, where there was a trend for a decrease in effect size over time
363 (Supplementary Figure 4). This is a common pattern in meta-analyses in ecology and
364 evolutionary biology (Jennions and Møller 2002). We have not used methods such as trim
365 and fill that try to compensate for publication bias, as they may perform poorly in high
366 heterogeneity datasets (Moreno et al., 2009, Moran et al. 2020). Regardless of the
367 underlying causes for this publication bias, it is important to take it into consideration when
368 interpreting the results, particularly in cases where confidence intervals are close to zero,
369 such as the effect of temperature on mating success (Figure 2b).

370 Another limitation of our study was that the sample size for the mating latency
371 ($k=29$) and choosiness datasets ($k=29$) was relatively small. As a result, subset analyses
372 testing for the effects of moderators had small sample sizes for each factor (Supplementary
373 Table 1). Most of these analyses did not detect any significant effects, with the exception of
374 an effect of the time of temperature treatment on mating success, which was discussed
375 above. The fact that the intensity and duration of the temperature treatment did not have an
376 overall effect on mating behaviour and mating success was surprising and may be due to
377 low statistical power.

378 Our meta-analysis focused on the effects of temperature on mating success and two
379 precopulatory traits, mating latency and choosiness. Nevertheless, temperature can also

380 influence postcopulatory processes (García-Roa et al. 2020). For example, the amount and
381 quality of sperm transferred during mating has been shown to vary with temperature
382 (Reinhardt et al. 2015, Sales et al. 2018, Gasparini et al. 2018, Walsh et al. 2019). A study
383 on the cigarette beetle (*Lasioderma serricone*) that examined both precopulatory and
384 postcopulatory traits actually found that temperature had a stronger effect on the latter
385 (Suzaki et al. 2018). We therefore suggest that a meta-analysis on how temperature
386 variation also influences postcopulatory traits, such as sperm production and sperm
387 competition, may be worthwhile.

388 Given rising temperatures due to global climate change, it is important to better
389 understand how changes in temperature may affect mating patterns and sexual selection
390 (García-Roa et al. 2020). Here, we show an increase in mating success when animals were
391 exposed to higher temperatures during mating, but not during early development or in
392 adulthood before mating. We found no evidence for directional effects of temperature on
393 mating latency or choosiness, suggesting it may be difficult to generate general predictions
394 for how the strength of sexual selection will change in a warming world. Nevertheless, we
395 also found a strong negative relationship between the effect sizes for mating latency and
396 mating success. This suggests that in species where a higher temperature leads to an increase
397 in mating latency, this may result in a decrease in mating success, and vice versa. Our meta-
398 analysis therefore provides new insights into the effects of temperature on mating behaviour
399 and sexual selection.

400

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404

405 **AUTHOR CONTRIBUTIONS**

406 AB carried out the data extraction, contributed to the data analysis, and provided comments
407 on the manuscript draft. NP conceived the study, contributed to data extraction and data
408 analysis, and wrote the manuscript.

409

410 **DATA AVAILABILITY STATEMENT**

411 All data used in this meta-analysis and the associated R code will be archived on the Dryad
412 Digital Repository upon manuscript acceptance.

413

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540 **Table 1.** Number of studies (n), species, and effect sizes (k) used in our meta-analysis on the
541 effects of temperature on mating latency, choosiness (strength of preference), and mating
542 success. We also show the breakdown by taxonomic group for each trait.

	Sample sizes		
	Studies (n)	Species	Effect sizes (k)
Mating latency	19	14	29
Arachnid	1	1	1
Insect	17	12	27
Mollusc	1	1	1
Choosiness	14	14	29
Amphibian	1	1	1
Bird	2	2	2
Crustacean	1	1	2
Fish	2	2	5
Insect	7	7	18
Reptile	1	1	1
Mating success	31	28	58
Collembola	1	1	1
Fish	1	1	2
Insect	29	26	55

543

544

545 **FIGURE LEGENDS**

546

547 **Figure 1.** Mean effect size estimates derived from multilevel intercept-only meta-analytic
548 models examining the effects of temperature on mating latency (diamond), choosiness
549 (square), and mating success (circle). The relative size of each symbol represents the number
550 of effect sizes included in that dataset (mating latency = 29, choosiness = 29, mating success
551 = 58).

552

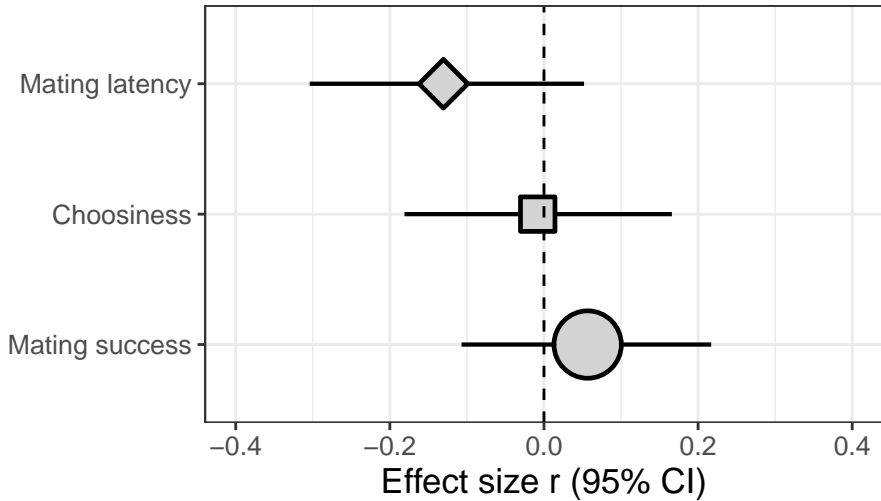
553 **Figure 2.** Mean effect size estimates derived from multilevel meta-regression models
554 examining how the “time of temperature treatment” moderator (early development,
555 adulthood before mating, or adulthood during mating) influences the relationship between
556 temperature and mating latency (diamond) or mating success (circle). The relative size of
557 each symbol represents the number of effect sizes included in that dataset (mating latency:
558 early development = 6, before mating = 11, during mating = 12; mating success: early
559 development = 6, before mating = 14, during mating = 38).

560

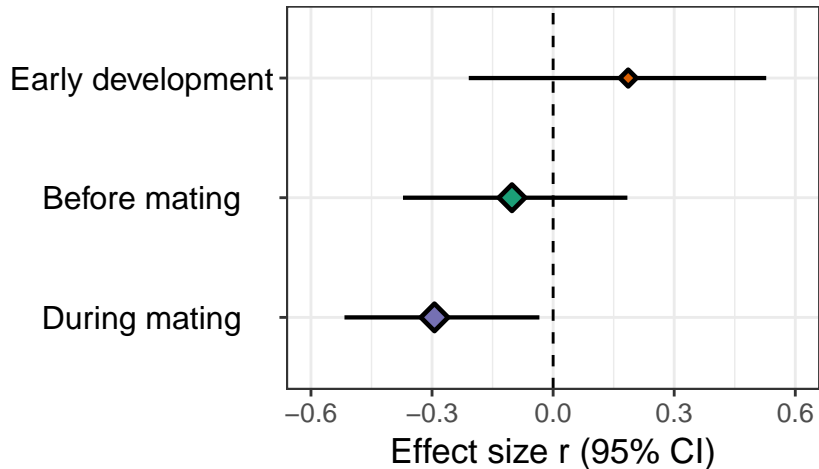
561 **Figure 3.** Fitted line and individual data points showing the relationship between Zr_{mating}
562 $_{\text{latency}}$ and $Zr_{\text{mating success}}$ for studies that measured both traits (14 effect sizes from 10 studies on
563 9 different species). The shaded area around the line of best fit indicates the 95% confidence
564 interval.

565

Main effects



Mating latency



Mating success

