Meta-analysis shows the evidence for context-dependent mating behaviour is inconsistent or weak across animals

Liam R. Dougherty

Institute of Integrative Biology, University of Liverpool, Liverpool, L69 7RB, UK

Email: liam.dougherty@liverpool.ac.uk Tel: (+44) 0151 795 7771

7261 words (main text), 149 words (abstract)

5 figures, 2 tables

Author contributions: LRD conceived the study, carried out the searches, collected the data, performed all analyses, and wrote the manuscript.

Data accessibility statement: I confirm that, should the manuscript be accepted, the data supporting the results will be archived in an appropriate public repository.

1 Abstract

2

3 Animals often need to invest significantly in mating behaviour in order to successfully mate.

4 However, the expression of mating behaviour can be costly, especially in unfavourable

5 environments, so animals are expected to adjust their behaviour in a context-dependent

6 way to mitigate these costs. I systematically searched the literature for studies measuring

7 animal mating behaviour (sexual signalling, response to sexual signals, or the strength of

8 mate choice) in more than one environment, and used a phylogenetically-controlled meta-

9 analysis to identify environmental factors influencing these behaviours. Across 222 studies,

10 the strength of mate choice was significantly context-dependent, and most strongly

11 influenced by population density, population sex ratio, and predation risk. However, the

12 average effect sizes were typically small. The amount of sexual signalling and the strength of

13 response to sexual signals were not significantly related to the environment. Overall, this

14 suggests that the evidence for context-dependent mating behaviour across animals is

15 surprisingly weak.

Introduction

16

17

18 For sexual animals, reproduction requires successfully mating with an individual of the

19 opposite sex. In order to achieve this, individuals may need to signal or display to potential

20 partners in order to attract and court them, or respond to the signals or displays of others.

21 Additionally, some individuals make better mates than others. Therefore, animals may gain

22 considerable benefits from choosing only to mate with partners of the highest quality,

23 leading to the expression of mate choice (Andersson 1994; Kokko *et al.* 2003; Rosenthal,

24 2017). However, both sexual signalling, and responding to sexual signals, can be expensive

25 in terms of time and energy (Andersson 1994; Kotiaho 2001). There are also costs associated

26 with mate choice, such as the energy and time needed to sample mates effectively (Sullivan

27 1994; Vitousek *et al.* 2007), or the risk of failing to mate if individuals are overly choosy

28 (Barry & Kokko 2010; Greenway *et al.* 2015). Therefore, the expression of these mating

29 behaviours should be influenced by the balance of these costs and benefits: a behaviour

30 should only be expressed when the benefits outweigh the costs.

31

32 Importantly, the costs and benefits of investing in mating behaviour are inherently linked to

33 the social, biological or physical environment. For example, at high predator density the cost

34 of mate searching or sexual signalling is increased when these behaviours make signallers or

35 searchers more conspicuous (Magnhagen 1991; Zuk & Kolluru 1998). In these conditions

36 animals may benefit from investing less into searching and signalling, at least in the short-

37 term. Importantly, the natural environment is complex, fluctuating, and unpredictable, both

38 spatially and temporally (Miller & Svensson 2014). Therefore animals will maximise their

39   fitness by identifying situations in which mate searching and choice are beneficial or costly,

40   and changing their behaviour accordingly. Indeed, evidence from a wide range of species

41   shows that individuals often alter their mating behaviour over the short-term, in response

42   to a wide range of social, biological, or physical factors (Jennions & Petrie 1997; Ah-King &

43   Gowaty 2016; Kelly 2018). For example, many species respond to an increased predation

44   risk by reducing signalling (e.g. Endler 1987; Fuller & Berglund 1996) or exhibiting weaker

45   mate choice (e.g. Hedrick & Dill 1993; Gong & Gibson 1996; Hughes et al. 2012).

46

47   These empirical examples show that the environment can be an important determinant of

48   mating behaviour in some species. Importantly, by identifying these effects in laboratory

49   studies, we may be able to better predict the expression of mating behaviour in the natural

50   environment, which is complex and highly dynamic (Miller & Svensson 2014). Further, mate

51   choice is a key component of sexual selection, which can influence population fitness and

52   drive the evolution of novel phenotypes, the action of which may in turn be influenced by

53   the expression of sexual signals (Andersson 1994). Therefore understanding the extent to

54   which both signalling and mate choice are context-dependent will help us to predict the

55   strength of sexual selection, and the resulting evolutionary change, in natural populations.

56   However, such predictions will only be possible if environmental effects are generally

57   consistent across species, and there is evidence that this may not be the case. For example,

58   many studies fail to find any significant effect of the environment on mating behaviour (e.g.

59   in relation to predation risk: Briggs et al. 1996; Billing et al. 2007). Other studies do detect

60   significant effects, but in contrasting directions (e.g. Beckers & Wagner 2018), suggesting

61   that environmental effects on mating behaviour may not be as clear as previously thought.

62   Importantly, to date there has been no quantitative synthesis of these data.

63

64   To address this problem, I systematically searched for studies reporting animal mating

65   behaviour in relation to seven environmental factors that are predicted to influence the

66   costs and benefits of expressing these behaviours. In order to estimate the degree of

67   context-dependence, I selected studies that reported mating behaviour in more than one

68   environmental context. I focused on three mating behaviours: a) the amount of sexual

69   signalling, the strength of response to mates or sexual stimuli (responsiveness), and the

70   strength of mate choice (choosiness). I examined these behaviours in relation to seven

71   social, biological or physical environmental factors: population density, adult sex ratio,

72   operational sex ratio (OSR), predation risk, travel cost, time cost, and variation in mate

73   quality. All of these factors potentially influence the costs and benefits of sexual signalling,

74   mate searching or mate choice. They do this by altering several key components of the

75   mating system: the number of potential mating opportunities, the cost of signalling, the cost

76   of sampling, and the benefits of choice (**Table 1**). Importantly, as much as possible I avoided

77   environmental factors which are likely to influence individual condition, because this is

78   predicted to influence mating behaviour independently of the external environment (Cotton

79   et al. 2006). This approach rules out other physical factors such as temperature or resource

80   availability, which have the potential to influence both individual condition and some of the

81   mating system components mentioned above.

82

83   Using this dataset I performed multiple phylogenetically-controlled meta-analyses

84   quantifying the difference in animal mating behaviour across environmental contexts.

85   Importantly, because I was interested in examining the overall effect of the environment on

86   the expression of mating behaviour, I combined all seven environmental factors into a single

87   analysis. However I performed separate analyses for each of the three behaviours, as they

88   are predicted to be influenced by the environment in different ways (see Predictions). I used

89   this analysis to ask three questions. First, does sexual signalling, responsiveness and

90   choosiness significantly differ across the animal kingdom in relation to the environment? Do

91   animals respond in a consistent way, as would be expected from sexual selection theory?

92   Second, does the magnitude of this difference depend on which aspect of the environment

93   is varied? Finally, are there any other aspects of the species tested, or experimental design

94   used, that influence the direction or magnitude of this difference?

95

Methods

97

98   **LITERATURE SEARCHES**

99   I searched for relevant papers in two ways. First, I obtained all papers cited by a recent

100   review of behavioural plasticity in mating behaviour by Ah-King & Gowaty (2016). Second, I

101   performed literature searches using the online databases Web of Science & Scopus on the

102   29th October 2018 (Table S1). The literature screening process is summarised in **Figure 1**.

103   After removing duplicate results, I screened all titles to remove obviously irrelevant studies

104   (e.g. studies on humans, other subject areas, review articles). I next imported all relevant

105   abstracts into the screening software Rayyan (Ouzzani *et al.* 2016), and excluded those that

106   did not appear relevant. This resulted in 701 relevant studies. I then read the full text of

107   these 701 studies to determine if they fit the inclusion criteria listed in the next section.
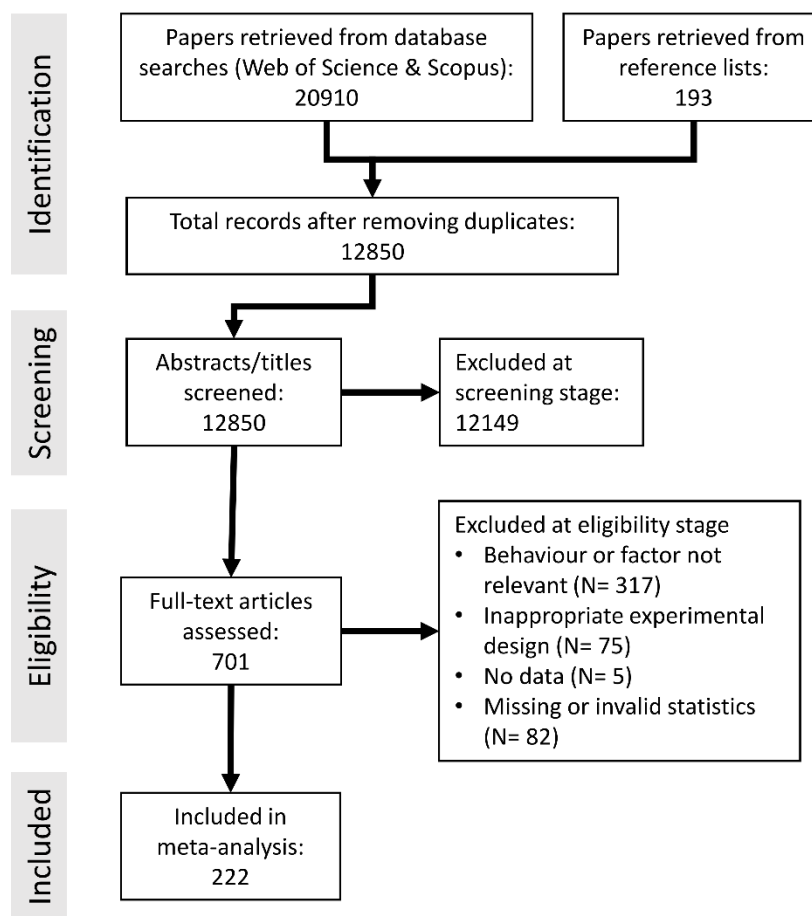
108

109

Figure 1. PRISMA diagram showing the literature search and selection process used to create the dataset.

110

111

112 **CRITERIA FOR INCLUSION**

113 I had several main criteria for including a study in the next stage of the analysis. Studies

114 were included that: a) measured one of the three mating behaviours listed above, b)

115 recorded this behaviour in more than one environmental context, in relation to one of the

116 seven environmental factors listed above, and c) provided sufficient statistical information

117 for an effect size to be calculated (see Effect size extraction and coding). I considered studies

118 examining all animal species, with the exception of humans. I included studies testing the

119 same subjects in multiple contexts, or different subjects in different contexts. I included

120   data on both males and females, and studies in which the environment varied naturally or

121   experimentally. I excluded studies if more than one environmental factor clearly differed

122   between contexts. I did not include cases for which mating behaviour was inferred from

123   mating outcomes (such as studies reporting metrics of sexual selection or mating frequency

124   using paternity tests), or in which behaviour could not be attributed to a single individual

125   (studies for which rivals or mates have some control over mating outcomes). I included

126   studies in which subjects experienced a variable environment before or during the

127   behavioural test. In the former case, the environment typically varied in the short term

128   (hours or days before the trial), and so any responses seen can be considered to represent

129   short-term behavioural plasticity. In a minority of cases, the environment was varied over a

130   longer time period. For example, subjects may have been reared under different

131   experimental conditions in the lab for several weeks, or compared the behaviour of wild-

132   caught subjects from populations that differed naturally in environmental conditions.

133

134   **MATING BEHAVIOURS AND ENVIRONMENTAL FACTORS**

135   Here, I briefly outline the inclusion criteria and predictions associated with the three

136   behaviours and seven environmental factors included in the analysis. For a more detailed

137   description of inclusion criteria and category definitions please see the supplementary

138   methods.

139

140   I focused on three mating behaviours: sexual signalling, response to sexual signals

141   (responsiveness), and the strength of mate choice (choosiness). In the sexual signalling

142   category I included any signalling behaviours that the authors suggest function to advertise

143   to or attract mates. I included both long-range attraction signals (such as song produced

144   when mates are not immediately present), and close-range courtship behaviours that are

145   expressed exclusively during mating interactions. I focused on signalling behaviours that

146   reflect the motivation to signal, or the energetic investment in signalling. I included acoustic,

147   chemical, tactile, and visual signals. For chemical signalling, I only included data on the time

148   spent signalling, or the likelihood of signalling, rather than the amount or composition of the

149   signals themselves. Importantly, signalling behaviour was instead classed as choosiness if it

150   was shown to be preferentially directed towards specific mates or phenotypes. I excluded

151   non-behavioural signals (e.g morphology or colouration), or cases where it was unclear

152   whether a signal had an exclusive sexual function (for example, male contest signals that are

153   also used by females to assess males).

154

155   Responsiveness can be defined broadly as the motivation to mate, or more strictly as the

156   average response to potential mates or sexual signals (Brooks & Endler, 2001; Edward,

157   2015). A highly responsive individual is one that shows the strongest behavioural response

158   across all presented mates or sexual stimuli. In other words, responsiveness is a measure of

159   the overall motivation to interact with potential mates or sexual stimuli, ignoring differences

160   between options. In this category I included any mating behaviour (with the exception of

161   sexual signalling, see above) summed or averaged across all options presented during a test.

162   When such behaviours could be shown to be directed towards any specific mate, or type of

163   mate, they were instead classed as choosiness (see supplementary methods for more

164   details).

165

166   Choosiness is a measure of the strength of mate choice, which I define following Reinhold &

167   Schielzeth (2015) as "the change in mating propensity in response to alternative stimuli". In

168 other words, the larger the difference in response to different stimuli, the choosier an

169 individual is. In this category I included any mating behaviour for which the *difference* in

170 response was compared between choice options. The greater the difference in response to

171 sexual stimuli, the choosier the focal individual. The choosiness category included any

172 behavioural measure that can be interpreted as reflecting the strength of a mating

173 preference. Preferences may be linked explicitly to a trait (either a specific stimulus or a

174 mate phenotype), but this was not required for inclusion.

175

176 I focused on seven environmental factors: population density, adult sex ratio, operational

177 sex ratio (OSR), predation risk, travel cost, time cost, and variation in mate quality (**Table 1**).

178 The three social factors (density of conspecifics, adult sex ratio and OSR of the population)

179 all provide information on the number of available mating opportunities (Kvarnemo &

180 Ahnesjo 1996; Kokko & Rankin 2006). The OSR is the ratio of reproductively active males to

181 females in a population (Kvarnemo & Ahnesjo 1996), and so is the most salient piece of

182 demographic information regarding current mating opportunities. In contrast, both the

183 population density and adult sex ratio are imperfect measures of reproductive competition,

184 but are much easier to assess. These three social factors also influence the amount of

185 intrasexual competition, which could influence the payoffs associated with different mating

186 tactics (Gross 1996; Weir *et al.* 2011). Finally, population density may also indirectly

187 influence individual predation risk (Krause & Ruxton 2002). The population density category

188 consisted of studies comparing mating behaviour at different population densities, while

189 controlling for the sex ratio perceived by subjects. In most cases, the sex ratio was equal

190 (1:1). Importantly, I did not include cases in which population density could influence the

191   amount of resources available to subjects, as this could potentially influence individual

192   condition (Cotton *et al.* 2006).

193

194

Table 1. Outline of the key ways in which the seven environmental factors included in the meta-analysis have the potential to influence the expression of mating behaviour.

Environmental factor	Environment potentially influences:			
	Mating opportunities	Cost of searching	Cost of signalling	Benefits of choice
Population density	✓	✓	✓	
Adult sex ratio	✓	✓	✓	
Operational sex ratio	✓	✓	✓	
Predation risk	✓	✓	✓	
Travel cost	✓	✓		
Time cost	✓	✓		
Variation in mate quality				✓

195

196

197   I included one factor related to the biological environment: predation risk. The risk of

198   predation could influence the cost of conspicuous signalling and of searching for and

199   sampling mates (Magnhagen 1991; Jennions & Petrie 1997; Zuk & Kolluru 1998). The level of

200   predation may also influence the expected number of future mating opportunities via its

201   effect on the density of conspecifics and average expected lifespan (Hubbell & Johnson

202   1987; Ah-King & Gowaty 2016). I considered studies which tested both direct and indirect

203   risk factors. Parasitoids can be considered ecologically similar to predators because they

204   lead to the death of the host, and so I also included studies examining the risk of parasitism

205   by parasitoids in this category (but not studies examining other forms of parasitism).

206

207   I also included two factors relating to the physical environment: travel cost and time cost.

208   The travel cost is the energetic cost (but not mortality cost) associated with movement,

209   which should influence the cost of searching for and sampling mates (Real 1990: Jennions &

210   Petrie 1997). The time cost is the amount of time remaining in the current breeding bout or

211   mating season (Sullivan 1994), which influences the number of future mating opportunities

212   for the current season (Jennions & Petrie 1997). There is also the potential for other aspects

213   of the environment to vary according to the season (such as population density or sex ratio),

214   and so I only included studies in this category if the time of year was not explicitly linked to

215   any other relevant environmental factors. I only included studies examining short-term time

216   costs, rather than long-term changes associated with animal age, as this time cost may be

217   confounded with other state-dependent effects when comparing individuals of different

218   ages (Cotton *et al.* 2006).

219

220   Lastly, variation in mate quality is the variation in mate phenotype experienced by the

221   chooser, which is assumed to reflect variation in the direct or indirect benefits that will be

222   received from mating with those individuals. Theory suggests that the benefits of being

223   choosy are higher when mates vary greatly in quality (Parker 1983; Real 1990). For the

224   variation in mate quality category, I excluded studies that did not control for the average

225   mate quality experienced by subjects. This category only applies to choosiness and

226   responsiveness.

227

228   There are other environmental factors that may influence mating behaviour in systematic

229   ways that I did not consider, because they do not influence the costs and benefits of

230   expressing mating behaviour. For example, differences in noise or light levels instead reduce

231   the ability of animals to *detect* or *discriminate between* signals (e.g. Seehausen *et al.* 1997;

232   Swaddle & Page 2007; Candolin 2019). Additionally, other environmental stressors such as

233   temperature could influence the costs and benefits of expressing mating behaviour

234   (Candolin 2019), but are also likely to influence individual state. For example, in high-stress

235   environments, individuals may have less energy reserves to spend on costly mating

236   behaviours (Coomes *et al.* 2019). I chose to exclude these types of stressors from the

237   analysis, as there is no way of determining whether any behavioural change is driven by a

238   context or state-dependent effect. I also excluded studies examining social-experience

239   effects that do not clearly influence the costs and benefits of choice, such as mate choices

240   influenced by the phenotypes of parents or opposite-sex individuals encountered during

241   development.

242

243   **PREDICTIONS**

244   I predicted that choosiness should be highest, and so individuals should mate least

245   randomly, when mating opportunities are common and the cost of sampling mates is low

246   (low costs of choice), and when there is large variation in mate quality (high benefits of

247   choice). Because of how I coded effect sizes (see Effect size extraction and coding), these

248   predictions will result in a positive average effect for choosiness for all environmental

249   factors (**Figure 2**). The predictions for sexual signalling and responsiveness are less clear,

250   because several processes could select for contrasting behavioural responses (**Table 1**). If

251   mate availability is most important for determining signalling and responsiveness, then

252   sexual signalling and responsiveness should be highest when mating opportunities are rare

253   and the cost of mate sampling is high, because in these situations each mating opportunity

254   is potentially more valuable. This type of response is analogous to the 'terminal investment'

255   observed in old or poor-condition individuals (Duffield et al. 2017). Alternatively, if signalling

256   and mate searching are moderately costly, then individuals could conserve energy by

257   reducing investment into these behaviours when the chances of securing a mate are low.

258   Further, because signalling and mate searching generally increase predation risk, the

259   expression of these behaviours may be greatest at a low predation risk (low cost of choice),

260   as with choosiness (Zuk & Kolluru 1998). Finally, plasticity in sexual signalling and

261   responsiveness could depend on the behaviour of chooser. If the more discriminating sex

262   becomes choosier when mate availability is high, then courters will need to invest more into

263   signalling and searching in these contexts in order to ensure a mating. Therefore, depending

264   on which processes are most important, the average effect size for sexual signalling and

265   responsiveness could be negative (if mate availability is most important) or positive (if

266   conserving available energy reserves or responding to choosers is most important) (**Figure**

267   **2**).

268

269   **EFFECT SIZE EXTRACTION AND CODING**

270   I used the correlation coefficient *r* as the measure of effect size. In this analysis, the effect

271   size represents the *difference* or *change* in a behaviour due to the environment. Larger

272   values therefore represent a greater difference in behaviour across contexts, and an effect

273   size of zero indicates no difference in behaviour across contexts. For all analyses, I used

274   Fisher's *Z* transform of the correlation coefficient (*Zr*), as r is constrained within ± 1 and so

275   does not adhere to a Gaussian distribution (Koricheva *et al.* 2013). The associated variance

276   for Zr (var Z) was calculated as 1/(n - 3) (Borenstein *et al.* 2009), with n being the total

277   number of animals used in the test.

278

279

Negative   Positive

Low mate availability   High mate availability
Low population density   High population density
Same-sex bias   Opposite-sex bias

High sampling costs   Low sampling costs
High predation risk   Low predation risk
High travel cost   Low travel cost
High time cost   Low time cost

Low benefits of choice   High benefits of choice
Low variation in mate quality   High variation in mate quality

-1   -0.5   0   0.5   1
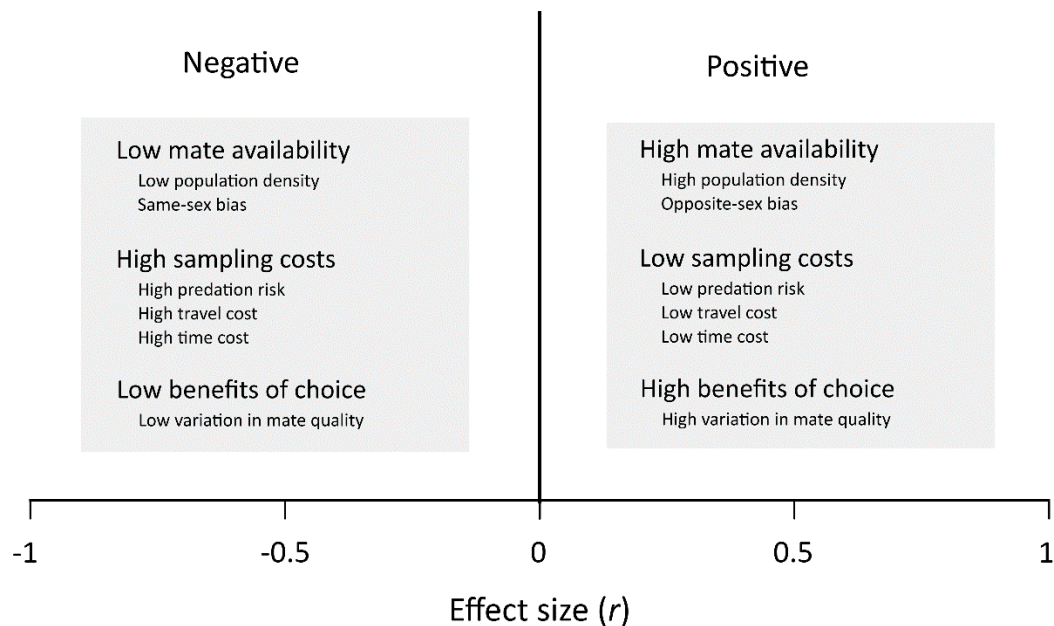
Effect size (r)

Figure 2. Diagram illustrating how differences in mating behaviour were assigned a positive or negative direction (in terms of the correlation coefficient r) in relation to environmental conditions. Positive effect sizes were assigned when mating behaviour was stronger under conditions of high mate availability, low costs of sampling mates and high benefits of mate choice. Negative effect sizes were assigned when mating behaviour was stronger under conditions of low mate availability, high costs of sampling mates and low benefits of mate choice. In all cases, 'high' and 'low' are relative terms, because environmental conditions were not standardised across studies.

280

281

282   I extracted all relevant effect sizes from each study. In many cases this resulted in multiple

283   effect sizes per study, because studies often report results from multiple experiments, or

284   compare several behaviours from the same experiment. The potential non-independence

285   arising from using multiple effect sizes per study is controlled for in the statistical analysis

286   (see Statistical Analyses). In many cases I obtained measurements for more than one

287 behavioural category from a single study (though I ran separate analyses for each category).

288 When statistical information was available, I obtained effect sizes directly, or using summary

289 data or the results of statistical tests, using a range of conversion equations (Lipsey & Wilson

290 2001; Koricheva *et al.* 2013). I used two approaches to obtain effect sizes when appropriate

291 statistics were missing. First, where possible I performed my own analyses using reported

292 summary statistics or raw data presented in the text, in tables and figures, or in available

293 supplementary results or data. I used the online tool WebPlotDigitizer v4 (Rohatgi 2019) to

294 extract raw data from scatter plots, and means and standard deviations from bar plots.

295 Second, I contacted authors directly and asked for either summary statistics or raw data. I

296 obtained data this way for 17 studies (Berglund 1994; Evans & Magurran 1999; Evans *et al.*

297 2002; Velez & Brockmann 2006; Wong & Svensson 2009; Young *et al.* 2009; Ziege *et al.*

298 2009; Lafaille *et al.* 2010; Makowicz *et al.* 2010; Willis *et al.* 2012; Pilakouta & Alonzo 2013;

299 Franklin *et al.* 2014; Wilgers *et al.* 2014; Breedveld & Fitze 2015; Pompilio *et al.* 2016; Filice

300 & Long 2017; Pilakouta *et al.* 2017). Information on methods for these calculations are

301 presented in **Table S2**.

302

303 The original direction of the extracted effect sizes is not meaningful, as it depends on the

304 type of data used (for example: association time is positively related to preference, whereas

305 approach latency is negatively related to preference), or which treatment is classed as the

306 control. I therefore manually assigned a direction to all effect sizes, in relation to the

307 environmental context under which behaviours were more strongly expressed. I assigned

308 directions based on the hypothesised costs of mate searching and mate choice (but not

309 sexual signalling). I assigned a positive direction to conditions in which the cost of expressing

310 mate searching and mate choice is expected to be low. This is associated with high mate

311   availability and low energetic or mortality costs of mate sampling. Conversely, I assigned a

312   negative direction to conditions in which the cost of mate searching and mate choice is

313   expected to be high, so that each mating encounter is more valuable. Therefore, the effect

314   size was assigned a positive direction when sexual signalling, responsiveness or choosiness

315   was highest when: the population density is high, the adult sex ratio or OSR is biased

316   towards the other sex, the predation risk is low, the travel and time costs are low, and there

317   is large variation in mate quality (**Figure 2**). Conversely, the effect size was assigned a

318   negative direction when sexual signalling, responsiveness or choosiness was highest when:

319   the population density is low, the adult sex ratio or OSR is biased towards the same sex, the

320   predation risk is high, the travel and time costs are high, and there is small variation in mate

321   quality (**Figure 2**). I note also that the terms 'high' and 'low' in this case are relative, because

322   the actual environmental conditions are not standardised across studies. So for example the

323   phrase 'high predation risk' is shorthand for 'the context in which predation risk in highest'.

324

325   In several cases, studies presented tests statistics that were non-significant, but provided no

326   descriptive or statistical information that allowed me to determine the direction of an effect

327   (for example, chi-squared statistics do not encode which cells have the highest frequencies).

328   These effect sizes would traditionally not be included in a meta-analysis in which effect size

329   direction is important. However, this systematically biases the dataset against non-

330   significant results (Harts *et al.* 2016), as such information is almost always available for

331   significant results. As a form of sensitivity analysis I assumed that these effect sizes were

332   equally likely to be weakly positive or negative, and assigned them a value of zero. I then ran

333   the analyses with and without including these directionless data points. This process

334   resulted in six separate datasets: a zeros included dataset and a zeros excluded dataset for

335   each behaviour category.

336

337   **PHYLOGENETIC TREES**

338   In order to control for the potential non-independence of effect sizes due to shared

339   evolutionary history (Hadfield & Nakagawa 2010; Koricheva *et al.* 2013) I created a

340   phylogeny of the species included in each of the six datasets. Given the broad range of

341   species included in each sample, no single published phylogeny was available that included

342   all species. I therefore constructed a phylogenetic supertree for each of the six datasets

343   using the Open Tree of Life (OTL) database (Hinchliff *et al.* 2015) and the rotl R package

344   (Michonneau *et al.* 2019). Given the absence of accurate branch length data for these trees,

345   all branch lengths were first set to one and then made ultrametric using Grafen's method

346   (Grafen 1989), using the R package ape v5.3 (Paradis *et al.* 2014). In cases where the OTL

347   database resulted in a polytomy, I manually searched for published phylogenies that could

348   resolve them (see supplementary methods for details). The final ultrametric trees for the

349   three full datasets (zeroes included) can be seen in the supplementary material (**Figures S1-**

350   **S3**).

351

352   **MODERATORS**

353   I tested for the effect of 10 categorical moderator variables (eight for each behaviour) on

354   the size or direction of context-dependent plasticity. For all three behaviours I examined the

355   effect of: environmental factor, focal sex, taxonomic class, environmental factor timing

356   (whether the environment was varied before or during behavioural trials), environmental

357   factor variation (whether the environmental varied naturally or experimentally), and animal

358   origin (whether subjects were lab-reared, wild-caught or wild). For sexual signalling I also

359   examined the effect of signalling modality (visual, acoustic, chemical, tactile, or mixed

360   signalling) and signalling type (close- or long-range signalling). For responsiveness and

361   choosiness I also examined the effect of preference measure (whether the study recorded

362   mating or a behavioural measure of mating preference) and stimuli type (whether subjects

363   were presented with conspecific signals only, or could choose between conspecific and

364   heterospecific signals). See the supplementary methods for details and predictions relating

365   to each moderator.

366

367   **STATISTICAL ANALYSES**

368   All statistical analyses were performed using R v3.6 (R development Core Team 2019). Meta-

369   analyses were performed using the package Metafor v2.1 (Viechtbauer 2010). In order to

370   determine the overall mean effect size for each dataset, I ran a multilevel random-effects

371   model using the rma.mv function, with study, species, and phylogeny as random factors

372   (Nakagawa & Santos 2012). Phylogeny was incorporated into the model using a variance-

373   covariance matrix, assuming that traits evolve via Brownian motion. The Fisher's Z

374   transformation was used as the effect size in all models, and model results were then

375   converted back to r for presentation. The mean effect size was considered to be significantly

376   different from zero if the 95% confidence intervals did not overlap zero. I ran these overall

377   models separately for each of the three behaviours. For each behaviour, I ran models with

378   and without the inclusion of directionless effect sizes.

379

380   I used I^2 as a measure of heterogeneity of effect sizes (Higgins *et al.* 2003). I^2 values of 25, 50

381   and 75% are considered low, moderate and high respectively (Higgins *et al.* 2003). I

382   calculated I^2 across all effect sizes, and also partitioned at different levels of the model using

383   the method of Nakagawa & Santos (2012). This allowed me to quantify the amount of

384   variation in effect size that could be attributed to differences in study, species, and

385   phylogenetic history.

386

387   I investigated potential moderators of the effect size using the full (zeroes included) dataset

388   for each behaviour. To test for the effect of moderators I ran meta-regression models, which

389   were identical to the above models except for the inclusion of categorical or continuous

390   fixed factors. For this I used two approaches. First, I ran a separate model for each fixed

391   effect. Second, I ran a full model including all fixed factors. I considered a moderator to

392   significantly influence the mean effect size by examining the Q_M statistic, which performs an

393   omnibus test of all model coefficients. For the full model, I specified which category levels to

394   compare using the anova function in R. For each behaviour I tested the effect of nine

395   moderators: eight categorical and one continuous (study year). I tested the effect of

396   different moderator variables depending on the behaviour examined. I used the method of

397   Nakagawa & Schielzeth (2013) to calculate marginal R^2 values for each fixed factor. In order

398   to estimate the average effect size for each level of a categorical factor I ran meta-

399   regressions including a single fixed factor, but excluding the model intercept. For sexual

400   signalling and responsiveness the number of effect sizes for some environmental factor

401   categories were small. Therefore, in order to check the sensitivity of the meta-regressions

402   testing the effect of environmental factor, I ran each of these tests first including all factors,

403   and second after removing any categories with 6 or less effect sizes (this does not apply to

404   the choosiness dataset).

405

406   Finally, I searched for signs of two types of publication bias using the full dataset for each

407   behaviour. I first searched for signs of time-lag bias, which arises when earlier published

408   studies have larger effect sizes than later published studies, which may indicate bias against

409   publishing studies of small effect in young research fields (Koricheva *et al.* 2013). To test for

410   any change in effect size over time, I ran a meta-regression with study year as a fixed effect.

411   Second, I searched for signs of publication bias against studies with small sample sizes or

412   non-significant results (Koricheva *et al.* 2013), by looking for funnel plot asymmetry using a

413   trim-and-fill test (Duval & Tweedie 2000) and Egger's regression (regression of *Zr* against

414   inverse standard error; Egger *et al.* 1997).

415

416   All data, R code, and supplementary materials are available at Dougherty (2020b).

417

418   ## Results

419

420   **SEXUAL SIGNALLING**

421   I obtained 260 effect sizes examining context-dependent sexual signalling, from 114 studies

422   and 68 species. I obtained data from seven taxonomic groups, though the majority of

423   studies focused on insects and fish (**Figure 3a**). Male signalling was much more common

424   than female signalling (males: k= 230; females: k= 24; no sex specified: k= 6).

425

426   Overall, sexual signalling behaviour did not consistently differ across contexts, either using

427   the full dataset (k= 260, mean= 0.07, 95% CI= -0.11- 0.24; **Figure 3b**) or the reduced dataset

428   (k= 209, mean= 0.095, 95% CI= -0.12- 0.18). The full dataset shows very high heterogeneity

429   across effect sizes (Total I^2= 93.4%), with 36.4% being attributable to between-study

430   differences, <1% to between-species differences, 11.24% to phylogenetic history, and 45.8%

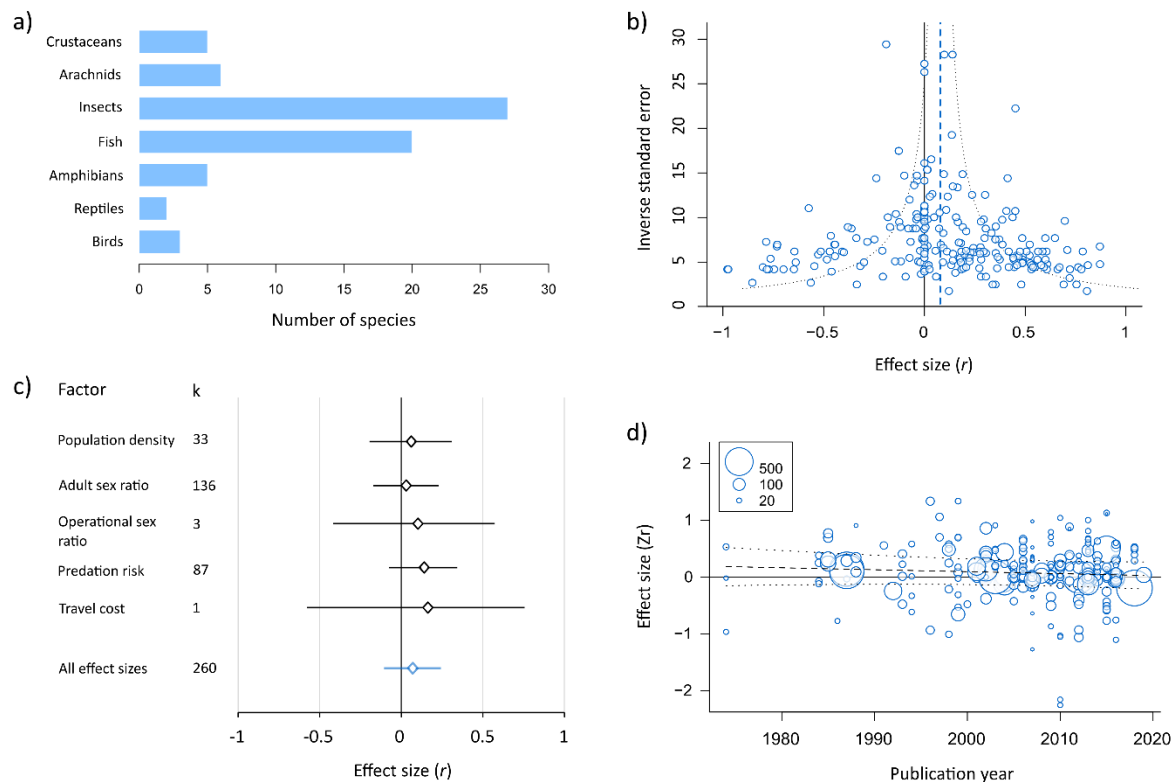431   to residual variance.

432

433

Figure 3. Summary results for context-dependent sexual signalling. a) Histogram showing the number of species included in relation to taxonomic grouping. b) Funnel plot showing the relationship between effect size (r) and sample size (inverse standard error). The dotted line shows the mean effect size for the full model. c) Forest plot showing the average effect size for each environmental factor separately. In all cases diamonds represent the mean effect size estimate, and the bars represent the 95% confidence interval. The mean effect size obtained from the full model, across all effect sizes, is shown in blue for comparison. k is the number of effect sizes in each category. d) Bubble plot showing the relationship between effect size (Zr) and publication year. The points are scaled by the sample size of each estimate. The broken line shows the predicted regression line from a meta-regression, and the dotted lines are the 95% confidence intervals.

434

435

436   The strength or direction of the signalling response did not differ for the five environmental

437   factors tested (**Table 2**; **Figure 3c**): for all environmental factors signalling was greatest

438   when the cost of choice was low (positive effect size), however the mean effect size did not

439   differ from zero for any environmental factor individually. This result remained after

440   removing the two environmental factors with 6 effect sizes or fewer (OSR and travel cost,

441    $Q_{M\ 2}$= 2.33, P= 0.31, k= 256). The average signalling response did not differ according to any

442   of the other moderators tested, including taxonomic class or focal sex, either when factors

443   were tested separately (**Table 2; Table S4**), or all factors were tested in a single model

444   (**Table S3**). The total variance explained by the fixed factors (marginal R^2) in the multiple

445   meta-regression model was 0.07.

446

447   Significant funnel plot asymmetry was detected for sexual signalling, with 24 'missing'

448   negative effect sizes (**Figure S4**). The overall mean was still not significantly different from

449   zero after included these missing effect sizes (k= 284, mean= 0.03, 95% CI= -0.02- 0.07). A

450   regression test did not detect any significant relationship between effect size and study

451   variance for sexual signalling ($F_{1,\ 258}$ = 0.41, P= 0.52; **Figure S5**).

452

453   **RESPONSIVENESS**

454   I obtained 176 effect sizes examining context-dependent differences in responsiveness,

455   from 86 studies and 53 species. I obtained data from eight taxonomic groups, though the

456   majority of studies focused on insects and fish (**Figure 4a**). I obtained an approximately

457   equal number of responsiveness effect sizes from both sexes (males: k= 78; females: k= 80;

458   no sex specified: k= 18).

459

Table 2. Meta-regression results for all three behaviours. Significance was determined using a Q_M test for both categorical and continuous fixed effects. Marginal R^2 is the amount of variance explained by each fixed factor. Each factor was tested using a separate mixed-effects model, with a single fixed factor and four random factors (Study ID, species, phylogeny and observation ID). Significant factors are highlighted in grey.

Fixed effect	Signalling			Responsiveness			Choosiness		
	Q_M	P	R^2	Q_M	P	R^2	Q_M	P	R^2
Environmental factor	2.44	0.66	0.014	9.50	0.09	0.09	8.89	0.18	0.04
Focal sex	1.08	0.58	0.005	0.85	0.65	0.01	5.40	0.07	0.02
Taxonomic class	2.19	0.9	0.036	2.44	0.93	0.02	3.33	0.85	0.04
Factor timing (Before vs during test)	2.78	0.25	0.02	3.48	0.18	0.04	0.39	0.82	<0.001
Factor variation (Manipulated vs natural)	1.09	0.3	0.005	0.01	0.93	<0.001	0.01	0.93	<0.001
Animal origin (Wild vs lab-reared)	0.42	0.81	0.004	3.64	0.16	0.04	1.81	0.61	0.02
Signalling modality	2.74	0.6	0.022	-	-	-	-	-	-
Signalling type (Short vs long range)	0.04	0.84	<0.001	-	-	-	-	-	-
Preference measure (Matings vs proxy)	-	-	-	0.20	0.66	<0.001	0.14	0.70	0.01
Stimuli type (Mate-quality vs species recognition)	-	-	-	0.07	0.79	0.03	1.37	0.24	0.01
Study year	0.78	0.38	0.005	0.001	0.98	<0.001	8.78	0.003	0.08

460

461

462   Overall responsiveness did not consistently differ across contexts, either using the full

463   dataset (k= 176, mean= -0.003, 95% CI= -0.082- 0.08; **Figure 4b**) or the reduced dataset (k=

464   146, mean= -0.001, 95% CI= -0.1- 0.1). The full dataset shows very high heterogeneity across

465   effect sizes (Total I^2= 91.6%), with 67.5% being attributable to between-study differences,

466   <1% to between-species differences or phylogenetic history, and 24.1% to residual variance.
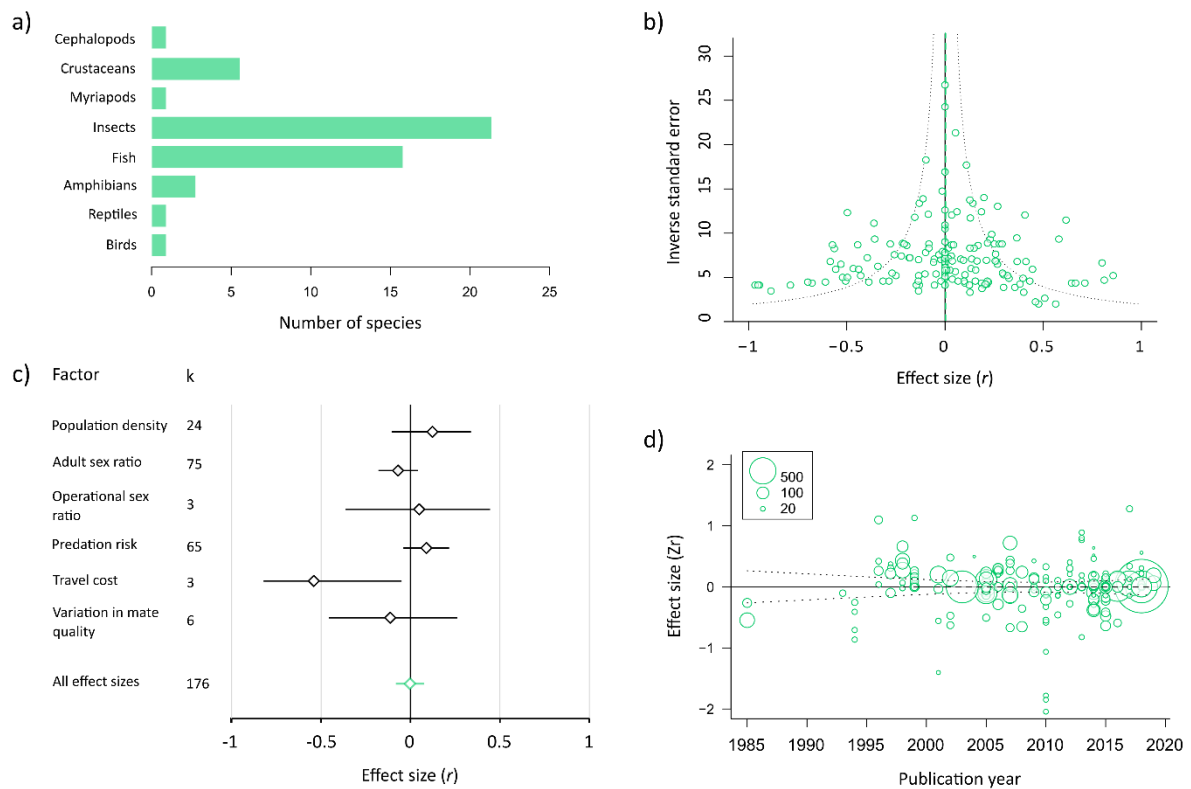
467

468

Figure 4. Summary results for context-dependent responsiveness. a) Histogram showing the number of species included in relation to taxonomic grouping. b) Funnel plot showing the relationship between effect size (r) and sample size (inverse standard error). The dotted line shows the mean effect size for the full model. c) Forest plot showing the average effect size for each environmental factor separately. In all cases diamonds represent the mean effect size estimate, and the bars represent the 95% confidence interval. The mean effect size obtained from the full model, across all effect sizes, is shown in green for comparison. k is the number of effect sizes in each category. d) Bubble plot showing the relationship between effect size (Zr) and publication year. The points are scaled by the sample size of each estimate. The broken line shows the predicted regression line from a meta-regression, and the dotted lines are the 95% confidence intervals.

469

470

471   The difference in responsiveness was not significantly influenced by environmental factor

472   (**Table 2**). There was a tendency for a positive effect size for predation risk, population

473   density and OSR and a negative effect size for adult sex ratio, travel cost and variation in

474   quality (**Figure 4c**). However, only one of the factors, travel cost, resulted in an average

475   estimate that differed significantly from zero. The non-significant effect of environmental

476   factor remained after removing the three environmental factors with 6 effect sizes or fewer

477   (OSR, travel cost and variation in mate quality, $Q_{M\ 2}$= 4.51, P= 0.11, k= 164). The average

478   difference in responsiveness was not significantly influenced by any of the other moderators

479   tested, either when factors were tested separately (**Table 2; Table S5**), or all factors were

480   tested in a single model (**Table S3**). The total variance explained by the fixed factors

481   (marginal R^2) in the multiple meta-regression model was 0.17.

482

483   Significant funnel plot asymmetry was detected for responsiveness, with 28 'missing'

484   negative effect sizes (**Figure S4**). Inclusion of these effect sizes resulted in a significantly

485   negative effect size for responsiveness (k= 204, mean= -0.07, 95% CI= -0.12 -0.02). A

486   regression test did not detect any significant relationship between effect size and study

487   variance for responsiveness ($F_{1,\ 174}$= 0.19, P= 0.67; **Figure S5**).

488

489   **CHOOSINESS**

490   I obtained 261 effect sizes examining context-dependent differences in choosiness, from

491   105 studies and 61 species. I obtained data from eight taxonomic groups, though the

492   majority of studies focused on insects and fish (**Figure 5a**). Female choice is more common

493   than male choice in the choosiness dataset (female choice: k= 159; male choice: k= 96; no

494   sex specified: k= 6).

495

496   Overall, choosiness was significantly higher when the costs of mate choice were low (k= 261,

497   mean= 0.098, 95% CI= 0.043- 0.16; **Figure 5b**). This result was the same after removing the

498   65 directionless effect sizes (k= 196, mean= 0.12, 95% CI= 0.05- 0.19). However, the overall

499   effect size is small (Cohen 1992). The full dataset shows very high heterogeneity (Total I^2=

500   81.2%), with 40.9% being attributable to between-study differences, 17.9% to between-

501   species differences, <1% to phylogenetic history, and 22.4% to residual variance.
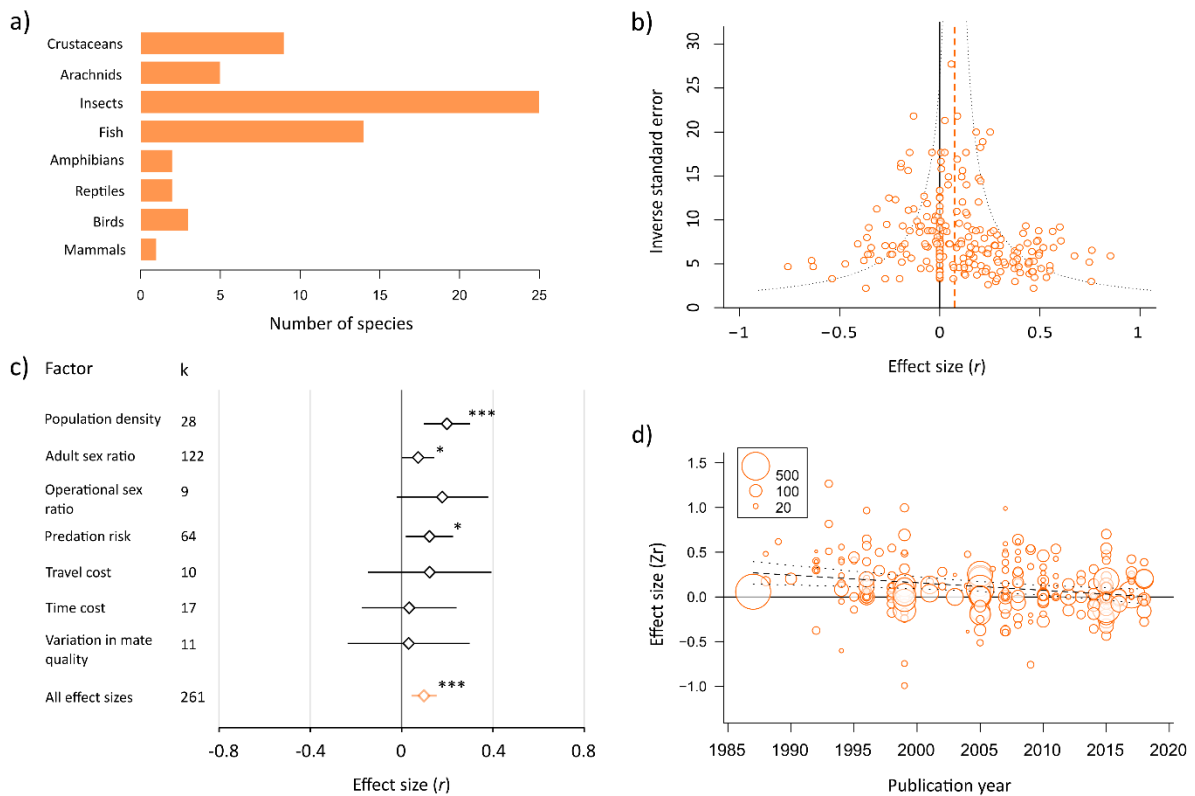
502

503

Figure 5. Summary results for context-dependent choosiness. a) Histogram showing the number of species included in relation to taxonomic grouping. b) Funnel plot showing the relationship between effect size (r) and sample size (inverse standard error). The dotted line shows the mean effect size for the full model. c) Forest plot showing the average effect size for each environmental factor separately. In all cases diamonds represent the mean effect size estimate, and the bars represent the 95% confidence interval. The mean effect size obtained from the full model, across all effect sizes, is shown in orange for comparison. k is the number of effect sizes in each category. Estimates that differ significantly from zero are marked with asterisks (*, P< 0.05; **, P< 0.01; ***, P < 0.001). Bubble plot showing the relationship between effect size (Zr) and publication year. The points are scaled by the sample size of each estimate. The broken line shows the predicted regression line from a meta-regression, and the dotted lines are the 95% confidence intervals.

504

505

506   The difference in choosiness across contexts was not significantly affected by environmental

507   factor (**Table 2**); the average estimate was positive for all factors, but significantly differed

508   from zero for predation risk, population density, and adult sex ratio (**Figure 5c**). The average

509   estimates for operational sex ratio, travel cost, time cost and variation in mate quality did

510   not differ significantly from zero, however all four categories consisted of a small number of

511   effect sizes (k <20), so this lack of an effect should be interpreted with caution. The average

512   choosiness response was not significantly influenced by any of the other categorical

513   moderators tested, either when factors were tested separately (**Table 2; Table S6**), or all

514   factors were in a single model (**Table S3**). However, the average choosiness response

515   decreased significantly over time (**Table 2**; **Figure 5d**). The total variance explained by the

516   fixed factors (marginal R^2) in the multiple meta-regression model was 0.15.

517

518   A trim-and-fill test did not detect any 'missing' effect sizes for choosiness. However, a

519   regression test revealed a significant negative relationship between effect size and inverse

520   standard error ($F_{1, 259}$= 4.87, P= 0.028; **Figure S5**). This latter effect seems to be driven by a

521   lack of negative effect sizes of low power, which is suggestive of publication bias.

522

523   ## Discussion

524

525   Investment in mating behaviour is often costly, and the fitness payoffs of this investment

526   can vary across contexts. Therefore, animals are expected to alter their mating behaviour

527   depending on the current context, in order to minimise the amount of investment needed

528   to secure matings, and maximise fitness outcomes. By synthesising the results of 222 studies

529   and 697 effect sizes examining animal mating behaviour across multiple contexts, I found

530   that choosiness (the strength of mate choice) differed significantly across environments.

531   Choosiness was significantly stronger in contexts where the cost of mate choice is low, such

532   as when mating opportunities are frequent and the perceived risk of predation is low.

533   However, the average effect of each factor alone was much weaker than expected, and

534   there was some evidence for a decrease in effect size over time. Neither sexual signalling

535   nor responsiveness differed across contexts in a consistent way, either across the whole

536   dataset or when each environmental factor was considered individually. Taken together,

537   these results suggest that the expression of mate choice is more context-dependent than

538   either sexual signalling or responsiveness, but that overall the evidence for context-

539   dependent mating behaviour across animals is currently surprisingly weak. The common

540   assumption that animal mating behaviour shows context-dependent expression may need

541   to be reassessed in light of these findings.

542

543   Why might mate choice be more consistently sensitive to the environment than sexual

544   signalling or responsiveness? One explanation is that the environmental factors examined

545   here are predicted to influence choosiness in the same way: when conditions become

546   unfavourable, choosiness should decrease. In contrast, there may be conflicting selection

547   pressures acting on signalling and responsiveness which cause the direction of plasticity to

548   differ across species or contexts. For example, when mate availability is low, the potential

549   value of each mate encounter is higher, but the cost of searching and signalling is also

550   higher. Here other factors, such as the severity of the environment or the age of the

551   individuals (Duffield et al. 2017), may be most important in determining whether individuals

552   increase or decrease expression of mate searching and signalling. An alternative explanation

553 relates to the relative importance of each behaviour for reproductive fitness. While

554 choosing the right partner can often provide strong fitness benefits to choosers (Andersson

555 1994; Kokko *et al.* 2003), even a total lack of choosiness still leads to mating, just with a

556 random partner. However, reduced signalling or mate searching may often lead to a

557 complete failure to mate, resulting in a fitness of zero. In many contexts gaining any mate,

558 which may require investment in mate searching and/or sexual signalling, may be more

559 important than gaining a *high-quality* mate. One consequence of this could be high

560 investment in sexual signalling and mate searching under most conditions, which will result

561 in reduced context-dependence.

562

563 All three datasets were characterised by very high heterogeneity in both the strength and

564 direction of the effect size. Sexual signalling and responsiveness in particular showed an

565 approximately equal number of positive and negative effect sizes. Partitioning of the model

566 variances suggested that little heterogeneity could be explained by species differences or

567 phylogenetic relatedness. I therefore tested whether a range of biological and

568 methodological moderating factors could explain this variation. Importantly, environmental

569 factor, sex or taxonomic group did not significantly explain the variation in any behaviour

570 (while choosiness was significantly context-dependent, this effect did not differ according to

571 which environmental factor was examined). In fact, for sexual signalling and responsiveness,

572 the mean effect size for each environmental factor considered alone did not differ

573 significantly from zero. Choosiness was highest when the costs of choice were lower for all

574 of the seven factors tested, though the mean effect size was significantly different from zero

575 only for population density, adult sex ratio, and predation risk. However, the lack of a

576 significant effect for travel cost, time cost and variation in mate quality are likely driven by

577   the small sample sizes for these groups, and so any conclusions relating to these factors

578   should be interpreted with caution. Interestingly, choosiness was more sensitive to

579   differences in population density than to differences in sex ratio, even though the latter is a

580   more accurate measure of the number of available mating opportunities. Individuals may be

581   more likely to respond to changes in overall population density if it is easier to assess

582   accurately. Alternatively, this effect could be driven by the fact that population density

583   tends to vary more than sex ratio in an absolute sense in this sample. Across all studies

584   included in the three datasets that measured or manipulated population density (N= 22),

585   the median number of conspecifics was 4 (±6.8) at low density and 20.5 (±56.3) at high

586   density. Assuming a 1:1 sex ratio, this corresponds to 2 and 10 'available' mates in these

587   studies. In comparison, for studies that measured or manipulated sex ratio across all three

588   datasets (N= 98), the median number of mates per focal individual is 0.5 (±1.4) at low mate

589   availability and 2 (±8.3) at high mate availability.

590

591   Importantly, the majority of heterogeneity in all three datasets remained unexplained after

592   testing the effects of ten moderating factors (the total amount of variance explained by all

593   fixed factors was 0.17 or less). It is unclear whether such heterogeneity represents real,

594   biological variation or stems from some other source. Some of this variation could be

595   explained by methodological limitations. For example, the effect size used here is only able

596   to detect linear effects. This means that significant quadratic effects, such as peak signalling

597   at intermediate densities (Kokko & Rankin 2006), will not be captured here. Alternatively,

598   the large variation observed may be the result of methodological differences between

599   studies that have not been accounted for (Dougherty & Shuker 2015; Rosenthal 2017;

600   Dougherty 2020a). For example, studies typically assume animals can accurately assess the

601 costs of expressing a behaviour in a given environment, but this may not always be the case.

602 Therefore, differences in the extent to which studies successfully manipulate these

603 perceived costs may lead to significant variation in context-dependent behavioural

604 responses. Experimental studies may also often use subjects that are especially eager to

605 mate, for example because they are virgin or have been isolated from members of the

606 opposite sex, and such individuals are predicted to show lower levels of context-dependent

607 behaviour than experienced individuals (Ah-King & Gowaty 2016; Kelly 2018). Finally, the

608 observed heterogeneity may stem from biological differences that are difficult assess for all

609 of the species sampled, for example in relation to mating system, life-history or the

610 energetic costs of signalling. Importantly, one key factor that is currently unaccounted for is

611 the cost of expressing mating behaviour in a given environment: plasticity should be largest

612 where behaviours are compared across environments that differ greatly in the costs and

613 benefits of expression. This is important, because the included studies differ in terms of the

614 range of environmental conditions subjects are tested in. Because these environmental

615 differences are not standardised, studies will differ also in the range of any environment-

616 induced costs. Unfortunately, we simply do not have accurate data on what these costs are,

617 even for a small number of behaviours or contexts. This is likely to be the case for some

618 time, given the difficulty in measuring fitness in ecologically relevant contexts. However,

619 without this data we also cannot rule out the possibility that experiments simply do not

620 present subjects with a sufficiently variable range of contexts to detect adaptive context-

621 dependent behaviour.

622

623 In conclusion, this study suggests that the evidence that animal mating behaviour varies in a

624 consistent way across different environments is currently quite limited. Across species,

625   sexual signalling and responsiveness do not appear to consistently respond to any of the

626   environmental differences tested. Choosiness did show consistent, significant differences in

627   relation to predation risk, population density and adult sex ratio, but the effect sizes are

628   generally weaker than expected. This is despite plenty of good empirical examples of

629   context-dependent mating behaviour as predicted by sexual selection theory, and narrative

630   reviews consisting almost entirely of affirmatory examples (e.g. Ah-King & Gowaty 2016;

631   Kelly 2018). Importantly, the datasets for all three behaviours were characterised by very

632   high heterogeneity in effect size which remains mostly unexplained. It therefore remains

633   unclear whether environmental variability is a less important driver of behavioural plasticity

634   than predicted, or whether the lack of a strong effect is due to unaccounted biological or

635   ecological variability across species. The best way to try to tease apart these alternatives in

636   the future will be to perform careful, well-designed studies. This work is needed if we are to

637   understand the expression of animal mating behaviour, and evolutionary forces driven by

638   mate choice and intrasexual competition, in complex and rapidly-changing natural

639   environments. Further, human-induced changes in the natural environment have the

640   potential to influence most of the factors considered here (e.g. population density, predator

641   density, travel cost, time cost). Therefore, understanding how mating behaviour and

642   population fitness respond to these increasingly challenging natural conditions will help us

643   to predict whether natural populations will be able to adapt and persist in the wild.

Acknowledgements

Competing interests

I declare no competing interests.

References

Ah-King, M. & Gowaty, P.A. (2016). A conceptual review of mate choice: stochastic demography, within-sex phenotypic plasticity, and individual flexibility. *Ecology and Evolution*, 6, 4607-4642.

Andersson, M.B. (1994). *Sexual selection*. Princeton University Press, Princeton.

Barry, K.L. & Kokko, H. (2010). Male mate choice: why sequential choice can make its evolution difficult. *Animal Behaviour*, 80, 163-169.

Beckers, O.M. & Wagner, W.E. (2018). Males and females evolve riskier traits in populations with eavesdropping parasitoids. *Behavioral Ecology and Sociobiology*, 72, 174.

Berglund, A. (1994). The operational sex ratio influences choosiness in a pipefish. *Behavioral Ecology*, 5, 254-258.

Billing, A.M., Rosenqvist, G. & Berglund, A. (2007). No terminal investment in pipefish males: only young males exhibit risk-prone courtship behavior. *Behavioral Ecology*, 18, 535-540.

Borenstein, M., Hedges, L.V., Higgins, J.P. & Rothstein, H. (2009). *Introduction to meta-analysis*. John Wiley, Chichester, UK.

Breedveld, M.C. & Fitze, P.S. (2015). A matter of time: delayed mate encounter postpones mating window initiation and reduces the strength of female choosiness. *Behavioral Ecology and Sociobiology*, 69, 533-541.

Briggs, S.E., Godin, J.G.J. & Dugatkin, L.A. (1996). Mate-choice copying under predation risk in the Trinidadian guppy (*Poecilia reticulata*). *Behavioral Ecology*, 7, 151-157.

Brooks, R. & Endler, J.A. (2001). Female guppies agree to differ: phenotypic and genetic variation in mate-choice behavior and the consequences for sexual selection. *Evolution*, 55, 1644-1655.

Candolin, U. (2019). Mate choice in a changing world. *Biological Reviews*, 94, 1246-1260.

Cohen, J. (1992). A power primer. *Psychological Bulletin*, 112, 155.

Coomes, C.M., Danner, R.M. & Derryberry, E.P. (2019). Elevated temperatures reduce discrimination between conspecific and heterospecific sexual signals. *Animal Behaviour*, 147, 9-15.

Cotton, S., Small, J. & Pomiankowski, A. (2006). Sexual selection and condition-dependent mate preferences. *Current Biology*, 16, R755-R765.

Dougherty, L.R. (2020a). Designing mate choice experiments. *Biological Reviews*, 95, 759-781.

[dataset] Dougherty, L.R. (2020b). Supplementary material for "Meta-analysis shows the evidence for context-dependent mating behaviour is inconsistent or weak across animals". Figshare. https://doi.org/10.6084/m9.figshare.12957422

Dougherty, L.R. & Shuker, D.M. (2015). The effect of experimental design on the measurement of mate choice: a meta-analysis. *Behavioral Ecology*, 26, 311-319.

Duffield, K.R., Bowers, E.K., Sakaluk, S.K. & Sadd, B.M. (2017). A dynamic threshold model for terminal investment. *Behavioral ecology and sociobiology*, 71, 185.

Duval, S. & Tweedie, R. (2000). Trim and fill: a simple funnel-plot–based method of testing and adjusting for publication bias in meta-analysis. *Biometrics*, 56, 455-463.

Edward, D.A. (2015). The description of mate choice. *Behavioral Ecology*, 26, 301-310.

Egger, M., Smith, G.D., Schneider, M. & Minder, C. (1997). Bias in meta-analysis detected by a simple, graphical test. *Bmj*, 315, 629-634.

Endler, J.A. (1987). Predation, light intensity and courtship behaviour in *Poecilia reticulata* (Pisces: Poeciliidae). *Animal Behaviour*, 35, 1376-1385.

Evans, J.P., Kelley, J.L., Ramnarine, I.W. & Pilastro, A. (2002). Female behaviour mediates male courtship under predation risk in the guppy (*Poecilia reticulata*). *Behavioral Ecology and Sociobiology*, 52, 496-502.

Evans, J.P. & Magurran, A.E. (1999). Male mating behaviour and sperm production characteristics under varying sperm competition risk in guppies. *Animal Behaviour*, 58, 1001-1006.

Filice, D.C. & Long, T.A. (2017). Phenotypic plasticity in female mate choice behavior is mediated by an interaction of direct and indirect genetic effects in *Drosophila melanogaster*. *Ecology and Evolution*, 7, 3542-3551.

Franklin, A.M., Squires, Z.E. & Stuart-Fox, D. (2014). Does predation risk affect mating behavior? An experimental test in dumpling squid (*Euprymna tasmanica*). *PloS One*, 9, e115027.

Fuller, R. & Berglund, A. (1996). Behavioral responses of a sex-role reversed pipefish to a gradient of perceived predation risk. *Behavioral Ecology*, 7, 69-75.

Gong, A. & Gibson, R.M. (1996). Reversal of a female preference after visual exposure to a predator in the guppy, *Poecilia reticulata*. *Animal Behaviour*, 52, 1007-1015.

Grafen, A. (1989). The phylogenetic regression. *Philosophical Transactions of the Royal Society of London. B, Biological Sciences*, 326, 119-157.

Greenway, E.V.G., Dougherty, L.R. & Shuker, D.M. (2015). Mating failure. *Current Biology*, 25, R534-R536.

Gross, M.R. (1996). Alternative reproductive strategies and tactics: diversity within sexes. *Trends in Ecology & Evolution*, 11, 92-98.

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

Harts, A.M., Booksmythe, I. & Jennions, M.D. (2016). Mate guarding and frequent copulation in birds: A meta-analysis of their relationship to paternity and male phenotype. *Evolution*, 70, 2789-2808.

Hedrick, A.V. & Dill, L.M. (1993). Mate choice by female crickets is influenced by predation risk. *Animal Behaviour*, 46, 193-196.

Higgins, J., Thompson, S.G., Deeks, J.J. & Altman, D.G. (2003). Measuring inconsistency in meta-analyses. *British Medical Journal*, 327, 557-560.

Hinchliff, C.E., Smith, S.A., Allman, J.F., Burleigh, J.G., Chaudhary, R., Coghill, L.M., Crandall, K.A., Deng, J., Drew, B.T. & Gazis, R. (2015). Synthesis of phylogeny and taxonomy into a comprehensive tree of life. *Proceedings of the National Academy of Sciences*, 112, 12764-12769.

Hubbell, S.P. & Johnson, L.K. (1987). Environmental variance in lifetime mating success, mate choice, and sexual selection. *The American Naturalist*, 130, 91-112.

Hughes, N.K., Kelley, J.L. & Banks, P.B. (2012). Dangerous liaisons: the predation risks of receiving social signals. *Ecology letters*, 15, 1326-1339.

Jennions, M.D. & Petrie, M. (1997). Variation in mate choice and mating preferences: a review of causes and consequences. *Biological Reviews*, 72, 283-327.

Kelly, C.D. (2018). The causes and evolutionary consequences of variation in female mate choice in insects: the effects of individual state, genotypes and environments. *Current Opinion in Insect Science*, 27, 1-8.

Kokko, H., Brooks, R., Jennions, M.D. & Morley, J. (2003). The evolution of mate choice and mating biases. *Proceedings of the Royal Society B: Biological Sciences*, 270, 653-664.

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

Koricheva, J., Gurevitch, J. & Mengeresen, K. (2013). *Handbook of meta-analysis in ecology and evolution*. Princeton University Press, Princeton.

Kotiaho, J.S. (2001). Costs of sexual traits: a mismatch between theoretical considerations and empirical evidence. *Biological Reviews*, 76, 365-376.

Krause, J., & Ruxton, G.D. (2002). *Living in groups*. Oxford University Press, Oxford.

Kvarnemo, C. & Ahnesjo, I. (1996). The dynamics of operational sex ratios and competition for mates. *Trends in Ecology & Evolution*, 11, 404-408.

Lafaille, M., Bimbard, G. & Greenfield, M.D. (2010). Risk trading in mating behavior: forgoing anti-predator responses reduces the likelihood of missing terminal mating opportunities. *Behavioral Ecology and Sociobiology*, 64, 1485-1494.

Lipsey, M. & Wilson, D. (2001). *Practical meta-analysis*. Sage Publications, London.

Magnhagen, C. (1991). Predation risk as a cost of reproduction. *Trends in Ecology & Evolution*, 6, 183-186.

Makowicz, A.M., Plath, M. & Schlupp, I. (2010). Male guppies (*Poecilia reticulata*) adjust their mate choice behaviour to the presence of an audience. *Behaviour*, 147, 1657-1674.

Michonneau, F., Brown, J.W. & Winter, D.J. (2016). rotl: an R package to interact with the Open Tree of Life data. *Methods in Ecology and Evolution*, 7, 1476-1481.

Miller, C.W. & Svensson, E.I. (2014). Sexual selection in complex environments. *Annual Review of Entomology*, 59, 427-445.

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

Nakagawa, S., & Schielzeth, H. (2013) A general and simple method for obtaining R2 from generalized linear mixed-effects models. *Methods in Ecology and Evolution*, 4, 133-142.

Ouzzani, M., Hammady, H., Fedorowicz, Z. & Elmagarmid, A. (2016). Rayyan—a web and mobile app for systematic reviews. *Systematic reviews*, 5.

Paradis, E., Claude, J. & Strimmer, K. (2004). APE: analyses of phylogenetics and evolution in R language. *Bioinformatics*, 20, 289-290.

Parker, G.A. (1983). Mate quality and mating decisions. In: *Mate choice* (ed. Bateson, P).

Cambridge University Press, Cambridge, pp. 141-166.

Pilakouta, N. & Alonzo, S.H. (2013). Predator exposure leads to a short-term reversal in

female mate preferences in the green swordtail, *Xiphophorus helleri*. *Behavioral*

Ecology, 25, 306-312.

Pilakouta, N., Correa, M.A. & Alonzo, S.H. (2017). Predation risk reduces a female preference

for heterospecific males in the green swordtail. *Ethology*, 123, 95-104.

Pompilio, L., Franco, M.G., Chisari, L.B. & Manrique, G. (2016). Female choosiness and

mating opportunities in the blood-sucking bug *Rhodnius prolixus*. *Behaviour*, 153,

1863-1878.

Real, L. (1990). Search theory and mate choice. I. Models of single-sex discrimination. *The*

American Naturalist, 136, 376-405.

Reinhold, K. & Schielzeth, H. (2015). Choosiness, a neglected aspect of preference functions:

a review of methods, challenges and statistical approaches. *Journal of Comparative*

Physiology A, 201, 171-182.

Rohatgi, A. (2019). WebPlotDigitizer. 4rd edn. Available at: Retrieved from:

https://apps.automeris.io/wpd/.

Rosenthal, G.G. (2017). *Mate choice*. Princeton University Press, Princeton.

Seehausen, O., Van Alphen, J.J. & Witte, F. (1997). Cichlid fish diversity threatened by

eutrophication that curbs sexual selection. *Science*, 277, 1808-1811.

Sullivan, M.S. (1994). Mate choice as an information gathering process under time

constraint: implications for behaviour and signal design. *Animal Behaviour*, 47, 141-

151.

Swaddle, J.P. & Page, L.C. (2007). High levels of environmental noise erode pair preferences in zebra finches: implications for noise pollution. *Animal Behaviour*, 74, 363-368.

R Development Core Team (2019). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna.

Vélez, M.J. & Jane Brockmann, H. (2006). Seasonal variation in female response to male calling song in the field cricket, *Gryllus rubens*. *Ethology*, 112, 1041-1049.

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

Vitousek, M.N., Mitchell, M.A., Woakes, A.J., Niemack, M.D. & Wikelski, M. (2007). High costs of female choice in a lekking lizard. *PLoS One*, 2, e567.

Weir, L.K., Grant, J.W.A. & Hutchings, J.A. (2011). The Influence of operational sex ratio on the intensity of competition for mates. *The American Naturalist*, 177, 167-176.

Wilgers, D.J., Wickwire, D. & Hebets, E.A. (2014). Detection of predator cues alters mating tactics in male wolf spiders. *Behaviour*, 151, 573-590.

Willis, P.M., Rosenthal, G.G. & Ryan, M.J. (2012). An indirect cue of predation risk counteracts female preference for conspecifics in a naturally hybridizing fish *Xiphophorus birchmanni*. *PloS one*, 7, e34802.

Wong, B.B. & Svensson, P.A. (2009). Strategic male signalling effort in a desert-dwelling fish. *Behavioral Ecology and Sociobiology*, 63, 543-549.

Young, K.A., Genner, M.J., Joyce, D.A. & Haesler, M.P. (2009). Hotshots, hot spots, and female preference: exploring lek formation models with a bower-building cichlid fish. *Behavioral Ecology*, 20, 609-615.

Ziege, M., Mahlow, K., Hennige-Schulz, C., Kronmarck, C., Tiedemann, R., Streit, B. & Plath, M. (2009). Audience effects in the Atlantic molly (*Poecilia mexicana*)–prudent male

mate choice in response to perceived sperm competition risk? *Frontiers in Zoology*, 6, 17.

Zuk, M. & Kolluru, G.R. (1998). Exploitation of sexual signals by predators and parasitoids. *The Quarterly Review of Biology*, 73, 415-438.