Phil. Trans. R. Soc. B. article template

PHILOSOPHICAL TRANSACTIONS B

Phil. Trans. R. Soc. B. doi:10.1098/not yet assigned

Mate choice in a polluted world: consequences for individuals, populations and communities

Ulrika Candolin¹ and Bob B. M. Wong²

¹Organsimal and Evolutionary Biology, University of Helsinki, Finland orcid.org/0000-0001-8736-7793 ²School of Biological Sciences, Monash University, Melbourne, Australia orcid.org/0000-0001-9352-6500

Keywords: environmental change, communication, courtship, mate preferences, sexual selection, signals

1

1 Pollution (e.g. by chemicals, noise, light, heat) is an insidious consequence of anthropogenic activity 2 that affects environments worldwide. Exposure of wildlife to pollutants has the capacity to adversely 3 affect animal communication and behaviour across a wide range of sensory modalities – by not only 4 impacting the signalling environment, but also the way in which animals produce, perceive and 5 interpret signals and cues. Such disturbances, particularly when it comes to sex, can drastically alter 6 fitness. Here, we consider how pollutants disrupt communication and behaviour during mate choice, 7 and the ecological and evolutionary changes such disturbances can engender. We explain how the 8 different stages of mate choice can be affected by pollution, from encountering mates to the final 9 choice, and how changes to these stages can influence individual fitness, population dynamics, and 10 community structure. We end with discussing how an understanding of these disturbances can help 11 inform better conservation and management practices and highlight important considerations and 12 avenues for future research.

1

1 1. Pollution and Mate choice

1 Environmental pollution is a serious and growing problem. In a human-dominated world, habitats

2 everywhere are increasingly being drenched by chemicals, disturbed by anthropogenic noise,

3 illuminated by artificial light, or thermally altered by human activities. Such pervasive pollutants not

4 only have the capacity to drastically change the environment, but can also interfere with key sensory

5 and physiological processes of exposed organisms [1-3]. In so doing, pollutants can influence the

6 ability of animals to receive and perceive information about their environment and potentially

^{*}Author for correspondence (ulrika.candolin@helsinki.fi).

7 impinge on their ability to mount an adaptive response [4-6]. In this regard, altered communication,

8 especially when it comes to sex, can have important fitness consequences [7, 8].

9 For many species, mate choice plays a fundamental role in determining which individuals are able to 10 successfully reproduce [9]. Typically, males compete vigorously for fertilisation opportunities, while 11 females make careful choices among potential mates (although large variation in this pattern is found 12 among species). Indeed, the elaborate male ornaments and conspicuous courtship displays that evolve 13 in response to female mate preferences can reflect a whole suite of direct and indirect fitness benefits 14 for choosy individuals, from access to mates that deliver superior parental care to the inheritance of 15 superior genes that increase offspring viability [10]. Display traits can also be non-informative, or 16 even deceptive, and evolve because signallers take advantage of pre-existing sensory biases in mate

17 choosers [10].

18 As an important fitness determinant that can influence both the quantity and quality of offspring

19 produced, mate choice relies on the capacity of individuals to exercise their reproductive decisions 20 prudently among the pool of suitors available to mate. For this to occur, choosy individuals must 21 accurately perceive and obtain reliable information about the quality of potential mates, as well as 22 process this information to make adaptive mating decisions [9]. In this regard, pollution-induced

23 changes to the environment – by altering these fundamental processes – can have a direct bearing on

24 individual mating decisions and mate choice.

25 Altered mate choice can have repercussions not only for individuals, but for the viability of

26 populations and the survival of species [11]. Changes in the number and quality of offspring can

27 affect population dynamics by influencing key demographic parameters resulting in population

declines [12]. Such changes, in turn, can affect species interactions and impact the structure and

29 function of the ecological communities they inhabit [13]. Disturbance to mate choice can also

30 influence vital evolutionary processes and the strength and direction of selection [14]. It can affect

31 premating reproductive isolation, which may promote population differentiation and speciation on

32 the one hand [15], or lead to interspecific matings and the loss of biodiversity, on the other [16].

33 Here, we discuss the effects that pollution has on communication and behaviours in a mate choice

34 context, and how these changes influence the dynamics of populations and, hence, the structure and

35 function of communities (figure 1). We begin by explaining how pollution affects the different stages

36 of the mate choice process. We then discuss how changes in mate choice can impact individual

37 fitness and, in so doing, population dynamics and species characteristics. We continue by reflecting

38 on the effect that changes in population characteristics can have on species interactions and

39 community structure. Finally, we consider how an improved understanding of the effects of pollution

40 on animal communication and mate choice can inform more effective conservation and management

41 outcomes.

42

43 **2. How does pollution influence mate choice?**

Mate choice is a multi-staged process that requires individuals to encounter potential suitors, acquire accurate information about the quality of these individuals, process the information gathered and make an informed choice. At each step, pollution has the potential to impinge on the mate choice process, and it can do so in three key ways: (1) by altering environmental conditions, (2) by affecting the intrinsic properties of potential mates and the individuals performing the mate choice, and (3) by impacting key population parameters (figure 1). Pollution may influence one or several stages of the mate choice process, and the changes it causes at one stage can alter its effects at other stages.

51

52 Mate encounter rate

53 Environmental conditions

54 Pollution can influence the ability of individuals to detect, attract and search for mates. For instance,

55 in glow-worms (*Lampyris noctiluca*), light pollution (artificial light at night) hinders the ability of

56 males to detect the bioluminescent glow of signalling females [17]. Similarly, in Lusitanian toadfish

57 (Halobatrachus didactylus), exposure to noise pollution from shipping activity affects the ability of

58 individuals to detect the courtship sounds of conspecifics [18]. Apart from these direct effects,

59 pollution can also affect mate encounter rates indirectly by altering species interactions (e.g. risk of

60 actual predation) that influence the cost of attracting and searching for mates.

61 Individual characteristics

62 Pollution that influences behavioural, morphological and physiological traits of individuals can alter

63 mate encounter rates. For instance, several herbicides influence the synthesis of pheromones in moths

64 and, hence, their ability to attract mates [19]. Stress-inducing pollutants, such as noise, can disturb

65 behaviours essential for maximising mate encounters, such as general activity and responsiveness to

66 cues of mates [20], or cause neurobiological changes that affect the perception or production of cues

67 [21]. Pollution can also influence investment into mate searching through effects on food intake,

68 metabolism, body condition, and the motivation to search for mates [22].

69 Population characteristics

70 Pollution that alters the size, structure, or distribution of populations can have a direct bearing on

71 mate encounter rates. For instance, toxic compounds that increase mortality and reduce population

72 density, or those that inhibit reproductive maturation, can reduce the number of individuals available

to mate, as well as the probability of encountering mates. Similarly, avoidance of pollutants, such as

reas [23].

76 Pollution that alters sex ratio can affect the intensity of competition for mates and, in so doing, the

benefit of investing in mate attraction and mate searching [24]. This can arise, for example, if

78 pollution-induced mortality is sex-dependent, or if sex determination is disrupted. In regard to the

79 latter, species with environmental sex determination may be particularly sensitive to pollutants that

80 can alter key environmental parameters, such as temperature [25]. Pollution-mediated changes in sex

81 ratio can also occur in species with primarily genetic sex determination, especially in the context of

so called endocrine-disrupting chemicals that disturb the normal hormone function of exposed

83 organisms [26]. For instance, the synthetic hormone estrogen, EE2, skews sex ratios towards females.

84 Such changes can relax competition among males for females, while increasing investment of

85 females into mate searching [27].

86 Pollution can also influence the expression of alternative reproductive strategies and, hence, the

87 mates that are encountered. For instance, light pollution that affects sleeping patterns of songbirds

88 can influence the possibility of cuckoldry, as individuals that delay the onset of daily activity are

89 more easily cuckolded [28].

90 Changes in the variation among individuals in mate quality can similarly alter the benefit of mate

91 attraction and mate search. In this respect, an increase in variation among individuals raises the

92 benefit of mate choice and, hence, may increase investment into mate searching, while reduced

93 variation may have the opposite effect [29].

94

95 Information reliability

96 Environmental conditions

97 Sexual signals are often finely attuned to the environment in which they have evolved. Pollution that 98 alters the physical characteristics of the landscape, including its visual, acoustic, and olfactory 99 properties, can therefore affect both the quantity and quality of the information being emitted and 100 transmitted through the signalling environment. This, in turn, can influence the information these 101 signals are purported to encode and, hence, their reliability. The low frequency din of urban noise, for 102 instance, can mask the low frequency components of the songs of birds, which alters their 103 information content [30]. Similarly, chemical compounds are known to interfere with the 104 transmission of olfactory signals by destroying or degrading them [31]. Global warming lowers in 105 turn the detectability and persistence of olfactory signals, as in the scent markings of mountain lizard

106 (*Iberolacerta cyreni*) [32].

107 Pollution can also impact the amount of resources available to individuals for investing into signals

108 used for advertising quality. If competition for limited resources intensifies, the reliability of signals

109 as indicators of resource-holding potential may improve [33]. However, pollution can also reduce

signal reliability by creating ecological traps [34]. Such a possibility can arise through the emergence

111 of novel cues that mimic those that individuals traditionally rely upon to guide their behavioural

112 decisions. Artificial light, for instance, attracts night-active insects, such as glow-worms and fireflies

113 that locate mates based on light emission [35].

114 Individual characteristics

115 It is well documented that exposure to certain pollutants can have a direct bearing on the expression

116 of sexual signals. Exposure of fish to municipal wastewater treatment effluent, in particular the

117 various pharmaceutical pollutants in the wastewater, is known to reduce male courtship behaviours

118 [36]. Exposures of tree frogs (*Hyla arborea*) to noise pollution elevates their stress hormone levels,

119 which reduces the colour of their vocal sacs used to attract females [21].

120 Changes in either the assessed trait, or in the quality of the assessed individuals, can disrupt the

121 relationship between the trait and the honesty of the information it is purported to convey. However,

122 while evidence exists of pollution altering signal and cue expression, much less is known about the

123 impact of altered signals on their reliability in guiding adaptive mating decisions. For example, in the

124 context of noise pollution, there is ample evidence documenting how animals, such as frogs, birds,

125 and insects, are able to adjust their acoustic signals to avoid vocal masking by, for example, calling

126 louder [37] or at higher frequencies [38, 39]. Yet, despite such changes, it remains unclear how signal

127 modification might affect the content of the signal and, hence, its reliability as an indicator of mate

128 quality. For instance, in frogs, females often prefer males that produce lower-pitched calls as these

advertise body size [40]. Hence, if males are forced to produce higher pitched calls in noisy

130 environments, such adjustments could potentially result in a conflict between signal audibility on the

131 one hand, and signal reliability, on the other [30]. In this regard, the utility of the signal will depend

132 on whether all signalling individuals are similarly affected by the pollutant, and whether signal

133 expression changes concomitantly with the quality of these individuals so that the signal continues to

134 function as an honest indicator of mate quality.

135 When pollution influences only one component of a multicomponent signal (e.g. ornament colour,

but not size), or only one sensory modality of a multimodal signal (e.g. colour, but not the intensity

137 of courtship), the different components may convey contradictory information that reduces signal

reliability [41]. Similarly when different components change in different directions, the resultant

139 signal may yield contradictory information.

140 Population characteristics

141 Investment into signals depends on the intensity of competition for mates [10]. If pollution relaxes 142 mate competition by altering the density or structure of populations, investment into signals may 143 decrease [42]. This, in turn, can reduce the reliability of signals as indicators of mate quality. For 144 instance, a reduced density of males can relax the social control over the expression of sexual signals 145 and allow subdominant males in poor physical condition to signal dishonestly [43, 44]. An example 146 of this seen in the electric signals produced by the fish *Brachyhypopomus gauderio*, where a lower 147 population density reduces social interactions and, hence, decreases the honesty of electric discharges 148 as indicators of body size [45]. Pollution that influences the perceived intensity of competition for 149 mates can similarly influence signal reliability without altering population size or structure. For 150 instance, increased water turbidity in eutrophied environments reduces visibility and the detection of 151 rival males in three-spined sticklebacks (Gasterosteus aculeatus). This relaxes the social control of 152 signals and, hence, their reliability as indicators of male condition and offspring viability [46, 47].

153

154 Information processing and choice

155 Environmental conditions

156 Pollution that alters food availability or predation risk can influence the costs and benefits of 157 engaging in mate choice. For instance, a reduced ability to find food may force individuals to spend 158 more time and energy on foraging and less on mate choice [48]. Similarly, a hampered ability to 159 detect predators can increase the perception of risk, resulting in individuals becoming less choosy to 160 mitigate the chances of being eaten [49]. An impaired ability to detect mates can, in turn, reduce the 161 opportunity for choice [50]. Grim future reproductive opportunities may cause individuals to 162 prioritize mating and become less choosy in order to maximise their chances of securing a mate [51]. 163 Such changes can also induce individuals to switch from the use of signals in one sensory modality to 164 another, such as paying less attention to acoustic signals in favour of visual signals in noisy 165 environments.

166 Individual characteristics

167 The ability of choosy individuals to receive and process the information that reaches them depends 168 on a range of intrinsic factors, including sensory and cognitive function, decision rules (e.g. mate 169 acceptance thresholds), hormonal levels, and body condition – all of which can potentially be 170 disturbed by pollution [52]. This is especially true of pollutants that interfere with the endocrine 171 system and alter sexual motivation and behaviour, as well as impinge on sensory systems and the 172 reception of information [31]. For instance, the insecticide endosulfan resulted in male red-spotted 173 newts (*Notophthalmus viridescens*) taking longer to detect female pheromones, which in turn reduced

- 174 mate encounter rates [53]. This illustrates how the impact of pollutants may influence several mate
- 175 choice stages, including the processing of signals as well as encounters with mates.
- 176 Pollution can also alter the body condition of choosy individuals and, hence, the amount of resources
- they can invest into mate choice [54]. For instance, female wolf spiders (*Schizocosa stridulans*) are
- 178 less selective for males in good condition when food is limited [55]. Considering the profound effects
- that pollutants often have on body functions, changes to the intrinsic properties of choosers is
- 180 probably a common pathway through which various pollutants can influence mate choice.
- 181 Population characteristics
- 182 Changes in the density and structure of populations can alter investment into mate assessment and
- 183 choice in a manner similar to the effects described earlier for other components of the mate choice
- 184 process. For instance, pollution that decimates a population increases the cost of choosiness by
- 185 increasing the prospects of remaining unmated [56].
- 186 Pollution that alters aggression and negative interactions among individuals can also impact the costs
- 187 of choice. For example, decreased population density may lower the frequency and intensity of male
- 188 sexual harassment and, hence, reduce the cost to females from having to fend off undesirable mates
- 189 [4]. It is becoming increasingly apparent that males, in attempting to maximise their own
- 190 reproductive payoffs, can also behave in ways that override or impinge on female mate choice [57].
- 191 An example of this is seen in guppies (*Poecilia reticulata*), with exposure to the agricultural pollutant
- 192 17β-trenbolone, a powerful synthetic steroid, increasing male coercive matings and, in so doing,
- 193 circumventing female choice [58, 59].
- 194

3. Adaptive or maladaptive mate choice?

196 Whether the response of an individual to pollution is adaptive or not depends on its genetically 197 determined reaction norm, and how the response can be altered through environmental effects, 198 learning and evolutionary (genetic) changes. Reaction norms have evolved under past conditions and, 199 hence, their adaptive value largely depends on the resemblance of the polluted conditions to earlier 200 encountered conditions [5, 60]. When the difference is large, the reaction norms are likely to be 201 maladaptive. For instance, individuals may lack the sensory and neuroendocrine functions required to 202 perceive changes in mate quality in a polluted environment, or they may not be able to overcome the 203 challenges that the pollutant imposes on mate detection and evaluation.

204 When polluted conditions resemble earlier encountered conditions, animals may be more adept at

- 205 plastically adjusting to pollution. For instance, individuals from environments with fluctuating noise
- 206 levels may have evolved the flexibility to pay more attention to visual cues when noise levels are
- 207 high. In general, species that can switch among cues may be better predisposed to deal with human-

208 induced pollution when the pollution reduces the efficiency of signals and cues in certain sensory

- 209 modalities, but not others [41]. However, when pollution alters the information content of different
- signals, and animals continue to pay attention to them, this could lead to contradictory information
- 211 being acquired, which can render mate choice more difficult.
- 212 Learning may also improve the ability of individuals to assess signals and cues and make favourable
- 213 choices. For instance, white-crowned sparrows (Zonotrichia leucophyrs) learn to adjust theirs song to
- 214 noise from tutor songs through cultural selection [61]. Individuals may also learn to pay less attention
- to cues that are unreliable indicators of mate quality, or to adjust the timing of their reproductive
- 216 activities. For instance, birds living near airports advance the timing of their chorus to avoid overlap
- 217 with periods of intense aircraft noise [62]. It is important to point out, however, that plastic
- adjustments are not always possible [63] or may simply not be enough to counter the effects of
- 219 pollution [64]. Under such circumstances, evolutionary changes may be required.
- 220

4. Consequences of altered mate choice

222 Individual level

Maladaptive mate choice may reduce the number of offspring that individuals produce if the chooser selects a mate that has a low fertilisation success or fecundity, has less resources to provide, or is a poor parent. Maladaptive mate choice can also influence the quality of the offspring produced, particularly if the selected mate is of low genetic quality. For instance, three-spined stickleback females are more likely to choose a mate that sires offspring of low viability when visibility is reduced due to algal blooms [46].

- When individuals increase their investment into mate choice in polluted habitats to compensate for a compromised ability to evaluate mates, this may reduce the amount of resources available to invest in
- 231 other reproductive components, such as fecundity, parental care, and future reproductive
- 232 opportunities [65]. Similarly, elevated costs of searching for, and evaluating, mates can reduce
- survival and fecundity and, hence, lifetime reproductive success.
- 234 When individuals reduce their investment into mate choice, maladaptive choices may follow that
- 235 lower the number and quality of offspring they produce. For instance, canaries (*Serinus canaria*)
- 236 produce smaller clutch sizes when choosing a mate in a noisy environment, probably because
- hampered male-female vocal communication reduces female motivation to reproduce [66]. Such
- 238 reduced investment can be adaptive under natural, fluctuating conditions if conditions improve with
- time. However, in human-modified habitats, conditions may not improve and the reduction in
- 240 investment may, instead, reduce fitness.

241 Pollution can, in some instances, facilitate mate choice, or reduce the cost of choosing a mate, and

242 improve reproductive success. For instance, the disappearance of predators from polluted

environments can allow prey species to spend more time searching for and evaluating mates [2].

244 Pollution that increases the randomness in mate choice may, in turn, improve the reproductive

success of individuals that may otherwise have low mating prospects [46]. In this regard, altered

246 distribution of mating success among individuals could have important population-level

- consequences.
- 248

249 Population level

250 Altered reproductive success of individuals can influence population dynamics and demographics. If

a large proportion of the population makes maladaptive mate choices and produces fewer offspring or

252 offspring of lower viability, the population may decline [67].

253 Altered mate choice can also influence the evolution of traits. Maladaptive preferences and signals

254 may be lost, while new traits may evolve [68]. However, the evolution of signals and preferences is

255 generally a slow process, as it depends on generation time and the presence of suitable genetic

variation [69]. Thus, evolution may frequently not be fast enough to rescue mate choice systems inrapidly changing environments.

258 Altered mate choice that influences selection on traits can, in turn, influence selection on correlated 259 traits. It can also influence selection later in life. For instance, relaxed selection at the mate choice 260 stage can strengthen selection at other life-history stages, such as among juveniles if more offspring 261 of low viability are born into the population when mate choice becomes more random [70]. There is 262 also evidence suggesting that mate choice and sexual selection may promote the evolution of 263 mechanisms that can allow animals to better cope with pollutants. An example of this is seen in flour 264 beetles (*Tribolium castaneum*), which evolved resistance to a pyrethroid pesticide faster under sexual 265 selection [71].

266

267 *Community level*

Changes in population dynamics can influence community composition. Species able to adapt their
 mate choice system to pollution may thrive, while those that cannot may flounder. For instance, the

270 composition of a community of nesting birds in New Mexico changed with increasing noise levels.

- 271 Species that adjusted their vocalisations during reproduction to the noise flourished, while those that
- did not declined [13]. Such changes may in turn influence species interactions. For instance, a
- 273 declining predator population may release its prey population from predation, or its competitors from

274 competition and, hence, influence the population dynamics of these species [72]. However, little is 275 currently known about such community-wide consequences of altered mate choice. 276 Pollution that impairs species recognition can increase the frequency of interspecific matings. This 277 can result in unviable offspring, or in hybrids that have a lower viability than their parental species. 278 Such maladaptive matings may use up valuable time and energy and, hence, decrease offspring 279 production. On the other hand, pollution that increases interspecific matings also have the potential to 280 select for traits that contribute to population divergence. This may promote species differentiation 281 and possible speciation [73]. Alternatively, interspecific matings because of pollution may result in 282 hybrids that are more adept at succeeding under altered conditions. This can lead to the loss of 283 biodiversity through the breakdown of species isolation mechanisms, as demonstrated, for example, 284 in African cichlids [16].

285

5. How can the knowledge be of use in conservation

287 management?

Studies of wildlife behavioural responses to human-altered conditions, including altered reproductive responses, such as mate choice, are crucial in understanding the harmful effects of pollution on species. Behavioural responses can be used as first indicators of changes to ecosystems, as well as reveal mechanisms and pathways through which pollution influences population dynamics and, further, how the effects spread through the species community [74].

Because behaviour is the manifestation of numerous complex developmental and physiological
processes, it is an exceptionally powerful and biologically relevant indicator of environmental
impacts. Hence, in the context of environmental monitoring, behaviour can be a much more

comprehensive and sensitive biomarker than standard laboratory assays used to test for pollutants in

the environment (e.g. chemicals), which typically target only one or a few biochemical or

298 physiological parameters [75]. Given the central role of mate choice in determining fitness and

299 population dynamics, it is a particularly important indicator of impacts of environmental pollution on300 species.

Indeed, from a practical management and conservation perspective, there are many lessons that can be gleaned from knowledge of how pollution affects mate choice. For instance, the finding that birds and anurans differ in their capacity to shift vocal frequencies [76] suggests that different approaches may be required to effectively manage anthropogenic noise pollution in different kinds of habitats. In the context of noise pollution, mitigation strategies that are already widely used to limit the imapct of anthropogenic noise on humans, such as sound barriers and noise curfews, may also be effective in managing the impact of noise disturbance on wildlife [77]. 308 Measuring mate choice in nature, however, can often be difficult, and what is measured in the 309 laboratory may not reflect processes in nature. Thus, care needs to be taken when planning how to 310 investigate the impact of pollutants on mate choice.

311

6. Future research directions

313 Much information exists on the effects of pollutants on mate choice behaviour, while less is known 314 about the consequences of altered mate choice for individual fitness, population dynamics, species 315 interactions and community structure [11]. Because mate choice is an important fitness determinant, 316 disruptions to the behaviour can have far reaching consequences for both ecological and evolutionary 317 processes, and need to be considered in studies on the effects of pollution on ecosystems. 318 The response of wildlife to pollutants often depend on the enormity of the disturbance. Thus, 319 researchers should be cognisant of employing exposure levels that are ecologically relevant [75]. 320 Here, it is important to realise that the relationship between the magnitude of the response and the 321 extent of the disturbance may not necessarily be linear. For instance, several studies examining the 322 behavioural responses of wildlife to chemical pollutants have reported non-monotonic dose 323 responses, whereby exposure to lower concentrations can induce effects not seen at higher exposure 324 levels [78]. Such findings underscore the importance of testing responses across multiple levels of 325 disturbance.

A better understanding of the longer term impacts of pollutants is also needed. Many pollutants are highly pervasive in the environment. Yet, there has been a tendency for experimental studies to employ extremely short exposure times (in some cases, only a matter of hours) [2]. This is true even though the impacts of pollutants, such as chemical contaminants, can take time to manifest. Moreover, there is now good evidence to suggest that exposure to pollutants can induce effects that transcend generations by causing developmental changes that are epigenetic [79]. For example, in

transcend generations by causing developmental changes that are epigenetic [79]. For example, in

332laboratory mice, exposure to an endocrine disruptor affects female mating preferences three

333 generations removed from the actual exposure [80]. Such studies underscore the fact that exposure to

pollutants need not even be permanent to exert long-lasting effects on the mate choice process.

In addition, greater emphasis needs to be given to understanding the impact of pollutants in

interaction with other environmental stressors. In the wild, animals are typically confronted with a

337 myriad of environmental challenges simultaneously (from both natural and anthropogenic sources).

338 Yet, despite this, there has been a tendency for researchers to examine the wildlife impacts of

pollution in a vacuum, isolated from the influence of other environmental factors. Predicting the

340 response of wildlife to pollutants in the presence of other kinds of environmental stressors cannot be

341 achieved by studying these different disturbances in isolation, as multiple stressors can interact to

induce effects that can be either greater (synergistic) or less (antagonistic) than the sum of their
 independent effects [81]. Multifactorial studies, in this regard, could be useful in disentangling the
 underlying mechanisms behind wildlife responses to pollutants under more realistic, multi-stressor
 environments.

346 Both within and between species differences are also important. Within species, responses can vary 347 among individuals, depending on a range of factors, such as life history stage, sex, age, and body 348 size. For instance, Bertram et al. [58] reported sex specific differences in the response of guppies to a 349 widespread agricultural contaminant, 17b-trenbolone, with altered reproductive behaviour in males, 350 but not females. Among species, the bulk of research effort focussing on the impacts of pollution on 351 mate choice have tended to focus on only a handful of taxa, even though the response of wildlife to 352 pollutants can vary. The effects of noise pollution provide a good case in point. Here, most studies 353 exploring the impacts of anthropogenic noise on acoustic signals have centred on terrestrial 354 environments, with a heavy emphasis on the mating calls of birds and frogs, while impacts of noise in 355 aquatic habitats have largely focussed on marine mammals (mostly in a non-reproductive context). 356 By contrast, far less attention has been given to understanding impacts of noise pollution on other 357 acoustically communicating taxa, such as fish, where the use of sound as a form of communication, 358 including in mate choice, appears to be underappreciated [3, 82]. Here, taxonomic differences in the 359 mechanisms of sound production and detection, as well as differences in the transmission properties 360 of sound in water and air, underscore the necessity for more direct testing of anthropogenic impacts 361 in taxa that have, to date, been largely neglected.

362 In advancing the field, an important challenge will be to overcome our own sensory biases. To date, 363 understanding of how pollution disrupts animal communication and mate choice has tended to focus 364 almost exclusively on visual, acoustic and olfactory communication [7]. Yet, non-human animals can 365 employ an extraordinarily diverse range of sensory channels for conspecific communication, many of which are very different from our own. Moreover, even in cases where the same sensory modalities 366 367 are employed, perceptual abilities are often strikingly different. For example, some species, in 368 contrast to humans, are able to see ultraviolet signals or hear infrasound. Yet, despite this, our current 369 understanding of how pollutants affect these systems remains rudimentary. A related issue is the 370 multimodality of animal communication systems. In this regard, impairment of any one (or 371 combination) of different sensory modalities can have implications that are likely to depend on a 372 range of factors, including environmental context, the relative importance of the different sensory 373 modalities, and the information being conveyed [7, 11]. Important insights will no doubt come from 374 research that is less encumbered by our own sensory tendencies and better informed by sensory

375 ecology [83].

- Finally, more information is needed on the relative importance of plastic responses and genetic
- 377 changes in coping with polluted environments. In particular, more attention needs to be paid to the
- 378 possibility of mate choice behaviour evolving to be better suited to polluted conditions: when is
- 379 evolutionary rescue likely and when is it not, and which factors determine whether a species will be
- able to adapt to pollution [60]? Insights into these questions will be pivotal in understanding the
- 381 longer term consequences of altered mate choice in an increasingly human-dominated world.
- 382
- 383

384 Additional Information

- 385 Acknowledgments
- We thank Jakob Bro-Jørgensen for inviting us to contribute to this special issue, and Jake Martin for the design and editing of the figure.
- 388

389 Data Accessibility

- 390 This article has no additional data.
- 391
- 392 Authors' Contributions
- Both authors contributed to the development and write up of the article's content, and gave final
- approval for its publication.
- 395

398

- 396 Competing Interests
- The authors have no competing interests.
- 399 Funding
- 400 Funding support was provided by the Academy of Finland (no. 277667) (to U.C.) and a Discovery
- 401 Grant from the Australian Research Council (DP160100372) (to B.B.M.W.).
- 402 403

404 References

- [1] Swaddle, J.P., Francis, C.D., Barber, J.R., Cooper, C.B., Kyba, C.C.M., Dominoni, D.M., Shannon, G., Aschehoug, E., Goodwin, S.E., Kawahara, A.Y., et al. 2015 A framework to assess evolutionary responses to anthropogenic light and sound. *Trends Ecol. Evol.* 30, 550-560. (doi:10.1016/j.tree.2015.06.009).
- [2] Saaristo, M., Brodin, T., Balshine, S., Bertram, M.G., Brooks, B.W., Ehlman, S.M., McCallum, E.S., Sih, A., Sundin, J., Wong, B.B.M., et al. 2018 Direct and indirect effects of chemical contaminants on the behaviour, ecology and evolution of wildlife. *Proc. R. Soc. Lond. B* 285, 10. (doi:10.1098/rspb.2018.1297).
- [3] van der Sluijs, I., Gray, S.M., Amorim, M.C.P., Barber, I., Candolin, U., Hendry, A.P., Krahe, R., Maan, M.E., Utne-Palm, A.C., Wagner, H.J., et al. 2011 Communication in troubled waters: responses of fish communication systems to changing environments. *Evol. Ecol.* 25, 623-640. (doi:10.1007/s10682-010-9450-x).
- [4] Wong, B.B.M. & Candolin, U. 2015 Behavioral responses to changing environments. *Behav. Ecol.* 26, 665-673. (doi:10.1093/beheco/aru183).

- [5] Tuomainen, U. & Candolin, U. 2011 Behavioural responses to human-induced environmental change. *Biol. Rev.* 86, 640-657. (doi:10.1111/j.1469-185X.2010.00164.x).
- [6] Sih, A. 2013 Understanding variation in behavioural responses to human-induced rapid environmental change: a conceptual overview. *Anim. Behav.* 85, 1077-1088. (doi:10.1016/j.anbehav.2013.02.017).
- [7] Rosenthal, G.G. & Stuart-Fox, D. 2012 Environmental disturbance and animal communication. In *Behavioural responses to a changing world: mechanisms and consequences* (eds. U. Candolin & B.B.M. Wong), pp. 16-31. Oxford, Oxford Unviersity Press.
- [8] Candolin, U. 2019 Mate choice in a changing world. Biol. Rev. in press.
- [9] Rosenthal, G.G. 2017 Mate choice. Princeton and Oxford, Princeton University Press.
- [10] Andersson, M. 1994 Sexual selection. Princeton, Princeton University Press.
- [11] Candolin, U. & Wong, B.B.M. 2012 Sexual selection in changing environments: consequences for individuals and populations. In *Behavioural responses to a changing world: mechanisms and consequences* (eds. U. Candolin & B.B.M. Wong), pp. 201-215. Oxford, Oxford University Press.
- [12] Holman, L. & Kokko, H. 2013 The consequences of polyandry for population viability, extinction risk and conservation. *Phil. Trans. R. Soc. B.* 368. (doi:10.1098/rstb.2012.0053).
- [13] Francis, C.D., Ortega, C.P. & Cruz, A. 2009 Noise pollution changes avian communities and species interactions. *Curr. Biol.* 19, 1415-1419. (doi:10.1016/j.cub.2009.06.052).
- [14] Candolin, U. & Vlieger, L. 2013 Estimating the dynamics of sexual selection in changing environments. *Evol. Biol.* 40, 589-600.
- [15] Pfennig, K.S. 2016 Reinforcement as an initiator of population divergence and speciation. *Curr. Zool.* 62, 145-154. (doi:10.1093/cz/zow033).
- [16] Seehausen, O., Alphen, J.J.M. & Witte, F. 1997 Cichlid fish diversity threatened by eutrophication that curbs sexual selection. *Science* 277, 1808-1811.
- [17] Bird, S. & Parker, J. 2014 Low levels of light pollution may block the ability of male glow-worms (*Lampyris noctiluca* L.) to locate females. *J. Insect Conserv.* 18, 737-743. (doi:10.1007/s10841-014-9664-2).
- [18] Vasconcelos, R.O., Amorim, M.C.P. & Ladich, F. 2007 Effects of ship noise on the detectability of communication signals in the Lusitanian toadfish. J. Exp. Biol. 210, 2104-2112. (doi:10.1242/jeb.004317).
- [19] Eliyahu, D., Applebaum, S. & Rafaeli, A. 2003 Moth sex-pheromone biosynthesis is inhibited by the herbicide diclofop. *Pest. Biochem. Physiol.* 77, 75-81. (doi:10.1016/s0048-3575(03)00101-9).
- [20] Wingfield, J.C. 2015 Coping with change: A framework for environmental signals and how neuroendocrine pathways might respond. *Front. Neuroendocrinol.* 37, 89-96. (doi:10.1016/j.yfrne.2014.11.005).
- [21] Troianowski, M., Mondy, N., Dumet, A., Arcanjo, C. & Lengagne, T. 2017 Effects of traffic noise on tree frog stress levels, immunity, and color signaling. *Conserv. Biol.* 31, 1132-1140. (doi:10.1111/cobi.12893).
- [22] Heuschele, J., Salminen, T. & Candolin, U. 2012 Habitat change influences mate search behaviour in three-spined sticklebacks. *Anim. Behav.* 83, 1505-1510.
- [23] Blickley, J.L., Blackwood, D. & Patricelli, G.L. 2012 Experimental Evidence for the Effects of Chronic Anthropogenic Noise on Abundance of Greater Sage-Grouse at Leks. *Conserv. Biol.* 26, 461-471. (doi:10.1111/j.1523-1739.2012.01840.x).
- [24] Weir, L.K., Grant, J.W.A. & Hutchings, J.A. 2011 The Influence of Operational Sex Ratio on the Intensity of Competition for Mates. Am. Nat. 177, 167-176. (doi:10.1086/657918).

- [25] Sandra, G.E. & Norma, M.M. 2010 Sexual determination and differentiation in teleost fish. *Rev. Fish. Biol. Fish.* 20, 101-121. (doi:10.1007/s11160-009-9123-4).
- [26] Wedekind, C. 2017 Demographic and genetic consequences of disturbed sex determination. *Phil. Trans. R. Soc. B.* 372, 10. (doi:10.1098/rstb.2016.0326).
- [27] Orton, F. & Tyler, C.R. 2015 Do hormone-modulating chemicals impact on reproduction and development of wild amphibians? *Biol. Rev.* 90, 1100-1117. (doi:10.1111/brv.12147).
- [28] Greives, T.J., Kingma, S.A., Kranstauber, B., Mortega, K., Wikelski, M., van Oers, K., Mateman, A.C., Ferguson, G.A., Beltrami, G. & Hau, M. 2015 Costs of sleeping in: circadian rhythms influence cuckoldry risk in a songbird. *Funct. Ecol.* 29, 1300-1307. (doi:10.1111/1365-2435.12440).
- [29] Owens, I.P.F. & Thompson, D.B.A. 1994 Sex-differences, sex-ratios and sex-roles. Proc. R. Soc. Lond. B 258, 93-99. (doi:10.1098/rspb.1994.0148).
- [30] Halfwerk, W., Bot, S., Buikx, J., van der Velde, M., Komdeur, J., ten Cate, C. & Slabbekoorn, H. 2011 Low-frequency songs lose their potency in noisy urban conditions. *Proc. Natl. Acad. Sci. USA* 108, 14549-14554. (doi:10.1073/pnas.1109091108).
- [31] Lurling, M. & Scheffer, M. 2007 Info-disruption: pollution and the transfer of chemical information between organisms. *Trends Ecol. Evol.* 22, 374-379. (doi:10.1016/j.tree.2007.04.002).
- [32] Martin, J. & Lopez, P. 2013 Effects of global warming on sensory ecology of rock lizards: increased temperatures alter the efficacy of sexual chemical signals. *Funct. Ecol.* 27, 1332-1340. (doi:10.1111/1365-2435.12128).
- [33] Shuster, S.M. & Wade, M.J. 2003 Mating Systems and Strategies. Princeton, NJ., Princeton University Press.
- [34] Schlaepfer, M.A., Runge, M.C. & Sherman, P.W. 2002 Ecological and evolutionary traps. *Trends Ecol. Evol.* 17, 474-480. (doi:10.1016/s0169-5347(02)02580-6).
- [35] Longcore, T. & Rich, C. 2004 Ecological light pollution. Front. Ecol. Env. 2, 191-198. (doi:10.2307/3868314).
- [36] Soffker, M. & Tyler, C.R. 2012 Endocrine disrupting chemicals and sexual behaviors in fish a critical review on effects and possible consequences. *Crit. Rev. Toxicol.* 42, 653-668. (doi:10.3109/10408444.2012.692114).
- [37] Brumm, H. & Todt, D. 2002 Noise-dependent song amplitude regulation in a territorial songbird. *Anim. Behav.* 63, 891-897. (doi:10.1006/anbe.2001.1968).
- [38] Parris, K.M., Velik-Lord, M. & North, J.M.A. 2009 Frogs Call at a Higher Pitch in Traffic Noise. Ecol. Soc. 14, 24.
- [39] Lampe, U., Schmoll, T., Franzke, A. & Reinhold, K. 2012 Staying tuned: grasshoppers from noisy roadside habitats produce courtship signals with elevated frequency components. *Funct. Ecol.* 26, 1348-1354. (doi:10.1111/1365-2435.12000).
- [40] Ryan, M.J. 1980 Female mate choice in a neotropical frog. *Science* 209, 523-525. (doi:10.1126/science.209.4455.523).
- [41] Partan, S.R. 2017 Multimodal shifts in noise: switching channels to communicate through rapid environmental change. *Anim. Behav.* 124, 325-337. (doi:10.1016/j.anbehav.2016.08.003).
- [42] Candolin, U. & Heuschele, J. 2008 Is sexual selection beneficial during adaptation to environmental change? Trends Ecol. Evol. 23, 446-452.
- [43] Candolin, U. 1999 Male-male competition facilitates female choice in sticklebacks. Proc. R. Soc. Lond. B 266, 785-789.
- [44] Candolin, U. 2000 Increased signalling effort when survival prospects decrease: male-male competition ensures honesty. *Anim. Behav.* 60, 417-422.

- [45] Gavassa, S., Goldina, A., Silva, A.C. & Stoddard, P.K. 2013 Behavioral ecology, endocrinology and signal reliability of electric communication. J. Exp. Biol. 216, 2403-2411. (doi:10.1242/jeb.082255).
- [46] Candolin, U., Tukiainen, I. & Bertell, E. 2016 Environmental change disrupts communication and sexual selection in a stickleback population. *Ecology* 97, 969-979.
- [47] Wong, B.B.M., Candolin, U. & Lindström, K. 2007 Environmental deterioration compromises socially-enforced signals of male quality in three-spined sticklebacks *Am. Nat.* 170, 184-189.
- [48] Jennions, M.D. & Petrie, M. 1997 Variation in mate choice and mating preferences: a review of causes and consequences. *Biological Review* 72, 283-327.
- [49] Magnhagen, C. 1991 Predation risk as a cost of reproduction. *Trends in Ecology and Evolution* 6, 183-186.
- [50] Engström-Öst, J. & Candolin, U. 2007 Human-induced water turbidity alters selection on sexual displays in sticklebacks. *Behav. Ecol.* 18, 393-398.
- [51] Backwell, P.Y. & Passmore, N.I. 1996 Time constraints and multiple choice criteria in the sampling behaviour and mate choice of the fiddler crab, Uca annulipes *Behav. Ecol. Sociobiol.* 38, 407-416.
- [52] Buchanan, K.L. & Partecke, J. 2012 The endocrine system: can homeostasis be maintained in a changing world? In Behavioural responses to a changing world. Mechanisms and consequences (eds. U. Candolin & B.B.M. Wong), pp. 32-45. Oxford, Oxford University Press.
- [53] Park, D. & Propper, C.R. 2002 Endosulfan affects pheromonal detection and glands in the male red-spotted newt, Notophthalmus viridescens. *Bull. Environ. Contam. Toxicol.* 69, 609-616. (doi:10.1007/s00128-002-0104-8).
- [54] Cotton, S., Small, J. & Pomiankowski, A. 2006 Sexual selection and condition-dependent mate preferences. *Curr. Biol.* 16, R755-R765. (doi:10.1016/j.cub.2006.08.022).
- [55] Hebets, E.A., Wesson, J. & Shamble, P.S. 2008 Diet influences mate choice selectivity in adult female wolf spiders. *Anim. Behav.* 76, 355-363. (doi:10.1016/j.anbehav.2007.12.021).
- [56] Willis, P.M., Ryan, M.J. & Rosenthal, G.G. 2011 Encounter rates with conspecific males influence female mate choice in a naturally hybridizing fish. *Behav. Ecol.* 22, 1234-1240. (doi:10.1093/beheco/arr119).
- [57] Wong, B.B.M. & Candolin, U. 2005 How is female mate choice affected by male competition? *Biol. Rev.* 80, 559-571.
- [58] Bertram, M.G., Saaristo, M., Baumgartner, J.B., Johnstone, C.P., Allinson, M., Allinson, G. & Wong, B.B.M. 2015 Sex in troubled waters: Widespread agricultural contaminant disrupts reproductive behaviour in fish. *Horm. Behav.* 70, 85-91. (doi:10.1016/j.yhbeh.2015.03.002).
- [59] Tomkins, P., Saaristo, M., Bertram, M.G., Tomkins, R.B., Allinson, M. & Wong, B.B.M. 2017 The agricultural contaminant 17 beta-trenbolone disrupts male-male competition in the guppy (Poecilia reticulata). *Chemosphere* 187, 286-293. (doi:10.1016/j.chemosphere.2017.08.125).
- [60] Sih, A., Ferrari, M.C.O. & Harris, D.J. 2011 Evolution and behavioural responses to human-induced rapid environmental change. *Evol. Appl.* 4, 367-387. (doi:10.1111/j.1752-4571.2010.00166.x).
- [61] Moseley, D.L., Derryberry, G.E., Phillips, J.N., Danner, J.E., Danner, R.M., Luther, D.A. & Derryberry, E.P. 2018 Acoustic adaptation to city noise through vocal learning by a songbird. *Proc. R. Soc. Lond. B* 285, 20181356.
- [62] Gil, D., Honarmand, M., Pascual, J., Perez-Mena, E. & Garcia, C.M. 2015 Birds living near airports advance their dawn chorus and reduce overlap with aircraft noise. *Behav. Ecol.* 26, 435-443. (doi:10.1093/beheco/aru207).
- [63] Lengagne, T. 2008 Traffic noise affects communication behaviour in a breeding anuran, Hyla arborea. *Biol. Conser.* 141, 2023-2031. (doi:10.1016/j.biocon.2008.05.017).
- [64] Nemeth, E. & Brumm, H. 2010 Birds and Anthropogenic Noise: Are Urban Songs Adaptive? Am. Nat. 176, 465-475. (doi:10.1086/656275).

[65] Roff, D. 1992 The evolution of life-histories. New York, Chapman and Hall.

- [66] des Aunay, G.H., Grenna, M., Slabbekoorn, H., Nicolas, P., Nagle, L., Leboucher, G., Malacarne, G. & Draganoiu, T.I. 2017 Negative impact of urban noise on sexual receptivity and clutch size in female domestic canaries. *Ethology* 123, 843-853. (doi:10.1111/eth.12659).
- [67] Kokko, H. & Brooks, R. 2003 Sexy to die for? Sexual selection and the risk of extinction. *Annales Zoologici Fennici* 40, 207-219.
- [68] McNair, A., Nakagawa, S. & Grimm, V. 2014 The Evolutionary Consequences of Disrupted Male Mating Signals: An Agent-Based Modelling Exploration of Endocrine Disrupting Chemicals in the Guppy. *Plos One* 9, 9. (doi:10.1371/journal.pone.0103100).
- [69] Barrett, R.D.H. & Hendry, A.P. 2012 Evolutionary rescue under environmental change? In *Behavioural responses to a changing world. Mechanisms and consequences.* (eds. U. Candolin & B.B.M. Wong), pp. 216-233. Oxford, Oxford University Press.
- [70] Winemiller, K.O. 1992 Life-history strategies and the effectiveness of sexual selection. *Oikos* 63, 318-327. (doi:10.2307/3545395).
- [71] Jacomb, F., Marsh, J. & Holman, L. 2016 Sexual selection expedites the evolution of pesticide resistance. *Evolution* 70, 2746-2751. (doi:10.1111/evo.13074).
- [72] Hoover, S.E.R. & Tylianakis, J.M. 2012 Species interactions. In *Behavioural responses to a changing world: mechanisms and consequences* (eds. U. Candolin & B.B.M. Wong), pp. 129-142. Oxford, Oxford University Press.
- [73] Boughman, J.W. 2002 How sensory drive can promote speciation. Trends Ecol. Evol. 17, 571-577.
- [74] Candolin, U. & Wong, B.B.M. 2012 *Behavioural responses to a changing world. Mechanisms and consequences.* Oxford, Oxford University Press; 280 p.
- [75] Zala, S.M. & Penn, D.J. 2004 Abnormal behaviours induced by chemical pollution: a review of the evidence and new challenges. *Anim. Behav.* 68, 649-664. (doi:10.1016/j.anbehav.2004.01.005).
- [76] Roca, I.T., Desrochers, L., Giacomazzo, M., Bertolo, A., Bolduc, P., Deschesnes, R., Martin, C.A., Rainville, V., Rheault, G. & Proulx, R. 2016 Shifting song frequencies in response to anthropogenic noise: a meta-analysis on birds and anurans. *Behav. Ecol.* 27, 1269-1274. (doi:10.1093/beheco/arw060).
- [77] Slabbekoorn, H. & Ripmeester, E.A.P. 2008 Birdsong and anthropogenic noise: implications and applications for conservation. *Mol. Ecol.* 17, 72-83. (doi:10.1111/j.1365-294X.2007.03487.x).
- [78] Martin, J.M., Saaristo, M., Bertram, M.G., Lewis, P.J., Coggan, T.L., Clarke, B.O. & Wong, B.B.M. 2017 The psychoactive pollutant fluoxetine compromises antipredator behaviour in fish. *Environ. Pollut.* 222, 592-599. (doi:10.1016/j.envpol.2016.10.010).
- [79] Walker, D.M. & Gore, A.C. 2011 Transgenerational neuroendocrine disruption of reproduction. *Nat. Rev. Endocrinol.* 7, 197-207. (doi:10.1038/nrendo.2010.215).
- [80] Crews, D., Gore, A.C., Hsu, T.S., Dangleben, N.L., Spinetta, M., Schallert, T., Anway, M.D. & Skinner, M.K. 2007 Transgenerational epigenetic imprints on mate preference. *Proc. Natl. Acad. Sci. USA* 104, 5942-5946. (doi:10.1073/pnas.0610410104).
- [81] Folt, C.L., Chen, C.Y., Moore, M.V. & Burnaford, J. 1999 Synergism and antagonism among multiple stressors. *Limnol. Oceanogr.* 44, 864-877. (doi:10.4319/lo.1999.44.3_part_2.0864).
- [82] Radford, A.N., Kerridge, E. & Simpson, S.D. 2014 Acoustic communication in a noisy world: can fish compete with anthropogenic noise? *Behav. Ecol.*
- [83] Lim, M.L.M., Sodhi, N.S. & Endler, J.A. 2008 Conservation with sense. Science 319, 281-281.

Figure caption

Figure 1. Impact of altered mate choice on individuals, populations and communities.

Figure

