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1 Pheromones-based sexual selection in a rapidly 2 changing world

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4 Q1
5 Insects utilise chemical cues for a range of different purposes
6 and the complexity and degree of specificity of these signals is
7 arguably unparalleled in the animal kingdom. Chemical signals
8 are particularly important for insect reproduction and the
9 selective pressures driving their evolution and maintenance
10 have been the subject of previous reviews. However, the world
11 in which chemical cues evolved and are maintained is changing
12 at an unprecedented rate. How (or indeed whether) chemical
13 signals used in sexual selection will respond is largely
14 unknown. Here, we explore how recent increases in
15 urbanisation and associated anthropogenic impacts may affect
16 how chemical signals are produced and perceived. We focus
17 on four anthropomorphic influences which have the potential to
18 interact with pheromone-mediated sexual selection processes;
19 climatic temperature shifts, exposure to chemical pollutants,
20 the presence of artificial light at night and nutrient availability.
21 Our aim is to provide a broad overview of key areas where the
22 rapidly changing environment of the future might specifically
23 affect pheromones utilised in sexual selection.

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32 Insects utilise chemical cues to detect the scents of their
33 own and other species (including other animals, plants
34 and fungi). The complexity and degree of specificity of
35 the chemical cues used by insects is dazzling and, has
36 perhaps unsurprisingly, been the subject of many studies
37 and review papers [1–9,10*]. Over the past two decades,
38 reviews of pheromone communication have explored the
39 processes underlying the evolutionary mechanism creat-
40 ing shifts in pheromone composition [9,11], highlighted
41 the interplay between signallers and receivers [5,12] and

provided comprehensive syntheses of their role in sexual
42 selection [4,7,8,13]. However, increasing urbanisation and
43 associated environmental impacts means that the world in
44 which chemical cues and signals had evolved and are
45 maintained is changing at an unprecedented rate. 46

Urbanisation has irreparably and rapidly altered the
47 living environment and increasing evidence suggests
48 that it may promote differences in the behaviour (for a
49 recent review, see [14]) or variation in phenotype [15]
50 between urban and rural populations of the same species.
51 Critically, such dramatic environmental change has the
52 potential to interfere with the long-evolved and well-
53 established communication systems of the species
54 inhabiting the Earth. Perhaps unsurprisingly, given our
55 own sensory bias, the effect of urban noise on acoustic
56 communication is relatively well documented for the
57 vertebrates [16,17] and some acoustically orienting
58 invertebrates [18,19]. In contrast, the degree to which
59 urbanisation may similarly influence chemical signals,
60 and particularly those employed in sexual selection in the
61 insects, is comparatively less well understood. Given
62 the inherent importance of pheromone signals for
63 intra-specific communication [20**] this knowledge
64 gap requires consideration. Moreover, as with other
65 sensory modalities, the efficacy of chemical signals is
66 inherently dependent on their efficient reception. Thus,
67 any environmental change that disrupts signal percep-
68 tion can influence signaller–receiver dynamics resulting
69 in damaging fitness consequences. 70

Here, we focus on four anthropomorphic influences which
71 have the potential to interact with pheromone-mediated
72 sexual selection processes in insects; climatic tempera-
73 ture shifts, exposure to chemical pollutants, the presence
74 of artificial light at night and nutrient availability. In all
75 cases, the impact may be on the capacity of an individual
76 to produce a chemical signal but, and perhaps more
77 significantly, such anthropogenic shifts may also affect
78 the capacity of the receiver to accurately perceive and/or
79 respond to the signal. We acknowledge that this list is not
80 exhaustive and it draws, in some cases, from excellent
81 recent reviews that have taken a different perspective.
82 Our aim is to provide a broad overview of key areas and
83 provide illustrative examples where the changing envi-
84 ronment might specifically affect pheromones utilised in
85 sexual selection in the insects, however, the issues cov-
86 ered are applicable more broadly across other taxa. We
87 hope that the review will prompt further consideration of
88 the potential for anthropogenically-driven environmental
89

2 Special section on pheromones

90 change to promote variation in one of the fundamental
91 signals driving species-specific variation in reproductive
92 success.

93 Anthropogenic influences

94 Climate and temperature

95 A well-documented outcome of industrialisation and
96 urbanisation is a shift in global temperature. Understand-
97 ing how this affects the physiology and behaviour of
98 sexually reproducing organisms is paramount if we are
99 to predict how (or indeed if) species might respond to
100 such change. In insects, climate change research typically
101 focuses on the distribution and expansion of key pest
102 species [21], however, temperature-related phenological
103 mismatches between hosts and prey are documented [22].
104 From the perspective of sexual selection, temperature
105 shifts are linked to variation in both signal production and
106 signal perception [23^{*}]. Temperature-modulated chemi-
107 cal communication is observed in the ladybeetle, *Adalia*
hipunctata [24]. In this species, females use chemical cues
108 produced by juveniles to assess resource quality, typically
109 resulting in a negative relationship between juvenile
110 pheromone production and the number of eggs laid
111 subsequently by females [24]. However, while the quan-
112 tity and quality of pheromones produced by juveniles
113 increases with temperature, at the highest temperature
114 (25 °C) ovipositing females did not distinguish between a
115 control site (with no juvenile pheromones) and one with
116 juvenile pheromones present, resulting in suboptimal
117 placement of eggs within the environment [24]. A similar
118 temperature-related shift in the reliability of the signal
119 occurs in the adult male beewolf, *Philanthus triangulum*. In
120 this species, higher rearing temperatures during the juve-
121 nile phase are beneficial to males as they promote
122 increased juvenile survival and adult male pheromone
123 production [25]. Conversely, at lower temperatures juve-
124 nile survival is reduced, males are physiologically con-
125 strained, and there is increased variance in male phero-
126 mone output. This temperature modulated shift has
127 important fitness consequences for females of this species
128 as they use male pheromone expression as signals of male
129 developmental condition. Thus, at lower temperatures
130 the perceived message accurately reflects male condition,
131 but at higher temperatures even lower quality males are
132 capable of producing the ‘high quality signal’ rendering
133 the honesty within the system effectively lost. In some
134 cases, temperature may be a stronger driver of pheromone
135 expression than the physiological or biochemical state of
136 the signaller. For example, in the moth *Caboptilla frax-*
irella, male response to female pheromones was more
137 strongly influenced by variation in temperature than a
138 hormone-induced variation in reproductive state [26].
139 Ultimately, if the honesty of a particular signal and
140 individual fitness returns are diminished, we would either
141 expect receivers to cease responding to the signal or that
142 alternative signals would need to be employed.

Exposure to chemicals

143 Chemical pollutants have the potential to directly alter
144 the pheromone signal and mask signal perception. In
145 their recent review exploring the effect of air pollution on
146 chemical signalling, McFrederick *et al.* [27] highlighted
147 aggregation pheromones and long-range mate attraction
148 pheromones as being ‘highly vulnerable to perturbation
149 by air pollution’ [27]. Chemical pollutants are perhaps
150 most challenging for long-range chemical orientation as
151 both the efficacy of the signal itself and the receiver
152 response may depend on the ‘scentscape’ of the given
153 environment (*sensu*, [27]). Moreover, extremely low
154 levels of largely abiotic chemical pollutants may act as
155 information disruptors or ‘info-disrupters’ for pheromone
156 communication [28]. For example, exposure to low con-
157 centrations of endocrine disrupters or ‘environmentally
158 safe’ levels of common pesticides can influence the
159 outcome of female choice and/or may shift male expres-
160 sion of pheromones leading to suboptimal female mating
161 preferences [29–32]. Such studies are often carried out on
162 targeted pest species with the view to some form of
163 control, but they have important general repercussions
164 for non-lethal effects of endocrine disruption and their
165 capacity to interfere with reproductive processes in
166 insects [31]. We note that comparable negative effects
167 of chemical pollutants are observed in aquatic environ-
168 ments [33]. Current research in the aquatic environment
169 is not directly related to sexual selection but such studies
170 are similarly concerning as the concentrations causing
171 negative fitness effects are largely below the concentra-
172 tions considered to be non-toxic in the environment
173 and the species-wide fitness implications are largely
174 unknown. 175

Anthropogenic light at night

176 Perhaps the least well recognised and yet arguably most
177 pervasive form of anthropogenic pollution is artificial light
178 pollution. The intensity and spread of artificial light at
179 night is unprecedented in the history of life on earth and
180 the ecological implications are documented for both
181 vertebrates and invertebrates [34]. Underpinning the
182 negative effects of light at night is its inhibitory influence
183 on metabolic pathways associated with biological rhythm
184 and antioxidant capacity [35–37]. At particular risk are
185 crepuscular or nocturnal species whose life-histories
186 and activity patterns are optimised for the nocturnal
187 environment. The capacity for anthropogenic light pol-
188 lution to affect chemical signalling is not intuitive but
189 recent studies suggest that its presence correlates with
190 variation in pheromone signals used in mate choice. In the
191 noctuid moth, *Mamestra brassicae*, the quantity of female
192 moth pheromones was reduced when pupae were reared
193 through to adults in the presence of artificial light at
194 night [38^{*}]. The resulting female pheromones were
195 also qualitatively compromised, containing less of a
196 known preferred male chemical attractant and an increase
197 in a known inhibitory compound [38^{*}]. A suggested
198

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