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8 **Title: Plasticity in a changing world: Behavioural responses to human perturbations**

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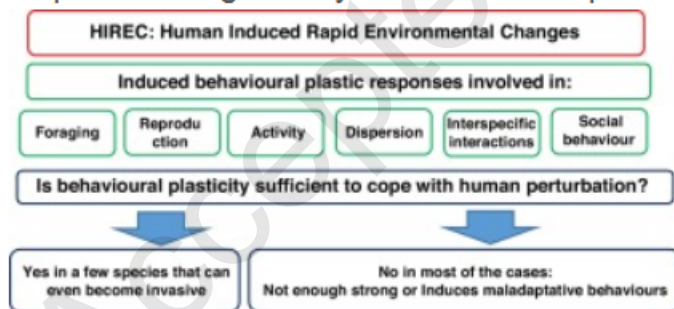
32 **Abstract**

33 Most insect species are affected by Human Induced Rapid Environmental Changes (HIREC). Multiple responses to
34 HIREC are observed in insects, such as modifications of their morphology, physiology, behavioural strategies or
35 phenology. Most of the responses involve phenotypic plasticity rather than genetic evolution. Here, we review the
36 involvement of behavioural plasticity in foraging, reproduction, habitat choice and dispersal; and how behavioural
37 plasticity modifies social behavior and inter-specific interactions. Although important, behavioural plasticity is rarely
38 sufficient to cope with HIREC. An increasing number of studies find species to respond maladaptively or insufficiently
39 to various anthropogenic disturbances, and less often is large degree of plasticity linked to success.

40

Graphical abstract

HIREC can induce plastic responses in all types of behaviours, but these responses are generally insufficient to cope with human perturbations.



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47 **Introduction**

48 Most insect species are affected by Human Induced Rapid Environmental Changes (HIREC, defined by Sih et al.
49 2011)[1], which include variable threats like climate change, habitat fragmentation, habitat loss, human harvesting,
50 and pollution. The species can respond to HIREC, as to any other environmental changes, through plasticity, genetic
51 evolution or dispersal. HIREC generally impact negatively the species. However some species cope well with HIREC and
52 their populations increase to a point where they become themselves a threat to other species. Multiple responses to
53 HIREC are observed in insects, such as modifications of their morphology (eg, size, wing area), physiology (eg, immune
54 response, metabolic rate), behavioural strategies or phenology [2]. Hendry et al. (2008) [3] used meta-analysis
55 dedicated to animals and found most of the responses to involve phenotypic plasticity rather than genetic evolution.
56 Moreover, when genetic changes or shifts in demography, distribution or phenology occurred, these were generally
57 preceded by a modification involving phenotypic plasticity [4]. Thus, behavioural plasticity appears important in
58 explaining variation in the success of species to resist HIREC [5] (Figure 1). The behavioural responses can be either
59 maladaptive, such as the incapacity to detect new predators that can precede species' decline [5], or be adaptive and
60 improve fitness, such as the finding of new host plant species by *Drosophila suzukii* when invading new areas [6]. In
61 this chapter, we examine how behavioural plasticity is involved in insect responses to HIREC during foraging,
62 reproduction, habitat choice and dispersal; and how behavioural plasticity modifies social behavior and inter-specific
63 interactions. We also examine if this plasticity is sufficient to respond adaptively to HIREC or not.

64 **Foraging behavior**

65 The Optimal Foraging Theory (OFT) predicts that generalist species should turn to specialist strategies when resources
66 become rare, such as after habitat changes due to HIREC. Species that show plasticity in their temporal or spatial
67 resource use, such as aphid parasitoids [7], may have a higher ability to resist HIREC. The main plastic response of
68 foraging insects to changes in their habitats is to modify or enlarge their diet choice. Evans & Moustakas (2017) [8]
69 showed with a model that if predators (or species at high trophic level), shift among prey species when the preferred
70 prey becomes unavailable because of climate change, they survive longer. This modification of diet has been observed
71 in phytophagous insects, and sometimes improves resistance to climate change, as shown by Raffa et al. (2016) [9] for
72 bark beetles, and sometimes not, as shown by Pol et al. (2017) [10] for ants. In some species, like the invasive
73 *Drosophila suzukii* that shows extreme plasticity in diet choice, including more than 30 plant species, diet breadth is
74 probably responsible for their success [6]. The capacity of this species to use transgenerational medication (preference

75 of oviposition in fruit containing an entomotoxic substance) contribute to its success [11]. However, *D. suzukii* also
76 oviposits on plants that prevent the development of their larvae. Such traps could represent a cost of extreme
77 plasticity [6].

78 Another solution to climatic stress is to selectively feed on particular types of food. The tropical butterfly *Bicyclus*
79 *anymana*, decreases its activity on hot days and increases its intake of polyphenols (antioxidant) in order to maintain
80 elevated antioxidant levels, which may confer fitness benefits by up-regulating endogenous antioxidant defenses. In
81 grasshoppers, individuals shift their nutrient intake between carbohydrates and proteins depending on temperature
82 and predation stress: indeed, it was shown that a chronic risk of predation (i.e. a chronic stress), induces an elevated
83 metabolism and then a change in nutrient demand and resource consumption and that a higher temperature stands
84 to exacerbate this stress and this diet modification. Growth or reproduction are protein-demanding whereas to cope
85 with stress, a diet balanced towards carbohydrates is more appropriate [12].

86 **Reproductive behaviour**

87 Changes in the environment can influence the ability of individuals to attract and locate mates, as well as their mate
88 choice behaviour. Such changes can alter the number and quality of offspring produced, as well as lead to a
89 demographic Allee effect, and, hence, influence population dynamics [13]. Traffic noise, for instance, interferes with
90 the ability of female field crickets *Gryllus bimaculatus* to locate singing males during mate searching, which can
91 influence their reproductive success [14]. To counteract negative effects of noise on mate location, individuals may
92 alter their mate attraction or mate location behaviour. For example, male grasshoppers *Chortippus biguttulus* elevate
93 the frequency of their courtship song so that it can be distinguished from traffic noise [15].

94 Another common environmental change influencing reproductive behaviours is the increased use of artificial light at
95 night. Male glow-worms *Lampyris noctiluca*, for instance, are less able to locate glowing females under artificial light
96 [16], while females of the Australian black field cricket *Teleogryllus commodus* become less selective in their mate
97 choice [17]. Increased light levels influence also sex pheromone production. For example, females of a noctuid moth
98 *Mamestra brassica* reduce their sex pheromone production when light levels are high [18].

99 Changes in habitat structure are common causes of altered reproductive behaviour. An example is the degradation of
100 tropical cloud forests, which has caused an Afrotropical butterfly *Salamis parhassus* to shift its mate search behaviour

101 from perching to patrolling [19]. Rising temperature and climate change influence in turn the production and
102 reception of sex pheromones [20], as well as the choice of oviposition site [21].

103 **Choice of micro-habitat**

104 The choice of micro-habitat in response to habitat and climate change has received much attention. For example,
105 Burdick et al. (2015) [22] showed that aphids modify their feeding location under increased UV radiation by feeding on
106 the underside of leaves, as this protects against radiation. Alford et al. (2017) [23] showed that aphid parasitoids
107 increase their thermal tolerance and, hence, resistance to climate stress by manipulating the settling place on
108 parasitized aphids.

109 **Activity**

110 As mentioned previously, Beaulieu et al. (2015) [24] recorded a decrease in daily activity of the tropical butterfly on
111 hot days. Physical activity elevates metabolic rate and the production of reactive oxygen species (ROS) and reduced
112 activity consequently limits these effects. The ant *Iridomyrmex purpureus* (Formicidae) employs a range of strategies
113 to overcome high temperature stress, such as adjusting time of foraging to the colder hours of the day, climbing grass
114 blades to cool down, and foraging only within shaded areas [25].

115 The reaction to thermal stress varies among species. For example, Kruse et al. (2008) [26] showed that spiders
116 increase their activity at high temperatures, whereas carabid beetles decrease their activity. Since both are predators
117 on the same prey (flies), these opposite reactions modify the predation rate on the prey.

118 At the seasonal level, Tougeron et al. (2017) [27] observed a change in overwintering strategy following winter
119 warming in aphid parasitoid wasps, from diapause to active state. This plasticity allows individuals to increase their
120 progeny production. The mechanism behind the change is a decrease in responsiveness to environmental signals,
121 rather than a genetic loss of diapause.

122 **Dispersion**

123 Poethke et al. (2010) [28] showed with a model that any persistent deterioration of the environment that decreases
124 expected fitness can induce dispersal behaviour in philopatric organisms. The model was developed for aphids
125 responding to declining population viability due to increased predation pressure, but the model can be applied to any
126 environment deterioration that reduces population viability.

127 **Interspecific interactions**

128 Interactions between species depend on local conditions and, hence, are sensitive to environmental change [29, 30].
129 Pesticides, for instance, shift the competitive relationship between two thrips species so that an intrinsically inferior
130 species *Frankliniella occidentalis* displaces an intrinsically superior competitor *Thrips tabaci* [31]. Climate change and
131 increases in temperature are similarly altering species interactions. Ground beetles, for instance, attack more mobile
132 prey at higher temperatures [32], while the parasitoid *Aphidius rhopalosiphi* attack fewer aphid hosts [33].
133 The invasion of alien species can profoundly alter species interactions and thereby the dynamics of populations [34].
134 When the mosquito *Aedes albopictus* - a vector of Zika, dengue, and chikungunya viruses - invaded North America, it
135 displaced the resident *Ae. aegypti* through interspecific matings that sterilized the resident species [35]. However,
136 invaders can as well have positive effects on ecosystems. When insect pollinators were introduced to the Galapagos
137 Islands, these made more visits to plants than the native species, which improved the stability of the interaction
138 network [36].
139 The loss of species can similarly alter species interactions. When large herbivores were lost from the African savanna,
140 *Acacia* trees invested less in food and shelter rewards for mutualistic ants, which defend the trees against large
141 herbivores and insect pests. A non-mutualistic ant could then occupy the trees, which caused the trees to suffer
142 increased attack by insect pests [37].

143 **Social behaviour**

144 Social behaviour is an important determinant of fitness in social insects. Thus, alteration of social behaviour because
145 of environmental change can have profound demographic consequences [38, 39]. For instance, higher temperature
146 induces a switch from solitary to social lifestyle in sweet bees *Halictus rubicundus*, which increases the number of
147 pollinators, which in turn could mitigate the current pollinator crisis [40]. On the other hand, a rise in temperature can
148 as well disrupt social interactions. For example, higher temperature increases variation in worker size in the ant
149 *Temnothorax nylanderii*, probably through reduced ability of nestmate workers to regulate larval development [41].
150 Changes in the distribution and abundance of resources are common causes of altered frequency or type of social
151 interaction. Changed shelter availability, for instance, influences the formation of social aggregations in the maritime
152 earwig *Anisolabis maritima* [42]. In the pharaoh's ant *Monomorium pharaonic*, changed resource distribution
153 influences pheromone deposition along trails to food sources, which allows ants to communicate and reach adaptive
154 collective decision in changing environments [43].

155 **Is behavioural plasticity sufficient to cope with human perturbation?**

156 In this review, we have shown that behaviourally plastic response to HIREC are common. However, whether the
157 plastic responses are sufficient to prevent population decline and extinction is poorly known. The research field is still
158 in its infancy, and examples are scarce for insects. Some species are able to adjust their behaviour in an adaptive
159 manner to changes, such as bark beetles that use multiple, integrated sensory modalities to adjust their choice of host
160 trees to local conditions [9]. However, an increasing number of studies find species to respond maladaptively or
161 insufficiently to various anthropogenic disturbances. For instance, plasticity in feeding behaviour of the harvester ant
162 *Pogonomyrmex mendozanus* is insufficient for coping with deteriorating food quality [9]. Similarly, most species have
163 limited potential to adjust behaviourally to extreme temperatures and many species are moving towards the poles to
164 escape climate change [25, 44].

165 Ecological traps can worsen survival prospects in changing environments. For instance, jewel beetles (*Julodimorpha*
166 *bakewelli*) copulate with beer bottles because the texture of the bottles resembles that of females [45], while mayflies
167 oviposit on asphalt because the surface reflects polarized light in a similar manner as water bodies [46].

168 Behavioural responses that are insufficient but still improve survival could facilitate evolutionary adaptation by
169 providing more time for genetic changes [47]. This is especially likely in species with short generation time, as
170 suggested for many pest and disease vectors [48].

171 **Conclusions and perspectives**

172 Behavioural plasticity is often not sufficient to cope with HIREC. One explanation is proposed by Sih (2013) [5]: if novel
173 items have been poor options in the evolutionary history of a species, this could explain neophobic behaviours, while
174 if novel items have been beneficial in the past, this could explain neophilic behaviours, which can help species to
175 respond to HIREC. Because HIREC often results in novel conditions, not experienced in the recent evolutionary past,
176 the responses may often be maladaptive and result in population decline. In rare cases, human induced changes can
177 have a positive effect on an ecosystem's stability. For instance, in the Galapagos Islands, an introduced pollinators
178 visited more plants than their native or endemics counterparts, which increased ecosystem stability [36, 49].

179 Two fields of research emerge from this review that need more attention: (1) from a fundamental point of view, more
180 research is needed on the effects of transgenerational plasticity on behavioural responses to environmental change,
181 ie, when environments experienced by the parents influence the responses of offspring. Transgenerational plasticity is
182 increasingly found to be involved in adjustments to variable environments, but the degree to which insects adjust to
183 HIREC through transgenerational plasticity in behaviour is a largely unexplored topic. (2) From an applied point of

184 view, the field of Conservation Behavior should receive more attention. This is a young discipline that investigates how
185 the knowledge of animal behaviour can be taken in consideration in actions for preventing the loss of biodiversity
186 [50].

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195

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323 Figure legend

324 **Figure 1 (adapted from Sih 2013 [5]). Extended reaction norms.** Within a range of normal past conditions, animals
325 **might show optimal reaction norms that match environmental optima reasonably well.** In condition A, just outside
326 **of the range of past conditions, organisms might simply extend their reaction norms;** however, beyond some
327 **threshold (condition B), lack of past selection might allow the maintenance of genetic variation in reaction norms,**
328 **some of which might come close to matching even a very different optimum in a novel condition that is well outside**
329 **the range of past conditions. The stars represent the optimal trait in each environment.**
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