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

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31 Abstract

32 Most insect species are affected by Human Induced Rapid Environmental Changes (HIREC). Multiple responses to HIREC

33 are observed in insects, such as modifications of their morphology, physiology, behavioural strategies or phenology.

34 Most of the responses involve phenotypic plasticity rather than genetic evolution. Here, we review the involvement of

35 behavioural plasticity in foraging, reproduction, habitat choice and dispersal; and how behavioural plasticity modifies

36 social behavior and inter-specific interactions. Although important, behavioural plasticity is rarely sufficient to cope with

37 HIREC. An increasing number of studies find species to respond maladaptively or insufficiently to various anthropogenic

38 disturbances, and less often is large degree of plasticity linked to success.

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Introduction

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

Foraging behavior

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

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

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

Reproductive behaviour

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

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

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

107 from perching to patrolling [19]. Rising temperature and climate change influence in turn the production and reception

108 of sex pheromones [20], as well as the choice of oviposition site [21].

109 Choice of micro-habitat

110 The choice of micro-habitat in response to habitat and climate change has received much attention. For example,

111 Burdick et al. (2015) [22] showed that aphids modify their feeding location under increased UV radiation by feeding on

112 the underside of leaves, as this protects against radiation. Alford et al. (2017) [23] showed that aphid parasitoids

113 increase their thermal tolerance and, hence, resistance to climate stress by manipulating the settling place on

114 parasitized aphids.

115 Activity

116 As mentioned previously, Beaulieu et al. (2015) [24] recorded a decrease in daily activity of the tropical butterfly on hot

117 days. Physical activity elevates metabolic rate and the production of reactive oxygen species (ROS) and reduced activity

118 consequently limits these effects. The ant *Iridomyrmex purpureus* (Formicidae) employs a range of strategies to

119 overcome high temperature stress, such as adjusting time of foraging to the colder hours of the day, climbing grass

120 blades to cool down, and foraging only within shaded areas [25].

121 The reaction to thermal stress varies among species. For example, Kruse et al. (2008) [26] showed that spiders increase

122 their activity at high temperatures, whereas carabid beetles decrease their activity. Since both are predators on the

123 same prey (flies), these opposite reactions modify the predation rate on the prey.

124 At the seasonal level, Tougeron et al. (2017) [27] observed a change in overwintering strategy following winter warming

125 in aphid parasitoid wasps, from diapause to active state. This plasticity allows individuals to increase their progeny

126 production. The mechanism behind the change is a decrease in responsiveness to environmental signals, rather than a

127 genetic loss of diapause.

128 Dispersion

129 Poethke et al. (2010) [28] showed with a model that any persistent deterioration of the environment that decreases

130 expected fitness can induce dispersal behaviour in philopatric organisms. The model was developed for aphids

131 responding to declining population viability due to increased predation pressure, but the model can be applied to any

132 environment deterioration that reduces population viability.

133 Interspecific interactions

134   Interactions between species depend on local conditions and, hence, are sensitive to environmental change [29, 30].

135   Pesticides, for instance, shift the competitive relationship between two thrips species so that an intrinsically inferior

136   species *Frankliniella occidentalis* displaces an intrinsically superior competitor *Thrips tabaci* [31]. Climate change and

137   increases in temperature are similarly altering species interactions. Ground beetles, for instance, attack more mobile

138   prey at higher temperatures [32], while the parasitoid *Aphidius rhopalosiphi* attack fewer aphid hosts [33].

139   The invasion of alien species can profoundly alter species interactions and thereby the dynamics of populations [34].

140   When the mosquito *Aedes albopictus* - a vector of Zika, dengue, and chikungunya viruses - invaded North America, it

141   displaced the resident *Ae. aegypti* through interspecific matings that sterilized the resident species   [35]. However,

142   invaders can as well have positive effects on ecosystems. When insect pollinators were introduced to the Galápagos

143   Islands, these made more visits to plants than the native species, which improved the stability of the interaction network

144   [36].

145   The loss of species can similarly alter species interactions. When large herbivores were lost from the African savanna,

146   *Acacia* trees invested less in food and shelter rewards for mutualistic ants, which defend the trees against large

147   herbivores and insect pests. A non-mutualistic ant could then occupy the trees, which caused the trees to suffer

148   increased attack by insect pests [37].

149   Social behaviour

150   Social behaviour is an important determinant of fitness in social insects. Thus, alteration of social behaviour because of

151   environmental change can have profound demographic consequences [38, 39]. For instance, higher temperature

152   induces a switch from solitary to social lifestyle in sweet bees *Halictus rubicundus*, which increases the number of

153   pollinators, which in turn could mitigate the current pollinator crisis [40]. On the other hand, a rise in temperature can

154   as well disrupt social interactions. For example, higher temperature increases variation in worker size in the ant

155   *Temnothorax nylanderi*, probably through reduced ability of nestmate workers to regulate larval development [41].

156   Changes in the distribution and abundance of resources are common causes of altered frequency or type of social

157   interaction. Changed shelter availability, for instance, influences the formation of social aggregations in the maritime

158   earwig *Anisolabis maritima* [42]. In the pharaoh's ant *Monomorium pharaonic,* changed resource distribution influences

159   pheromone deposition along trails to food sources, which allows ants to communicate and reach adaptive collective

160   decision in changing environments [43].

161   Is behavioural plasticity sufficient to cope with human perturbation?

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

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

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

Conclusions and perspectives

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

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

the field of Conservation Behavior should receive more attention. This is a young discipline that investigates how the

knowledge of animal behaviour can be taken in consideration in actions for preventing the loss of biodiversity [50].

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339   Figure legend

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