Insect Evolutionary Traps: An Anthropogenic Decoupling of Preference and Performance

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Insects like any other animals use environmental cues to find suitable resources and execute behaviours which can increase their fitness (Robertson *et al.,* 2013). This kind of cue-response system (*e.g.* response to the smell of food by attacking, response to the sight of mate by copulating *etc.*) becomes adaptive over generations but the problem arises when human-induced rapid environmental changes (HIREC) alter these environmental cues in such a way that the previously adaptive behaviour becomes associated with novel habitats that are dangerous or novel resources that can drastically reduce the fitness creating an 'evolutionary trap' (Robertson and Hutto, 2006 and Greggor *et al.,* 2019). These kinds of behavioural maladaptation in the context of habitat selection, foraging, navigation, oviposition and mate selection act as attractive population sinks which not only drive the animals away from positive-fitness resources but rapidly reduce their numbers, even, threatening the species persistence (Fletcher *et al*., 2012 and Robertson *et al*., 2017). In this mini-review, we will first discuss few notable examples of evolutionary traps related to insects, then try to understand the ecological and evolutionary principles underlying this phenomenon and close with a short note on its implication and future areas of research.

Beer is one of the popular beverages among Australians but back in the '80s, they were quite careless in dumping their 'stubbies' – an Australian nickname for beer bottles. People often used to casually throw them out of the car's window and filled the roadsides of Western Australia. These fellows never realized that a group of six-legged males can make use of those stubbies to satisfy their 'forbidden lust'. *Julodimorpha bakewelli* (Buprestidae: Coleoptera) is a jewel beetle inhabiting the arid regions of Australia. The females of this beetle are larger than the males and dimples on their shiny brown elytra serve as a cue for a potential mate to the males. During the mating seasons (August-September) in the '80s, the light reflected from dimpled glass rims at the bottom of the brown stubbies started attracting the male beetles (Gwyne and Rentz, 1983). To the male *J. bakewelli*, a beer bottle lying on the ground looks like a big, sexy and irresistible female. A male immediately mounts the bottle (Fig.1a), tries to insert his penis and during this hardcore sex, he either dies because of scorching sun and mating injuries or gets consumed by the local ants. The males busy with their beer bottles not only ignored the females but experienced reduced survival over the years pushing the species to the verge of extinction. This apparently funny but ecologically depressing incident forced the beer companies to change the shape of their bottles.

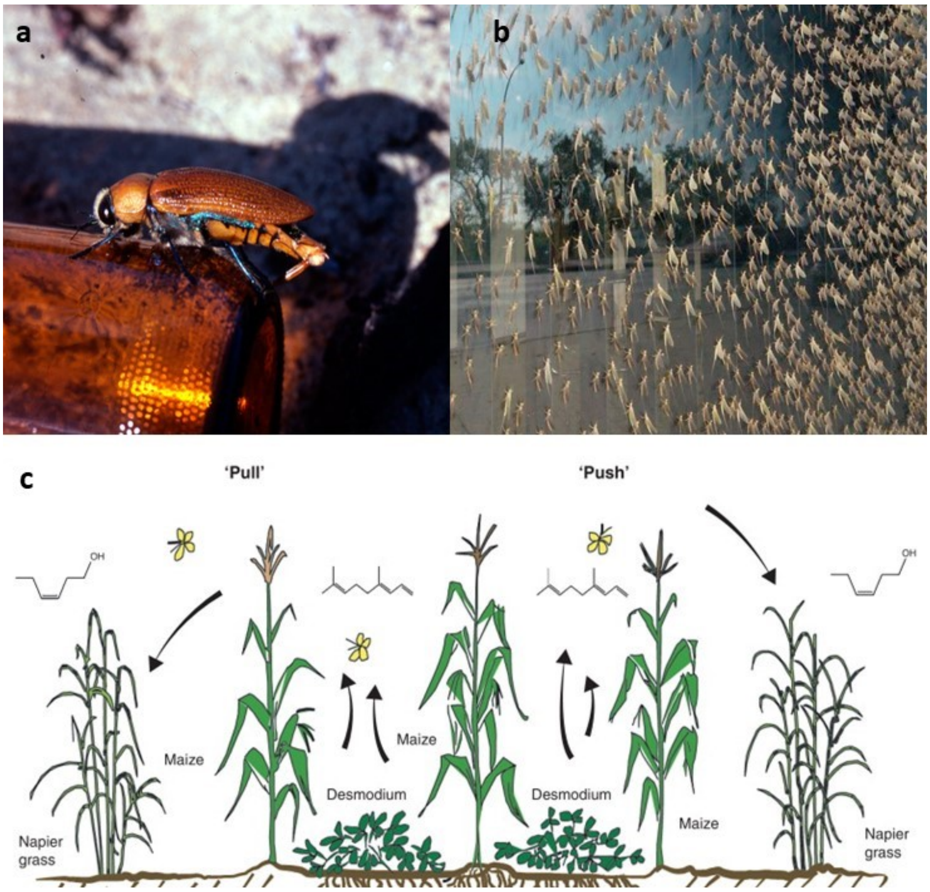

Fig. 1. Example of few evolutionary traps triggering maladaptive behaviour in insects. a) Male *Julodiomorpha bakewelli* mounting a beer bottle(©Darryl Gwynne), b) a group of mayflies attracted to polarized light from a glass window pane(©Will Milne), (Both adapted from Robertson *et al*., 2013) c) push-pull farming involving Napier grass as trap crop to attract the maize borers (modified from Pickett *et al*., 2014).

The search for effective utilization of non-conventional sources of energy has led mankind to invent photovoltaic solar panels with the aim of reducing environmental pollution and boosting ecological sustainability. Surprisingly, the solar panels have been identified as a strong source of polarized light pollution attracting water-seeking (semi)aquatic insects (Horvath *et al*., 2010). Especially the (most widely used) dark coloured solar panels which horizontally polarize the reflected sunlight (90-100% compared to 30-80% from natural water bodies) mimicking the cue a lot of aquatic insects rely upon to identify water bodies suitable for mating or oviposition. In addition to solar panels, other man-made dark coloured objects like glass buildings, and asphalt roads equally influence the decision making of these insects (Fig. 1b) (Kriska *et al*., 1998 and 2008). These supernormally polarized light sources have become preferentially attractive for the aquatic insects and as a result, the adults fail to find a mate and the eggs fail to hatch ultimately bringing their population down (Robertson and Chalfoun, 2016). Aquatic insects have an innate preference for surface areas with increasingly higher percentages of polarized light which eventually make them susceptible to fall prey to such rapid anthropogenic changes (Robertson *et al*., 2019). Recently, a field experiment with adult water-seeking insects across four taxonomic groups *viz*., Chironomidae (10,102), Simuliidae (556), Trichoptera (181) and Ephemeroptera (147) has shown more than 40% adjusted capture for the first three groups and nearly 30% of the same for Ephemeroptera on entirely black solar panels compared to the manipulated panels with different width and density of white gridding where the adjusted capture was reduced to nearly 95% (Black and Robertson, 2020). Of course, the result highlights the severity of such 'solar traps' but it also suggests a way to mitigate the challenge by modest reduction of photoactive area (2-3%) of the panels. Besides aquatic insects, light pollution by artificial city lights has immensely contributed to a rapid decline of nocturnal insects (including pollinators and predators of pests) by impairing their navigation abilities, ocular sensitivity, host-seeking and ovipositional behaviour, pupation and diapause (Owens and Lewis, 2018).

In the earlier examples, the evolutionary traps were created unintentionally, yet drastically affected the species performance creating a higher preference towards negative fitness resources, but such traps can also be set intentionally to manage pestiferous and invasive species. Professor Zeyaur Khan, an IARI graduate and Indo-African scientist, has spent decades for the development of 'push-pull farming' targeting insect's olfactory behaviour of host selection. Thousands of farmers in East Africa have adopted this strategy to protect their maize and sorghum from borer pests (*Chilo partellus*, *Busseola fusca*, *Sesamia calamistis* and *Eladna saccharina*). Molasses grass (*Melinis minutiflora*) and desmodium (*Desmodium uncinatum* and *D. intortum*), when intercropped with maize or sorghum, repel the stem borers and additionally volatiles from molasses increase parasitism by *Cotesia sesamiae*. On the other hand, volatiles from the so-called 'trap crop' of Napier and Sudan grass (*Pennisetum purpureum* and *Sorghum vulgare sudanense*) surrounding the main crop field not only attract the stem borers for oviposition but restricts the larval development with physiological impairments and recruitment of natural enemies (Fig. 1c) (Khan *et al.,* 1997 and 2006). This approach of utilizing an evolutionary trap contributed to increased crop yields, livestock production, enhanced food security and ecological sustainability (Khan and Pickett, 2004 and Robertson *et al.,* 2017). The same principles are now widely used to control *Helicoverpa* in Cotton, Colorado beetle in potatoes, maggots in onion, thrips in chrysanthemum, bark beetles in conifers and different pests of medical and veterinary importance (Cook *et al.,* 2007). In addition to planting crops emitting volatiles attractive to pests, several other traps targeting the insects' visual and olfactory responses such as light trap, yellow sticky plates and pheromone lures have been recommended as an integral part of conservation agricultural practices. The innate phototactic behaviour of many nocturnal insects has provided the basis of designing insecticide based light traps and electric insect killers. Equipped with fluorescent electric tubes the electric insect killers have been widely used for managing household and glasshouse pests such as mosquitoes, moths and beetles. Insecticide based light traps with blue fluorescent light were widely used to control rice borers *Tryporyza incertulus* and *Chilo suppressalis* in Japan during World war-II and afterwards (Ishikura, 1950). Yellow sticky plates and roles have become popular tools to attract and trap a lot of diurnal insects possessing an innate attraction for yellow colours such as planthoppers, leafhoppers, aphids, whiteflies, thrips and leafminers (Shimoda *et al.,* 2013). The pheromone lures, on the other hand, are designed to manipulate the olfactory behaviour of insects. Semiochemicals released from either of the sexes inducing aggregation, foraging or mate searching responses have been synthesized in-vitro and implemented in crop fields, orchards and vineyards for pest monitoring, mating disruption and mass trapping purposes. Pheromone dispensers releasing synthetic sex pheromone plumes at a fixed rate confuse the males and reduce the frequency with which they encounter calling females and thus disrupt the mating and reproduction. The technique has been successfully implemented against bollworms, fruit sucking moths, stem borers, gypsy moths, oriental beetles *etc* (Tewari *et al.,* 2014). Mass trapping involves the use of attractive semiochemicals to lure the pest population towards killing devices such as small amount of insecticides, adhesives, water or other physical killing agents. This strategy gained huge success inmanaging bollworms, tephritid fruitflies, boll weevil, codling moth, bark beetles and palm weevils (El-Sayed *et al.,* 2009 and Tewari *et al.,* 2014).

From the examples cited above, it is quite clear that the 'insect evolutionary trap' occurs when human activity creates or manipulates the environment in such a way that an insect's adaptive strategies no longer correlate with increased fitness and as a result, it prefers to choose dangerous resources or behaviours despite having better options (Robertson and Chalfoun, 2016). In case of any organism, including insects, natural selection should align the relative preference for a resource (*e.g.* mate, food item, territory) with its fitness value such that resources which provide better fitness rewards are preferred over those with a lower fitness value. But human-induced rapid environmental change may decouple this preference-performance correlation such that organisms preferentially exploit negative fitness resources (evolutionary traps) or avoid high-quality resources, which would otherwise increase its fitness (undervalued resources) (Fig. 2) (Robertson *et al*., 2017).

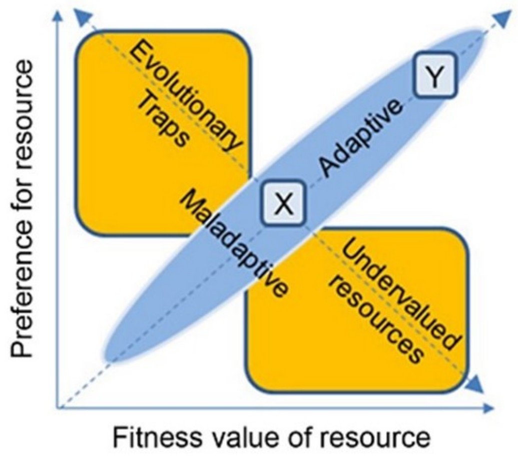

Fig. 2. A conceptual diagram showing the relationship between preference for resources with fitness value associated with the resources. Blue ovoid region indicates the effect of natural selection and yellow rectangles represent trajectories under human induced environmental changes (Adapted from Robertson *et al.,* 2017).

A deep understanding of sensory, cognitive and behavioural mechanisms of a species is necessary to discern its susceptibility towards a trap. Animals often need to generalize cues from experiences as familiar cues also vary in time and space. It is a pitfall where novel environmental changes may also be perceived under the generalized cue. This is the reason why the male *Julodiomorpha* beetles fell for the stubbies. The degree of difference between a familiar and a novel cue determines whether an insect should behave adaptively or it requires further presentation of cues to learn and act accordingly (Ferrari *et al.,* 2007, 2016). Individuals within and between populations differ greatly in their behavioural tendencies (Sih *et al.,* 2004). The bolder individuals are more likely to explore novel cues compared to the shy ones. In that case aggressive, bolder individuals will be easily attracted towards post-HIREC novel dangers and succumb to such evolutionary traps. In this way, even if some traps cannot cause an abrupt decline in species or population, they may exert strong selection pressure depending on personality phenotypes (Madden and Whiteside, 2014). The success of an evolutionary trap also depends on whether it is a single opportunity or a multiple opportunity trap. In case of a single opportunity trap (like toxic food or oviposition site), the outcome of an error is fatal leaving no place for learning but a multiple opportunity trap (such as unpleasant but not fatal gustatory response) can offer scope for learning and avoiding the danger (Greggor *et al*., 2019)

A comprehensive understanding of insect evolutionary traps is necessary both for the conservation of endangered insects and controlling pestiferous and invasive species. The biological principles that cause the decline of nocturnal pollinators by night light pollution are the same to be used for light trapping of nocturnal pests, the quantity and quality of stimulus being the difference. From the conservation point of view, an evolutionary trap can be disarmed by reducing the attractiveness of a trap; increasing its fitness values; or both (Robertson *et al*., 2013). Assessing an anthropogenic novel change as a potential evolutionary trap is of first and foremost importance which require overall consideration of key components of an ecosystem and their interactions. Cautious ecological restoration by increasing habitat connectivity between positive-fitness patches can increase the habitat availability for mobile species making them less vulnerable to succumb to patches with negative fitness value. From the pest management point of view, the efficacy of an evolutionary trap depends on its attractiveness. In simple words, to trap a pest, a negative fitness resource must be (made) attractive over other options available to the pest. Farmers and folks have been using different kinds of evolutionary traps to deter or kill agricultural, livestock and household pests since ages even before the term was scientifically defined. The major risk associated with exploiting an evolutionary trap is its direct and indirect effect on non-target organisms (Robertson *et al*., 2017). However, the framework of an evolutionary trap has a great potential for large scale population control and eradication by making it more taxon-specific, and resistant to escape based on physiological, ecological and evolutionary responses. Multidisciplinary research oriented towards behavioural biology, sensitive and cognitive ecology, the molecular and physiological basis of phenotypic plasticity may yield deeper insights about how well an evolutionary trap can be utilized for pest management or disarmed for the conservation of biodiversity.

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