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Use of habitat odour by host-seeking insects

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USE OF HABITAT ODOUR BY HOST-SEEKING INSECTS

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For Review Only

9 ABSTRACT

10 Locating suitable feeding or oviposition sites is essential for insect survival. Understanding
11 how insects achieve this is crucial, not only for understanding ecology and evolution of
12 insect-host interactions, but also for the development of sustainable pest control strategies
13 that exploit insects' host-seeking behaviours. Volatile chemical cues are used by foraging
14 insects to locate and recognise potential hosts but in nature these resources usually are
15 patchily distributed, making chance encounters with host odour plumes rare over distances
16 greater than 10s of meters. The majority of studies on insect host-seeking have focussed on
17 short-range orientation to easily-detectable cues and it is only recently we have begun to
18 understand how insects overcome this challenge. Recent advances show that insects from a
19 wide range of feeding guilds make use of 'habitat cues', volatile chemical cues released over
20 a relatively large area that indicate a locale where more specific host cues are most likely to
21 be found. Habitat cues differ from host cues in that they tend to be released in larger
22 quantities, are more easily detectable over longer distances, and may lack specificity, yet
23 provide an effective way for insects to maximise their chances of subsequently encountering
24 specific host cues. This review brings together recent advances in this area, discussing key
25 examples and similarities in strategies used by haematophagous insects, soil-dwelling insects
26 and insects that forage around plants. We also propose and provide evidence for a new theory
27 that general and non-host plant volatiles can be used by foraging herbivores to locate patches
28 of vegetation at a distance in the absence of more specific host-cues, explaining some of the
29 many discrepancies between lab and field trials that attempt to make use of plant-derived
30 repellents for controlling insect pests.

31 *Key words:* habitat cues, host location, olfaction, semiochemicals, insect-host interactions,
32 insect behaviour.

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34	47	I. INTRODUCTION	

48 Over the years considerable knowledge has accumulated on how insects use volatile chemical
 49 cues to locate and recognise their respective host species. These cues usually consist of
 50 specific-characteristic blends of volatile compounds or, in some cases, individual volatiles
 51 that are restricted to a narrow range of related host species (Bruce, Wadhams & Woodcock,
 52 2005; Bruce & Pickett, 2011). These cues offer an effective means of locating a host at short
 53 range but, due to the physical properties of odour plumes, chance encounters with host odour
 54 at longer distances are rare. Volatiles emanating from an odour source in wind form an odour
 55 plume that meanders downwind. Molecular diffusion occurs at too small a scale to contribute
 56 significantly to plume structure and the distribution of odours within the plume's overall
 57 boundaries is mainly dictated by the forces of turbulence, which creates discrete filaments of

1
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3 58 relatively undiluted odour interspersed with clean air (Murlis, Elkinton & Cardé, 1992;
4
5 59 Voskamp, Den Otter & Noorman, 1998; Koehl, 2006). Many insects are adept at following
6
7 60 these plumes (Murlis *et al.*, 1992; Cardé & Willis, 2008; Bau & Cardé, 2015). Voskamp *et al.*
8
9 61 (1998) showed that tsetse flies detected odour plumes up to 10-20 m downwind of an odour
10
11 62 source in an open field and up to 60 m in woodland. At longer distances, however, odourant
12
13 63 concentration can fall below insect detection thresholds (Murlis, Willis & Cardé, 2000;
14
15 64 Koehl, 2006) and, together with increased intermittency of plume encounter (Koehl, 2006;
16
17 65 Beyaert & Hilker, 2014), this means that insects' abilities to use host-originating odour to
18
19 66 locate a feeding or oviposition site becomes increasingly difficult. This presents an enormous
20
21 67 challenge to host-seeking insects. In areas with high plant species diversity, suitable hosts for
22
23 68 phytophagous insects may be patchily distributed (Randlkofer *et al.*, 2010) and insects may
24
25 69 not come close enough to detect odour plumes using random foraging movements alone,
26
27 70 particularly if hosts are hidden within dense patches of non-host vegetation that may obstruct
28
29 71 or adsorb odour (Beyaert & Hilker, 2014). Haematophagous insects face a similar problem
30
31 72 since their animal hosts may occupy large home ranges with distances of up to many
32
33 73 kilometres between individuals or groups of individuals (Potts & Lewis, 2014).

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39 74 Where host odour cues are difficult to locate, the use of 'habitat odour cues' provides insects
40
41 75 with a means of increasing their foraging success. As opposed to 'host cues' in the traditional
42
43 76 sense, which are used to locate specific feeding or oviposition sites, habitat cues indicate a
44
45 77 general area where such sites or associated cues are *most likely* to be found (Bell, 1990;
46
47 78 Meiners, 2015). From a behavioural ecology perspective, habitat odour may be many things.
48
49 79 Habitat odour may comprise the collective volatile emissions of all organisms inhabiting a
50
51 80 potential foraging patch. Many of the volatile compounds that insects can detect are found
52
53 81 ubiquitously across the plant or animal kingdoms, produced by host and non-host alike. For
54
55 82 example, green leaf volatiles and other ubiquitous plant volatiles can indicate the presence of
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3 83 a patch of vegetation in a heterogeneous landscape. Respiratory CO₂ emissions produced by
4
5 84 plant roots or animals can provide information on the presence of a patch of vegetation to
6
7 85 below-ground feeding herbivores or a group of animals to blood-feeding insects.
8
9
10 86 Alternatively, habitat odour may be associated with the collective secretions or excretions of
11
12 87 host organisms, for example odours associated with dwellings or nests of animals that are
13
14 88 hosts to blood-feeding insects. Since they tend to be produced over larger areas or by many
15
16 89 different organisms within a habitat, habitat odour is generally emitted in greater quantities
17
18 90 and detectable at greater distances than host odour, providing insects with information on a
19
20 91 location to search for more host-specific volatile cues. The main ways in which habitat and
21
22 92 host odour cues differ are summarised in Table 1.

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26 93 Habitat cues may serve to increase foraging efficiency in a number of ways (Fig. 1). Insects
27
28 94 may fly upwind in response to a habitat-odour plume before engaging in hierarchical plume
29
30 95 switching (Beyaert & Hilker, 2014), abandoning the former long-range cue in favour of
31
32 96 following the host plume to its source. Alternatively, habitat cues present as background
33
34 97 odour may induce non-directional localised searching behaviours, for example through
35
36 98 increases in rates of turning or changes in speed of movement in order to increase the
37
38 99 probability of intercepting a host plume, after which movement upwind toward the host can
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40
41 100 occur. In these first two scenarios, habitat and host odour are encountered sequentially and
42
43 101 encounter with host odour must override any behavioural response to the habitat odour cue.
44
45
46 102 Habitat cues may also act in conjunction with host cues, reinforcing behavioural responses
47
48 103 when detected by insects at the same time by providing important contextual information.
49
50 104 Here, detection of habitat odour may sensitise insects to host volatiles, enhancing their
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52 105 responsiveness to these cues (Dekker, Geier & Cardé, 2005; Schröder & Hilker, 2008). This
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54 106 sensitization may work in conjunction with upwind flight and localised search behaviours in
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3 107 response to habitat cues (Fig 1a & b), ensuring that insects respond strongly to host cues once
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5 108 they are encountered.
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8 109 Since habitat odour is generally released over a relatively large area and in large quantities,
9
10 110 foraging insects will find themselves exposed to habitat odour cues for lengthy periods of
11
12 111 time. Constant exposure to these background odourants can eventually result in olfactory
13
14 112 adaptation and habituation (Schröder & Hilker, 2008), meaning insects may become less
15
16 113 responsive to habitat cues over time. This may serve to allow insects to ‘give up’ on a
17
18 114 resource patch after failing to locate any host cues within it. Alternatively, constant exposure
19
20 115 to habitat odour could lead to sensitisation, reinforcing the behavioural response over time.
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24 116 **II. USE OF HABITAT CUES BY FORAGING INSECTS**

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26
27 117 The majority of studies on insect host location have focussed on easily detectable, short-range
28
29 118 cues originating from the host and it is only recently that evidence of habitat cue use has
30
31 119 emerged. Their use now appears to be exceptionally widespread, employed by insects from a
32
33 120 diverse range of feeding guilds including soil-dwelling insects, haematophagous insects,
34
35 121 predatory and parasitic insects, above-ground herbivores, and pollinators. The seemingly
36
37 122 widespread use of these cues suggests they are a fundamental component of insect host
38
39 123 location. Key examples from each of these insect feeding guilds are described below.
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43 124 **(1) Soil-dwelling insects**

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46 125 Herbivorous insects that dwell within the soil make use of exudates from roots to locate
47
48 126 suitable feeding sites (Johnson & Gregory, 2006a; Johnson & Nielsen, 2012) and these often
49
50 127 confer species-specific information on host identity (Soni & Finch, 1979; Rogers & Evans,
51
52 128 2013a). Respiratory CO₂ emissions have also been shown to elicit behavioural responses
53
54 129 from a range of root-feeding insects, suggesting a role in host location (Johnson *et al.*, 2012).
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3 130 Carbon dioxide is generally produced in much higher quantities than other root exudates and
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5 131 diffuses relatively rapidly through the soil (Payne & Gregory, 1988), making it detectable at
6
7 132 greater distances (Johnson & Nielsen., 2012). Carbon dioxide emission from roots is
8
9 133 ubiquitous, produced by all respiring tissue, and also exhibits strong vertical gradients
10
11 134 between the upper soil and air and, in areas of high root density, horizontal concentration
12
13 135 gradients may not always be perceptible to soil-dwelling insects (Johnson *et al.*, 2006b). This
14
15
16 136 led Johnson and Gregory (2006a) to question the role of CO₂ in host location, particularly for
17
18 137 specialist root herbivores for which CO₂ is unlikely to confer sufficient information. Instead,
19
20 138 they proposed that CO₂ serves to inform as to the presence of a nearby patch of plants where
21
22 139 more specific root exudates may subsequently be searched for, thus functioning as a ‘search
23
24 140 trigger’ rather than a host cue. This hypothesis was supported by behavioural studies on the
25
26 141 larvae of the root-feeding clover weevil, *Sitona lepidus* (Johnson *et al.*, 2006b). In
27
28 142 behavioural experiments, no evidence of oriented movement towards point emissions of CO₂
29
30 143 was observed, regardless of emission rates. In the presence of constant CO₂ emissions,
31
32 144 however, larvae made more tortuous and intensive searching movements compared to CO₂-
33
34 145 free experiments, allowing insects to increase their chances of intercepting other root-derived
35
36 146 chemical cues. Similar effects were observed for larvae of the wheat bulb fly, *Delia*
37
38 147 *coarctata*, which displayed increased rates of turning and track length in elevated CO₂ but did
39
40 148 not orientate toward point emissions in arena-based behavioural experiments (Rogers *et al.*,
41
42 149 2013b).

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48 150 Reinecke *et al.* (2008) showed that exudates from undamaged roots of dandelion inhibited
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50 151 behavioural responses of the European cockchafer (*Melolontha melolontha*) to CO₂. This was
51
52 152 interpreted as a possible plant defence strategy, with exudates serving to mask the
53
54 153 attractiveness of the long range cue. An alternative hypothesis is that these exudates may be
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56 154 used by host-seeking larvae to switch off responses to CO₂ when close enough to a plant
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3 155 patch to be able to make use of more specific host cues or localised searching behaviours.
4
5 156 Once host root exudates reach sufficient concentrations for inhibition of CO₂ detection, they
6
7 157 are presumably also in sufficient concentrations to be used for host orientation, making CO₂ a
8
9 158 redundant and, due to large horizontal gradients in CO₂ concentration close to dense plant
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11 159 patches, potentially disruptive signal at short range (Johnson & Gregory, 2006a). These two
12
13 160 hypotheses are not mutually exclusive but further work is needed to validate either,
14
15 161 preferably involving realistic plant densities that would be encountered by root-feeding larvae
16
17 162 in field conditions. The use of host-originating CO₂ inhibitors may be a widespread
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19 163 phenomenon and future studies may uncover their use by other soil-dwelling insects.
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24 (2) Haematophagous insects

25
26 165 Like root-feeding herbivores, haematophagous insects make use of a combination of CO₂ and
27
28 166 more specific host volatiles, as well as heat, to locate a feeding site. The malaria mosquito,
29
30 167 *Anopheles gambiae*, prefers to feed on human hosts and readily responds to human body
31
32 168 odour in a wind tunnel by flying upwind but tends not to land on the source of emission
33
34 169 unless it is heated (Spitzen *et al.*, 2013). We recently found that, when placed in a screen cage
35
36 170 containing a source of human odour female *An. gambiae* did not land on the human odour
37
38 171 source unless CO₂ was delivered through the side of the cage, instead preferring to rest on the
39
40 172 walls and ceiling in the absence of CO₂ (Webster, Lacey & Cardé, 2015). Similar
41
42 173 observations were made for the yellow fever mosquito, *Aedes aegypti*, which was found not
43
44 174 to feed through a membrane when presented with human odour alone but nevertheless flew
45
46 175 upwind upon detection of human odourants (Lacey, Ray & Cardé, 2014; McMeniman *et al.*,
47
48 176 2014). Anthropophilic mosquitoes such as *An. gambiae* search for blood meals in and around
49
50 177 human dwellings. In our study we suggested that human odour, in the absence of carbon
51
52 178 dioxide or heat, serves as a means for mosquitoes to locate a human dwelling since these
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54 179 continuously emit human odour even when its occupants are absent (Webster *et al.*, 2015).
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3 180 On its own, human odour therefore likely serves as a habitat cue for these species, inducing
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5 181 location of and arrestment within a human dwelling, an ideal habitat within which to
6
7 182 subsequently search for a blood meal. Once CO₂ or heat indicates a human is present, human
8
9 183 odour acts together with these other cues to function as a host cue. This is an example of how
10
11 184 the same volatile compounds can function as both habitat and host cue depending upon the
12
13 185 context in which they are detected. Similar habitat cues are also used by mosquitoes feeding
14
15 186 on non-human animals. The southern house mosquito, *Culex quinquefasciatus*, preferentially
16
17 187 obtains blood meals from birds and is attracted by the odour of fresh chicken faeces, an
18
19 188 effective cue indicating a physical location recently occupied by potential hosts (Cooperband
20
21 189 *et al.*, 2008). Behavioural responses of haematophagous insects to urine and faecal odour are
22
23 190 widespread and these offer effective and sometimes host-characteristic cues indicating a nest
24
25 191 or general area regularly inhabited by potential hosts (Becker *et al.*, 1995; Baldacchino *et al.*,
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27 192 2013; Nordéus *et al.*, 2014).

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31
32 193 Exhaled CO₂ is generally considered a host cue for haematophagous insects (Cardé &
33
34 194 Gibson, 2010) but recent studies have led us to question this hypothesis. Exhaled CO₂ offers
35
36 195 little information regarding host species but is detectable over large distances (Zöllner *et al.*,
37
38 196 2004; Lorenz *et al.*, 2013) and, since many haematophagous insects tend to prefer social
39
40 197 animals as hosts (Lehane, 2005), combined exhalations of a group of animals offers an
41
42 198 effective long-range cue indicating a general area inhabited by potential hosts. Whilst CO₂
43
44 199 elicits upwind flight and plume following, haematophagous insects tend not to orient toward
45
46 200 or land on the source at close range (Spitzen, Smallegange & Takken, 2008), instead
47
48 201 initiating rapid 'zigzag' flight behaviour in the general vicinity of the CO₂ source (Spitzen *et*
49
50 202 *al.*, 2008; Lacey *et al.*, 2014). This suggests a switch to localised searching behaviour in order
51
52 203 to make contact with more specific host cues indicating potential feeding sites. Carbon
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54 204 dioxide therefore seems to function more as a 'habitat' cue by indicating a general area
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3 205 occupied by potential hosts where more specific host cues may be subsequently located,
4
5 206 similar to the model proposed by Johnson and Gregory (Johnson *et al.*, 2006a) used by root-
6
7 207 feeding herbivores. Support for this hypothesis comes from that fact that at close range CO₂
8
9 208 is almost completely ignored in favour of skin odour by most haematophagous insects. *Aedes*
10
11 209 *aegypti* readily flies upwind along a plume of CO₂ but, when presented with a human foot-
12
13 210 odour plume in parallel, the CO₂ plume was completely ignored (Lacey *et al.*, 2014). Similar
14
15 211 observations were made for *Cx. quinquefasciatus*, which also seemed to orient at long range
16
17 212 to CO₂ but only used human odour at close range for landing (Lacey & Cardé, 2011).

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21 213 As with root-feeding herbivores, volatiles that inhibit detection of CO₂ by haematophagous
22
23 214 insects have recently been uncovered (Tauxe *et al.*, 2013). These compounds were identified
24
25 215 using *in-silico* screening to predict chemical structures likely to interact with the CO₂
26
27 216 receptor (Boyle, McNally & Ray, 2013), providing a large range of compounds only a few of
28
29 217 which have been tested and so the possible ecological function of these CO₂ inhibitors
30
31 218 remains unclear for now. As with root-feeding herbivores, inhibition of long-range habitat
32
33 219 cue detection may represent a defensive strategy by the host or, alternatively, a mechanism
34
35 220 employed by the insect to facilitate switching from habitat cues to host cues at shorter ranges.
36
37 221 Further work is needed to test either hypothesis and could lead to novel strategies for
38
39 222 controlling these important public health pests.

223 (3) Predatory and parasitic insects

224 Among the most widely-recognised examples of use of habitat cues comes from predatory
225 and parasitic insects. This topic has already been reviewed extensively (Vet & Dicke, 1992;
226 Hare, 2011; Heil, 2014; Pierik, BallarÉ & Dicke, 2014; Hilker & Fatouros, 2015; Meiners,
227 2015) and so is only discussed briefly here. When searching for prey or insect hosts for
228 oviposition, predatory and parasitic insects can make use of volatiles directly emanating from

1
2
3 229 their host's body or emitted as pheromones (Afsheen *et al.*, 2008). Due to the small size of
4
5 230 such odour sources these are often emitted in minute quantities, however, and so use of such
6
7 231 cues in long-range host location is difficult. The plant on which the host is feeding represents
8
9 232 a larger and far more easily detectable target at long range. Predatory and parasitic insects use
10
11 233 plant odours to locate their hosts' habitat at a distance and subsequently engage in more
12
13 234 localised foraging behaviour once on the plant (Bukovinszky *et al.*, 2012; de Rijk, Dicke &
14
15 235 Poelman, 2013). For example, the rove beetle *Aleochara bipustulata*, which feeds on and
16
17 236 whose larvae parasitise the pupae of cabbage root flies, *Delia radicum*, uses volatiles emitted
18
19 237 from fly-infested roots to locate a suitable area for foraging at a distance. Once in the vicinity
20
21 238 of the root beetles can then make use of volatile cues from larval tracks and pupae (Goubert
22
23 239 *et al.*, 2013). Plants can benefit from recruitment of natural enemies of their herbivores and
24
25 240 consequently tend to produce elevated quantities of volatiles upon herbivory (Vet & Dicke,
26
27 241 1992; Heil, 2014) or in response to herbivore egg deposition (Hilker & Fatouros, 2015).
28
29 242 Herbivore-induced volatile blends may also provide specific information reflecting
30
31 243 infestation by specific herbivore species (De Moraes *et al.*, 1998; McCormick, Unsicker &
32
33 244 Gershenson, 2012), greatly facilitating eventual host-location by specialist parasitic insects.
34
35 245 While herbivore-induced volatiles can substantially increase the detectability of prey at short-
36
37 246 mid range, at distances of more than a few 10s of meters predatory and parasitic insects face
38
39 247 the same challenge as other insects in that plume encounters may be too rare to provide an
40
41 248 effective means of locating an infested plant. Larger-scale habitat cues that indicate an area of
42
43 249 vegetation provide a solution to this problem, and evidence for use of such cues comes from
44
45 250 pollinators and above-ground foraging herbivores.

51 52 53 251 **(4) Pollinators and above-ground foraging herbivores**

54
55 252 The use of habitat cues by insects foraging above-ground around plants remains largely
56
57 253 unexplored but tantalizing indirect evidence exists for their use. Foliage offers a large source

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3 254 of odour but at greater distances downwind falls in concentration within odour plumes
4
5 255 (Murlis *et al.*, 2000; Koehl, 2006) and increasing intermittency (Koehl, 2006; Beyaert &
6
7 256 Hilker, 2014) means they may be difficult to detect. Host plants located within the middle of
8
9
10 257 a patch may be even harder to detect due to obstruction or adsorption of volatiles onto
11
12 258 surfaces of downwind vegetation (Beyaert & Hilker, 2014). In the absence of specific host
13
14 259 plumes, orienting first toward a broad patch of vegetation could substantially increase the
15
16 260 foraging insect's chances of subsequently encountering host cues. This is particularly true in
17
18 261 areas where vegetation coverage is not complete and broken up by bodies of water, rocky
19
20 262 areas, urban constructions etc. Even where vegetation coverage is fairly extensive, localised
21
22 263 regions containing higher abundances/diversity of plants will generally offer the most
23
24 264 promising locations to search for a suitable host. Many plant volatiles are ubiquitous,
25
26 265 produced by a wide range of different plant species in large quantities and can indicate such
27
28 266 areas of vegetation. Even non-host volatiles, normally avoided at short-range (Bruce *et al.*,
29
30 267 2005), may be used to indicate such areas at long range and may facilitate eventual host
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32
33
34 268 encounter.

37 269 **(a) Green leaf volatiles**

38
39
40 270 To be of any use, habitat cues should be detectable at relatively large distances and thus
41
42 271 emitted from a larger area and/or in higher concentrations. Green leaf volatiles (GLVs) are C-
43
44 272 6 fatty acid derivatives, produced ubiquitously throughout the plant kingdom, and may offer
45
46 273 such a cue. Whilst GLVs are generally only produced in large quantities following herbivory
47
48 274 or physical stress (Mwenda & Matsui, 2014), in nature such stresses are common and so most
49
50 275 plant patches produce large quantities of GLVs. Strong behavioural responses of herbivorous
51
52 276 insects to GLVs have been shown by a number of insect species, even for those which are
53
54 277 generally thought to recognise their hosts using highly species-specific blends. The black
55
56 278 bean aphid, *Aphis fabae*, is attracted to specific blends of volatiles emitted by its host *Vicia*
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3 279 *faba* (Webster *et al.*, 2008a; Webster *et al.*, 2008b) and the requirement for a blend is so
4
5 280 pronounced that, when presented with individual host volatiles outside the context of the
6
7 281 complete blend, aphids were repelled (Webster *et al.*, 2010a). Notable exceptions to this
8
9 282 trend, however, were the GLVs (Z)-3-hexenol and 1-hexenol, both of which were attractive
10
11 283 on their own at levels similar to those emitted by plants (Webster *et al.*, 2010b). Given the
12
13 284 strict preference for host-specific blends by this aphid, and the total lack of host-specific
14
15 285 information provided by GLVs, these responses are at first glance surprising. Such responses
16
17 286 to GLVs are fairly widespread, however, with many insects responding positively to them
18
19 287 despite normally showing preferences for highly host-specific volatile blends (Birkett *et al.*,
20
21 288 2004; Ruther & Mayer, 2005; Alagarmalai *et al.*, 2009; Li *et al.*, 2014). Their possible role as
22
23 289 habitat cues, indicating general areas of vegetation worthy of closer inspection by host-
24
25 290 seeking insects, may explain this pattern. GLVs may also be used to inform of habitat
26
27 291 suitability once the insect is already within a habitat. (Z)-3-hexenol is not attractive to the leaf
28
29 292 beetle *Cassida denticollis* but the presence of this volatile as background odour dramatically
30
31 293 increased the speed at which beetles discriminate host tansy (*Tanacetum vulgare*) stems from
32
33 294 non-odorous dummy stems (Muller & Hilker, 2000), possibly by informing on overall
34
35 295 habitat quality.

296 **(b) Non-host volatiles**

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37 297 Aside from GLVs, general vegetative odours from plants other than hosts may serve to
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39 298 inform as to the location of a plant patch. Unmated female cotton leafworm (*Spodoptera*
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41 299 *littoralis*) feed from nectar-rich lilac flowers and respond to their odour in a wind tunnel
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43 300 (Saveer *et al.*, 2012). Cotton plants, which are used for oviposition and are only attractive to
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45 301 mated females, were not landed on by unmated females but their odour elicited increased
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47 302 take-off flights compared to dummy plants (Saveer *et al.*, 2012). This suggests that 'non-host'
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49 303 odour may play a role in long-range orientation even if they do not induce orientation at short
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3 304 range. In fact, non-host volatiles that are repellent at short range may be attractive over longer
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5 305 distances when used as habitat cues. The idea that non-host volatiles may be used in host
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7 306 location is contrary to many long-held assumptions in insect behavioural ecology. A huge
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9 307 number of studies have demonstrated that insects will move away from non-host odours but
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11 308 the overwhelming majority of these studies used short-range olfactometers. Olfactometers are
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13 309 simple walking assays that are extremely efficient at screening short-range behavioural
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15 310 responses but do not account for long-range behavioural responses to volatile cues. Few
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17 311 studies have compared long- and short-range responses to the same odours but those that did
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19 312 showed surprising contradictions. Calatayud *et al.* (2014) showed that female cereal stem
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21 313 borers (*Busseola fusca*) avoided non-host Napier grass in preference of host maize in a Y-
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23 314 tube olfactometer (short-range orientation) but showed no such preference in a wind tunnel
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25 315 (longer-range orientation). Even more striking discrepancies come from *Drosophila* for
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27 316 which, in an olfactometer designed to assess walking behaviour, addition of CO₂ to vinegar
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29 317 odour decreased its attractiveness whereas in a free-flying cage assay the addition of CO₂
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31 318 raised the attractiveness of vinegar (Faucher, Hilker & de Bruyne, 2013). It is impossible to
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33 319 draw broad conclusions from the few studies that use both short- and long-range behaviour
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35 320 assays but in these examples at least, odours which are avoided at short range at the host
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37 321 location stage may elicit different, or opposite, responses at long range during the habitat
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39 322 location stage.

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41 323 Use of non-host odours in the field to deter insect pests have met with mixed results.
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43 324 Although there are numerous examples of non-host plants being extraordinarily effective at
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45 325 reducing pest numbers when planted alongside hosts (Pickett *et al.*, 2014), there are many
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47 326 more that fail to have any effect in the field or that deliver opposite than expected results. In
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49 327 an attempt to use a range of non-host plant odours to protect roses against Japanese beetle
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51 328 (*Popillia japonica*) it was found that addition of supposedly repellent non-host species
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3 329 actually increased numbers of invading beetles (Held, Gonsiska & Potter, 2003). Similar
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5 330 effects were observed when plants deterrent to the Colorado potato beetle (*Leptinotursa*
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7 331 *decemlineata*) were planted amidst potato plants, resulting in larger number of beetles than in
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10 332 untreated plots (Moreau, Warman & Hoyle, 2006). If non-host volatiles are avoided at short
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12 333 range but used to indicate the presence of a plant patch at longer ranges this may explain why
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14 334 attempts to incorporate non-host volatiles into integrated pest management strategies have
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16 335 often had opposite than expected outcomes in these, and other (Legaspi, Simmons & Legaspi,
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18 336 2011; Moreno & Racelis, 2015) field experiments.

21 337 **III. IMPLICATIONS**

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24 338 The use of habitat cues by foraging insects has now been demonstrated in a number of
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26 339 systems spanning several different feeding guilds. Despite this, use of habitat cues by insects
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28 340 is still widely overlooked. This is probably in part due to the difficulty of identifying such
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30 341 cues. Most studies use olfactometers that only record simple attractive/repellent behaviours
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32 342 used in short-range orientation. Some habitat cues may only operate at long range (thus
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34 343 walking assays may not always be appropriate) and may also elicit more complex non-
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36 344 directional searching behaviours that are difficult to detect without using advanced tracking
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38 345 techniques in suitably large arenas. Video-tracking technology has advanced considerably in
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40 346 recent years allowing detailed three-dimensional flight paths to be constructed for small
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42 347 insects both inside the lab and outdoors (Spitzen *et al.*, 2013; Manoukis *et al.*, 2014). Insect
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44 348 movement can also be tracked effectively using radar or by fitting insects with active
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46 349 transmitters and tracking using radio telemetry (Chapman, Drake & Reynolds, 2011;
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48 350 Kissling, Pattemore & Hagen, 2014). These techniques have been successfully employed to
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50 351 track insect movement in the field, often over large distances, and can provide important
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52 352 insights into how insects move within and between different habitats (Negro *et al.*, 2008;
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54 353 Hagen, Wikelski & Kissling, 2011; Lihoreau *et al.*, 2012). As use of these advanced tracking

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3 354 techniques becomes more widespread, we predict that identification of new habitat cues will
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5 355 accelerate.
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8 356 Evidence for the use of habitat cues by above-ground-foraging herbivorous insects remains
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10 357 tentative with much work still to do. The possibility that non-host odours can function as
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12 358 habitat cues at long range deserves particular attention since this has obvious implications for
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14 359 the use of non-host volatiles as deterrents in integrated pest management strategies. The
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16 360 occurrence of habitat cue inhibitors in both soil-dwelling and haematophagous insects
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18 361 (Reinecke *et al.*, 2008; Turner & Ray, 2009; Tauxe *et al.*, 2013) suggests a widespread
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20 362 phenomenon and could fuel new pest management strategies. Attempts could be made to
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22 363 screen host volatiles for their ability to inhibit behavioural responses to known habitat cues
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24 364 when presented to insects simultaneously. Any identified habitat cue inhibitors could then
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26 365 potentially be used to disrupt habitat location at a distance if placed around the perimeter of
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28 366 an area to be protected, reducing the influx of pests. This would probably be more effective in
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30 367 situations where points of entry are limited, such as vents in a glasshouse or other man-made
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32 368 structure, where inhibitors can be most easily applied. A better understanding of habitat cues
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34 369 may also help with monitoring or mass-trapping strategies. For example, some
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36 370 haematophagous insects use CO₂ as a long-range habitat cue but may not orient towards it at
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38 371 close range, yet many modern CO₂ commercial traps still aim to trap insects at or very near to
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40 372 the point of CO₂ release (Vaidyanathan & Feldlaufer, 2013). More careful arrangement of
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42 373 habitat and host cues in such traps may lead to far more effective trapping rates (Spitzen *et*
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44 374 *al.*, 2008; Cooperband & Cardé, 2006).
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51 375 Future studies on host-location behaviour should seek to better distinguish between habitat
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53 376 and host cues. This could easily be achieved by using a combination of long- (e.g. wind
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55 377 tunnel) and short- (e.g. olfactometer) range behavioural assays to observe differences in
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57 378 responses to volatiles at different spatial scales and also by precisely tracking movement
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3 379 paths of insects rather than simply recording their final destinations. Cues that elicit upwind
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5 380 orientation at long range but are ignored or avoided at short range are more likely to be
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7 381 habitat than host cues. Volatiles that elicit non-directional searching behaviour rather than
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9 382 directed movement to the point of emission are also more likely to be habitat cues, as are
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11 383 those whose presence as background odour enhances insects' responses to other host cues.

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14 384 Whilst this review has focussed on examples from insects, use of habitat cues has also been
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16 385 recorded in vertebrates (e.g. use of dimethyl sulphide to indicate regions of biodiversity by
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18 386 procellariiform seabirds (Nevitt, 2008)), suggesting they are a near-universal component of
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20 387 host location. An improved understanding of habitat cue use would greatly improve our
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22 388 understanding of insect foraging behaviour and ecology and may also lead to improved
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24 389 development of pest control strategies that aim to exploit or disrupt insect host-seeking
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26 390 behaviours.

30 31 391 **IV. CONCLUSIONS**

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34 392 1. Habitat cues are used to improve chances of ultimately locating a host cue by inducing
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36 393 orientation toward, or triggering foraging behaviour within, a physical area that is likely to
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38 394 harbour hosts. Habitat cues differ from host cues in that they tend to be produced in larger
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40 395 quantities and detectable at greater distances than host cues and tend to provide less host-
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42 396 specific information.

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46 397 2. Habitat odour comprises the collective volatile emissions of a habitat or physical region.

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48 398 These volatiles may originate collectively from the different organisms that inhabit the area.

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50 399 Many habitat cues are ubiquitous volatiles that, while offering little information on species
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52 400 identity, tend to be produced in large quantities from a wide range of plants/animals including
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54 401 host and non-host alike (e.g. GLVs from foliage, respiratory CO₂ emissions from roots or
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56 402 animals) and thus may be used to indicate patches of vegetation or groups of animals.

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3 403 Alternatively, habitat cues may originate from excretions or secretions of host organisms, for
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5 404 example indicating a dwelling or nesting area of a group of animals.
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8 405 3. In recent years evidence of habitat cue use by insects has accelerated. There are now
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10 406 numerous clear examples of their use by soil-dwelling herbivores, haematophagous insects,
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12 407 predatory and parasitic insects, above-ground foraging herbivorous insects, and even birds.
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14 408 Use of habitat cues is thus rapidly emerging as an essential component of host location for
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16 409 many host-seeking organisms.
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20 410 4. Numerous field and laboratory experiments suggest that non-host plant volatiles may
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22 411 function as habitat cues for host-seeking herbivorous insects, used to indicate patches of
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24 412 vegetation where potential hosts may be searched for if host-specific cues are unavailable.
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27 413 Non-host volatiles that are repellent at short range can be attractive over larger distances,
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29 414 further evidencing their role as habitat cues with important implications for their use in
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31 415 integrated pest management.
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34 416 5. Research into host-location behaviour has largely involved use of short-range olfactometer
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36 417 behavioural assays that, while possessing many advantages for rapid screening of behavioural
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38 418 responses and assessment of short-range orientation, are unsuitable for identification of
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40 419 habitat cues. This is likely a reason for the slow progress made in identifying new habitat
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42 420 cues and future research making use of state of the art tracking technologies will undoubtedly
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44 421 result in discoveries of new habitat cues.
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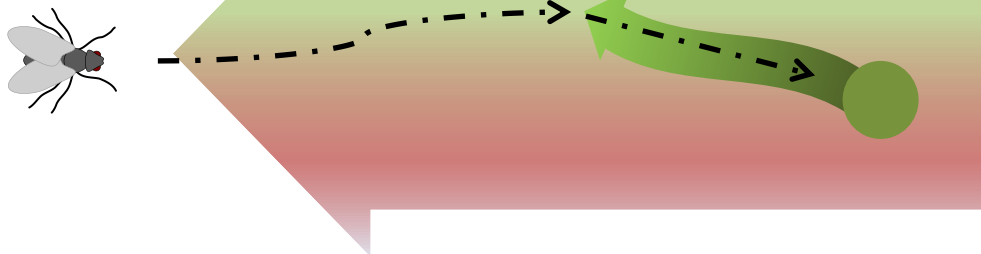
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49 639 Figure 1. Use of habitat cues by foraging insects. Shown are three main ways in which habitat
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51 640 odour can be used for eventual location of a suitable host for feeding/oviposition (green circle):
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53 641 a) The large red/green arrow represents odour from a potential resource patch. Insects follow
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55 642 this toward the patch before eventually encountering host odour (small green arrow).
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58 643 Encounter with host odour leads to a switch in behaviour, where insect ceases to move in
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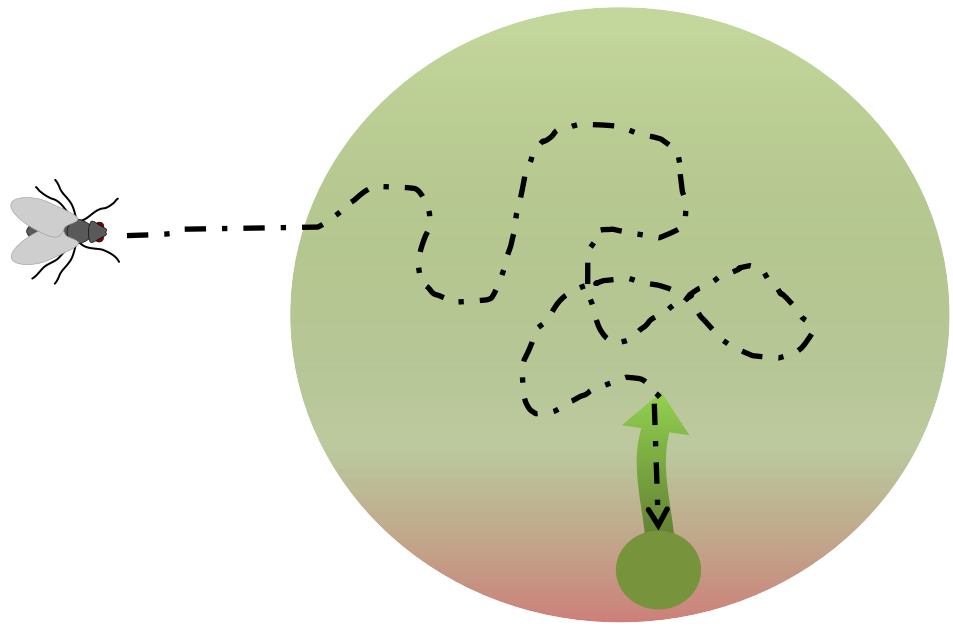
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3 644 response to habitat odour and instead follows host odour to its source. b) Habitat odour
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5 645 (red/green area) present in the background induces non-directional localised searching
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7 646 behaviour in the form of increased rates of turning and changes in movement speed,
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9 647 increasing the probability of chance encounter with host odour. Once host odour is detected,
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11 648 the insect abandons this localised searching behaviour and instead follows the host odour
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13 649 toward its source. c) Habitat cues present as background odour gate behavioural responses to
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15 650 host cues. When relevant background odour is detected that indicates the insect is in a
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17 651 suitable habitat, insects become more responsive to host-odour cues. When this relevant
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19 652 background odour is lacking, host-odour cues that the insect detects are either responded to
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21 653 weakly or ignored.
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a)

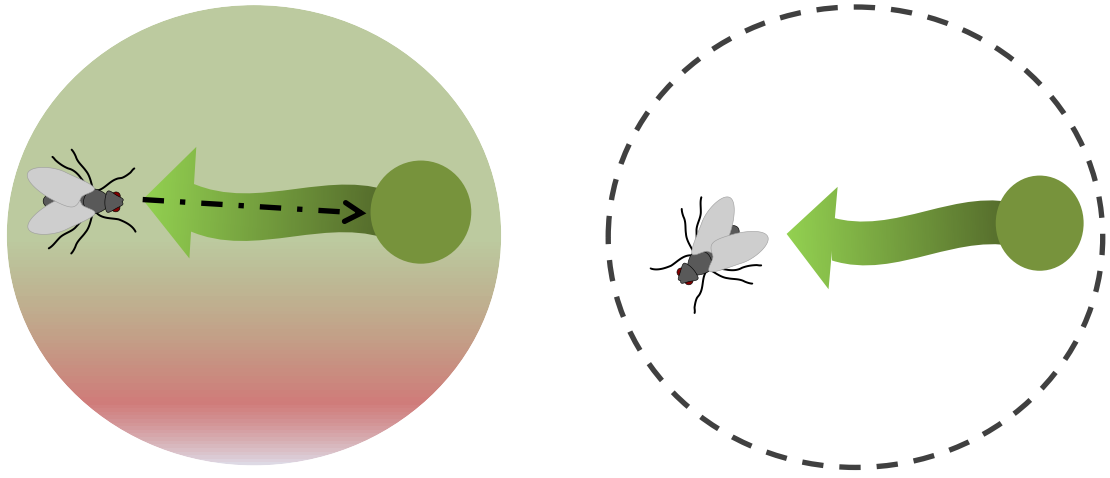
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b)



c)



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3 Table 1 Host cues vs. habitat cues. ‘Host cue’ has become a general term used to refer to any
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5 cue used at any stage in host location. There is an important distinction, however, between
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7 cues used to locate a feeding/oviposition site (host cues) and cues used to inform of a general
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9 area where host cues may subsequently be found (habitat cues). We propose the following
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11 broad criteria to help distinguish between the two. This list is not intended to be overly
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13 prescriptive since there are undoubtedly exceptions to each and should instead serve only as a
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15 general guide to distinguish between the two.
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Feature	Host cues	Habitat cues
Function	Indicate location of a feeding/oviposition site	Indicate a general area/location where host cues are most likely to be encountered
Source	Emitted from host	Emitted from host’s habitat, which may include the host itself as well as non-hosts
Quantities emitted in	Lower quantities	Higher quantities
Detectability	Detectable at short distances	Detectable at longer distances
Specificity	Often host-specific	Not necessarily host-specific
Behaviours elicited	Directed movement towards odour source	General upwind movement, localised searching behaviour, or enhanced responses to host cues

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