REVIEW

The “sequential cues hypothesis”: a conceptual model to explain host location and ranking by polyphagous herbivores

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Abstract  Successfully locating a host plant is crucial for an insect herbivore to feed and/or oviposit. However, locating a host within a complex environment that may contain an array of different plant species is a difficult task. This is particularly the case for polyphagous herbivores, which must locate a host within environments that may simultaneously contain multiple suitable and unsuitable hosts. Here we review the mechanisms of host selection used by polyphagous herbivores, as well as exploring how prior experience may modify a generalist’s response to host cues. We show that recent research demonstrates that polyphagous herbivores have the capacity to detect both common cues from multiple host species, as well as specific cues from individual host species. This creates a paradox in that generalists invariably rank hosts when given a choice, a finding at odds with the “neural limitations” hypothesis that says generalist insect herbivores should not have the neural capacity to identify cues specific to every possible host. To explain this paradox we propose a model, akin to parasitoid host location, that postulates that generalist herbivores use different cues sequentially in host location. We propose that initially common host cues, associated with all potential hosts, are used to place the herbivore within the host habitat and that, in the absence of any other host cues, these cues are sufficient in themselves to lead to host location. As such they are true “generalist” cues. However, once within the host habitat, we propose that the presence of a smaller group of cues may lead to further host searching and the location of preferred hosts: these are “specialist” cues. This model explains the current conflict in the literature where generalists can respond to both common and specific host-plant cues, while also exhibiting specialist and generalist host use behavior under different conditions.

Key words  diet breadth; foraging; insect behavior; insect–plant relationship; learning; neural constraints; visual cues; volatile cues

Introduction

Herbivorous insects make up nearly half of all eukaryotic species on earth (Gilbert, 1979). Approximately 98% of such insects are regarded as specialists, that is, they feed on only one or a small number of closely related plant species within a single plant family (Jaenike, 1990). Because of this vast diversity of specialist herbivores, the theory supporting the evolution of specialism is well developed (Jaenike, 1990; Futuyma & Moreno, 1998; Janz, 2003). This theory says, in part, that specialism will evolve in response to selective pressure to locate suitable host plants. Natural landscapes are complex, full of different potential host-plant cues, and natural selection should act to reinforce the ability of a herbivore to find host specific cues. The corollary of this is that selection should act against generalist herbivores, and this is seen to be evidenced by the lack of generalists in most herbivore lineages (Loxdale et al., 2011). While clearly valuable, this
Explaining polyphagy

It has been argued that polyphagy represents a survival mechanism, allowing the generalist herbivore to survive in environments where the composition of plant communities varies over space and time in an unpredictable way (Walter, 2003; Wiklund & Friberg, 2009). By utilizing alternative, albeit less suitable host plants, polyphagous herbivores can persist even when conditions are not suitable for their primary host plants (Velasco & Walter, 1993; Milne & Walter, 2000; Doak et al., 2006; Dingle & Drake, 2007). For example, the pentatomid bug *Nezara viridula* moves from one host plant species to another as the season progresses: this host-switching behavior is said to be an adaptive response to the limited food resources available (Velasco & Walter, 1993). However, even though there are purposive ecological advantages of polyphagy, generalist herbivores still present special problems for ecological theory (Walter, 2003).

There is a continuing debate about feeding generalism in nature. Loxdale et al. (2011) argues about the evolutionary “improbability” of generalism in nature, with the core argument being that the majority of animal species on earth are specialized forms that arose as a result of natural selection to occupy distinct ecological niches; thus evolution could not operate were organisms generalists. These authors further argue that generalism is an intermediate or poorly adapted trait on the road to specialization, or that apparent generalist herbivores may actually be unrecognized specialists; that is, given a choice such herbivores will show specialist feeding behavior (Loxdale et al., 2011; Loxdale & Harvey, 2016). Indeed, generalist herbivores have been viewed by several authors as being resource specialists, rather than host specialists, preferring to feed and lay eggs on particular plant structures, such as a fruit or growing tips (Clarke et al., 2005; Malacrida et al., 2007; Loxdale et al., 2011; Cini et al., 2012; Cunningham & Zalucki, 2014). Further adding to the debate, Walter (2003) argued that classifying organisms using generic terms such as “specialist” or “generalist,” monophagous or polyphagous is unwarranted, rather focus should be made on understanding the functional interactions that occur between an herbivore and its host plant.

In this review we do not intend to touch further on this debate, rather we choose to accept the fact that there are polyphagous insect herbivores in nature with host ranges that routinely extend across multiple plant families. Given this position, this review aims to focus on the possible mechanisms by which polyphagous herbivores may optimize their foraging to locate hosts. We limit the review to herbivorous or frugivorous insects, and exclude pollinators. Pollinators are thought to have beneficial relationships with their hosts (Mitchell et al., 2009) and so the evolutionary drivers between pollinator and plant are likely to be quite different from herbivores, where the plant–animal interactions are normally considered negative (Johnson, 2011). First we concentrate on the problems faced by foraging polyphagous herbivores. Then we detail the mechanisms by which generalist herbivores can optimize foraging for suitable hosts, showing that polyphagous herbivores have the olfactory mechanisms necessary to detect common host-plant volatile cues. We discuss how prior experiences with olfactory and visual cues can further enhance host location. We then detail the fact that there is a paradox in host plant selection by polyphagous herbivores. Although generalist herbivores can detect general host cues, they can also detect host specific cues (either olfactory or color cues). In the remainder of the review, we propose a novel, and testable model of host selection by polyphagous herbivores which we believe resolves this paradox.

Problems with being a polyphagous herbivore

Host selection is crucial for herbivorous insects and is central to individual fitness. However, choosing a host in often complex environments comprising a large number of different plant species can be a neurologically difficult task. This is particularly the case for polyphagous herbivores as they need to evaluate a greater diversity of host plants and associated cues than do specialist herbivores. It is widely believed that generalist herbivores may find it difficult to choose among alternative host plants due to an insect’s limited neural capacity to process multiple sensory inputs (Agrawal, 2001; Bernays, 2001; Carrasco et al., 2015). Such neurological constraints are thought to infer restrictions on an insect’s ability to make complex decisions based upon the array of sensory information being emitted from potential hosts (Bernays, 1999, 2001; Bernays & Funk, 1999; Janz, 2003; Egan & Funk, 2006). Additionally, making decisions and choosing among host plants takes time due to the competing sensory inputs from the potential hosts, and so polyphagous herbivores are thought to respond slower to host cues than specialists (Bernays, 1999; Bernays & Funk, 1999). Despite these issues polyphagous herbivores do occur in nature (Normark & Johnson, 2011; Clarke, 2017), but determining how such herbivores recognize and locate their hosts remains a major challenge (Bruce & Pickett, 2011; Cunningham, 2012).
Proposed solutions to problems faced by polyphagous herbivores

Host location using common olfactory cues

One solution to the “too many signals not enough processing” problem is that it is now evident that polyphagous herbivores have the capacity to detect common volatiles which arise from across their potential host ranges (Ramachandran et al., 1990; Light & Jang, 1996; Stranden et al., 2003; Bruce et al., 2005; Del Socorro et al., 2010; Bruce & Pickett, 2011; Becher et al., 2012; Cunningham & Zalucki, 2014; Cunningham et al., 2016; Wang et al., 2017; Biasazin et al., 2018), and this offers a mechanistic basis of how these herbivores locate hosts. Volatile compounds may be conserved across plant species, genera and families: for example, a small subset of pigeon pea volatiles are conserved across tobacco, cotton, and bean (Rajapakse et al., 2006), while the green leaf volatiles (a group of several compounds) are highly conserved across the plant kingdom (Dudareva et al., 2004; Carrasco et al., 2015). Studies have demonstrated that various polyphagous herbivores have olfactory neurons that are capable of detecting these common host volatiles (Bruce et al., 2005). The antennae of the western flower thrips, Frankliniella occidentalis, contain an array of olfactory receptor neurons that are capable of detecting a green leaf volatile and floral volatiles that are common across many of its host plant species (Koschier et al., 2000; Abdullah & Butt, 2015). Likewise the polyphagous hawkmoth Hyles lineata, rice leaf-roller Cnaphalocrocis medinalis, and the heliothine moths Helicoverpa armigera and H. virescens have all been shown to be capable of detecting common host-plant volatiles (Ramachandran et al., 1990; Raguso & Light, 1998; Stranden et al., 2003). Similarly, Cunningham et al. (2016) showed that while the antennae of the fruit fly Bactrocera tryoni was capable of detecting a suit of volatiles associated with fruit ripening, a simple blend of three esters (ethyl acetate, ethyl propionate, ethyl butyrate) was common across many ripening fruits and were sufficient in themselves to provide the cues needed for successful host location.

By having olfactory mechanisms capable of detecting common host volatiles, polyphagous herbivores are able to locate and utilize multiple host species and, more specifically, this has been argued to be an evolutionary adaptation allowing the utilizing of multiple hosts (Mustaparta, 1990; Bruce et al., 2005; Cunningham et al., 2016). Additionally, this olfactory mechanism also allows polyphagous herbivores to overcome an insect’s limited capacity to process information. Instead of having to evaluate a great diversity of volatiles from different host plants, polyphagous herbivores only need to be attentive to the volatiles that are shared across host species.

Using previous experience to optimize host foraging

Prior experience with a host plant, through oviposition or feeding, can refine subsequent foraging behavior through the learning and memory of host-associated cues (Papaj & Prokopy, 1989; Anderson & Anton, 2014; Jones & Agrawal, 2017). Oviposition or feeding experiences can improve the neurosensory processes that enable insect herbivores to detect and locate suitable hosts and this enhances foraging efficiency by allowing those insects to be more attentive to the host cues that previously led to successful host location (Anderson & Anton, 2014; Carrasco et al., 2015). The advantages of host learning to a polyphagous herbivore are immediately obvious (Cunningham & West, 2008), and indeed it has been argued that polyphagous herbivores make more significant use of learning than specialists (Bernays, 2001; Bernays et al., 2004). This difference in learning capacity has been demonstrated at a genetic level, with differences in the expression of genes associated with learning between polyphagous and specialist herbivores. Tapia et al. (2015) showed that there was higher expression of the learning-associated foraging gene (for) in the generalist aphid Myzus persicae s. str than in its specialist sub-species, Myzus persicae nictoianae.

Different forms of learning have been demonstrated in insects and, ultimately, the learning type utilized by a species depends on life-history attributes and the amount of variation in the cues that they encounter (Jones & Agrawal, 2017). It has been argued that since polyphagous herbivores have large host ranges and are exposed to environments containing many different potential hosts, associative learning, rather than habituation or sensitization, is likely to be exhibited (Jones & Agrawal, 2017). Associative learning occurs when herbivores associate specific cues of a host plant (e.g., color, odors, taste, or shape) with a positive reward, such as successful oviposition or acquiring suitable food resources (Jones & Agrawal, 2017). The cues associated with the positive reward will be the most receptive in later foraging and thus allow the herbivore to more rapidly locate its host (Cunningham et al., 1998, 2004, 2006; Cunningham et al., 1999; Mery & Kawecki, 2002; Riffell et al., 2008; Simões et al., 2011; Zrelec et al., 2013). As examples, desert locusts, Schistocerca gregaria, are able to associate plant odors with food rewards and this improved subsequent attraction to such odors following learning trials (Simões et al., 2011). Similarly, the attraction of the noctuid moth
H. armigera toward flowers was strongly influenced by prior experiences with specific floral volatiles in association with feeding. In a series of experiments Cunningham et al. (2004) showed that when moths fed on flowers that were odor-enhanced using either phenylacetaldehyde or \( \alpha \)-pinene, the moths subsequently showed a significant preference for the flower type on which they fed. In these examples, attraction toward a particular odor was enhanced through the association of a food reward.

Experience during the immature stage has also been shown to affect adult host selection behavior among polyphagous herbivores, with adults actively seeking hosts on which they developed (Akhtar & Isman, 2003; Facknath & Wright, 2007; Blackiston et al., 2008; Videla et al., 2010; Anderson et al., 2013; Anderson & Anton, 2014; Gregório et al., 2015). For example, female Spodoptera littoralis prefer to oviposit on the host species they were raised on; when reared on cotton, adult moths deposited more eggs on cotton than on clover or alfalfa (Anderson & Anton, 2014). Similarly, when the agromyzid leafminers Liriomyza trifolii and Liriomyza huidobrensis were raised on potato, adults showed preferential orientation toward potato in olfactometer tests (Facknath & Wright, 2007). The mechanism by which learnt information is transferred from larvae to adult is still unknown but different mechanisms have been suggested. The chemical legacy hypothesis proposes that traces of chemicals (mostly from food) inside or outside an immature insect can directly affect their sensitivity/preference for food containing these chemicals when they become adults (Corbet, 1985). A second proposed mechanism states that neural tissue from larval mushroom bodies is preserved through metamorphosis and are incorporated into the mushroom bodies of adults, thus providing a substrate to transfer learned information (Tully et al., 1994; Armstrong et al., 1998; Marin et al., 2005; Blackiston et al., 2008). Whatever the mechanism, this field of research demonstrates that larval experiences can influence adult host selection behavior and for polyphagous herbivores this can, once again, fine-tune detection for host cues.

The paradox of host location—polyphagous herbivores using specific host cues

Host location using specific olfactory cues

As previously mentioned there is now clear evidence to demonstrate that polyphagous herbivores have the capacity to detect common host volatiles. However, what is also evident is that polyphagous herbivores exhibit preference hierarchies for their hosts (Jallow & Zalucki, 2003; Rajapakse et al., 2006; Clarke et al., 2011; Thöming et al., 2013; Conchou et al., 2017; Wang et al., 2017). This is due to the fact that, as with specialist herbivores, polyphagous herbivores have also been shown to be capable of distinguishing between hosts using specific plant volatiles. For example, B. tryoni showed an oviposition preference hierarchy among five citrus varieties; oviposition was higher on Murcott and grapefruit, lower on lemon and intermediate on Navel and Valencia (Muthuthantri & Clarke, 2012). Similarly, in a behavioral study, S. littoralis also showed an oviposition preference hierarchy among five plants; oviposition was higher on clover and cowpea, intermediate on maize and cotton, and lowest on cabbage (Thöming et al., 2013). Such preference hierarchies can be attributed to the ability of polyphagous herbivores to detect host-specific volatiles emitted by plants/fruits. For the case of S. littoralis, subsequent electrophysiological bioassays showed that the moth had the sensory ability to distinguish each of five tested host plants (clover, cowpea, maize, cotton, cabbage) through specific volatile combinations that elicited different electrophysiological responses in the antenna of the moth (Conchou et al., 2017). Behavioral studies followed by electrophysiological bioassays have also shown that H. armigera was also capable of detecting host-specific volatiles, with different electrophysiological antennal responses to volatiles from different host plants (Stranden et al., 2003; Rostelien et al., 2005; Rajapakse et al., 2006).

Host location using herbivore-induced olfactory cues

Further evidence to demonstrate that polyphagous herbivores are capable of detecting host-specific volatiles can be seen in their behavioral responses toward host plants damaged by other herbivores. Insect herbivory results in the synthesis and emission of herbivore-induced plant volatiles (HIPVs) (Karban & Baldwin, 1997; Agrawal, 1998; Zhuang et al., 2012). Although it is often assumed that the emission of HIPVs is a defensive response against further herbivory (Brussow et al., 2010), HIPVs can also mediate interactions between plants and their herbivorous insects as specialist herbivores exploit HIPVs as cues to forage for and locate suitable plants for oviposition (Lu et al., 2004; Silva & Furlong, 2012). But there is now evidence to suggest that some polyphagous herbivores can also exploit HIPVs for the same purpose (Silva et al., 2013; Silva et al., 2014; Coapio et al., 2016; Rizvi et al., 2016; Sarkar et al., 2016; El-Sayed et al., 2018; Karmakar et al., 2018).

In olfactometer bioassays the polyphagous beetles Epilachna vigintioctopunctata and Aulacophora foveicollis were more attracted to Solena amplexicaulis damaged by
con specifics than to undamaged plants: the beetles were specifically attracted to three compounds present in the volatiles of the herbivore-damaged plants, linalool oxide, nonanal and E-2-nonenal (Sarkar et al., 2016). Similarly, in a field study, El-Sayed et al. (2018) showed that the pandemic leafroller moth, Pandemis pyrusana, was more attracted to apple trees damaged by con specifics than to undamaged trees. These authors determined that the increased attraction to, and subsequent oviposition on, herbivore damaged trees was due to the moth’s attraction to specific volatiles emitted by herbivore-damaged plants. While the above studies do not, in themselves show the mechanism by which the herbivores could discriminate the different plant species, they do however demonstrate that polyphagous herbivores have the capacity to detect specific volatiles.

**Host location using specific color cues**

In addition to volatile cues, studies have demonstrated that polyphagous herbivores also have mechanisms to locate and exploit a particular host using specific color cues. Insects possess photoreceptor cells with different visual pigments, which allows them to discriminate the colors of flowers or fruits (Chittka & Menzel, 1992). However, this ability to discriminate color and distinguish between hosts ultimately depends on the specific range of the optical spectrum that stimulates the different receptors within the eye and the subsequent neural integration of this input (Chittka & Menzel, 1992; Kevan et al., 1996). For insects, in general, color is arbitrary; it is the spectral reflectance patterns and the ability to detect differences in reflectance patterns that are crucial for locating and selecting hosts. Floral and fruit hosts, particularly, can have very different patterns of reflectance and insect photoreceptors can detect different spectral ranges of light from ultraviolet (300 nm) through to blue (450 nm), green (540 nm) and red (above 620 nm) (Bernays & Chapman, 1994; Kevan et al., 1996; Briscoe & Chittka, 2001; Yaku et al., 2007).

Studies have demonstrated wavelength-specific behavioral responses elicited by various polyphagous herbivores (Robacker, 1992; Henneman & Papaj, 1999; Drew et al., 2003; Yaku et al., 2007). For example, *F. occidentalis*, *F. schultzei*, and *F. tritict*, all of which inhabit petallate flowers, have all shown specialized color responses that correlate to the reflectance patterns of their most preferred floral hosts (Walker, 1974; Matteson & Terry, 1992; Terry, 1997). Similarly, among polyphagous tephritids, *B. tryoni* has been shown to be more attracted to blue or white fruit mimics than to red, orange, yellow, green, or black fruit mimics (Drew et al., 2003). That this is a species-specific response pattern is illustrated through comparison with the congeneric *B. dorsalis*, which in similar experiments was more attracted to white fruit mimics than any other color (Vargas et al., 1991; Cornelius et al., 1999).

To further elaborate the highly specific nature of wavelength-specific responses, polyphagous herbivores have also been shown to be able to discriminate against hosts that appear to be of similar color. Blumthal et al. (2005) showed that *F. occidentalis* was more attracted to yellow Transvaal daisy than to yellow chrysanthemum, even though both flowers were of similar color to the human eye. This preference for one flower type over another was due to the difference in their spectral reflectance patterns; yellow Transvaal daisy had a relatively high red reflectance which made the flower more visible to *F. occidentalis*. Specialized color responses have even been shown in nocturnal polyphagous herbivores: foraging *Deilephila elpenor* can discriminate colors at night (Kelber et al., 2002; Balkenius & Kelber, 2004). Such studies demonstrate that polyphagous herbivores have highly focused mechanisms to locate and exploit a particular host using specific color cues.

**The paradox**

The above literature makes it evident that polyphagous herbivores are capable of host location using specific host cues, as well as generic host cues, and this creates a paradox. On the one hand the use of common host cues is thought to be a mechanism to overcome the neural limitation hypothesis; while the response to specific host cues is thought to create the neural limitation problem in the first place. How then can polyphagous herbivores be simultaneously generalists (utilizing very large host ranges) and specialists (ranking hosts)? Additionally if, through learning, polyphagous herbivores can still optimize their foraging using general host cues, then it begs the question why do they also need to rank hosts using specific host cues?

**Overcoming the paradox: a new model for host location by polyphagous herbivores**

Based on the demonstrated ability of polyphagous insects to utilize both generic and specialist host cues, we propose a hierarchical host location model detailing how host selection is achieved when a foraging polyphagous herbivore encounters a habitat consisting of many different host plant species suitable for either oviposition or feeding (Fig. 1). First, we propose that a flying herbivore or frugivore will detect the common volatiles emanating from
Explaining polyphagy

Plant species A

Host specific volatiles

Common volatiles

shared across the six plant species

Plant species B

Plant species C

Plant species D

Plant species E

Plant species F

Herbivore

Frugivore

Fig. 1 A simplified schematic diagram to illustrate how host selection is achieved by foraging polyphagous herbivores or frugivores. Numbers represent insect behavioral steps 1–6 (see text).

multiple different plant species (Fig. 1, step 1). Importantly, in the absence of other cues, our model predicts these common volatiles are sufficient on their own to lead to host location and acceptance (Fig. 1, step 2). But, if while in the host habitat the foraging insect detects more refined cues, it may show selective behavior between different hosts (Fig. 1, steps 3 and 4). For instance, the herbivore might be more attracted to a specific color (Fig. 1, step 5) or the frugivore might be attracted to specific fruit volatiles (Fig. 1, step 6). We believe that this model solves the paradox of host selection by polyphagous herbivores, by allowing for both the utilization of many hosts, but also the preferential selection of hosts.

Within this model, the ranking of hosts by polyphagous herbivores could be the result of two different mechanisms. In the first case, specific hosts could have a unique combination of traits (additional to the common traits), which allow unique identification of each potential highly ranked host. In this case the ability to rank hosts is limited by the insect’s neural capacity to retain and process host-cue information for each unique host. The second mechanism is an additive one. The herbivore may still utilize only a small number of cues (e.g., the common volatiles, a few additional volatiles, a shape profile, and a preferred reflectance spectrum), and as a host exhibits more of these (additional to the cue[s] common to all potential hosts) the host becomes more attractive. In this scenario the polyphagous herbivore can rank hosts, but not uniquely as different host species are likely to share at least some combination of these traits. We suspect the second mechanism to be more likely and it fits with the observation that polyphagous herbivores are often resource specialists (e.g., for fruit, pods, or growing tips) (Clarke et al., 2005; Malacrida et al., 2007; Loxdale et al., 2011; Cini et al., 2012; Cunningham & Zalucki, 2014), as these resource types are most likely to have additional common characteristics.

In our model we also need to consider the fact that foraging will lead to encounters with nonhosts. A specialist herbivore may land on many unsuitable plants before ultimately finding a suitable host for either oviposition or feeding. Finch and Collier (2000) developed a theory based on such insect behavior known as the “appropriate/inappropriate landings” theory. This theory is based on the fact that specialist phytophagous insects will land indiscriminately on green objects such as the leaves of host plants ( = appropriate landing) and nonhost plants ( = inappropriate landings). The Finch and Collier argue that once landing on a nonhost plant the decision as to whether to stay and oviposit or feed is primarily

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determined by the chemicals that an insect detects via its contact chemoreceptors. This theory should also work for a generalist herbivore and thus can be incorporated into our model. However, our model does suggest that inappropriate landing on a nonhost is more likely for a generalist than for a specialist herbivore, due to a generalist herbivore’s detection and response to generalist cues, such as common volatiles. A generalist herbivore landing on such a nonhost may subsequently reject that host and recommence flight if the cues emanating from the host are not sufficient (i.e., above a quantitative threshold) to lead to host acceptance. However, under our model, we also predict that common cues emanating from a nonhost may lead to oviposition or feeding on a nonhost. This leads to the potential issue of sub-optimal host use, which we consider in the last section of this discussion.

Also to be considered in our model are motivation-based models of host plant selection by herbivorous insects (Miller & Strickler 1984; Courtney et al., 1989). For example, the hierarchy-threshold model proposes that each host plant species has an intrinsic acceptability threshold that is determined by the positive stimuli received by the insect from the host plant (Courtney et al., 1989). If a host plant has a higher intrinsic acceptability threshold over another host plant, then that host will be accepted over the one that has a lower threshold. But if a host has a low intrinsic acceptability threshold, then it will be accepted only when the insect’s state has changed (e.g., by hunger, a high internal egg load, etc.). The important assumption here is that for an insect to accept a low ranked host, factors influencing acceptance threshold levels are not just related to intrinsic host plant properties but are also dependent on the insect’s physiological state. Age, prior experience, food deprivation, and egg load can all reduce an insect’s acceptance threshold thus allowing it to accept low ranked hosts (Courtney et al., 1989). On this basis another variable that can be included in our model is the physiological state of a foraging polyphagous herbivore. Herbivore foraging can be influenced by egg load (Jaenike, 1990), with the most common observation being that female herbivores are more likely to accept low ranking hosts as egg load increases (Courtney et al., 1989; Minkenberg et al., 1992). From our model, we predict that a polyphagous female herbivore with a large egg load is likely to rapidly orientate to common volatile cues so as to locate a host more quickly. In contrast, females with a lower egg load are more likely to be more selective in their foraging and may well spend more time foraging for specific host cues before “defaulting” to a host producing only the common cue.

Our model has distinct commonalities to natural enemy (parasitoid or predator) host foraging. Natural enemies first locate a host using the general cues emitted by the different plant species that make up the host-habitat; once in the habitat specific cues emitted by host feeding are used to accurately locate the host (Doutt, 1959; Meiners, 2015). This model was subsequently extended to foraging insects more generally (including herbivores) to cover the sequence of host habitat location, host patch location, host location and host acceptance (Hassel & Southwood, 1978). Light & Jang (1996), as an example, provide evidence for the use of multiple cues in foraging choices by the polyphagous fruit fly Ceratitis capitata, identifying the importance of generic green leaf volatiles, whole fruit odours, and specific fruit ripening esters and alcohols. Our model also proposes the sequential fashion use of generic and then more specific cues for host location, and as such has a strong link with existing models, but has what we believe to be a key important difference. In order for a specialist herbivore to successfully locate its host all, or nearly all, the necessary host-specific cues need to be detected in order to determine whether a host is present or absent. Whereas for a polyphagous herbivore we propose only a small set of common host cues are necessary to lead to locating any host, with any utilised sequential cues then helping to rank hosts. Hassel and Southwood’s (1978) sequential model recognises that polyphagous insects may spend more time searching for a preferred host, but do not offer a mechanism to explain why.

Optimal or suboptimal host use

Our sequential cues hypothesis explains how host plant location by polyphagous herbivores is achieved by responding to both common and specific host plant cues, ultimately resulting in either a specialist or a generalist form of host use behavior (Fig. 1). However, it can be argued that our model does not take into consideration the perceived view that host selection/acceptance by herbivorous insects is also a result of optimal oviposition (Jaenike, 1978; Stephens & Krebs, 1986; Scheirs & De Bruyn, 2002). According to this theory, female insect herbivores will lay eggs on sites best suited for offspring survival, thus optimizing their own fitness (Jaenike, 1978). However, the issue of all foraging for suitable oviposition sites being optimal is debatable. Many empirical studies have shown that various insect species (including polyphagous herbivores) make poor oviposition choices (Stephens & Krebs, 1986; Mayhew, 1997; Ballabeni et al., 2001; Scheirs & De Bruyn, 2002; West & Cunningham, 2002), often referred to as “suboptimal oviposition” (Jaenike, 1978; Scheirs & De Bruyn, 2002). Often these poor oviposition choices result in offspring dying or emerging as deformed or
sterile adults (Zalucki & Kitching, 1983; Xue & Yang, 2007).

Cunningham (2012) argued that observed suboptimal oviposition behavior was a result of an insect’s limited capacity to process information, which leads to a failure by the insect in rejecting unsuitable plant species. Thus we base our model solely on the fact that host location by insect herbivores is primarily driven by the host cues an insect herbivore is attracted to, rather than locating host cues that are optimal for offspring survival. From this our model can explain why polyphagous herbivores may select hosts that are bad for offspring survival. A host that is bad for offspring survival may still produce common volatile cues, or even specific cues, that are attractive to a foraging polyphagous herbivore. In such cases our model predicts that the herbivore would be equally attracted to that particular plant even though it is not suitable for offspring development and survival.

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Disclosure

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