

Evol Ecol (2015) 29:905–925  
DOI 10.1007/s10682-015-9800-9



ORIGINAL PAPER

# Adaptive and maladaptive consequences of “matching habitat choice:” lessons from a rapidly-evolving butterfly metapopulation

Michael C. Singer<sup>1</sup>

Received: 26 November 2014 / Accepted: 14 September 2015  
© Springer International Publishing Switzerland 2015

**Abstract** Relationships between biased dispersal and local adaptation are currently debated. Here, I show how prior work on wild butterflies casts a novel light on this topic. “Preference” is defined as the set of likelihoods of accepting particular resources after encountering them. So defined, butterfly oviposition preferences are heritable habitat adaptations distinct from both habitat preference and biased dispersal, but influencing both processes. When a butterfly emigrates after its oviposition preference begins to reduce realized fecundity, the resulting biased dispersal is analogous to that occurring when a fish emigrates after its morphological habitat adaptations reduce its feeding rate. I illustrate preference-biased dispersal with examples from metapopulations of *Melitaea cinxia* and *Euphydryas editha*. *E. editha* were feeding on a well-defended host, *Pedicularis*, when humans created patches in which *Pedicularis* was killed and a less-defended host, *Collinsia*, was rendered phenologically available. Patch-specific natural selection favoured oviposition on *Collinsia* in logged (“clearing”) patches and on *Pedicularis* in undisturbed open forest. Quantitative variation in post-alighting oviposition preference was heritable, and evolved to be consistently different between patch types. This difference was driven more by biased dispersal than by spatial variation of natural selection. Insects developing on *Collinsia* in clearings retained adaptations to *Pedicularis* in clutch size, geotaxis and oviposition preference, forcing them to choose between emigrating in search of forest habitats with *Pedicularis* or staying and failing to find their preferred host. Insects that stayed suffered reduction of realized fecundity after delayed oviposition on *Collinsia*. Those that emigrated suffered even greater fitness penalty from consistently low offspring survival on *Pedicularis*. Paradoxically, most emigrants reduced both their own fitness and that of the recipient populations by dispersing from a benign natal habitat to which they

---

**Electronic supplementary material** The online version of this article (doi:[10.1007/s10682-015-9800-9](https://doi.org/10.1007/s10682-015-9800-9)) contains supplementary material, which is available to authorized users.

---

✉ Michael C. Singer  
michael.singer@plymouth.ac.uk

<sup>1</sup> School of Biological Sciences, Plymouth University, Drake Circus, Plymouth, Devon PL4 8AA, UK

were maladapted into a more demanding habitat to which they were well-adapted. “Matching habitat choice” reduced fitness when evolutionary lag rendered traditional cues unreliable in a changing environment.

**Keywords** Butterfly · Matching habitat choice · Biased dispersal · Oviposition preference · Host shift · Fluctuating environment · Niche expansion

## Introduction

There is undiminished interest in local adaptation in its multiple roles: as a potential cause and symptom of incipient speciation (Jiggins et al. 2001; Nosil et al. 2002; Soria-Carrasco et al. 2014); as a handmaiden of rapid environmental change (Thomas et al. 2001; Cook and Saccheri 2013; Buckley and Bridle 2014); as a driver of indirect competition and species richness (Farkas et al. 2013); as a predictor of resilience to future environments (Bennett et al. 2015) and as a window into the genetic mechanisms of response to natural selection (Mullen et al. 2009; Hubbard et al. 2010; Wheat et al. 2011; Marden et al. 2013). Alongside this diversity of interests come conceptual re-imaginings of the roles of evolutionary forces and ecological events both natural and anthropogenic, in generating local adaptation (Kawecki and Ebert 2004). Gene flow often acts to reduce adaptive divergence between populations (e.g. Hendry and Taylor 2004; Nosil et al. 2006) and may thereby limit species’ ranges (Kirkpatrick and Barton 1997). In contrast, recent studies have emphasized that, when dispersal is biased by genotype, it can become a force generating adaptive differentiation rather than reducing it. Matching habitat choice (MHC; see Glossary) refers to the situation in which dispersing individuals choose to settle in the habitats to which they are best adapted (Ravigne and Olivieri 2004). This process is expected to reinforce habitat-specific selection in generating local adaptation (Edelaar et al. 2008; Edelaar and Bolnick 2012; Bolnick et al. 2009; Bolnick and Otto 2013; Richardson et al. 2014).

Here, I illustrate how prior work on butterflies casts a novel light on this current theme. This illustration requires separating the concepts of host preference, habitat preference and dispersal, phenomena that are partially synonymized in current literature. I argue that oviposition preferences of butterflies are heritable traits best viewed as distinct both from habitat preferences and from biased dispersal. By influencing habitat-specific rates of resource (=host) acquisition, oviposition preferences act as habitat adaptations. They cause, rather than comprise, biased dispersal among habitat types, playing a similar role in evolution of local adaptation to that of morphological traits that affect habitat-specific rates of feeding success. In making the case for this view, I hope to bring insect–host interactions more fully into discussion of biased dispersal and, in so doing, suggest avenues for both empirical and theoretical exploration.

New analyses of habitat-specific fitness consequences of oviposition preference are presented and combined with previously-published (but misunderstood) studies of biased dispersal in two Melitaeine butterflies, *Melitaea cinxia* and *Euphydryas editha*. The biology of these insects is reviewed in Ehrlich and Hanski (2004) and Hanski (2011). Biased dispersal of *M. cinxia* met definitions of MHC as defined in the Glossary, and generated “microgeographic adaptation” as predicted by Edelaar and Bolnick (2012). Although biased dispersal by *E. editha* also met definitions of MHC, its consequences were maladaptive both for many dispersing insects and for the populations into which they

immigrated. To set the context for these conclusions, the following sections describe butterfly habitat choice, oviposition behavior, host preference and dispersal.

## Habitat preference, host preference, motivation and dispersal

### Distinguishing between habitat preference and host preference

Butterflies are amenable to empirical studies of dispersal (supplemental appendix). These studies reveal that some species show open population structure, with individuals roaming widely across diverse habitats, seeking mates, nectar sources and oviposition sites as they fly. For these butterflies the term “habitat patch” may not be meaningful (Dennis et al. 2003, 2014). However, most butterflies, including those studied here, occur in discrete populations occupying habitat patches comprising areas of distinct vegetational and physical structure covering hundreds to thousands of square metres. A suitable habitat patch contains food resources for adults (nectar, honeydew, fruit, guano or carrion) and larvae (host plants), though these resources may be spatially separated (Gilbert and Singer 1973; Wiklund 1977). Habitats must also contain physical sites for pupation, mating, roosting, thermoregulation and diapause (Pratt and Emmel 2010). These complex requirements mean that a “habitat patch” is not a patch of hosts, but a larger area that contains the diverse physical and biological resources used by the insects in the course of their complex life cycles.

Butterflies can detect and respond to boundaries between habitats of different type or between suitable and unsuitable habitats. Consequently, the characterization of habitat patches, delineation of patch boundaries and provision of appropriate “corridors” for individuals moving among patches has been important in butterfly conservation. Literature on butterfly dispersal, reviewed by Dover and Settele (2009) and Stevens et al. (2010), tackles flight behavior at boundaries between habitat and non-habitat (Kuussaari et al. 1996; Boughton 2000; Ries and Debinski 2001; Schultz and Crone 2001; Kallioniemi et al. 2014), and ability to navigate across non-habitat to find habitat patches (Harrison 1989; Haddad 1999; Ricketts 2001; Conradt and Roper 2006; Schtickzelle et al. 2007).

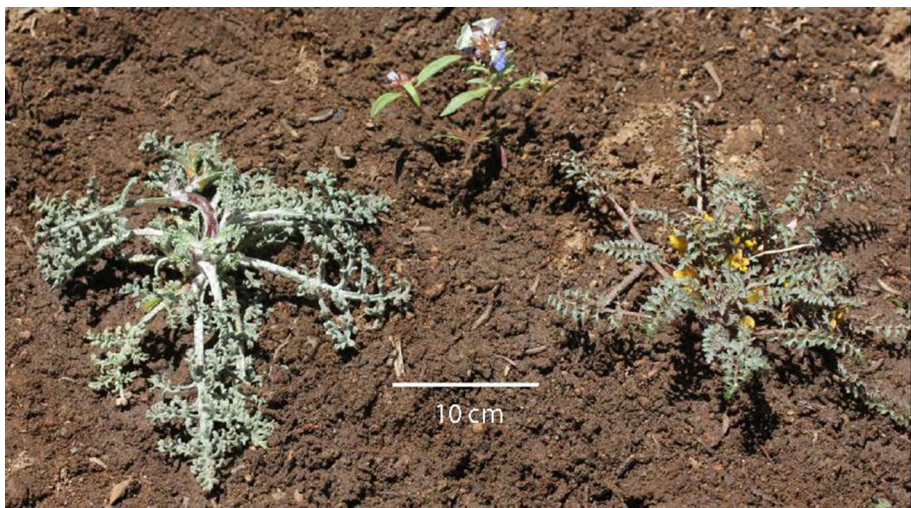
Most butterflies, including our study species, *M. cinxia* and *E. editha*, are more sedentary than their flight capability suggests, and maintain population integrity by some combination of home-range behavior and loyalty to particular specialized habitat types. *M. cinxia* populations in Finland occur in “dry meadows” where thin soil overlays granite substrate. The vegetation of these meadows is more xeric than surrounding forests and agricultural fields, and the dry meadow habitat patches have visible boundaries that the insects perceived and from which they were typically reflected (Kuussaari et al. 1996). Likewise Bay Checkerspots (*E. editha bayensis*) were reflected from the boundaries of their barren serpentine grassland habitats, turning around when they reached chaparral (shrubby) vegetation, or even grasses taller than 20 cm, growing on less toxic soil (Ehrlich 1961). Ehrlich titled his paper “Intrinsic barriers to dispersal...” to emphasize that *E. editha* had the physical capacity to cross the habitat boundaries from which they shrank. *E. editha* also showed ecotypic variation of habitat preference: after larvae originating from a chaparral habitat were experimentally introduced to the same patchwork of grassland and chaparral where Ehrlich (1961) had worked, the emerging adults flew in the chaparral, expressing the opposite habitat preference to that of the Bay Checkerspots that had flown a month previously (anecdote in Gilbert and Singer 1973).

Butterflies use vision as the principal means of initial detection of both hosts and habitats, but these detections are made at different times, from different distances. *Pararge aegeria* butterflies released 100 m from suitable habitat adopted straight-line flight towards that habitat at mean distances of 60–80 m (Ockinger and van Dyck 2012). In contrast, within a habitat patch, female *Cissia libye* turned towards individual host plants from a mean distance of only 0.42 m (Mackay and Singer 1982).

As a result of this difference in scale between host-finding and habitat-finding, and because individual hosts are unlikely to be re-visited by adult insects, choosing a host hasn't been described in butterfly literature as "habitat choice" from the adult's perspective, even though a single host may serve as the habitat of a larva. Butterflies are described as first choosing habitat patches, then searching within them for both adult and larval resources. For example, Friberg et al. (2008a, b) described sister species as having identical host preferences but achieving different diets by preferring physically different habitats. The use of different principal hosts was driven by a difference in habitat preference, not host preference.

### Oviposition behavior of study organisms

The first component of butterfly oviposition behaviour is the choice of plants on which to alight. When frequencies of alighting by *E. editha* searching for oviposition sites were compared with random samples of the vegetation, the butterflies showed alighting biases based on plant growth form and leaf shape, regardless of plant taxonomic relationship or status as hosts or non-hosts (Parmesan 1991; Parmesan et al. 1995). Figure 1 illustrates the similarity between a host of *E. editha*, *Pedicularis semibarbata* (Orobanchaceae) and a non-host, *Chaenactis douglasii* (Asteraceae), growing at our Rabbit Meadow study site in Sequoia National Forest, California. Unsurprisingly, the visually-searching insects failed to distinguish between these plants prior to alighting, showing strong alighting biases towards



**Fig. 1** At right, a host of *Euphydryas editha*, *Pedicularis semibarbata* (Orobanchaceae); at left, a structurally similar but unrelated non-host, *Chaenactis douglasii* (Asteraceae). Center the host *Collinsia torreyi* (Plantaginaceae)

both of them. These alighting biases were fixed: Parmesan et al. (1995) found identical bias towards *Pedicularis* in natural search by experienced insects and in the very first alights made by naïve females performing the first host searches of their lives in the same habitat patch.

After alighting, *E. editha* tasted plants by tapping them with their atrophied foretarsi, as seen in this video clip from time 0:06 to 0:09: <https://www.youtube.com/watch?v=pXT4qinQ0KM>. If the response to plant chemistry was acceptance, the butterfly curled her abdomen, extruded her ovipositor and pressed it against the undersides of leaves, searching for acceptable tactile stimuli. If the response to tactile stimuli was acceptance, the butterfly laid a clutch of eggs. These post-alighting components of preference were crucial in host selection, since butterflies observed in prolonged search alighted at least occasionally on all herbaceous plant species in their habitat. They frequently tasted non-hosts such as *Chaenactis* and were also observed searching, with frequent tasting, in habitat patches that contained no hosts at all. Despite the strong alighting bias towards it, *Chaenactis* received no eggs, since, like other non-hosts, it was always rejected after being tasted.

Evidence that abdominal curling was a chemotactic response comes from an experiment in which leaves of *Pedicularis* and *Collinsia* were dipped in ethanol for 30 s and the ethanol evaporated onto filter paper. When placed on dampened filter papers, insects from *Pedicularis*-adapted and *Collinsia*-adapted populations showed abdominal curling and ovipositor extrusion most readily in response to extracts of their own hosts (Singer and McBride 2010).

Geotaxis was also an important part of the post-alighting oviposition sequence. After accepting chemical stimuli, a positively geotactic insect would tumble to the ground and search the base of the plant. This video, from McBride and Singer (2010) <https://www.youtube.com/watch?v=V6NE89u46pc&feature=youtu.be> shows behaviour of a positively geotactic *E. editha* after a staged encounter with an acceptable host, *Pedicularis*. The previous video shows a non-geotactic insect ovipositing close to the point of staged “alighting” on *Collinsia*.

## Defining and measuring host preference and motivation

Ecologists often define resource “preference” in terms of the use of resources relative to their availability, while behavioural biologists define preference in terms of responses to stimuli. I use a behavioural definition, “the set of likelihoods of accepting specified resources that are encountered” (Glossary; Singer 2000), since this renders preference a trait of the insect that can vary among individuals and populations. In contrast, ecological definitions render preference effectively an emergent trait from the plant–insect interaction, equally subject to influence from variation among insects or among plants (Singer and Parmesan 1993; Singer 2000).

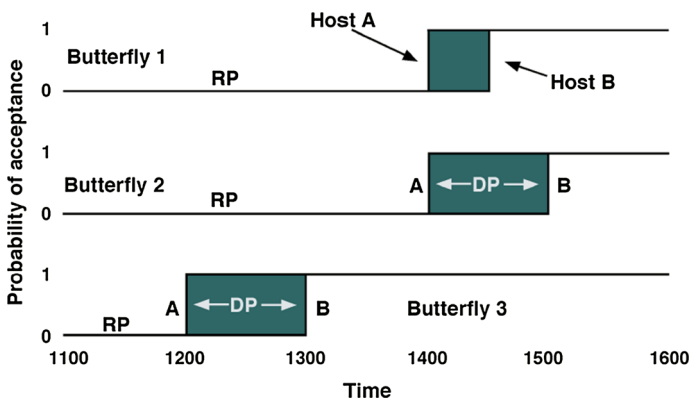
Two aspects of Melitaeine behaviour have assisted assessment of post-alighting host preferences. First, the response to host  $X$  at time  $t$  was unaffected by the identities of plants previously encountered or by the frequency of encounters with them. Despite learning which resources to use and how to use them when foraging for nectar, *E. editha* showed no evidence of learning when foraging for oviposition sites (Thomas and Singer 1987; Parmesan et al. 1995; McNeely and Singer 2001). The second useful aspect is that these butterflies behaved naturally after staged encounters with hosts (see videos). This ability of manipulated butterflies to replicate natural behavior makes it possible to stage a succession of encounters and observe acceptances and rejections of host chemistry without allowing

oviposition, judging acceptance from the abdominal curling and ovipositor extrusion that precede oviposition. When this is done, we observe that Melitaeines behave like a person on a long drive looking for a nice restaurant and failing to find one, but gradually becoming willing to eat worse and worse food as time goes by. The probability of accepting each host jumps quickly from zero to nearly one, but this change happens at different times for different hosts (Singer 1982). Therefore, if a butterfly that prefers host A over host B is prevented from ovipositing and offered staged encounters with the two hosts in alternation, we see a rejection phase when both hosts are rejected, then a discrimination phase during which host A is consistently accepted and host B consistently rejected. The final phase, in which both hosts are accepted, continues until oviposition is allowed (Fig. 2).

The figure shows changes in behaviour by three butterflies in trials of the type just described, again with actual oviposition not permitted. Individual 2 has a stronger preference for A over B than individual 1 because it would search for longer, accepting only host A, before reaching the “motivation” at which either host would be accepted. The difference between these insects is described as a difference in strength of preference, which is a heritable trait (Singer et al. 1988), with approximately equal paternal and maternal contributions (Singer and Moore 1991; McBride and Singer 2010).

On the other hand, butterflies 2 and 3 are described as having identical preferences, since their discrimination phases are the same length. However, they would show different behaviour if tested at the same time; for example, at 14:30 butterfly 3 would accept either host, while butterfly 2 would accept only host A. This difference is described as a difference in “motivation” to oviposit (see Glossary), which is not expected to be heritable, since in nature high motivation would result from prolonged failure to find the preferred host (Singer et al. 1992).

The practical measure of post-alighting preference for these insects is the minimum length of discrimination phase, the time from first acceptance of host A to last rejection of host B in trials where encounters with the hosts are staged in frequent alternation and oviposition is not allowed.



**Fig. 2** Stylized depiction of changes over time in the probability of accepting two hosts, with host A being preferred over host B by three butterflies differing in either preference or motivation (see text). Butterflies are offered repeated staged encounters with the two hosts in alternation, and are prevented from ovipositing. RP = rejection phase, when both hosts are rejected; DP = discrimination phase, during which the preferred host is accepted and the less-preferred host rejected. If oviposition is still prevented, the discrimination phase is followed by an acceptance phase when either host would be accepted, if encountered

## Oviposition preference as a habitat adaptation: effects of preference on fitness and preference as a driver of MHC

Butterfly flight consumes resources that would otherwise be directed to egg maturation (Gibbs et al. 2010; Saastamoinen et al. 2010; Bonte et al. 2012). Therefore, we expect butterflies to evolve oviposition preference for the most abundant hosts, reducing search costs and increasing realized fecundity. However, we also expect evolution of preference for hosts that support high offspring survival. The most abundant hosts will not always be those that support highest survival, so there will frequently be tension between these requirements. The result of this tension could be preference for hosts that are highly suitable but scarce or for hosts that are abundant but suboptimal for offspring performance. Hosts of *E. editha* vary considerably in suitability for larvae, and the insect has responded by evolving local preferences for hosts that supported high offspring survival, even if they were scarce (Singer et al. 1989, 1994; Singer and Wee 2005). In contrast, the two hosts of *M. cinxia*, *Veronica spicata* and *Plantago lanceolata*, supported identical offspring survival both in the laboratory and across a seven-year field study (van Nouhuys et al. 2003; Appendix 2). Therefore, we expect evolution of post-alighting preferences to respond principally to local host abundance and this expectation is fulfilled (Kuussaari et al. 2000).

Applying our concepts of ‘preference’ and ‘motivation,’ we perceive that a Melitaeine failing to quickly find its preferred host in its natal habitat patch has two options: it can stay and continue to search until its motivation rises to the point at which an acceptable host is encountered, or it can emigrate in search of a patch that contains its preferred hosts. In nature both options are taken, by different individuals. Evidence for the second option, preference-biased emigration, will be discussed later; here I discuss the first option, staying despite failing to find preferred hosts. Two examples show that many female *E. editha* chose this tactic.

First, in a population at Sonora Junction (Mono Co., California) a low-ranked host that was not preferred by any tested butterfly received 80 % of the eggs laid (Singer et al. 1989). The preferred host was rare, the low-ranked host was abundant and discrimination phases were short, so oviposition was not long delayed. Around 20 % of the butterflies succeeded in ovipositing on their preferred host, thereby gaining the highest offspring survival (Singer et al. 1994).

The second example comes from a metapopulation of *E. editha* along the Generals’ Highway (Sequoia National Forest, California). Starting in 1967, humans cut down trees and made clearings in which the insects’ traditional host, *Pedicularis semibarbata* (Fig. 1) was killed and the lifespan of the ephemeral annual *Collinsia torreyi* (Fig. 1) was extended, suddenly rendering it a suitable host. The insects responded by colonizing *Collinsia* in clearings and retaining their diet of *Pedicularis* in patches of open forest (“outcrops” in previous accounts) where widely-spaced trees remained (Singer 1983; Thomas et al. 1996). A mosaic of plant–insect association was created. At the metapopulation level, the insects underwent dietary niche expansion, a process shown by experiment to incur unexpected hazards in addition to its obvious benefits (Agashe and Bolnick 2012).

In 1979–1984 we tested both alighting biases and post-alighting preferences of female *E. editha* collected newly-eclosed in a large (3 ha) clearing at Rabbit Meadow, within the Generals’ Highway metapopulation. Although these butterflies had developed on *Collinsia* from eggs naturally laid on that host, they uniformly retained a strong bias towards alighting on plants such as *Chaenactis* that physically resembled *Pedicularis*, alighting on *Collinsia* (Fig. 1) even less frequently than random expectation (Parmesan et al. 1995).

After alighting, 64 % were tested as *Pedicularis*-preferring, 31 % without preference and only 5 % *Collinsia*-preferring ( $n = 55$ ; Singer 1983; Singer and Thomas 1996). In consequence, oviposition searches in the clearing patch were both longer and less successful than in open-forest. Parmesan et al. (1995) gathered naïve (teneral) female butterflies emerging from the clearing at Rabbit Meadow and released some of them in each patch type, observing the first oviposition search made by each insect. Mean lengths of search were  $28.7 \pm 15.9$  min in the clearing compared to  $10.8 \pm 12.1$  min in the open-forest. Only 20 % of searches ( $n = 40$ ) culminated in oviposition on *Collinsia* in the clearing, compared to 89 % ( $n = 27$ ) resulting in oviposition on *Pedicularis* in the open-forest.

Despite showing both visual (pre-alighting) and chemical (post-alighting) preferences for an absent host, *Pedicularis*, and despite being forced by these preferences into prolonged oviposition searches, many butterflies in the clearing failed to emigrate. Evidence for this comes from two experiments. First, preference tests were applied to recaptured butterflies that had either moved between habitat types or stayed in the patch of first capture. An estimated 20 % of the insects that stayed in the clearing ( $n = 41$ ) had done so despite preferring *Pedicularis* (Table 1). In a second experiment, insects captured in the clearing accepted *Pedicularis* sooner after capture than those from the adjacent open-forest site. We judged that the clearing butterflies were operating at higher mean motivation, caused by prolonged search (Singer et al. 1992).

The cost to realized fecundity of remaining in the clearing was estimated by sampling teneral females eclosing from *Collinsia* in the clearing and splitting them into two treatment groups. For the first 5 days of life, during which about half the potential fecundity was realized, one group was offered only *Pedicularis* for oviposition and the other only *Collinsia*. The experiment was carried out in the field, under natural conditions, so the two groups were tested simultaneously to control for effects of weather. The timing of each oviposition was noted and the number of eggs in each clutch counted.

As expected from the tested preferences, the first oviposition by insects offered only *Collinsia* was, on average, delayed (Table 2). On day 2 of life, when the first eggs were laid, the proportion of insects ovipositing on *Collinsia* was 0.18 with 95 % CI 0.09–0.32; the proportion ovipositing on *Pedicularis* was 0.75 with 95 % CI 0.54–0.89. On no other date was there a significant difference; frequency of oviposition by insects offered

**Table 1** Preferences of butterflies marked in June 1984 that moved between habitat patches at Rabbit Meadow or stayed in the patch where they were first marked (not necessarily their natal patch)

	Prefer <i>Pedicularis</i>	No preference	Prefer <i>Collinsia</i>
Stay in clearing ( $n = 41$ )	8 (20 %)	26 (63 %)	7 (17 %)
Move clearing to forest ( $n = 23$ )	8 (35 %)	14 (61 %)	1 (4 %)
Stay in forest ( $n = 55$ )	28 (51 %)	26 (47 %)	1 (2 %)
Move forest to clearing ( $n = 14$ )	1 (7 %)	10 (70 %)	3 (21 %)

Data from Thomas and Singer (1987)

Among butterflies first captured in forest, preferences *Pedicularis*:*Collinsia* were 28:1 for sedentary insects and 1:3 among emigrants.  $p = 0.003$  by two-tailed Fisher exact test

Among butterflies first captured in clearing, preferences *Pedicularis*:*Collinsia* were 8:7 for sedentary and 8:1 among emigrants.  $p = 0.18$ , NS by two-tailed Fisher exact test

The ratio of sedentary: emigrants was 36:2 among butterflies first caught in sympatry with their preferred host and 52:24 among butterflies with no preference.  $p = 0.002$  by two-tailed Fisher exact test (*Collinsia* was present in both habitats)



*Collinsia* perked up on day 3 and from then on was not significantly different from the frequency in the *Pedicularis* group. Insects that delayed their first oviposition laid larger first clutches on both hosts (Table 2) but this trend was insufficient to equalize overall fecundities between insects offered different hosts. As a result of greater delay on *Collinsia*, mean total fecundity for insects that survived for the full 5-day experiment was significantly lower than on *Pedicularis*: (119.8 vs 171.1, Mann–Whitney  $U$  test:  $p = 0.003$ , Table 2).

Interpretation of this experiment as an influence of host preference on realized fecundity rather than vice versa depends on the assumption that variation in strength of preference was not mechanistically driven by variation in fecundity. This assumption was justified by experiment. Although entomologists might expect insects with short discrimination phases to be maturing eggs faster, this was not the case here: the rate of egg maturation and the length of discrimination phase were independent variables (Agnew and Singer 2000).

### Justification for describing oviposition preference as causing, rather than comprising, biased dispersal and MHC

“Dispersal” is defined by Richardson et al. (2014) as “movement of offspring away from their parents or natal site of origin.” As such, it appears distinct from our definition of “preference.” However, preference and dispersal can be conflated in current literature. Bolnick and Otto (2013) write: “plant-feeding insects often exhibit biased oviposition .... a pattern of nonrandom dispersal that contributes to local adaptation.” When “biased oviposition” appears synonymous with “nonrandom dispersal,” it is not possible to ask whether variable oviposition preferences might cause biased dispersal or whether genetic differentiation among habitats in oviposition preference might be driven by biased

**Table 2** Daily and total fecundities and clutch sizes of *E. editha* collected as mating pairs in Rabbit clearing in 1983 and offered only *Pedicularis* or only *Collinsia* for 4 days, until day 5 of life (mating occurred on day 1)

	Day 2	Day 3	Day 4	Day 5	Total 5-day
Pedicularis mean fecundity	49.3 (28)	34.6 (33)	43.0 (25)	38.8 (15)	171 (15)
Collinsia mean fecundity	10.2 (41)	38.0 (38)	30.6 (35)	44 (29)	120 (29)
Pedicularis mean clutch size	65.8 (21)	54.3 (21)	56.6 (19)	64.7 (9)	
Collinsia mean clutch size	59.9 (7)	85.0 (17)	51.0 (21)	70.9 (18)	
Proportion laying on <i>Pedicularis</i>	0.75 (28)	0.60 (28)	0.78 (27)	0.60 (15)	
Proportion laying on <i>Collinsia</i>	0.18 (38)	0.45 (38)	0.60 (35)	0.62 (29)	
Mean size first clutch <i>Pedicularis</i>	65.8 (21)	71.0 (6)	91.0 (1)	No data	
Mean size first clutch <i>Collinsia</i>	59.9 (7)	85.0 (17)	85.2 (6)	109 (6)	
Mean total fecundity on <i>Pedicularis</i> for each date of first oviposition	180 (11)	152 (3)	133 (1)	(None)	
Mean total fecundity on <i>Collinsia</i> for each date of first oviposition	114 (3)	135 (14)	114 (5)	109 (6)	

Measures of daily “mean fecundity” include zeros from insects that did not lay on that day. Measures of “clutch size” exclude zeros. Mean sizes of first clutches refer to the first clutches of each insect. So, under “Day 4 and first clutch” the Table shows mean sizes of day 4 clutches deposited by insects that had not laid previously. Sample sizes in parentheses. Two insects offered *Collinsia* and one offered *Pedicularis* survived to day 5 without ovipositing and are not included in the summary. Data partly published by Singer (1986)

dispersal. These questions would seem circular. Here, I argue that, if we define host preference, habitat preference and dispersal as separate behaviors, then we can both ask these questions and document phenomena that we might not otherwise detect. Viewing host preference as a potentially independent, heritable, adaptation to habitat should bring it more informatively into discussions of genotype-biased dispersal.

Previous sections describe experiments and observations that collectively support two inferences about the role of butterfly oviposition in dispersal:

1. oviposition preferences are separate traits from habitat preferences; a habitat is chosen first, and only then is an oviposition search conducted within it, using different criteria from the habitat search.
2. oviposition preferences comprise adaptations to habitat, in the sense that they influence rates of fitness gain within particular habitats.

Does oviposition preference-biased dispersal fit the definition of MHC? A reviewer suggested that emigration from a patch in which the preferred host is scarce or absent might be a simple consequence of prolonged oviposition search, rather than an explicit decision by the insect, based on its search experience, to seek a new habitat patch and search elsewhere. If this were true, then biased dispersal would not fit the concept of MHC (Glossary; Edelaar et al. 2008).

For wide-ranging butterflies that roam diverse landscapes searching for hosts the reviewer's suggested scenario would likely apply, but for butterflies with discrete population structure, including our study species, it does not. For such a butterfly to leave a habitat patch it must make a decision to deviate from its normal behaviour. It must either cross a boundary that it can detect and from which it would normally be reflected or leave a memorized home range to which it has previously been confined. Such a decision to emigrate is not a direct response to hosts, since hosts typically occur only in parts of the habitat patch and frequently also occur outside the habitat (Dennis et al. 2003, 2014). Patch-leaving is not an automatic consequence of prolonged search, since normal reflection from habitat boundaries is observed during individual oviposition searches. This relative independence of host search from emigration decisions allows two additional inferences:

3. A decision by a butterfly to respond to its rate of fitness gain from oviposition by either emigrating from a habitat or remaining in it is analogous to the same “stay or go” decision made by a vertebrate in response to its feeding rate, when that rate is influenced by (for example) body shape or morphology of feeding structures.
4. when butterflies are biased towards leaving habitats to which their oviposition preferences do not well adapt them and migrating to habitats to which their oviposition preferences do adapt them, this behaviour does fit definitions of MHC (Glossary).

By viewing oviposition preference as a habitat adaptation and generator of MHC, the following sections address fitness consequences of MHC in both study butterflies. *M. cinxia* occupied a relatively stable environment, in which MHC generated results concordant with current theory. In contrast, *E. editha* inhabited a fluctuating environment in which recent anthropogenic intervention had generated habitat patches of very different quality. Here, the effects of MHC failed to match theory, being at times adaptive and at times maladaptive, both for the insects dispersing and for the populations into which they dispersed.

## Adaptive influence of biased dispersal in *M. cinxia*

*M. cinxia* in Finland inhabited habitat patches varying spatially in the availability of two Plantaginaceous hosts, *Veronica spicata* and *Plantago lanceolata*. Within the part of the butterfly's range where both hosts occurred (c.30 × 50 km), Hanski's group had assembled total counts of *M. cinxia* larval groups on each host, in every known habitat patch, recording extinctions and colonizations each year. Recorded colonizations from 1993 to 1997 totalled 317 out of 2356 possibilities (empty patch/year combinations). Hanski and Singer (2001) then asked whether these colonizations were biased by host composition of the patches and whether butterfly host preferences might drive any such bias.

For each target patch available for colonization (i.e. empty) we calculated connectivities to larval groups found on *Veronica* and on *Plantago* in other patches, weighting each larval group by its distance from the target patch. Note that an occupied, non-target, patch containing larvae on both hosts contributed to both connectivities. Higher relative connectivity to larvae on *Veronica* versus *Plantago* was associated with increased colonization rates of empty patches dominated by *Veronica* and decreased colonization of empty patches dominated by *Plantago*. Reciprocal-transplant preference experiments excluded regional variation in host acceptability as a cause of this pattern, since the species-identity of the preferred plant depended only on the origin of the insects and not on that of the plants. Therefore, we could use the patch-specific relative connectivity to larvae on *Veronica* as a surrogate for the preferences of females encountering the patch, and ascribe the biased colonization to an effect of preference genotype.

In summary, females that emigrated from their natal patches and roamed the landscape chose to colonize patches that best matched their own post-alighting preferences (Hanski and Singer 2001). Males, in contrast, didn't colonize empty patches, but arrived passively as sperm carried by females (Hanski et al. 2004). Biased gene flow had no effect on offspring fitness, because overall survival was identical on the two hosts and there was no trend for preference-performance correlation (van Nouhuys et al. 2003; see Glossary and online Appendix 2). Nonetheless, local adaptation should be enhanced by efficient host search within the newly-colonized habitats. In addition, the colonization bias interacted with the structure of patch networks to cause adaptive evolution of host preference within those networks (Hanski and Heino 2003).

In the Introduction I remarked that work on butterflies had been “misunderstood.” The Hanski and Singer (2001) study is a case in point. Clobert et al. (2009) wrote: “insects developing on a given host often search for similar hosts on which to lay their eggs when sexually mature (Hanski and Singer 2001)—a process known as natal habitat preference *induction*” (my italics). The use of “induction” wrongly implies that *M. cinxia* were induced by their larval experience to prefer, as adults, plants they had used as larvae, and that inter-patch differentiation in oviposition preference was not genetically based.

The idea that that larval induction of adult preference occurs widely in herbivorous insects was once popular (Thorpe 1930), but has been refuted as a generality (Barron 2001). For example, the apparent effect of larval experience on preferences of adult *Drosophila* disappeared when pupae were washed (Jaenike 1983). With two striking exceptions (Thoming et al. 2013; Cahenzli et al. 2015) experimental manipulation of Lepidopteran larval experience has not influenced adult preferences (Wiklund 1973; Janz et al. 2009).

So, it isn't surprising that there was no induction in the Hanski and Singer study (Singer and Lee 2000) nor in *E. editha*, in which preferences were likewise heritable within populations (Singer et al. 1988) and preference differences between populations were maintained on a common host in captivity (Singer and Parmesan 1993). Individuals that developed in the field on one host genus, from eggs laid naturally on that host, could have genotypes causing them to prefer to oviposit on a different host genus as adults (Singer 1983). The fact that insects originating from the same host at the same site can have genetically variable oviposition preferences is one of the features that lends these systems evolutionary interest.

## Adaptation, maladaptation, biased dispersal and MHC in *E. editha*

### Traits of *E. editha* adapted to *Pedicularis* or *Collinsia*

The section on “oviposition preference as a habitat adaptation...” described colonization of *Collinsia* by *E. editha* in a series of anthropogenic clearings at Generals' Highway, creating a mosaic of populations concentrated on two hosts: on *Collinsia* in clearings and on *Pedicularis* in open-forest patches. In order to evaluate adaptation by *E. editha* to their novel and traditional hosts, we examined traits of isolated metapopulations with long-term use of either *Collinsia* or *Pedicularis*. This examination revealed parallel variation among metapopulations in a suite of traits adapting the insects to their local hosts (Singer and McBride 2010, 2012). These traits included alighting bias, post-alighting chemical preferences, adult and larval geotaxis, clutch size and larval performance. Effects of local adaptation on larval performance were asymmetric: larvae adapted to *Collinsia* were not able to use *Pedicularis*, while larvae adapted to *Pedicularis* had no difficulty with *Collinsia*, implying that *Collinsia* was the less defended of the hosts (Rauscher 1982; Singer and McBride 2010).

Natural selection responsible for variation of egg height and clutch size was investigated by field observation and experiment. Leaf tips of *Pedicularis* were grazed by vertebrates, causing selection for positive geotaxis (Bennett et al. 2015). Conversely, *Collinsia* was not grazed, but leaves close to the ground were less nutritious, supporting slower larval development than higher leaves, causing selection for higher egg placement (McBride and Singer 2010). Host-associated natural selection on clutch size was revealed by experimental placement of neonate larvae in the field. These larvae survived better in large than in small groups on *Pedicularis* and better in small than in large groups on *Collinsia* (McBride and Singer 2010).

In apparent response to this host-specific natural selection on egg placement and clutch size, insects in *Pedicularis*-adapted populations typically laid one clutch per day, averaging around 50 eggs, at height <1 cm., while *Collinsia*-adapted insects laid 7–15 clutches per day averaging 4–12 eggs/clutch, at height >4 cm (Singer and McBride 2010).

Although these adaptations were heritable, there was no overall genomic signature of host affiliation in *E. editha* (Mikheyev et al. 2013). Hybrids between butterflies adapted to different hosts were vigorous and fertile, and showed intermediate trait values to their parents—for example, accepting both hosts readily and laying clutches of 20–30 eggs 2–3 times per day (McBride and Singer 2010). The sets of host-associated populations did not (yet) constitute cryptic species.

## Maladaptation of *E. editha* to their novel host, *Collinsia*

Within the Generals' Highway metapopulation of *E. editha*, we studied a *Collinsia*-feeding population in a 3 ha. clearing at Rabbit Meadow. In the absence of *Pedicularis*, the insects retained *Pedicularis*-adaptive traits. Despite their alighting bias towards *Chaenactis* and against *Collinsia*, most searching insects did eventually encounter *Collinsia*. Those that decided to seek an oviposition site on this species treated it as though it were a *Pedicularis*, laying mean clutch sizes of 51.0 eggs ( $n = 50$ ) at mean height 0.58 cm. This compared with mean clutch size of 43.5 ( $n = 79$ ) at mean height 0.55 cm on *Pedicularis* in the adjacent open-forest habitat patch (Supplemental Table 1).

In sum, *Collinsia*-feeding butterflies in the Rabbit Meadow clearing lacked adaptation to their host in at least four traits: in alighting bias, post-alighting preference, geotaxis and clutch size. Even though they achieved higher fitness on *Collinsia* than that achieved by insects using *Pedicularis* in the adjacent open-forest patch (see below), I describe these *Collinsia*-feeders as “maladapted” to their host (see definition of “local adaptation” in Glossary).

## Effects of post-alighting preference on reciprocal dispersal among patch types

For *Pedicularis*-preferring *E. editha* eclosing in the clearing the alternate strategy to staying at home with reduced realized fecundity was to emigrate to a habitat patch that did contain their preferred, traditional host. We (Thomas and Singer 1987) investigated this possibility by performing mark-release-recapture in both patches of the adjacent patch-pair at Rabbit Meadow, and then blind-testing the preferences of recaptured females that had moved or stayed. With marginal significance ( $p = 0.053$  by Fisher's exact, two-tailed), the per-capita rate of emigration was higher from the clearing: 23 out of 64 (36 %) migrated from clearing to forest while 14 of 69 (20 %) moved in the opposite direction.

Dispersal was biased as expected with respect to post-alighting preferences. Females that dispersed between patch types were more likely than sedentary insects to prefer the host used in their target patch. Further, females first captured in the patch where their preferred host occurred were less likely to emigrate from that patch than females with no preference (Table 1).

## Identifying local adaptation caused by biased dispersal

We expect effects of MHC on trait divergence among habitat patches to mimic and complement effects of patch-specific natural selection (Bolnick and Otto 2013). At Rabbit Meadow we obtained a clear demonstration of this complementarity and we identified biased dispersal as an influential driver of population differentiation.

Natural selection on host use (Glossary) differed between the two patch types, clearing and open-forest (qualitative summary in Supplemental Table 2). A combination of experimental placement of eggs and observation of natural oviposition showed that, across both habitat types, the highest fitness resulted from oviposition on (long-lived) *Collinsia* in clearings, the second highest from oviposition on *Pedicularis* in open-forest habitat and lowest (close to zero) from using the (short-lived) open-forest *Collinsia* (Moore 1989; Boughton 1999; Thomas et al. 1996; Singer and Thomas 1996). So, although *Collinsia* was everywhere abundant and available to ovipositing butterflies, selection opposed acceptance of this host in open-forest habitat patches and favoured it in clearings. Logging by humans had created a patchwork landscape with opposing directions of natural selection on host use and hence, less directly, on host preference.

Within each year there was a consistent difference in post-alighting preference, in the expected direction, between insects in the Rabbit clearing and the adjacent open-forest patch. This difference was heritable: it was maintained when insects from the adjacent patches were raised in captivity on *Collinsia* (Singer and Thomas 1996). The difference could have been caused by either or both of two documented effects: biased dispersal and habitat-specific natural selection.

An unexpected natural event allowed us to identify a strong role of biased dispersal in the differentiation of preference among patches. A summer frost ( $-5^{\circ}\text{C}$ ) in June 1992 killed *Collinsias* in all the clearings throughout the metapopulation, after the butterflies had finished ovipositing but before larvae could diapause. Larvae starved and the clearing populations were extinguished, while the open-forest populations were unaffected. Because insects in the open-forest patches developed more slowly than those in the clearings, open-forest adults eclosed about a week later than clearing adults and immigrants to clearings in 1993 arrived so late that their offspring were killed by host senescence. The clearing was not recolonized until later (Boughton 1999).

Thus, adults captured in clearings in 1994 were all immigrants. By good luck we had estimated the inter-patch difference in preference at the Rabbit patch-pair in 1992, immediately prior to the natural elimination of the clearing population. We repeated this estimate in 1994. With reasonable sample sizes in both patches in both years (40 and 45 in 1992, 44 and 37 in 1994) we observed identical inter-patch differences in preference in 1992 and 1994 (Fig. 3 of Singer and Thomas 1996). Classifying preference into five categories (Table 3) illustrates how the interpatch differentiation of preference was adaptive for insects in the clearing, where it would reduce the time wasted in searching for *Pedicularis* by butterflies that were forced to use *Collinsia*, whether or not they preferred it. Because both biased dispersal and patch-specific selection were operating in 1992 but biased dispersal was the sole mechanism at work in 1994, we concluded that biased dispersal had been the more influential force in driving differentiation of post-alighting preference between the patches (Singer and Thomas 1996).

### A paradox? Fitness of migrants reduced by choosing habitats to which they were adapted

Dispersal by Generals' Highway *E. editha* was not density-dependent on a per-capita basis (Boughton 2000), but nonetheless the high absolute density in clearings, plus the tendency for insects with post-alighting preference for *Pedicularis* to emigrate from clearings to their traditional host and habitat, caused net migration from clearings to open-forest

**Table 3** Preference difference between adjacent patches of a patch-pair

	C	N	P0	P1	P2
Rabbit clearing	5	5	10	12	5
Rabbit open-forest	0	4	6	23	11

Preferences of *E. editha* females captured flying in Rabbit Meadow clearing and open-forest patches in 1994 (data from Singer and Thomas 1996). Butterflies were compared side-by-side, in blind tests, using the same test plants still rooted in the ground. C = *Collinsia* preference; N = no preference; P0 = preferring *Pedicularis* but with first acceptance of both hosts on the same day; P1 = accepting *Pedicularis* on day 1 of testing with first acceptance of *Collinsia* on day 2; P2 = insects accepting *Pedicularis* on day 1 but still rejecting *Collinsia* at the end of day 2.  $p = 0.007$  by Mann–Whitney test, after assigning numbers to each preference category (C = 1, N = 2, P0 = 3, P1 = 4, P2 = 5)

patches (Table 1; Boughton 1999, 2000). A system of sources and pseudosinks was set up, with clearings acting as sources and open-forest populations suffering increasing competition and acting as pseudosinks (Boughton 1999). Thus, there was an overall trend for butterflies to emigrate from the habitat type that supported higher fitness.

The trend for preference difference between emigrants and sedentary butterflies reaches significance only when analyzed in both directions (Table 1). However, it is highly likely that emigrants from clearings were biased towards *Pedicularis*-preferers that would have suffered fitness reduction from prolonged search if they had stayed. Therefore, we cannot conclude that these emigrants were reducing their fitness just because they were moving to a habitat that supported lower fitness in general. To assess this question we can use evidence from the experiment, already summarized in Table 2, that simulated the behaviour of staying in the clearing and estimated the consequent reduction of fecundity. The experiment was conducted in 1983, mid-way through the evolution of increasing *Collinsia* acceptance, using only butterflies emerging in the clearing habitat, that had developed on *Collinsia* from eggs naturally laid on it. Among insects offered only *Collinsia*, mean egg production was 120, a reduction of 30 % from the mean of 171 among insects offered *Pedicularis* (Table 2). The estimated fecundity reduction among strong *Pedicularis*-preferers, that did not lay on *Collinsia* until day 5, was 36 %, from 171 to 109 (Table 2).

These fecundity reductions estimate the penalty incurred by insects choosing to remain in the clearing. How do they compare with the penalty associated with emigration to the open-forest habitat? Prior to 1989 the anthropogenic habitat at Generals' Highway was so benign, and the host *Collinsia* so poorly-defended, that in most years butterfly population growth was several times higher on *Collinsia* in clearings than on *Pedicularis* in open-forest patches (Moore 1989; Thomas et al. 1996). Therefore, for the majority of butterflies, the reduction of fitness from lowered fecundity caused by remaining in the clearing and failing to find their preferred host was less than the reduction from poor offspring survival caused by emigration to the more challenging open-forest habitat. Most of the insects that emigrated from the clearing reduced their lifetime fitness by doing so, despite correctly perceiving that they were maladapted to their natal habitat.

### **Another paradox? Maladaptive evolution in populations receiving immigrants despite MHC**

Still at Generals' Highway in the 1980's, would we expect immigration from *Collinsia*-feeding populations in clearings to have driven maladaptive evolution in open-forest *E. editha* populations, where selection strongly opposed oviposition on *Collinsia*? Perhaps not, because biased dispersal caused immigrants from the clearing to be biased against *Collinsia* acceptance? However, that bias was measured within the population of origin, the clearing, where increased *Collinsia* acceptance was rapidly evolving. Butterflies captured eclosing from *Collinsia* in the Rabbit clearing in 1989 were significantly more *Collinsia*-preferring than equivalent insects tested in 1984: ratios of *Pedicularis* preference: no preference: *Collinsia* preference were 13:5:0 in 1984 and 10:23:10 in 1989 (Singer and Thomas 1996).

Because of the opposing influences on immigration to open-forest of biased dispersal and rapid evolution in the clearing, we cannot predict whether local natural selection against *Collinsia* acceptance in open-forest would have been reinforced or opposed by gene flow from clearings. However, preference testing showed that the net influence of immigration was to oppose local selection, and that the open-forest populations suffered "migration load" (Bolnick and Nosil 2007). In the mid-1980s both larval density and post-

alighting acceptance of *Collinsia* in the set of open-forest patches became significantly associated with isolation from populations in clearings. The better-connected a forest patch was to clearings, the higher the larval density and the greater the locally-maladaptive acceptance of *Collinsia*. These metapopulation-level effects had completely disappeared by 1994, 2 years after the extinction of clearing populations had caused migration from clearings into open-forest patches to cease (Thomas et al. 1996; Singer and Thomas 1996). Acceptance of *Collinsia* in open-forest patches was no longer associated with isolation from clearings. Both the appearance of this metapopulation-level pattern in the 1980's, and its subsequent disappearance, suggest that migration from clearings into open-forest, despite comprising MHC, had driven increasing, maladaptive, *Collinsia* acceptance in the habitats receiving the migrants.

If our inference about the cause of maladaptation in open-forest patches is correct, the maladaptation should have persisted after immigration from clearings ceased in 1992. In 1994, we tested this hypothesis by comparing oviposition preferences of butterflies at the Rabbit open-forest site and those from a similar site at Colony Meadow, 12 km distant in Sequoia National Park, where no logging had occurred, and there had been no colonization of *Collinsia*. Even though in 1994 all the tested butterflies from both Rabbit and Colony had developed from eggs laid naturally on *Pedicularis*, the insects from Rabbit were significantly more accepting of *Collinsia*, indicating a locally-maladaptive legacy of prior gene flow from the (now extinct) Rabbit clearing (Singer and Thomas 1996).

## Conclusion

To resist coining novel jargon, I adopt simple definitions of established concepts. I follow Friberg et al. (2008a, b) in separating host choice and habitat choice to make two relatively simple concepts rather than combining them into a single complex one. I follow Richardson et al. (2014) in defining dispersal as “movement of offspring away from their parents or natal site of origin” and I follow myself (Singer 2000) in defining preference as the “set of likelihoods of accepting resources that are encountered.” I follow Kawecki and Ebert (2004) in defining “local adaptation” without reference to performance outside the focal habitat and I choose the simpler definitions of MHC listed in the Glossary (Ravigne and Olivieri 2004; Edelaar et al. 2008) rather than the detailed, teleological definition of Edelaar and Bolnick (2012) that requires organisms to behave “in order to increase their expected fitness.” By using these definitions I am able to describe oviposition preference as an adaptation to habitat and a potential driver of MHC. I can also avoid circularity when describing oviposition preferences as influencing biased dispersal, while the same biased dispersal causes evolutionary divergence of preference among habitats. This approach has enabled me to describe unusual, and, perhaps, unexpected phenomena operating in natural populations, without recourse to novel terminology.

Our work with *E. editha* at Generals' Highway showed that spatial variation of a single habitat adaptation, oviposition preference, had three distinct and identifiable causes operating at different scales (Singer and Thomas 1996). Preference differences between adjacent habitat patches of different type, separated by as little as 150 m, were caused principally by MHC, which acted to complement the difference between patch types in local natural selection. Differences across the metapopulation (1–4 km) among undisturbed open-forest patches with different isolation from disturbance were caused by traditional effects of gene flow working in opposition to local natural selection. Finally, at the



landscape scale (across 12 km), spatial variation of natural selection brought about the preference difference between metapopulations at Colony Meadow in the National Park and at Generals' Highway in the National Forest.

Cues used in habitat choice are expected to evolve to optimize fitness. However, in the case of *E. editha* at Generals' Highway, the combination of rapid anthropogenic environmental change and evolutionary lag by the butterflies resulted both in fitness-reducing habitat choices by individuals and maladaptive evolution of preference in the undisturbed forest habitats. Anthropogenic intervention had created habitat diversity on both spatial and temporal scales sufficiently rare in the past that insects had not evolved reduced host specialization or plasticity necessary to deal with it adaptively (cf Ronce and Kirkpatrick 2001). This type of effect should be common, as anthropogenic tinkering with natural communities is already pervasive (Fahrig 2007).

**Acknowledgments** Melitaeine butterflies first attempted to explain their oviposition behaviour to Singer in 1956; Paul Ehrlich introduced Singer to *E. editha* in 1967. Extension from Singer's (1983) "two-patch" study to the metapopulation level was initiated by Chris Thomas, resulting in Singer's collaboration with Hanski. Carolyn McBride, Camille Parmesan and Davy Boughton all made essential contributions to the work. Discussions with Carol Boggs, Dan Bolnick, Roger Dennis, Pim Edelaar, Andy Foggo, Kelsey Jiang, Mark Kirkpatrick, Isabelle Olivieri, Paul Severns and Rachel Steward have been most helpful. Anonymous reviewers and the associate editor were exceptionally willing to accommodate the manuscript's conceptual peregrinations and unconventional format. This work benefitted from NSF grants to Paul Ehrlich in 1967–1971 and to Singer in 1978–1980, 1984–1986, 1993–1995 and 2002–2004.

## Glossary

### Preference

"the set of likelihoods of accepting specified resources that are encountered" (Singer 2000). This definition should apply both to host preference and to habitat preference when "resources" are habitats. "Preference" refers to multiple resources, "acceptance" to a single resource. "Acceptance" is either the act of accepting a resource or the tendency to accept a single resource. So, from a starting point at which most insects strongly prefer *Pedicularis*, "an evolutionary increase in *Collinsia* acceptance" could refer to a decrease in strength of preference for *Pedicularis* over *Collinsia*, an increase in proportion of insects with no preference, and/or an increase in preference for *Collinsia*.

### Preference-performance correlation

Variation of oviposition preference among individual females is associated with variation of performance among their offspring (Singer et al 1988).

### Motivation to oviposit

Readiness to respond to stimuli from hosts by ovipositing. In our study organisms, the trend for insects to accept a wider range of hosts as they search is attributed to increase of "motivation" over time; however, insects that search for only a short time for their preferred host before accepting a lower-ranked host are described as possessing "weak preference" rather than "rapidly-increasing motivation." The practical reason for this approach is that it distinguishes a potentially heritable trait, "preference," from short-term effects of encounter rates that are classed as "motivation" (see text and Fig. 2).

<b>Host use</b>	Actual use of particular host resources, typically resulting from interactions between encounter, preference and motivation.
<b>Local adaptation</b>	“evolution of traits that provide an advantage under local environmental conditions.... regardless of the consequences of these traits for fitness in other habitats” (Kawecki and Ebert 2004). This usage allows the possibility that an individual can have lower fitness in a habitat to which it is well-adapted than in a habitat to which it is maladapted, if the habitat to which it is adapted is in some sense demanding, as described here for <i>E. editha</i> adapted to the host <i>Pedicularis</i> .
<b>Matching habitat choice (MHC)</b>	(1) Preference by individuals for “the habitat to which they are best adapted” (Ravigne and Olivieri 2004). (2) “Dispersing individuals sample and compare environments and settle in environments that best match their phenotype, causing directed gene flow” (Edelaar et al. 2008).

## References

- Agashe D, Bolnick DI (2012) Dietary niche and population dynamic feedbacks in a novel habitat. *Oikos* 121:347–356
- Agnew K, Singer MC (2000) Does fecundity drive the evolution of insect diet? *Oikos* 88:533–538
- Barron AB (2001) The life and death of Hopkins’ host-selection principle. *J Insect Behav* 14:725–737
- Bennett NL, Severns PM, Parmesan C, Singer MC (2015) Geographic mosaics of host preference, phenology, adult size and microhabitat choice predict butterfly resilience to climate warming. *Oikos* 124:41–53
- Bolnick DI, Nosil P (2007) Natural selection in populations subject to a migration load. *Evolution* 61:2229–2243
- Bolnick DI, Otto S (2013) The magnitude of local adaptation under genotype-dependent dispersal. *Ecol Evol* 3:4722–4735
- Bolnick DI, Snowberg LK, Patenia C et al (2009) Phenotype-dependent native habitat preference facilitates divergence between parapatric lake and stream stickleback. *Evolution* 63:2004–2016
- Bonte D, Van Dyck H, Bullock JM et al (2012) Costs of dispersal. *Biol Rev* 87:290–312
- Boughton DA (1999) Empirical evidence for complex source-sink dynamics with alternative states in a butterfly metapopulation. *Ecology* 80:2727–2739
- Boughton DA (2000) The Dispersal System of a Butterfly: a test of source-sink theory suggests the intermediate-scale hypothesis. *Am Nat* 156:131–144
- Buckley J, Bridle JR (2014) Loss of adaptive variation during evolutionary responses to climate change. *Ecol Lett* 17:1316–1325
- Cahenzli F, Wenk BA, Erhardt A (2015) Female butterflies adapt and allocate their progeny to the host-plant quality of their own larval experience. *Ecology* 96:1966–1973
- Clobert J, Le Gaillard JF, Cote J et al (2009) Informed dispersal, heterogeneity in animal dispersal syndromes and the dynamics of spatially structured populations. *Ecol Lett* 12:197–209
- Conradt L, Roper TJ (2006) Nonrandom movement behavior at habitat boundaries in two butterfly species: implications for dispersal. *Ecology* 87:125–132
- Cook LM, Saccheri I (2013) The peppered moth and industrial melanism: evolution of a natural selection case study. *Heredity* 110:207–212
- Dennis RLH, Shreeve TG, van Dyck H (2003) Towards a functional resource-based concept for habitat: a butterfly biology viewpoint. *Oikos* 102:417–426
- Dennis RLH, Dapporto L, Dover JW (2014) Ten years of the resource-based habitat paradigm: the biotope-habitat issue and implications for conserving butterfly diversity. *J Insect Biodivers* 2:1–32
- Dover J, Settele J (2009) The influences of landscape structure on butterfly distribution and movement: a review. *J Insect Conserv* 13:3–27

- Edelaar P, Bolnick DI (2012) Nonrandom gene flow: an underappreciated force in evolutionary ecology. *TREE* 27:659–665
- Edelaar P, Siepielski AM, Clobert J (2008) Matching habitat choice causes directed gene flow: a neglected dimension in evolution and ecology. *Evolution* 62:2462–2472
- Ehrlich PR (1961) Intrinsic barriers to dispersal in the checkerspot butterfly *Euphydryas editha*. *Science* 134:108–109
- Ehrlich PR, Hanski I (2004) On the wings of checkerspots: a model system for population biology. Oxford Univ Press, Oxford
- Fahrig L (2007) Non-optimal animal movement in human-altered landscapes. *Funct Ecol* 21:1003–1015
- Farkas TE, Mononen T, Comeault AA et al (2013) Evolution of camouflage drives rapid ecological change in an insect community. *Curr Biol* 23:1835–1843
- Friberg M, Bergman M, Kullberg J et al (2008a) Niche separation in space and time between two sympatric sister species—a case of ecological pleiotropy. *Evol Ecol* 22:1–18
- Friberg M, Olofsson M, Berger D et al (2008b) Habitat choice precedes host plant choice—niche separation in a pair of a generalist and a specialist butterfly. *Oikos* 117:1337–1344
- Gibbs M, Breuker CJ, Hesketh H et al (2010) Maternal effects, flight versus fecundity tradeoffs, and offspring immune defence in the Speckled Wood butterfly, *Pararge aegeria*. *BMC Evol Biol* 10:345
- Gilbert LE, Singer MC (1973) Dispersal and gene flow in a butterfly species. *Am Nat* 107:58–72
- Haddad NM (1999) Corridor use predicted from behaviors at habitat boundaries. *Am Nat* 153:215–227
- Hanski I (2011) Eco-evolutionary dynamics in the Glanville fritillary butterfly. *PNAS* 108:14397–14404
- Hanski I, Eralahti C, Kankare M et al (2004) Variation in migration propensity among individuals maintained by landscape structure. *Ecol Lett* 7:958–966
- Hanski I, Heino M (2003) Metapopulation-level adaptation of insect host plant preference and extinction–colonization dynamics in heterogeneous landscapes. *Theor Pop Biol* 64:281–290
- Hanski I, Singer MC (2001) Extinction–colonization dynamics and host plant choice in butterfly metapopulations. *Am Nat* 158:341–353
- Harrison S (1989) Long-distance dispersal and colonization in the Bay checkerspot butterfly. *Ecology* 70:1236–1243
- Hendry AP, Taylor EB (2004) How much of the variation in adaptive divergence can be explained by gene flow? An evaluation using lake-stream stickleback pairs. *Evolution* 58:2319–2331
- Hubbard JK, Uy JAC, Haubler ME et al (2010) Vertebrate pigmentation: from underlying genes to adaptive function. *Trends Genet* 26:231–239
- Janz N, Soderlind L, Nylén S (2009) No effect of larval experience on adult host preferences in *Polygonia c-album* (Lepidoptera:Nymphalidae): on the persistence of Hopkins' host selection principle. *Ecol Entomol* 34:50–57
- Jaenike J (1983) Induction of host preference in *Drosophila melanogaster*. *Oecologia* 58:320–325
- Jiggins CD, Naisbit RE, Coe RL et al (2001) Reproductive isolation caused by colour pattern mimicry. *Nature* 411:302–305
- Kallioniemi E, Zannese A, Tinker JE, Franco AMA (2014) Inter- and intra-specific differences in butterfly behaviour at boundaries. *Insect Conserv Divers* 7:232–240
- Kawecki TJ, Ebert D (2004) Conceptual issues in local adaptation. *Ecol Lett* 7:1225–1241
- Kirkpatrick M, Barton NH (1997) Evolution of a species' range. *Am Nat* 150:1–23
- Kuussaari M, Nieminen M, Hanski I (1996) An experimental study of migration in the Glanville Fritillary butterfly, *Melitaea cinxia*. *J Anim Ecol* 65:791–801
- Kuussaari M, Singer MC, Hanski I (2000) Local specialization and landscape-level influence of host use in a herbivorous insect. *Ecology* 81:2177–2187
- Mackay DA, Singer MC (1982) The basis of an apparent preference for isolated plants by ovipositing *Euptychia libye* butterflies. *Ecol Ent* 7:299–303
- Marden JH, Fescemyer HW, Schilder J et al (2013) Genetic variation in HIF signaling underlies quantitative variation in physiological and life-history traits within lowland butterfly populations. *Evolution* 67:1105–1115
- McBride CS, Singer MC (2010) Field studies reveal strong postmating isolation between ecologically divergent butterfly populations. *PLoS Biol* 8(10):e1000529. doi:10.1371/journal.pbio.1000529
- McNeely C, Singer MC (2001) Contrasting the roles of learning in butterflies foraging for nectar and oviposition sites. *Anim Behav* 61:847–852
- Mikheyev AS, McBride CS, Mueller UG et al (2013) Host-associated genomic differentiation in congeneric butterflies: now you see it, now you don't. *Mol Ecol* 22:4753–4766
- Moore SD (1989) Patterns of juvenile mortality within an oligophagous insect population. *Ecology* 70:1726–1731

- Mullen LM, Vignieri SN, Gore JA, Hoekstra HE (2009) Adaptive basis of geographic variation: genetic, phenotypic and environmental differences among beach mouse populations. *Proc R Soc B* 276:38–9–3818
- Nosil P, Crespi BJ, Sandoval CP (2002) Host–plant adaptation drives the parallel evolution of reproductive isolation. *Nature* 417:440–443
- Nosil P, Sandoval CP, Crespi BJ (2006) The evolution of host preference in allopatric versus parapatric populations of *Timema cristinae* walkingsticks. *J Evol Biol* 19:929–942
- Ockinger E, van Dyck H (2012) Landscape structure shapes habitat-finding ability in a butterfly. *PLoS One* 7:e41517
- Parmesan C (1991) Evidence against plant “apparency” as a constraint on evolution of insect search efficiency (Lepidoptera: Nymphalidae). *J Insect Behav* 4:417–430
- Parmesan C, Singer MC, Harris I (1995) Absence of adaptive learning from the oviposition foraging behaviour of a checkerspot butterfly. *Anim Behav* 50:161–175
- Pratt GF, Emmel JF (2010) Sites chosen by diapausing or quiescent stage quino checkerspot butterfly *Euphydryas editha quino* (Lepidoptera: Nymphalidae) larvae. *J Insect Conserv* 14:107–114
- Rausher MD (1982) Population differentiation in *Euphydryas editha* butterflies: larval adaptation to different hosts. *Evolution* 36:581–590
- Ravigne V, Olivier I (2004) Implications of habitat choice for protected polymorphisms. *Evol Ecol Res* 6:125–145
- Richardson JL, Urban MC, Bolnick DI, Skelly DK (2014) Microgeographic adaptation and the spatial scale of evolution. *TREE* 29:165–176
- Ricketts TH (2001) The matrix matters: effective isolation in fragmented landscapes. *Am Nat* 158:87–99
- Ries L, Debinski DM (2001) Butterfly responses to habitat edges in the highly fragmented prairies of Central Iowa. *J Anim Ecol* 70:840–852
- Ronce O, Kirkpatrick M (2001) When sources become sinks: migrational meltdown in heterogeneous habitats. *Evolution* 55:1520–1531
- Saastamoinen M, van der Sterren D, Vastenhout N et al (2010) Predictive adaptive responses: condition-dependent impact of adult nutrition and flight in the tropical butterfly *Bicyclus anynana*. *Amer Natur* 176:686–698
- Schtickzelle N, Joiris A, Van Dyck H, Baguette M (2007) Quantitative analysis of movement behavior within and outside habitat in a specialist butterfly. *BMC Evol Biol* 7:4. doi:10.1186/1471-2148-7-4
- Schultz CB, Crone EE (2001) Edge-mediated dispersal behavior in a prairie butterfly. *Ecology* 82:1879–1892
- Singer MC (1982) Quantification of host preference by manipulation of oviposition behavior in the butterfly *Euphydryas editha*. *Oecologia* 52:224–229
- Singer MC (1983) Determinants of multiple host use by a phytophagous insect population. *Evolution* 37:389–403
- Singer MC (1986) The definition and measurement of oviposition preference. In: Miller J, Miller TA (eds) *Plant–insect interactions*. Springer, Berlin, pp 65–94
- Singer MC (2000) Reducing ambiguity in describing plant–insect interaction: “preference”, “acceptability” and “electivity”. *Ecol Lett* 3:159–162
- Singer MC, Lee JR (2000) Discrimination within and between host species by a butterfly: implications for design of preference experiments. *Ecol Lett* 3:101–105
- Singer MC, McBride CS (2010) Multi-trait host-associated divergence among sets of butterfly populations: implications for reproductive isolation and ecological speciation. *Evolution* 64:921–933
- Singer MC, McBride CS (2012) Geographic mosaics of species’ association: a definition and an example driven by plant–insect phenological synchrony. *Ecology* 93:2658–2673
- Singer MC, Moore RA (1991) Genetic variation in oviposition preference between butterfly populations. *J Insect Behav* 4:531–535
- Singer MC, Ng D, Thomas CD (1988) Heritability of oviposition preference and its relationship to offspring performance within a single insect population. *Evolution* 42:977–985
- Singer MC, Parmesan C (1993) Sources of variation in patterns of plant–insect association. *Nature* 361:251–253
- Singer MC, Thomas CD (1996) Evolutionary responses of a butterfly metapopulation to human and climate-caused environmental variation. *Am Nat* 148:S9–S39
- Singer MC, Thomas CD, Billington HL, Parmesan C (1989) Variation among conspecific insect populations in the mechanistic basis of diet breadth. *Anim Behav* 37:751–759
- Singer MC, Thomas CD, Billington HL, Parmesan C (1994) Correlates of speed of evolution of host preference in a set of twelve populations of the butterfly *Euphydryas editha*. *Ecoscience* 1:107–114

- Singer MC, Vasco D, Parmesan C et al (1992) Distinguishing between preference and motivation in food choice: an example from insect oviposition. *Anim Behav* 44:463–471
- Singer MC, Wee B (2005) Spatial pattern in checkerspot butterfly–host interactions at local, metapopulation and regional scales. *Annales Zoologici Fennici* 42:347–361
- Soria-Carrasco V, Gompert Z, Comeault AA et al (2014) Stick insect genomes reveal natural selection’s role in parallel speciation. *Science* 344:738–742
- Stevens VM, Turlure C, Baguette M (2010) A meta-analysis of dispersal in butterflies. *Biol Rev* 85:625–642
- Thomas CD, Bodsworth EJ, Wilson RJ et al (2001) Ecological and evolutionary processes at expanding range margins. *Nature* 411:577–581
- Thomas CD, Singer MC (1987) Variation in host preference affects movement patterns in a butterfly population. *Ecology* 68:1262–1267
- Thomas CD, Singer MC, Boughton DA (1996) Catastrophic extinction of population sources in a butterfly metapopulation. *Am Nat* 148:957–975
- Thoming G, Larsson MC, Hansson BS, Anderson P (2013) Comparison of plant preference hierarchies of male and female moths and the impact of larval rearing hosts. *Ecology* 94:1744–1752
- Thorpe WH (1930) Biological races in insects and allied groups. *Biol Rev* 5:177–212
- van Nouhuys S, Singer MC, Nieminen M (2003) Spatial and temporal patterns of caterpillar performance and the suitability of two host plant species. *Ecol Ent* 28:193–202
- Wheat CW, Fescemeyer HW, Kvist J et al (2011) Functional genomics of life history variation in a butterfly metapopulation. *Mol Ecol* 20:181301828
- Wiklund C (1973) Host plant suitability and the mechanism of host selection in larvae of *Papilio machaon*. *Entomol Exp Appl* 16:232–242
- Wiklund C (1977) Oviposition, feeding and spatial separation of breeding and foraging habitats in a population of *Leptidea sinapis* (Lepidoptera). *Oikos* 28:56–68