

Ilkka Hanski: The legacy of a multifaceted ecologist

Attraction of *Melitaea cinxia* butterflies to previously-attacked hosts: a likely complement to known Allee effects?

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Clumped distributions of herbivorous insect eggs often result from independent assessments of individual plants by different ovipositing females. Here we ask whether, in addition, plants might be rendered more or less attractive to ovipositing *Melitaea cinxia* butterflies by presence of conspecific eggs and/or by prior larval attack. Both eggs and larval damage rendered *Veronica spicata* plants significantly more acceptable; the effect of eggs was particularly strong. Larval damage caused a marginally significant increase in acceptability of *Plantago lanceolata*, but there was no trend for an effect of eggs on this host. Variable oviposition preferences of Melitaeine butterflies are known to drive their metapopulation dynamics by affecting rates of emigration and patch colonization. Therefore variable host acceptability, as documented here, should do likewise, reducing emigration rates at high population densities where *V. spicata* is present in the landscape and complementing Allee effects that are already known in this system.

Introduction

With typical panache, Ilkka Hanski began a talk in 1994 like this: “We have sequenced an entire landscape comprising 1.6 kilopatches.” Each year for five years he and his entourage had counted the conspicuous communal larval webs of the Glanville fritillary butterfly, *Melitaea cinxia*, on each of two host plants, *Veronica spicata* and *Plantago lanceolata*, in 1600 habitat patches across the Åland Islands. Early analyses of these

data examined influences of patch size, spacing and dispersal on metapopulation dynamics (Hanski *et al.* 1994, 1995, Kuussaari *et al.* 1996). As the dataset grew over the years, including ever more kilopatches (Ojanen *et al.* 2013), it became possible to analyse how patch colonization and metapopulation dynamics were influenced by host composition of the patches and host preferences of the butterflies (Kuussaari *et al.* 2000, Hanski & Singer 2001, Hanski & Heino 2003). Individuals from patch networks in which the

insects fed principally on *Veronica* were not at all different from those sampled from *Plantago*-feeding networks in terms of larval performance (van Nouhuys et al. 2003). In contrast, they were clearly and genetically different in oviposition preference (Kuussaari et al. 2000). The adaptive significance of this differentiation is not known, but if it exists it is probably connected with host-finding efficiency (Singer 2015).

Genetic variation of post-alighting oviposition preference for host species, coupled with variable host composition of habitat patches, drove biases in both emigration and patch colonization. Two metapopulation-level effects of these biases emerged. First, in local patch networks where *Veronica* was more preferred, empty patches containing principally *Veronica* were more likely to be colonized than *Plantago*-dominated patches (Hanski & Singer 2001). Second, again in local patch networks where *Veronica* was more preferred, host use in occupied patches was more biased towards *Veronica* than expected from its relative abundance in each patch (Kuussaari et al. 2000).

These metapopulation-level effects were driven by matches and mismatches between the genetically-determined oviposition preferences of the insects and the host compositions of the patches in which they found themselves. In consequence, any factor that systematically affected host acceptability to the butterflies would be expected to add to these metapopulation effects. Here, we ask whether prior attack by *M. cinxia* affects host acceptability to females arriving subsequently and assessing those hosts for oviposition. Increases in host acceptability in response to attack would be expected to complement the Allee effects already documented in this system (Kuussaari et al. 1998) by reducing emigration rates from patches with dense local *M. cinxia* populations. The metapopulation level effect of this would be to increase the stability of established patches, and decrease the successful colonization of new patches by one or just a few founder individuals.

Methods

Our aim was to study whether experimentally-

manipulated attacks on host plants by adult and larval *M. cinxia* affected the acceptabilities of those hosts to searching butterflies arriving after those attacks. To do this, we obtained stocks of *M. cinxia*, *P. lanceolata* and *V. spicata* from the Åland Islands (Finland), within the intensively-studied *M. cinxia* metapopulation. To study the effect of butterfly eggs on *P. lanceolata*, the plants were grown in a greenhouse in Åland in potting soil mixed with sand from Åland. The plants for the rest of the experiments were grown in a greenhouse in Austin, Texas, in sterilized granitic sand from Sequoia National Forest, California, resembling soil in the plants' natural habitat.

For the experiment using eggs laid on *V. spicata* we selected matched pairs of plants that were either clones or siblings from the same habitat patch. Criteria used in matching included size, morphology and phenology. We then randomly selected one member of each pair to receive eggs from a motivated *M. cinxia* female that had not been allowed to lay eggs for one day prior to the experiment and that could therefore be readily induced to oviposit on a plant chosen by the experimenter. Eggs were laid on the chosen plants without disturbing the plants in any way, other than by placing the butterflies upon them. The experiment was repeated with plants that were not clones, with members of each pair chosen from different habitat patches.

For the experiment using eggs laid on *P. lanceolata* plants were paired by size and phenology. One member of each pair was chosen randomly to have eggs laid on it. This plant was put in a sleeve cage with a mated fed *M. cinxia* female that had oviposition experience but had not laid eggs in the last 24 hours. The other plant was placed in a sleeve cage with no butterfly, and they were both left for the day in the greenhouse.

For the experiments on responses to prior larval damage we again used matched plant pairs and randomly chose one member of each pair to receive post-diapause larvae, which were removed after they had eaten around 50% of the foliage. To assess effects of experimental treatments on host acceptability to the butterflies we waited from 2 to 5 days after eggs had been laid or one month after larvae had been removed. We then tested each experimental plant pair with a different female butterfly.

For all experiments except the one using eggs laid on *P. lanceolata* butterflies were fed and allowed to bask in natural sunlight before each set of trials. We then staged repeated encounters between each insect and the two members of a plant pair in alternation, following a protocol described in Singer *et al.* (1992). Insects were not allowed to oviposit, but attempts to do so were scored as acceptances of the test plant. If the attacked plant was accepted by the insect and the unattacked plant subsequently rejected, we recorded a preference for the attacked plant. Insects that did not discriminate between the test plants were allowed to lay eggs and re-tested. If, after several re-tests, they made no discrimination, the result for that plant pair was recorded as no difference in acceptability.

The experiment on response to eggs laid on *P. lanceolata* was done differently. Four 1 × 1 × 0.8 m mesh cages were placed in the greenhouse, spread several meters apart. A pair of plants (with and without eggs) was set in each cage 50 cm apart. Fed mated female butterflies were introduced to each cage in the morning, and left for the day with access to honey water. At the end of the day we searched for and counted egg clusters on the plants. When only one plant received a cluster, that plant was recorded as more acceptable; when both plants received eggs, we recorded them as equal acceptability. This procedure was repeated with 32 different butterflies and plant pairs on eight sunny days. The number of eggs in each cluster was counted.

Analyses of oviposition choice were by a two-tailed binomial test, using the null hypothesis of equal acceptability of control or experimental plants and excluding from analysis those

plant pairs within which the insects failed to discriminate. We analysed the egg clutch size for the experiment on response to eggs laid on *P. lanceolata* using a *t*-test. In the cases that both plants received eggs in that experiment we compared the egg cluster size using a paired *t*-test.

Results

Effects of larval feeding on plant acceptability were significant and equivalent on the two hosts (Table 1), with greater acceptability to ovipositing adults of plants that had experienced prior herbivory. In contrast, effects of eggs were apparently diverse. Eggs laid on *V. spicata* caused a clear increase of plant acceptability, while those laid on *P. lanceolata* had no detectable influence (Table 1). The result from *P. lanceolata* (which were not cloned) was significantly different from the result from *V. spicata* clones (binomial test: $p = 0.02$) but not from the result using non-cloned *V. spicata* (binomial test: $p = 0.2$). In the experiment using *P. lanceolata*, in which oviposition occurred, there was no significant difference in egg clutch sizes between those laid on plants that already contained eggs, and those laid on empty plants, even in trials in which both plant types received eggs (paired *t*-test: $t_4 = 0.1708$, $p = 0.30$).

Discussion

Group living in animals often arises incidentally, with no mean benefit, when individuals attempt to use each other as cover against predators

Table 1. Number of plant pairs (*Veronica spicata* and *Plantago lanceolata*) in which the test butterflies preferred the attacked or unattacked individual.

Experiment	Attacked plant more acceptable	Unattacked plant more acceptable	No difference	<i>p</i> (binomial test)
<i>V. spicata</i> cloned, with/without eggs	18	2	2	0.0002
<i>V. spicata</i> non-cloned with/without eggs	9	2	2	0.04
<i>P. lanceolata</i> with/without eggs	8	7	12, 5*	1.0
<i>V. spicata</i> with/without larval damage	16	5	1	0.02
<i>P. lanceolata</i> with/without larval damage	15	6	8	0.05

* No oviposition occurred in 12 trials and both plants were used in five trials.

(Hamilton 1971). It can also confer benefits by enhancing adaptive functions such as camouflage, aposematic display, vigilance and feeding efficiency. Conversely, negative effects of grouping stem from increased competition for food and apparency to enemies. It is not surprising, then, that ovipositing herbivorous insects show a diversity of responses to conspecifics that affect group size, ranging from aversion through neutrality to conspecific attraction. Conspecifics can enhance oviposition, either directly by their presence or indirectly, by their modification of plant quality (Judd & Borden 1992, Navasero & Ramaswamy 1993, Prokopy & Reynolds 1998, Raitanen *et al.* 2014, Desurmont *et al.* 2014, Durisko *et al.* 2014). However, by far the most frequently reported effect is that insects tend to avoid host plants that bear conspecific eggs or larvae (Rothschild & Schoonhoven 1977, Williams & Gilbert 1981, Shapiro 1981, Roitberg & Prokopy 1987, Pettersson 1992, Kumari *et al.* 2016). The tendency of the butterfly *Pieris brassicae* to avoid conspecifics was documented more than 100 years ago (Kerbey & Spence 1858, as cited in Prokopy & Reynolds 1998). *Pieris brassicae* are now known to avoid eggs of related species also (Schoonhoven *et al.* 1990). Shapiro (1981) showed that Pierid butterfly species that laid red eggs avoided them, while those that laid cryptic eggs did not. The avoidance of bright yellow congeneric eggs by *Heliconius* butterflies has apparently led to the multiple evolutionary origins of specific *Heliconius* egg mimics produced by their hosts and effective as defences against butterfly oviposition (Gilbert 1982). Many ovipositing insects apply to their hosts a pheromone that deters subsequent oviposition, interacting with other aspects of host quality but generally reducing the acceptability of pheromone-marked hosts. This behaviour has been well studied in true fruit flies, reviewed by Nufio and Papaj (2000).

Insects often have good reason to avoid conspecific eggs. Competition and cannibalism are rife (Wise *et al.* 2006). Large groups may be apparent to predators or parasitoids (Stamp 1981) and parasitoids may locate their insect hosts using volatiles produced by plants in response to herbivore eggs (Fatouros *et al.* 2014). Conversely, there may be benefits to some insects of

ovipositing preferentially on plants that already have eggs. Prokopy and Reynolds (1998) and Papaj *et al.* (1992) suggested that adult female Mediterranean fruit flies cue in to the presence of other conspecific adults as an indicator of host plant quality, using “public information” (Danchin *et al.* 2004) in a manner analogous to the phenomenon of “mate copying” in which females increase their preference for individual males after observing them being accepted by other females. Herbivorous insects may benefit from large group size by enhancement of anti-predator defence (Lawrence 1990, Hunter 2000, Riipi *et al.* 2001), by being better able to overcome host defences (Clark & Faeth 1997, Campbell & Stastny 2014, Desurmont *et al.* 2014) or by constructing better protection against harsh climate (Kuussaari *et al.* 2004, Kuussaari & Singer 2017).

The consequences of conflicting effects of local density or group size are sometimes manifest in ambivalent insect behaviour. In walnut flies the physical act of oviposition is facilitated when flies use holes in fruit bored by individuals that have oviposited previously (Nufio & Papaj 2000). These flies are simultaneously repelled from prior oviposition sites by oviposition deterrent pheromone and attracted to oviposition holes already drilled in the fruit (Nufio & Papaj 2000).

Clumped egg distributions in the field may occur even when conspecific eggs are avoided, if this avoidance is insufficiently strong to overcome effects on egg distribution of habitat heterogeneity, host dispersion and variance in host plant quality. For instance, oviposition by *M. cinxia* increases with *P. lanceolata* plant size, and differs between genotypes (Reudler Talsma *et al.* 2008). Therefore, the documented naturally occurring clumping of egg clusters in the field by Melitaeine butterflies including *M. cinxia* (Rauscher *et al.* 1981, Kuussaari *et al.* 2004) does not necessarily indicate attraction to conspecifics.

Here, we give evidence that past attack by larvae on both hosts rendered them more attractive to ovipositing butterflies. The effect of the presence of eggs was significant on *V. spicata* but not on *P. lanceolata*. However, because of the difference in experimental design between the experiments with *P. lanceolata* and *V. spicata* that gave significantly different results, we cannot

conclude with significance that effects on the two hosts were different, although this is likely. Correspondingly, and potentially through the same mechanism of induced plant response, *V. spicata* becomes attractive to the specialist parasitoid wasp *Hyposoter horticola* after *M. cinxia* eggs are laid on it, but *P. lanceolata* does not (Castelo *et al.* 2010).

We do not know whether the effect of eggs is direct or indirect. Butterflies may detect eggs directly, as do *Heliconius* (Gilbert 1982) and *Pieris* (Shapiro 1981). Alternatively eggs laid on *V. spicata* might have caused induced plant responses (Hilker & Fatouros 2016), which then rendered the plants more acceptable to ovipositing butterflies. In fact both oviposition and herbivory by *M. cinxia* induce changes in the volatile profile of *V. spicata* (Pinto-Zevallos *et al.* 2013).

Like walnut flies, our study insects clearly experience both positive and negative effects of the enhanced larval group size that results when egg clusters share the same small herbaceous host individual. Prediapause *M. cinxia* larval groups have been observed to starve after defoliating their hosts (first author's pers. obs.), and the rate of parasitism of caterpillars by the specialist parasitoid *Cotesia melitaeorum* increases with group size (Lei & Camara 1999). Conversely, larvae benefit from the strength of the winter nests that only large groups can spin (Kuussaari 1998) and larval survival increases with increasing group size, despite the opposing influence of parasitism (Kuussaari & Singer 2017).

Local *M. cinxia* populations in Finland are short-lived and founded by very few individuals, often apparently by single mated females. This conclusion is drawn from the observation that newly colonized populations often contain only a single winter nest of diapausing larvae (Austin *et al.* 2011). Our experimental results lead to the expectation that these single nests should sometimes comprise amalgamated groups from more than one oviposition event by different females. This mixing can be caused both by multiple oviposition events on the same plant and/or by merging of family groups as the caterpillars move between adjacent plants during feeding. Both of these processes have been documented in Finnish *M. cinxia* (Kuussaari *et al.* 2004; Kuussaari & Singer 2017).

How might the behaviours we discuss here affect (meta)population dynamics? We would expect both hosts, particularly *V. spicata*, to be more acceptable to adults in habitat patches with high insect density. In Melitaeine butterflies the match/mismatch between adult oviposition preferences and the acceptabilities of hosts that those adults encounter influences both emigration rates (Thomas & Singer 1987) and rates of colonization of empty habitat patches (Hanski & Singer 2001). Therefore, we expect that the increased acceptability of attacked plants should reduce emigration rates at high population densities and increase them at low densities. These responses would create an Allee effect, augmenting the known Allee effects that result from poor mate location at low densities and from direct responses of adult *M. cinxia* to encounters with conspecifics (Kuussaari *et al.* 1998). Both male and female butterflies tended to remain longer in patches where they encountered more conspecifics.

The effects shown here thus join a constellation of other factors which complement each other, causing Allee effects, positive density-dependence and clumped population distributions of adults at both within-patch and between-patch scales. In order to assess the importance of these various factors for clumped population distributions, we would need to know the strength, not just the direction, of these responses. This would enhance our understanding of the forces affecting population dynamics in this system from which very detailed long-term dynamic data are now available for testing mechanistic hypotheses.

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