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Selection for enemy-free space: eggs placed away from the host plant increase survival of a neotropical ithomiine butterfly

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Abstract. 1. The selection of an oviposition site by a phytophagous insect can depend on many factors, including the risk of predation. Many species avoid predators by laying eggs where enemies searching host plants are unlikely to find them.

2. Females of the Peruvian butterfly, *Oleria onega* Hewitson (Lepidoptera: Nymphalidae: Danainae: Ithomiini) lay most of their eggs (76 ± 9%) off the host plant, *Solanum mite* Ruiz & Pav. These off-host eggs may be laid up to 0.5 m from the nearest host-plant individual, on twigs or leaf litter, as well as on living plants of species unsuitable for larval food.

3. Disappearance of eggs on and off the host plant was recorded by transferring eggs laid in captivity to known locations in the wild and recording rates of disappearance before the larvae emerged. After 2 days, eggs on the host were significantly more likely to have disappeared compared to eggs laid elsewhere.

4. We conclude that a high risk of predation is a likely trigger that caused *O. onega* to evolve a behaviour of laying eggs off its host plant.

Key words. Enemy-free space, host plant, Ithomiini, Lepidoptera, *Oleria onega*, oviposition, predation, survival.

Introduction

The survival and growth of larvae of phytophagous insects depend critically on adult selection of oviposition site. Selection of a host plant of good quality ensures that the larvae have the best chance of survival or that their growth performance is maximised (Craig *et al*., 1989). Nevertheless, oviposition preference and larval performance are often poorly correlated (Janz, 2002; Verdon *et al*., 2007); eggs are sometimes deposited on poor quality hosts (Singer & Stireman, 2003; Moon & Stirling, 2006) or occasionally not on the host plant at all (Singer, 1984; Wiklund, 1984; Verdon *et al*., 2007).

The choice of oviposition site can be a compromise between opposing needs. Females must select a suitable site for larvae to obtain food while considering the availability of the host plant and plant density to maximise fecundity, host-plant size and quality (Wiklund, 1984; Thompson & Pellmyr, 1991; Heisswolf *et al*., 2005; Agosta, 2008; Albanese *et al*., 2008), risk of predation (Sendoya *et al*., 2009) and parasitoids (Singer & Stireman, 2003; Carrasco *et al*., 2009), avoidance of intraspecific competition (Craig *et al*., 2000); larval mobility (Janz, 2002) and the concentration of chemical compounds required by the larvae for defence or perhaps as a means of avoiding competition by generalised herbivores (Peñuelas *et al*., 2006).

Predators and parasitism are important causes of mortality in herbivorous insects (Keese, 1997). Insects may respond evolutionarily by choosing a novel host that provides a refuge from predation or parasitism (Novotny *et al*., 1999). Resource competition is often invoked as a primary constraint on an ecological niche. However, natural enemies rather than competitors may play the major role in shaping the phytophagous niche, and it is likely that insects switch hosts primarily in order to seek enemy-free space (Jeffries & Lawton, 1984). A host shift can be catalysed if the new host lacks enemies that have accumulated on the original host (Murphy, 2004). Predators and parasites often use visual or chemical cues from the host to locate their prey, and herbivores that shift to new hosts can reduce their detectability (Keese, 1997). Even shifts to nutritionally inferior plants can be favourable when predation is intense (Ballabeni *et al*., 2001; Zangerl *et al*., 2002; Murphy,

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2004), and natural enemies may promote diversification of insect lineages as a result (Gratton & Welter, 1999; Drès & Mallet, 2002).

An alternative is to minimise contact with an unchanged host. In temperate climates, selecting oviposition sites away from the host plant on substrates unfavourable for larval development may be a strategy to prevent oviposition on plants vulnerable to senescence, or alternatively to avoid predators and parasitism. For example, a newly formed alpine species of the genus *Lycaeides* lays eggs on the host, *Astragalus whitneyi*, but with so little glue that they readily fall off the plant after oviposition. This alpine-associated adaptive trait is probably essential for their survival because *Lycaeides* overwinter as diapausing eggs. Eggs remaining attached to the senesced host plant would be blown with the plant by strong winter winds away from sites of new host growth (Gompert *et al*., 2006). In contrast, the papilionid *Parnassius apollo* uses an evergreen herb, *Sedum album*, as host, but deposits its eggs 1–2 m away from the plant. This may be an anti-predator tactic: if eggs are deposited some distance from the host they become less predictable in space (Wiklund, 1984). Oviposition away from the host has been rarely reported in the tropics. One exception is the Trinidadian satyrine, *Euptychia hermes*. The female butterfly alights on various plant species before encountering a host plant, which it tests by drumming with the foretarsi. If the plant is deemed acceptable, the female deposits an egg singly on dead plant material or an alternative low growing plant close by (Singer, 1984). Oviposition sites vary within a single bout of egg-laying suggesting these butterflies actively make decisions based on their immediate experience (M. Singer, pers. comm.).

We here report similar behaviour in another tropical butterfly, and investigate its evolutionary significance. *Oleria onega* Hewitson (Nymphalidae: Danainae: Ithomiini) is a member of clearwing Müllerian mimicry rings of the neotropical rainforest understorey (Beccaloni, 1997). *Oleria onega* ssp. nov. is an endemic subspecies to north-east Peru where its distribution centres on the Departments of San Martín, Huánuco, and Loreto. It specialises on Solanaceae, feeding mainly on *Solanum mite* Ruiz & Pav. Adult ithomiine butterflies sequester dehydroxypyrollizidine alkaloids from nectar sources, particularly in the families Boraginaceae and Asteraceae, and these act as defensive compounds (Brown, 1984) but pyrollizidine alkaloids are not passed to larvae (although they may be passed to eggs – see Brown, 1987: Table 5). Although almost all Ithomiini are specialised on Solanaceae, there is no evidence to suggest that larvae synthesise or sequester defensive chemistry from their host plants (Brown, 1987; Trigo *et al*., 1996).

Oleria onega lay eggs intermittently on and off the host plant (see results and Fig. 2). This behaviour is not limited to this subspecies but may be characteristic of other members of the *O. onega* species group (Gallusser, 2002; de-Silva *et al*., 2010). Mallet and Knapp (cited in Knapp & Helgason, 1997) reported *O. onega* ssp. nov. females testing *Solanum anceps*, before ovipositing on another non-solanaceous plant or leaf litter some distance away.

Predation can be a significant selection pressure on insect herbivores (Smiley, 1985; Floren *et al*., 2002; Davidson *et al*., 2003). In the Tarapoto area, ants numerically dominate the insect fauna, and probably represent an important predation threat (Gallusser, 2002). Natural predators of *O. onega* potentially include ants of the genera *Ectatomma* sp. and *Camponotus* sp. (Formicidae) (Gallusser, 2002). We hypothesise that the threat of predation is high, and in the absence of alternative host plants *O. onega* may exploit enemy-free space by laying eggs off its host.

Here we assess whether the oviposition decisions of *O. onega* increase survival in the field. We test whether predation plays an important role in the egg-laying behaviour of this species by comparing disappearance of eggs deposited on and off the host plant.

Materials and methods

Study sites

Fieldwork was conducted near Tarapoto in the Department of San Martín along the course of the Río Shilcayo, which originates from and lies south-west of the Cerro Escalera mountain range (red square, Fig. 1). *Oleria onega* ssp. nov. is locally abundant along the course of the river and its distribution is largely coincident with that of its host, *S. mite*. This plant is found mainly in secondary forest where it is clustered along paths next to the river and in treefall gaps in partial shade. The adult butterfly is found year-round but is particularly abundant during the dry season. The egg survival experiment was carried out during the main dry period between August and September 2007 when adults were abundant.

Fig. 1. Map of Peru, and the Department of San Martin, showing the area (red square) where work was conducted.

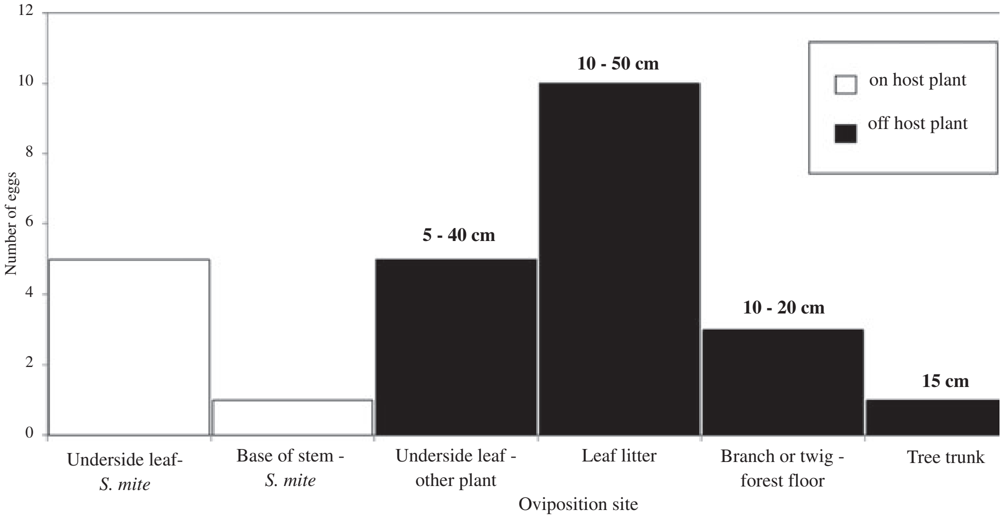

Fig. 2. Observations of oviposition at the study site. Eggs were laid up to 0.5 m from the nearest host plant, *Solanum mite*. Straight-line distances to the nearest host individual were measured for each off-host location. Distance ranges are shown for each substrate. A total of 21 wild females were followed during these observations.

Study organism

Oleria onega adult females lay solitary white, sub-spherical eggs approximately 1 mm in height. Between 1 and 12 eggs are laid by a female in quick succession or over 3–4 days but on average 4–6 eggs are laid once oviposition begins. Eggs hatch 3–4 days after oviposition and are laid year-round but more so during the main dry season (June to September).

Egg survival experiment

Butterflies were collected approximately 2 km from the Río Shilcayo study site. Multiple females were collected to ensure replication of the experiment over consecutive days. These butterflies were transferred to individual cages, 1 m × 0.7 m, containing a single *S. mite* plant, previously collected and transplanted from the capture area. A 10% sucrose solution was supplied as a food source and replenished daily. Plants were maintained within the cages, and any found to be unhealthy were discarded. Each butterfly remained in captivity for 3 days, during which time most eggs were laid, and was then returned to and released in to the area of capture. Eggs were collected from the cages and transferred immediately to the field site on the day they were laid. Eggs laid in captivity were deposited either on the undersides of leaves of *S. mite* or on soil surrounding the plant. Eggs laid on the plant were transferred to a plant in the field where possible and eggs laid on the soil surface were transferred with the soil and located off the host plant.

Egg transfers were of two types: (i) to the underside of leaves of tagged *S. mite* plants or (ii) to other substrates including the leaves of other plants, leaf litter or twigs and small branches within 50 cm of the nearest *S. mite* plant in accordance with observations of oviposition by butterflies in the field (Fig. 2).

Solanum mite plants were chosen at random at the study site along a measured distance of 30 m and were selected in order to maximise coverage of the area. All sites were selected within an area of 500 m^2 at equal elevation where *O. onega* and *S. mite* are particularly abundant. Each egg was glued via a small section of leaf or substrate to its new position using natural resin from a locally abundant tree, *Himatanthus sucuuba* (Apocynaceae) known locally as 'bellaco caspi'. Forceps were used to avoid direct finger contact with either egg or attachment during transfer. This procedure was carried out to prevent accidental deposition of organic compounds or salts from the skin, which are potentially attractive to ants. Presence or absence of transplanted eggs was recorded on days 1 and 2 following relocation to ensure that this was before larval emergence (on day 3 or 4). A thorough search was made of each area surrounding the attachment site if the egg was absent to ensure it had not fallen from its attachment. Eggs were recorded as absent only when completely removed leaving the transferred substrate intact. A total of 297 eggs were transferred to 23 separate study areas over a period of 24 days (Table 1). Daily egg transfers were divided approximately equally between on- and off-host attachment sites.

Statistical analyses

Rates of disappearance of eggs from *S. mite* and alternative substrates was recorded and compared using likelihood ratio tests based on the beta-binomial distribution (authored by ZihengYang; see appendix in Jiggins *et al*., 2001). This provides a powerful method to compare binomial probability parameters for count data among treatments (in this case disappearance rates of eggs on different substrate types) when mean binomial probabilities vary among replicates within treatments.

Table 1. Survival rates of eggs laid on and off the host plant, *Solanum mite*, and on other substrates between the day of transfer and days 1 and 2 following transfer.

Days 0 and 1 Substrate	Total no. of eggs – day 0	Total no. of eggs – day 1	Mean survival after 1 day*	Standard error*	$2\Delta\log_e L \simeq \chi^2$	*P*	d.f.
S. mite	153	92	0.61	0.055	0.089	0.7649	1
Off host	144	93	0.63	0.060			
Days 0 and 2 Substrate	Total no. of eggs – day 0	Total no. of eggs – day 2	Mean survival after 2 days*	Standard error*			
S. mite	153	58	0.37	0.051	5.08	0.0242	1
Off host	144	81	0.56	0.059			
Days 1 and 2† Substrate	Total no. of eggs – day 1	Total no. of eggs – day 2	Mean survival between days 1 and 2*	Standard error*			
S. mite	91	58	0.63	0.057	12.61	0.0004	1
Off host	93	81	0.87	0.045			

*As estimated while allowing for variable means within treatments in Yang's beta-binomial test.

†Data from one site were removed, as no eggs remained there after 1 day.

Results

Oviposition behaviour in the wild

When females were followed during flight, they were observed to alight on and test leaves of the host, *S. mite*. Following this behaviour, each female oviposited either on the underside of a leaf, or alternatively, flew up to 0.5 m from the plant before laying an egg on dead plant material or other low-growing non-host plant species (Fig. 2). A large fraction, 76 ± 9%, of eggs were laid off the host. The remaining 24% of eggs were laid mainly on the undersides of leaves of the host, *S. mite* (Fig. 2).

Survival of transplanted eggs

During the first 2 days after egg transfer ('day 0'), egg survival was low, with only 47% of eggs remaining on average across substrates. We tested for heterogeneity of binomial parameters across study sites. Likelihood ratio tests did not reject the hypothesis that mean disappearance rate and variance of disappearance rate parameters were homogeneous within treatments for days 0–1, days 1–2, or days 0–2. Nonetheless, there was a small positive correlation of the fraction disappearing from days 0–1 to 1–2 ($r = +0.32$ on host plants, and $r = +0.22$ off hosts). Although these correlations were not significant and explain little variance, we have conservatively analysed comparisons among treatments using a test based on the beta-binomial distribution (see methods) to allow for sitewise heterogeneity of means of disappearance rates within treatments, and different variances around the mean binomial probability in the two treatments. Thus we compared the hypothesis of a single overall mean (for both on- and off-host survival) to the hypothesis of different overall means between treatments while in both cases allowing the means to vary at different subsites within treatments, and the variances of the means to differ between treatments. The *P*-values in the relevant tests in Table 1 use this conservative assumption, but they were similar to those obtained as if there were no heterogeneity of means within treatments or variances among treatments.

There was no significant difference in egg survival between the day of egg transfer and the first day following transfer with 61 ± 6% survival on *S. mite*, compared to 63 ± 6% on other substrates (Table 1; Fig. 3). However, after 2 days, overall mean survival of eggs on the leaves of the host plant *S. mite* was 37 ± 5% compared to 56 ± 6% survival off the host, a significant difference. Most of this mortality occurred in the first period, although survival of eggs between days 1 and 2 also differed highly significantly among substrates.

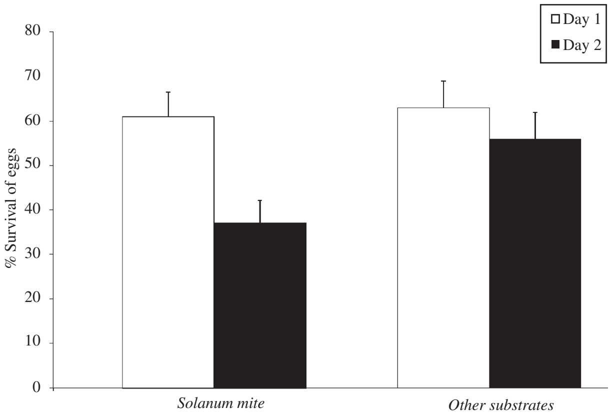

Fig. 3. Fraction of *Oleria onega* eggs remaining after 1 or 2 days after transplanting to *Solanum mite* or alternative substrates. Error bars show standard errors estimated via Yang's beta-binomial test.

Discussion

Oleria eggs placed away from the host plant on alternative substrates had significantly enhanced survival compared to those laid on the host plant, *S. mite*. Therefore, it is reasonable to assume that the threat from predators is a significant factor that prompts *O. onega* to lay eggs away from its normal host plant.

It is possible that visual and/or chemosensory cues can be used to detect the presence of ants, and it is this that leads to oviposition off the host plant. *Eunica* butterflies (Nymphalidae) have been shown able to detect ants visually, and that this alters their oviposition behaviour (Sendoya *et al*., 2009). Female *Eunica* avoid laying eggs on leaves frequented by ants (Freitas & Oliveira, 1996). Although *O. onega* lays most of its eggs off the host, almost a quarter of eggs are still laid on the host, and it is possible that these particular hosts have been assessed by the female to be safe compared to other *S. mite* plants. Further investigation of this possibility is planned.

Predation by ants is a major cause of caterpillar mortality in tropical forests (Smiley, 1985; Freitas & Oliveira, 1996; Machado & Freitas, 2001). In lowland tropical rainforests, ants are considered the most abundant and important predators, and the very low abundance of less mobile arthropods correlates with the numerical dominance of ant fauna (Floren *et al*., 2002). When predation pressure is high some insect herbivores switch to an alternative host, even though that host may be nutritionally inferior (Ballabeni *et al*., 2001; Zangerl *et al*., 2002; Moon & Stirling, 2006), because the reduced risk of predation on a novel host offsets maladaptation resulting from the shift (Heard *et al*., 2006). However, physiological constraints may limit opportunities to switch to an alternative and chemically different host, particularly in insects that specialise on plants containing defensive compounds such as the Solanaceae: costs associated with maintaining detoxification enzymes for any one group of compounds are high (Keese, 1997). Moreover, intense interspecific competition is likely to limit opportunities for host shift. In the absence of an alternative host, *O. onega* may well take advantage of the only enemy-free space available: other plants and leaf litter in the vicinity of its host.

Dethier (1959) suggested that chance plays an important role in how specialised phytophagous insects choose their hosts. Sensory abilities of lepidopteran larvae are limited until contact is made with the host plant. For example, caterpillars of the Oregon silverspot butterfly, *Speyeria zerene hippolyta* are able to distinguish bare ground from vegetation, but larvae were not able to orient towards the host from distances of >3 cm (Bierzychudek *et al*., 2009). Larvae as well as adults use plant volatiles in host recognition, and secondary compounds found in Solanaceae and other plants are important cues in butterfly–plant associations. For example, larvae of the papilionid *Battus polydamas* are attracted to and feed on *Aristolochia*, which contain toxic aristolochic acids. Larvae disperse and become solitary at the third or fourth instar and at this stage their sensory abilities are sufficiently developed for them to be able to locate alternative host-plant individuals (Pinto *et al*., 2009).

Whether a newly emerged larvae of *O. onega* is similarly able to use chemical cues from its host, or whether it finds its host by chance is uncertain. At present, we know nothing about the undoubtedly perilous journey the first-instar larva must undertake from its hatch site to what may be a single host plant in the vicinity. If the stem of its host is 0.5 cm wide, and the egg is laid 0.5 m away, simple trigonometry indicates that this tiny, 1.5 mm-long caterpillar must navigate across the complexities of the forest floor to within an almost incredible accuracy ($\sim \frac{1}{2}^{\circ}$ of arc), in order to find a stem of its host. For off-host oviposition to be adaptive, the survival benefits for the egg must outweigh the costs for young larvae of finding their host from such a great distance. It will now be of great interest to study the navigation of and fitness consequences to the newly hatched larva on its odyssey towards its host, in order to gain a more complete understanding of the survival advantages of this extreme off-host oviposition behaviour.

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