

**THE EFFECTS OF EXPERIENCE
ON HOST ACCEPTANCE
IN OVIPOSITING MOTHS**

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LIST OF ORIGINAL PAPERS

- I Tammaru T, Javoiš J 2000 Responses of ovipositing moths (Lepidoptera: Geometridae) to host plant deprivation: life-history aspects and implications for population dynamics. *Environmental Entomology* 29: 1002–1010
- II Javoiš J, Tammaru T 2004 Reproductive decisions are sensitive to cues of life expectancy: the case of a moth. *Animal Behaviour* 68: 249–255
- III Javoiš J, Tammaru T, Käär M 2005 Oviposition in an eruptive moth species, *Yponomeuta evonymellus*, is insensitive to the population density experienced during larval period. *Entomologia Experimentalis et Applicata* 115: 379–386
- IV Tammaru T, Javoiš J 2005 When being alive implies being safe: variation in mortality rates can cause oviposition selectivity to increase with age. *Oikos*, in press.
- V Javoiš J, Tammaru T. The effect of egg load on motivation to oviposit is weak and inconsistent in a geometrid moth. Submitted manuscript
- VI Javoiš J, Tammaru T. Decreasing egg quality as a cost of oviposition selectivity in insects. Manuscript

The thesis is based on these studies, in the text referred to by their Roman numerals. The author of the thesis contributed substantially to the studies: participated in planning the experiments, gathered all the empirical data, had the main responsibility of data analysis and writing in II, III, V, VI, participated in data analysis and writing of I, and participated in writing of IV. Permission has been given by the original publishers to reproduce the articles.

1. Host choice for oviposition in insects

Much of an adult female insect's time is dedicated to oviposition. In some species, females leave their eggs right in the place where they have eclosed from pupa (e.g. Tammaru et al. 2002). As another extreme, females express postnatal care (Tallamy & Brown 1999). However, in most species the final step of an insect's maternal care is moving around and actively choosing substrates for egg laying (Bernays & Chapman 1994). Different insect species use different substrates for oviposition, be these either individual plants or parts of these (Bernays & Chapman 1994), animals on which the larvae are going to parasitize or travel (e.g. Godfray 1994), other kinds of larval food sources (e.g. Ward et al. 1999), or just be habitat in which the larvae have to search for food sources by themselves (e.g. Bergman 1996).

Handling of an oviposition host involves a number of actions, from initial perception of the host, through testing stages by different sensory systems, until the final decision of rejection, or acceptance: i.e. laying eggs (Bernays & Chapman 1994). The acceptance decision can include considerations over the number of eggs (clutch size) (Mangel 1987, Pilson & Rausher 1988, I, II), or the quality of the eggs (Fox & Czesak 2000, VI) laid.

Her genes dictate the insect mother much of the information of which types of hosts to choose and how many eggs to lay on different host items she finds (e.g. Prokopy et al. 1982b, Jaenike & Grimaldi 1983, Thompson 1988, Thompson & Pellmyr 1991). However, the fitness value of oviposition decisions depends on the exact environmental situation (Roff 1992, Stearns 1992), while environment varies both temporally and spatially, too quickly for evolution to follow its each change (Papaj & Prokopy 1989). In other words, the genes never "know" exactly what environmental conditions the organism carrying them is going to meet. The only way to learn more about the situation is to let the mother just go and see herself, i.e. "keep her eyes open" and let her remember what happens to her (Bradshaw 1965, Houston & McNamara 1992). Hence, in addition to the genetic information, an ovipositing insect should largely rely on its individual *experience*.

2. The effect of experience on optimal acceptance of hosts for oviposition

In the current thesis, I will present six studies which aim to clarify the effect of experience on optimal host acceptance in ovipositing insects. One of these is a theoretical model, while in the five empirical studies different moth species served as model insects. In the current concluding article, I will place the results of the presented studies in the context of the present knowledge about the subject. To do this, I will shortly review main relevant hypotheses and add examples of empirical evidence. Therein, I will consider the results of my original studies.

In principle, previous experience could modify an insect's perception of three main factors which, in turn, should influence optimal decision on the acceptance of the potential host an insect has just encountered. First, the experience can modify the insect's estimate of the **suitability of the particular host type** for her offspring, or for oviposition. Second, it can modify the **insect's physiological potential**, either the potential to find new hosts, or to have new eggs for laying. Third, it can modify the **insect's estimate of the environmental promises** for these actions. If the probability to find a new host is high, then the insect should be more fastidious about the host encountered. In other words, it should elevate its acceptance threshold (*sensu* Courtney et al. 1989) of host choice, and accept only host types of highest preference rank. While, if the amount of eggs available (or potential to produce those) is high, the fastidiousness should be low, i.e. acceptance threshold should be lowered. This is because the risk of becoming egg-limited, i.e. the probability of having no(t enough) eggs when a higher quality host will be encountered in future, is low.

The factors determining host range can also affect the clutch size laid on a host (Pilson & Rausher 1988). Under conditions where a larger clutch implies a lower fitness per egg (i.e. no Allee effect: e.g. Wertheim et al. 2002), but still a higher cumulative fitness per whole clutch (i.e. the clutch size does not exceed the so-called Lack clutch: e.g. Skinner 1985), insects should lay larger clutches if probability to find a new host is lower, or if more eggs are available (Iwasa et al. 1984, Parker & Courtney 1984).

The effect of experience on the three main factors of acceptance will be considered in separate chapters below, although different factors act in concert (Courtney et al. 1989, I, II, IV, V) and, in practice, their effects can be largely interrelated and hard to distinguish (e.g. Rosenheim & Rosen 1991, Fletcher et al. 1994). Also, the effects of preimaginal and imaginal experience will be considered in separate chapters. Insect larvae are temporally separated from the oviposition environment, and their biology often leads to spatial and sensory separation as well. Moreover, in holometabolous insects (as are the study

species of the experiments presented in the thesis), much of the memory may be lost during metamorphosis (Barron 2001, III). It can be assumed, therefore, that larval experience influences oviposition behaviour largely in a different way than adult experience.

2.1. Preimaginal experience

2.1.1. Host suitability

A hypothesis, well-known under the name of “Hopkins’ host selection principle”, proposes that adults prefer for oviposition the host type which they have experienced in the larval stage (Barron 2001). Such behaviour could be adaptive, if a “search-image” to recognize the most probably encountered suitable host type is needed by the adult, and the shaping of the image is more adequate or energetically less costly in the larval than in the adult stage.

There have appeared several empirical demonstrations of such larval conditioning in holometabolous insects (reviewed in Barron 2001). For instance, *Drosophila melanogaster* (Diptera: Drosophilidae) adults laid more eggs on host types on which they grew up as larvae (Jaenike 1983). However, a suspicion has arisen that such experiments rather demonstrate conditioning of the adults with remnants of larval hosts shortly after their emergence (Jaenike 1988, Barron & Corbet 1999). The boundary between adult and larval experience is faint here: particles of larval hosts may remain also inside the body of the pupa, and affect the adult’s decisions thereby (Corbet 1985). A study which supposedly demonstrated the “true” learning in the larval stage and persistence of the memory through metamorphosis was conducted on *Hyssopus pallidus* (Hymenoptera: Eulophidae) parasitoids (Gandolfi et al. 2003). Compared to controls, adult parasitoids which had been exposed to apple odour in the egg- and early larval stage were more eager to search for hosts (fruit-infesting moth larvae) in response to apple odour. No such increase of the search activity was found, however, in individuals to which the odour was exposed later: in late larval or early adult stages. The authors did not propose an adaptionistic explanation for why the learning ability vanishes at later ages, but this fact itself makes the scenario of adult conditioning to chemical contamination from larval habitat improbable.

If an adult weighs laying its eggs in the habitat (or even the same host organism) it has itself developed in, against emigrating to find a new habitat, then the larval stage could provide plenty of time to estimate the suitability of the native habitat (e.g. Rhainds et al. 2002). Indeed, several characteristics of the larval habitat can modify the propensity of the adult to refuse oviposition in native habitat and emigrate.

Best known examples come from Orthoptera and other hemimetabolous insects, in which high population density, or otherwise harsh conditions lead to development of specific migration morphs. These morphs clearly express, both morphologically and behaviourally, their “intention” to disperse from their adverse habitat. Moreover, in locusts the morph development of offspring can be determined by population density experienced by the mother (reviewed in e.g. Harrison 1980, Pener 1991, Pener & Yerushalmi 1998, Applebaum & Heifetz 1999). Some evidence for the intention to emigrate from the overcrowded habitat comes from holometabolous insects as well. Usually, this intention is accompanied by, and experimentally recorded as some kind of altered potential of the adults descending from different larval habitats. Such alterations in development will be considered in the next chapter.

2.1.2. Insect potential

Many species, in response to larval overcrowding show a shift of insect potential towards better ability for searching new habitats, probably at the expense of lower reproductive capacity, or longer larval development. The migration morphs of various hemimetabolous insects often possess (larger) wings, higher moving activity, altered sensillary complement, postponed reproduction, higher abdominal lipid content, smaller size, and/or extended adult lifespan. Often, these traits have been shown to be accompanied by reduced total reproductive potential, or longer larval development (reviewed in e.g. Harrison 1980, Pener 1991, Pener & Yerushalmi 1998, Applebaum & Heifetz 1999).

In holometabolous insects, somewhat analogous increase of emigration potential can occur. For instance, some of crowded *Callosobruchus maculatus* (Coleoptera: Bruchidae) beetles develop into distinct dispersing morphs as adults, and the proportion of the “active” morphs is the higher, the denser is the population. The adults from the crowded populations also emerge later, weigh less, and live longer (Messina & Renwick 1985).

If developed under high density, *Spodoptera exempta* (Lepidoptera: Noctuidae) adults showed better flight ability. Supposedly this ability enhances dispersal from the habitat where population becomes too concentrated (Woodrow et al. 1987). In another noctuid moth, *Agrotis ipsilon*, larval crowding resulted in smaller adults with higher flying activity (Lewis & Keaster 1989). In yet another noctuid, *Anticarsia gemmatilis*, larval crowding resulted in less-weighting adults, which exhausted approximately two times less of their energy storages during a long-lasting flight (Fescemyer 1993).

Several holometabolous insect species, if larvally overcrowded, develop into adults with lower wing loading (lower body-mass/wing-area ratio) (reviewed in Ruohomäki 1992). For instance, larvae of *Epiphyas postvittana* (Lepidoptera: Tortricidae) moths, if exposed to crowding (without food shortage!), develop

into smaller adults with relatively larger wings (Danthanarayana et al. 1982). This was suggested to enhance their dispersal from the overcrowded habitat.

In *Plutella xylostella* (Lepidoptera: Yponomeutidae) moths, lower proportion of females were sexually mature at adult emergence, when grown at higher density. Supposedly, such a pattern enhances prereproductive dispersal of the moths from the overcrowded habitats (Branco & Gatehouse 1999). In *Mythimna convecta* (Lepidoptera: Noctuidae) moths, larval crowding lead to delayed reproductive maturation in adults – during this delay the moths supposedly emigrate from the overcrowded habitat (McDonald & Cole 1991). In this context, the ability of some ant and termite species to respond to unfavourable environment by developing increased proportion of dispersal morphs in adults (Cremer & Heinze 2003, Korb & Lenz 2004) must also be mentioned.

In our study on *Yponomeuta evonymellus* (Lepidoptera: Yponomeutidae) moths (III), we hypothesized that moths grown up on a defoliated host or under suboptimally high larval crowding have been selected to reject the host as an oviposition substrate, and leave it in search of a new one. This could be expected, because the species regularly goes through defoliation of hosts during density outbreaks, accompanied by low fitness of the offspring laid on defoliated hosts. We also hypothesized, that the adaptation to emigrate would be reflected in the oviposition schedules of the moths: mating, egg maturation or oviposition should be postponed in favour of emigration. This prediction was largely inspired by our finding in other moth species (I) in which the response to oviposition host deprivation is mainly expressed in the delay of oviposition, during which, most likely, dispersal from the area of low host availability takes place. Nevertheless, neither in lab-grown nor naturally-collected moths did we detect alteration of oviposition schedules, except a minute tendency towards earlier and smaller first clutch in response to natural defoliation, which, in fact, contradicted our expectations. Such results were reinforced by the finding, that experimentally increased adult density did not alter either timing of oviposition or fecundity. It is possible, that the species does not consider density of conspecifics as a criterion of host acceptance which, in turn, could provide a basis for population outbreaks.

Other kinds of effects of larval environment on oviposition host acceptance could be possible. For instance, the more an insect has acquired resources in the larval stage, the higher is usually its fecundity (Honěk 1993). Optimality models predict that high fecundity should lead to higher oviposition rates, and thereby lower selectivity, wider host range, and larger clutches. On the other hand, resource-rich larval life could also lead to longer life expectancy and higher searching efficiency which, in turn, could elevate host acceptance threshold.

2.1.3. Environmental promises

On the assumption of temporally stable environment quality, insects which have preimaginally experienced a hostile environment should expect less from it when being adults. In this context, it should be mentioned that the experiment studying larval conditioning in *Drosophila* (Jaenike 1983, see above) also provided some “puzzling” results. Developing in larval stage on some particular host types resulted in increased oviposition not only on these types, but also on some others. Possibly, larval experience of a low-quality host lowered the general (i.e. not host-specific) acceptance threshold of oviposition in adults (Courtney et al. 1989).

2.2. Imaginal experience

2.2.1. Host suitability

2.2.1.1. Host suitability for larvae

Adult experience could, in principle, reorder an insect’s innate preference rank of host types in two ways. First, the experience could influence the estimate of the “direct” benefits of a host type for the ovipositing individual itself (see below). Second, adult experience could influence an insect’s estimate of suitability of a host type for larval development. The latter is not easy to imagine, because an insect mother probably cannot put itself in the situation of its offspring, and hence seems ought to rely here purely on the guidance of its genes. However, herebelow I will consider proposed scenarios under which experience can help her, and some empirical evidence of this to occur.

Insects can learn to associate preliminary signals received from hosts with the probability that the host type will turn out to be acceptable in course of further testing. Thereafter, the insects preferentially search for the promising host types. As an example, in the field, *Battus philenor* (Lepidoptera: Papilionidae) butterflies switch between visual search-images for two host species with different leaf-shapes (Rausher 1978). This is related to phenological changes in relative leaf-qualities of the hosts. In the beginning of the season the two host species are of similar leaf quality, and most butterflies search for the more abundant host (see below for the likely reasons). Nevertheless, later in the season, the leaf quality in the more abundant host species decreases, while remaining the same in the rarer host (Rausher 1981), and accordingly, most butterflies start to search for the latter (Rausher 1980). The switch between the two search images probably takes place when the host type initially searched for becomes relatively too often rejected at further (post-alighting, i.e. contact) stages of testing compared to the alternative type, initially

alighted on only accidentally (Rausher 1978, Papaj & Rausher 1987). As predicted, butterflies with stronger search images discovered hosts at higher rates (Rausher 1978), which shows that the image forming ability indeed is adaptive.

In hymenopteran parasitoids, there are numerous reports of associative learning, where the females prefer the types of microhabitats for oviposition, in which they have previously encountered host insects (e.g. Kester & Barbosa 1991, Wardle & Borden 1991, Cortesero et al. 1995). For instance, *Biosteres arisanus* (Hymenoptera: Braconidae) parasitoids were shown to associate one fruit type with the presence of host eggs, and the other with the absence of those. In a subsequent experiment with the possibility to examine and lay eggs on both fruit types, the trained wasps laid eggs at higher rates and produced more offspring than untrained wasps, which shows the adaptive value of such associative learning (Dukas & Duan 2000).

Proximity to acceptable substrates (previously oviposited on) can, itself, form a character of a substrate, facilitating the acceptance of it for oviposition. Such a sensitization would be adaptive, if hosts use to be aggregated, and if the ovipositing female is time-limited rather than egg-limited. For instance, *Leptopilina boulardi* (Hymenoptera: Figitidae) parasitoids shortly (2 h, but not 24 h) after a previous oviposition event showed increased probability of probing a fruit model in search of host larvae (Kaiser et al. 2003). The species is supposedly relatively time-limited on daily scale (daily activity period lasts for few hours only, and an adult is carrying hundreds of eggs). Also, aggregations of hundreds of host larvae often occur in nature, so a host encounter signals of other suitable hosts nearby.

In contrast, in some species risk spreading could enhance the expected success of offspring (Mangel 1987, Cronin & Strong 1993). In a spatial risk spreader, acceptance should depend on how close in space are the eggs last laid. In a temporal risk spreader, accordingly, it should depend on how long ago last eggs were laid. It could be possible, that some females spread risks between different host types. In this case, the preference rank of a host type would be inversely related to the number of eggs this type has already received.

As an example of risk spreading, *Anagrus delicatus* (Hymenoptera: Mymaridae) parasitoids, both in the laboratory and in the field, rejected numerous potentially suitable hosts in a patch, and left the patches in search of new ones instead. Supposedly, such a behaviour decreases the potential fitness loss caused by extinction of the hosts in some patches (Cronin & Strong 1993).

In some species, the offspring may benefit from having been placed on the most abundant host type. In particular, it would be the case if the larvae need to switch between host individuals, while their fitness would be reduced if they switch between host types (reviewed in Cunningham et al. 2001). If the abundances of host types are largely unpredictable on the evolutionary time-scale, the adults could benefit from being able to remember the abundances of

different hosts met, and thereafter prefer the more abundant host types (Cunningham et al. 2001).

2.2.1.2. Host suitability for the ovipositing individual

In addition to characteristics important for larval development, a certain host type can comprise direct values and dangers for the ovipositing individual itself. For instance handling times (Courtney 1983, Jones & Kim 1994), predation risk (Jaenike 1978, Iwasa et al. 1984), mating opportunities (Rohde 1979), or value as a source of adult nutrition (Janz et al. 2005) could differ between hosts and thereby affect oviposition preferences. It is possible, that insects gain information about these properties during their adult life and, moreover, learn to associate these with particular host types, thereafter preferentially accepting the more beneficial types.

As seen, for instance, in the *Battus philenor* example above (Rausher 1978), insects sometimes preferentially accept more abundant hosts, i.e. those which they have encountered more times during their earlier adult life. As discussed above, such a behaviour could increase offspring fitness in some species. There are two ways how it could be beneficial also for the ovipositing adult, in terms of energetic gain.

First, during each handling of a host, insects could gain more skill in handling the particular type (e.g. McNeely & Singer 2001). The skill progressively decreases the amount of energy spent on each handling. Therefore, the relative benefit gained from more abundant host types can progressively increase throughout adulthood. So should do the acceptance probability of these types.

Second, it has been suggested in several insect species that, during their adult lives, females form search-images of more abundant or more apparent host types, and exploit only these hosts, rejecting (leaving unrecognized) others even if they are suitable for acceptance otherwise. The adaptiveness of such behaviour proposedly arises from energetical benefit, if the simplified host choice process outweighs the fitness loss related to rejecting some potentially suitable hosts (Papaj & Prokopy 1989, Bernays & Wcislo 1994). Such a search-image forming, where previous experience of a host type leads to higher relative preference of this type, has been found in several insects (e.g. Prokopy et al. 1982a, Landolt & Molina 1996, Cunningham et al. 1998)

2.2.2. Insect potential

2.2.2.1. Residual fecundity

Residual fecundity, i.e. the residual number of eggs potentially available, has been considered an important factor influencing host acceptance. When residual fecundity is higher, an insect should incorporate lower-quality hosts in its host

range. This is because the risk of becoming egg-limited, is lower (e.g. Iwasa et al. 1984, Courtney et al. 1989, McGregor 1997). For instance, younger *Gargaphia solani* (Hemiptera: Tingidae) bugs, with higher reproductive value, showed a tendency to “dump” their eggs in nests of conspecifics instead of guarding these themselves, compared to the older individuals (Tallamy 1986). In the field, older *Antiochris scolymus* (Lepidoptera: Pieridae) butterflies more frequently, compared to younger ones, rejected those hosts which already carried conspecific eggs (Nomakuchi et al. 2001). Supposedly, this was caused by their lower residual reproductive value.

In many species, however, residual fecundity is a rather ambiguous term. Resources which could be used for egg production can also be reallocated to increase the individual’s lifespan or to other energetic demands (Papaj 2000). Moreover, in some species mature eggs can be resorbed for this purpose (Bell & Bohm 1975). Such a reallocation usually takes place when hosts for laying eggs are not readily available.

Additionally, some insects are able to choose between producing few large eggs or many small ones (Fox & Czesak 2000). So, we cannot always make a clearcut prediction that an insect of higher potential fecundity should, *ceteris paribus*, necessarily have lower acceptance threshold and accept hosts of lower quality. Alternatively, insects may choose to increase their residual lifespan, and thereby have more time to search for high quality hosts, or produce larger eggs for enhancing fitness per larva.

A reallocation of egg-production reserves probably took place in three species of *Dacus* (Diptera: Tephritidae) flies, which still refused to accept low-quality host species, after a 16-days host deprivation (Fitt 1986). Instead, they had ceased egg-production. Solely the fourth studied *Dacus* species accumulated high egg loads during the deprivation, and accordingly accepted low-ranked hosts after the deprivation period. *Callosobruchus maculatus* (Coleoptera: Bruchidae) beetles, if deprived of hosts for six days, thereafter laid fewer eggs but had longer lifespans than controls (Wang & Horng 2004). Interestingly, resource for lifespan elongation was achieved partly by resorbing some of the eggs matured during the deprivation period. *Meligethes aeneus* (Coleoptera: Nitidulidae) beetles ceased egg production, and remained with lower lifetime fecundity, when deprived of preferred host (Hopkins & Ekbom 1999). This was explained by a possible reallocation of energy to host searching. In our study on three geometrid moths (I), the absence of hosts resulted in reduced egg production in all the species. Another study we performed on one of these species, *Scotopteryx chenopodiata* (Lepidoptera: Geometridae), showed that lifespan of the moths on a host of lower quality was longer, on average (VI). As an example of reallocation from egg number to egg size, *Stator limbatus* (Coleoptera: Bruchidae) beetles laid fewer eggs on a lower quality host species, however, these eggs were progressively larger, supposedly in order to avoid high mortality of smaller offspring, characteristic for this host type (Fox et al. 1997).

Empirical studies often measure the effect of egg load (i.e. the amount of mature eggs in the abdomen) on host acceptance. Although, in theory, this factor should affect optimal host acceptance through principally different pathways in different insect types (e.g. income vs capital breeders: Jaenike 1978, Iwasa et al. 1984, Mangel 1987) the outcome should be universally similar: higher egg load should lead to a higher probability of acceptance (Iwasa et al. 1984, Mangel & Roitberg 1989, McGregor 1997, Sirot et al. 1997).

Indeed, in numerous studies, ovipositing females with higher egg loads have been shown to accept for oviposition a wider range of host types and deposit larger clutches (Minkenberg et al. 1992). For instance, *Venturia canescens* (Hymenoptera: Ichneumonidae) parasitoids with higher egg-loads laid eggs in already parasitized (i.e. low-quality) hosts more frequently (Fletcher et al. 1994, Sirot et al. 1997). In the field, *Aphytis aonidiae* (Hymenoptera: Aphelinidae) parasitoids with higher egg loads were less selective when choosing hosts for oviposition (Heimpel et al. 1996). Such effect of egg load on acceptance of a host for oviposition is reinforced in species, where host feeding (Iwasa et al. 1984, McGregor 1997), or just searching for proteins (Prokopy et al. 1995), and increasing the egg load thereby, is an alternative for oviposition.

In many of the numerous findings of the positive effect of egg load on host acceptance, however, egg load needed not be involved in the causal linkage, and may just have been correlated to the true causal factors (Agnew & Singer 2000). This suspicion is reinforced by results showing that the positive effect of egg load need not be universal in insects (Browne et al. 1990, Rojas 1999, Babendreier & Hoffmeister 2002). The lack or weakness of the statistical effect of egg load on host acceptance in some studies may be explainable by a positive correlation of egg load with other factors, that influence host acceptance in the opposite direction (V).

In particular, in our experiment on *S. chenopodiata* (V), we found that the effect of egg load on host acceptance was weak and inconsistent. We recorded if wild-caught moths started to lay eggs within one day, when exposed to a low-ranked hostplant. We also directly estimated the egg loads: moths were killed instantly after the trial day, and the number of eggs found at dissection plus the number of eggs laid was used as the estimate of egg load. The overall effect of egg load on the probability of host acceptance was not statistically significant. In subsamples caught on different days, the effect was either negative, positive, or lacking. Similar inconsistent results were obtained in our earlier experiments, which, however, estimated egg load indirectly (I, II). A probable underlying cause of these inconsistencies is the likely change of the effect of egg load with age. At high age, mortality risk may become a more important factor of host acceptance than egg load.

Potential fecundity sooner or later starts to decrease even if no eggs are laid (e.g. Leather & Burnand 1987, Proshold 1996, Fraser & Trimble 2001). Additionally, it has been found in many insects and other organisms, that the size of the eggs laid (and thereby often the fitness of emerging larvae: reviewed

in Fox & Czesak 2000, but see e.g. Harvey 1977, Lalonde 2005) decreases with aging of an individual (Fox & Czesak 2000, VI). In some species, it has been shown that if oviposition is delayed, the first (i.e. the most earlier produced, and largest therefore) eggs in the oviduct will be resorbed (Torres-Vila & Rodriguez-Molina 2002).

In our study on *S. chenopodiata* moths (VI), we proposed that the decreasing quality of the eggs laid through insect life could form a selective pressure pushing the moths to accept low-quality hosts if deprived of high-quality ones (I, II). By such behaviour, the moths could reduce the potential cost of lower egg quality resulting from postponement of oviposition. To test this hypothesis, we investigated whether egg quality decreases throughout the oviposition period in this species, and if moths manipulated to postpone oviposition, by depriving them of high-quality hosts, show lower egg quality. Indeed, egg quality decreased throughout the life of the moths. Also, a four-day host-deprivation lead to decreased hatching success of the eggs laid immediately thereafter. Plausibly, these eggs were mature carried already before the deprivation period, and experienced some kind of deterioration during the oviposition delay.

2.2.2.2. Life expectancy

Additionally to the number of eggs available for laying, acceptance decisions should be influenced by another factor, the potential number of new hosts to be encountered in the future. Life expectancy is an important determinant of the future opportunities to lay eggs on new hosts. In contrast to high potential fecundity which should lower acceptance threshold, high life expectancy should increase the threshold, because chances to encounter better hosts in the future are higher (Ward 1987, McGregor 1997, Sirot et al. 1997, II). Any decrease in perceived life expectancy should thus bring along widening of the range of acceptable hosts.

Indeed, starved *Venturia canescens* (Hymenoptera: Ichneumonidae) parasitoids, with a reduced life expectancy, laid eggs in already parasitized (i.e. low-quality) hosts more frequently than those which were fed and therefore had longer expected lifespans (Fletcher et al. 1994, Sirot et al. 1997). *Acheta domesticus* (Orthoptera: Gryllidae) crickets increased their oviposition rate the next day after infection with bacteria, although not in response to infection by a parasitoid larvae (Adamo 1999). Ageing *Episyrphus balteatus* (Diptera: Syrphidae) predatory hoverflies reduced discrimination between oviposition substrates with aphid species of different quality (Sadeghi & Gilbert 2000).

In our experiment with three geometrid moth species (I), we found a positive effect of hunger on the acceptance of a nonhost substrate for oviposition in one of the studied species, *S. chenopodiata*. We hypothesized, that the moths perceived decreased life-expectancy, and this caused the accelerated oviposition. In further experiments with this species (II) we confirmed that the

moths could perceive decrease of their life expectancy and increase their acceptance of low-quality hosts in response. Increased oviposition rate and decreased delay of oviposition on a low-quality host was found in response to natural injuries, approaching “natural” death, manipulative wing injuries, and hunger (the latter was found in only two experiments of three altogether: I, II).

2.2.2.3. Various abilities

Host searching ability (sensory and locomotory abilities), or physiological ability for assimilation or reproductive processes can change throughout adult life (Dixon & Agarwala 2002). Such abilities are important factors influencing host acceptance, either mechanistically or as input variables in adaptive decision making (Courtney 1986, Bernays & Weislo 1994). For instance, increased wear of aculeus may cause older females of tephritid flies (Diptera: Tephritidae) to accept some host types (e.g. hard unripe cherries) less readily, and prefer others instead (e.g. fruits with preexisting holes), or lay multiple clutches (Jones & Kim 1994).

Older *Adalia bipunctata* (Coleoptera: Coccinellidae) ladybirds hesitated less before accepting sites with conspecific oviposition-detering pheromone (Frechette et al. 2004). The authors suggest that this could either be caused by reduced life-expectancy, or the weakened moving ability, which increased the time until locating a new patch. The proximate reason could supposedly be the loss of chemoreceptors efficacy associated with senescence. Associative learning ability of the preference of microhabitat for oviposition declined with adult age in *Exeristes roborator* (Hymenoptera: Ichneumonidae) parasitoids (Wardle & Borden 1985).

In the absence of hosts *Callosobruchus maculatus* (Coleoptera: Bruchidae) beetles soon start to “dump” eggs to substrates totally unsuitable for larval development. Even if such eggs are wasted, the behaviour itself may be adaptive. It was demonstrated (Wang & Horng 2004), that the more active dumpers retain higher egg maturation rates and thereby can be more fecund also after being provided with the host.

Once again, a relevant original result is the one with *S. chenopodiata* moths (II). In particular, as already mentioned, we found that moths with a part of their wing complement cut off increased their readiness to accept a low-quality host. A likely adaptationistic explanation, alternative to the one given above, is that the injured moths perceived decreased moving ability, while this ability is clearly crucial for searching of hosts.

2.2.3. Environmental promises

2.2.3.1. Host availability

As seen above, an ovipositing insect can attain and remember valuable information about suitability of different host types for oviposition, and adjust its oviposition decisions accordingly. Similarly, it is plausible that it can remember and make use of information about its oviposition environment in general.

It can be advantageous for an insect to remember general host availability experienced in the past and, based on that information, to predict the availability in the future. If host encounter rate is higher (hosts are more abundant or apparent in the environment), the insect should be more choosy (Iwasa 1984, Mangel 1987, Ward 1987, Mangel & Roitberg 1989, McGregor 1997). More specifically, the larger is the probable number of higher-, equal-, or even lower-quality (Ward 1987, but see Jaenike 1978, Courtney and Forsberg 1988) hosts encountered in the future, the lower should be the probability of accepting the present host.

In the field, *Battus philenor* (Lepidoptera: Papilionidae) butterflies decreased the probability of oviposition when the density of hosts increased. This was supposedly caused not merely by the constraints on egg maturation rates, but a true increase of host selectivity (Rausher 1983). After long dispersal flights, *Antiochris cardamines* (Lepidoptera: Pieridae) butterflies accepted host types otherwise unacceptable – host leaves (poor larval food), and sites already occupied by cannibalistic conspecifics (Courtney & Courtney 1982).

Adalia bipunctata (Coleoptera: Coccinellidae) ladybirds, when having been exposed for days to conspecific oviposition-detering pheromone, laid eggs in the presence of this pheromone faster than the naïve controls. This could be explained by the reduced “hope” of the pheromone-experienced ladybirds to find a patch not inhabited by conspecifics (Frechette et al. 2004).

Aptesis nigrocincta (Hymenoptera, Ichneumonidae) parasitoids were much more selective against already parasitized hosts, when having an experience of higher host encounter rate (Babendreier & Hoffmeister 2002). This did not result from lower egg loads (because a separate experiment found no effect of egg load on superparasitism probability), but rather was a consequence of altered host availability perception.

2.2.3.2. Mortality risk

Threat to an ovipositing individual’s life discounts the value of the future eggs laid. This should make an insect less choosy when deciding about the present host (Mangel 1987, Ward 1987). For instance, when *Leptopilina heterotoma* (Hymenoptera: Eucoilidae) parasitoids were exposed to shorter photoperiod,

which supposedly marks fall season and therefore short life-expectancy to them, they were more ready to superparasitize, i.e. to accept low-quality hosts (Roitberg et al. 1992). The same was found in this species in response to lowered air-pressure, marking an impending thunder storm (Roitberg et al. 1993).

Our result with *S. chenopodiata* moths (II), showing that the moths increased acceptance of low-quality hosts in response to hunger or injuries could also be interpretable in this context. Wing injuries probably are quite common in lepidopterans, not least because of bird attacks. Instead of being factors shortening life directly, and being perceived as such by the moths, hunger and injuries could rather serve as signals of environmental hostility (i.e. increased mortality risk) for them, and thereby influence host acceptance. Further experiments would be necessary to detect which of the proposed exact pathways acts in real.

Short adult lifespan and high probability of death in response to e.g. predator attacks makes it difficult for the adults to directly estimate environmental mortality risk. In a modelling study considering optimal host acceptance by hypothetical insects (IV), we simulated the possibility, that insects could estimate environmental mortality risk indirectly: in particular, they could make use of their own age as an indicator of the expected residual life span. Such an estimation could be adequate, if environmental mortality remains stable throughout adult life of the insect. We found that under certain conditions (for instance, if there are large enough differences between mortality risks in alternative patches an insect can be born into) this should result in dynamic optimization of host acceptance threshold during adult life. In particular, oviposition selectivity, i.e. probability of rejecting low-quality hosts, should increase throughout adult lives, which indeed has been detected in some empirical studies (Nomakuchi et al. 2001, II).

2.3. The importance of the subject

Herebelow, I would bring forward some aspects of the importance and applicability of my thesis. How could we gain from the understanding of the role of an insect's experience in its oviposition? First, it is pretty obvious that insects are ecologically important, on one hand from the perspective of biodiversity, as the most species-rich class of animals, on the other hand as our main competitors and (carriers of) important natural enemies (Price 1997, Speight et al. 1999). Better knowledge of their behaviour can improve the management of insect populations both from the perspectives of nature conservation and pest control (e.g. Wardle & Borden 1985, Castelo & Corley 2004). Also, from the viewpoint of basic sciences, insects are one of the most studied animal groups, and therefore serve as particularly valuable model

organisms for studying life history evolution in general (e.g. Roff 1992). No doubt, feasibility of handling and short generation length will promote scientific investigation on these animals also in the future. Oviposition behaviour of and individual differences in it can be particularly important determinants of population dynamics (Price 1994, I), spatial population structure (Courtney & Courtney 1982, Rausher 1983, Herzog 1995, I) and host range (Singer 1983, Fitt 1986, Larsson & Ekblom 1995) of an insect population.

An explicit appreciation of the fact that insects' reproductive strategies can be flexibly adjusted to the environment they are born into, is not very old. Despite of rapidly accumulating literature, we still often have to admit the existence of a lot of unexplainable variation of oviposition in seemingly similar conditions (e.g. Leather & Burnand 1987, Braby & Jones 1995, Tammaru et al. 1996, I, II, V). Nevertheless, the understanding of flexibility in insects' reproductive behaviour can be of crucial importance when improving population management methods. Saying figuratively, farmers could benefit from considering pests as living, experiencing, and evolving objects, not simple devastative substance, spread over their fields by some mysterious evil force.

For instance, in our study on three common and rather abundant species of geometrid moths (I), we investigated in which ways behaviour of ovipositing females could contribute to the stable (i.e. non-outbreaking) population dynamics of the species. The stable population dynamics could be a prerequisite avoiding local damages to host populations, and also extinctions of local insect populations. Several insect species display outbreaking dynamics in some environments, while they are stable in others (e.g. Alonso et al. 2000), and getting "the finger behind" the reason of such differences would provide effective tools for nature managers. In our study (I), we found that the moths delayed oviposition if deprived of host species, while oviposition rate and egg production were influenced only relatively slightly. This behaviour contrasted to that of a moth species with outbreaking population dynamics, studied earlier, in which acceptance was not affected by the species of the host (Tammaru et al. 1995). We concluded that when availability of larval resource is low in a habitat, the females of the "stable" species probably disperse to reproduce elsewhere. This could "help" to avoid both population outbreaks and extinctions. Because behavioural patterns were qualitatively similar between the three species, we also concluded that such a mechanism is plausible to act more generally, in other insect species of similar ecology. We suggested that the delay of oviposition in response to low host quality could serve as a general index of sensitivity of oviposition towards environmental conditions in different insects, and experimental measuring of this index could allow for predictions about various aspects of a species' ecology.

The current thesis is based on the optimality approach, i.e. it attempts to explain the behavioural patterns under the assumption that behaviour would maximize fitness of the studied genotype in the environment it has evolved in. The applicability and usefulness of the optimality approach for studies of insect

oviposition has been put under doubt. In particular, adaptationistic models of host selection have sometimes been suspected to be too naive or, on the other hand, not applicable generally enough over taxa of different phylogenies (reviewed in Mayhew 1997). Nevertheless, optimality approach has its valuable advantages. If, in our experiments, animals do not follow optimality predictions, this points out where we know too little about the environment the studied organism has evolved in, or too little about the genetic constraints on the evolution of the particular lineage, or that we have measured fitness in an inadequate currency. This is the way, how testing optimality predictions, rather than simple empirical models, shepherds us towards valuable information about the ecosystem under study.

I give a few examples from our studies. In our experiments with *S. chenopodiata* moths (I, II), we detected only a weak and inconsistent effect of adult feeding on host acceptance, while the effect could be predicted by optimality models to be strong. One of the plausible reasons for such inconsistency lays in the native environment of the species: lack of adult food may not occur frequently enough to effectively select for a response in oviposition behaviour (II). Another optimality prediction, strong effect of egg load on host acceptance, also turned out not to hold in this species (V). Probably, constraints on life expectancy or physiological ability at high age may force the insects to low host selectivity, even despite their low egg loads. Moths of another species, *Y. evonymellus*, did not follow our prediction of postponing oviposition in response to larval crowding (III). Genetic constraints on evolution of memory are a possible reason, however, alternatively, we may have missed some important aspects of the species ecology when making our predictions. Searching for an adequate currency of fitness is dealt with e.g. in the VI study, which demonstrates “inflation” of eggs and proposes ways how this may affect behaviour of insects.

Knowledge of the behaviour of a species without attempts to explain it through evolutionary history may not be sufficient to make predictions about the response to management or stress on a population. If the management expresses different selection pressures on the species than those under which the observed behavioural patterns have evolved, especially in short-generation organisms like insects, rapid microevolutionary changes can take place (Singer 1971, Kellner & Shapiro 1983, Thompson 1988), and the behaviour can change. To predict the potential for and direction of such microevolution, we need to know the nature of different constraints on behaviour. To understand the nature of the constraints, we need to apply the optimality approach, simple descriptive data is not sufficient here.

2.4. What next?

The subject of my thesis, although relatively narrow, has evoked a truly vast amount of studies in recent years, only a minute fraction of which are discussed in my review of literature. The accumulation of empirical case studies, as well as discovery of qualitatively new patterns of phenotypic plasticity in reproductive behaviour of insects, surely continues to accelerate.

Within this general flow, I would like to draw out two directions, the following of which, in my opinion, would be especially valuable. First, comparative studies and meta-analyses of behaviour over different phylogenetic lineages and ecological groups of insects should impetuously come beside intensive studies of few model organisms. Most of the effects described in the current thesis have not yet been analysed in this respect. Such analyses would increase reliability of our predictions about taxa not previously studied. The clarification of the general patterns requires high attention also to negative results of empirical studies, the submission and publishing of which unfortunately is “out of fashion” nowadays.

Second, experimental studies should more vigorously make their way out of the lab into the field. The more we attain knowledge about insect behaviour, the more clearly we understand how sensitive and alterable by experimental environment it is. Minutest unnaturality of environment, unnoticed by “blunt” humans, can turn qualitative behavioural responses in experiments upside down, and can thereby lead our investigations to “wrong traces” and deform our theories for long time.

SUMMARY OF ORIGINAL RESULTS

The current thesis comprises six studies on the effect of insects' individual experience on their acceptance of substrates for oviposition. One of the studies (IV) is a theoretical model, while the other five involved experiments with different moth species. In the experiments, we placed insects in individual vials furnished with various substrates, and measured the effects of their experience, either natural or manipulated, on various oviposition parameters. The results of the studies, together with the theoretical background, are shortly outlined below.

Where environmental stochasticity does not allow for genetic canalization of behaviour, it is often optimal to adjust decisions to ontogenetic experience of the individual. There are three possible pathways, along which previous experience can affect the optimal decision of acceptance or rejection of an encountered host for oviposition. First, the experience can directly influence perceived suitability of the host type. Second, it can influence the potential of the insect: either the potential for laying eggs, or the potential for searching new host items. If the potential for laying eggs becomes higher, lower-quality host types become acceptable, while, if the potential for finding new hosts is higher, the acceptance threshold is elevated, and only high-quality hosts are acceptable. Third, previous experience can influence the estimate of environmental promises for oviposition or host search by the insect, and the acceptance threshold thereby.

Adequate cues of oviposition habitat quality can be present already during larval stage. This has, in various insects, led to evolution of specific adult migration morphs, or caused milder adaptive behavioural responses in the adults which have developed under overcrowding in the larval stage. Higher potential for emigration and for searching a new habitat is often associated with postponing of reproduction and lower fecundity. In our study on an outbreaking moth species (III), we hypothesized that the moths are adapted to respond to larval overcrowding by postponing reproduction or altering fecundity schedules otherwise. This, nevertheless, was not found: fecundity schedules tended to be altered only minimally, and in the direction opposite to expected. Also, oviposition was insensitive to adult overcrowding. Such a low sensitivity of host acceptance to population density may contribute to the population outbreaks (I), characteristic of this species.

This hypothesis seems especially plausible in the light of the results of our study on three geometrid moth species which, on one hand, show stable (i.e. not outbreaking) population dynamics, and on the other hand, expressed a clear delay of acceptance of a nonhost substrate for oviposition, compared to when provided a high-ranked host (I). We proposed that such a delay could serve as an adequate experimental indicator of sensitivity of an insect species' distribution of eggs to environmental conditions, and as such, be a valuable

basis for predictions about the population-level behaviour, and life history of the species.

The same study (I) provided an unexpected result about the effect of insect physiological state on host acceptance. In particular moths fed as adults, and thereby carrying higher egg loads (i.e. loads of mature eggs in abdomens), nevertheless, did not accept a nonhost plant for oviposition earlier than those in hunger and therefore being more egg-limited. Moreover, in one species the fed moths tended to accept the nonhost later, on average, than the unfed individuals. This contradicts the conventional theory. We proposed that the moths in hunger perceived decreased life expectancy, and this tended to be a more important factor of host acceptance than egg load in that species. In further experiments (II), we confirmed that perceived life expectancy indeed affects host acceptance threshold in this species. We showed that both natural and manipulated variation of life expectancy brings along expected variation of host acceptance: moths which experienced higher mortality risk accepted a low-quality host faster than those with lower mortality risk.

However, insects probably possess only limited ability to perceive cues of adult mortality risk. In a modeling study on a “generalized” insect (IV), we showed that insects could improve this ability by using their own age as an indicator of the probable further life expectancy. Under certain conditions, this could cause the evolution of dynamic optimization: quality threshold of host acceptance should change with age. In particular, elevating the threshold (i.e. increasing selectivity of host choice) with age could lead to higher total fitness, compared to if oviposition selectivity was not affected by age. It remains to be shown, however, if such adaptation is present in some real species.

As discussed above, the effect of egg load turned out to be a less important factor of host acceptance than expected (I). This effect was detected weak also in another experiment (II). We further investigated the effect of egg load on acceptance of a low-quality host in a special experiment (V), in which, in contrast to our previous studies, we determined egg loads directly. We confirmed that the effect was weak and inconsistent in this species, having either positive, negative, or no effect on host acceptance in different subsamples. Again, we hypothesized the covariance of egg load with life expectancy to be the underlying cause: older moths could take life-expectancy as a relatively more important cue for optimal acceptance than do younger ones.

The number of eggs available for laying is not the only measure of residual reproductive value in insects. The quality of eggs can vary also, and has been shown to decrease throughout oviposition period in numerous insect species. We proposed that such temporal decrease of egg quality could act as a cost of oviposition selectivity in insects (VI). Relatively rapid acceptance of low-quality hosts, when deprived of high-quality ones, shown in numerous insects, could (partly) manifest avoidance of this cost. We conducted an experiment (VI) to test the plausibility of this mechanism in a geometrid moth, in which the described lowering of acceptance threshold indeed has been shown to occur

(I, II). We showed that the assumption of decreasing egg-quality throughout adult life indeed was met. We also demonstrated that delay of oviposition, resulting from temporal host deprivation, reduced hatching success of eggs. Probably, eggs already mature in the abdomens deteriorated during the delay. Such a deterioration may act as a cost of selectivity, and thereby affect host acceptance behaviour in the species.

In conclusion, I would like to believe that the studies presented in the current thesis have made a contribution to the empirical evidence, as well as understanding, of the effect of experience on host acceptance in insect oviposition. Mainly, they have clarified the role of time- and egg-limitation scale in determining host acceptance, but also the roles of preimaginal conditioning and egg-quality dynamics, and shed light on the role of host acceptance behaviour in determining population dynamics.

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SUMMARY IN ESTONIAN

Kogemuse mõju munemissubstraadi aktsepteerimisele liblikatel

Käesolev doktoritöö hõlmab kuut uurimust, mis selgitavad putukaisendi kogemuse mõju munemissubstraadi aktsepteerimisele. Üks neist uurimustest (IV) on teoreetiline mudel, ülejäänud viis aga kätkevad katseid erinevate liblikaliikidega. Katsetes paigutasime putukad ühekaupa munemissubstraadiga sisustatud anumatesse ja mõõtsime nende poolt kogetu mõju erinevatele munemise parameetritele. Allpool on lühidalt välja toodud uurimuste tulemused ja teoreetiline taust.

Keskkonnatingimused on tihti peale liialt varieeruvad võimaldamaks käitumismustrite geneetilist kanaliseerumist. Sellises olukorras võib looduslik valik viia käitumise plastilisusele vastavalt isendi ontogeneetilisele kogemusele. Kogemus võib mõjutada putuka optimaalset otsust kohatud munemissubstraadi aktsepteeritavuse kohta kolmel erineval viisil. Esiteks võib see otseselt mõjutada putuka hinnangut konkreetse substraaditüübi kvaliteedi kohta. Teiseks võib see mõjutada putuka võimekust muneda ja otsida uusi substraate. Kui võimekus munemiseks on kõrge, on adekvaatne muneda ka madalakvaliteedilistele substraatidele. Samas, kui võimekus otsida uusi substraate on kõrge, on kasulik jätta madalamakvaliteedilistele substraatidele munemata. Kolmandaks võib kogemus mõjutada putuka hinnangut keskkonna soodsusele munemise ja uute substraatide leidmise aspektist ja sedakaudu nihutada substraadi-kvaliteedi aktsepteerimisläve.

Adekvaatseid signaale elupaiga kvaliteedi kohta munemissubstraadina võib hankida juba vastseeas. Nii näiteks arenevad paljudel putukatel vastusena ebaoptimaalselt kõrgele populatsioonitihedusele vastseeas välja emigreerumiseks kohanenud valmikumorfid või on kooruvad valmikud muul viisil parema levimisvõimega. Paljudel liikidel kaasneb sellise arenguga hilinevad sigimine ja väiksem viljakus. Uurides liblikaliiki, mille populatsioonitihedus on looduslikult tugevasti kõikumine ja viib sageli vastsetoidu täielikule hävitamisele elupaigas, püstitasime hüpoteesi, et adaptiivne vastus liigsele vastsete populatsioonitihedusele võiks olla edasilükatud sigimine (III). Selline kohastumus võimaldaks enne sigimist vahetada munemispaika ja sedakaudu tõsta järglaste kohasust. Sellist efekti siiski ei leitud, vastsete tihedus mõjutas koorunud valmikute munemist kui üldse siis üksnes minimaalselt ja sedagi ennustatule vastupidises suunas. Ka valmikute kõrge tihedus ei mõjutanud munemist. Selline aktsepteerimiskäitumise vähenemine tundlikkus populatsioonitihedusele võib olla põhjuseks uuritud liigile looduslikult omasele populatsioonitiheduse suurele kõikumisele.

Viimatimainitu näib eriti tõenäoline meie teise uurimuse (I) tulemuste valguses. Kolmele uuritud vaksikuliigile on omane stabiilne populatsiooni-

dünaamika ning katses ilmutasid nad vastavalt selgelt tundlikkust munemis-substraadi kvaliteedi suhtes, lükates sobiva substraadi puudumisel munemist edasi. Selline munemise edasilükkamine võiks olla heaks eksperimentaalseks näitajaks liigi munemise keskkonnatundlikkuse kohta ja sellisena olla väärtuslikuks aluseks ennustustele liigiomase populatsioonidünaamika ja liigi elukäigu kohta.

Sama uurimuse (I) käigus ilmnes aga ka üks ootamatu tulemus, mis puudutab putuka füsioloogilise seisundi mõju aktsepteerimisotsusele. Nimelt ei alustanud valmikuna toidetud vaksikud, kel seetõttu oli suurem munalast (st. rohkem küpseid mune tagakehas), munemist ebasobivale substraadile varem kui nälginud, väiksemate munalastidega vaksikud. Ühel vaksikuliigil kaldusid toidetud vaksikud alustama munemist nälginutest koguni hiljem. Selline tulemus on vastuolus üldtunnustatud teooriaga munalasti positiivsest mõjust substraadi aktsepteerimisele. Püstitasime hüpoteesi, et nälginud vaksikud tajusid jääkeluea vähenemist, mis viiski nad suhteliselt kiirele munemisele, ja osutus ühel liigil isegi tähtsamaks aktsepteerimisotsuse mõjutajaks kui munalast. Edasistes katsetes (II) näitasime, et sellel liigil suremisrisk tõesti mõjutab aktsepteerimisotsust. Nimelt, nii looduslik kui menetluslik suremisriski varieerumine tõi kaasa vastava varieerumise aktsepteerimiskäitumises: kõrgema suremisriskiga vaksikud munesid madalakvaliteedilisel substraadil kiiremini kui madalama suremisriskiga vaksikud.

Putukate võime hinnata keskkonnategurite poolt põhjustatud suremisriski on siiski ilmselt üsnagi piiratud. Modelleerides hüpoteetilist putukat (IV) näitasime, et putukad võiksid kasutada oma vanust valmikuna jääkeluea indikaatorina. Teatud eeldustel võiks see evolutsiooni käigus viia aktsepteerimisläve ealise muutumiseni. Täpsemalt, elu jooksul kasvav selektiivsus munemis-substraatide suhtes võiks olla kohasem strateegia kui ealiselt muutumatu selektiivsus. Kas sellist kohastumust ka mõnel liigil reaalselt esineb, jääb edasiste uurimuste selgitada.

Nagu eelpool öeldud, osutus munalasti mõju aktsepteerimisele eeldatust väiksemaks (I). Munalasti nõrk mõju tuvastati ka teises uurimuses (II). Uurisime munalasti mõju eraldi katses (V). Erinevalt varasematest katsetest, millede käigus munalastid hinnati kaudselt, mõõtsime seekord katsealuste munalastid otseselt. Munalasti nõrk ja ebajärjekindel mõju aktsepteerimisotsusele uuritud liigil leidis taas kinnitust. Erinevates valimites oli mõju madalakvaliteedilise substraadi aktsepteerimisele erinev, olles positiivne, negatiivne või puududes sootuks. Selline ebajärjekindel mõju võib tuleneda munalasti ja jääkeluea kovariatsioonist, kusjuures vanematele isenditele võib võrreldes noorematega olla jääkeluiga suhteliselt olulisem aktsepteerimist määrav tegur.

Munetud munade arv pole putukatel ainus kohasuse komponent. Munade kvaliteet võib samuti varieeruda ja paljudel liikidel on näidatud, et see väheneb valmiku vananedes. Püstitasime hüpoteesi, et see nähtus võib suurendada substraadivalivuse hinda putukate munemisel (VI). Paljude putukaliikide emaste valmidus hakata kõrgekvaliteediliste substraatide puudumisel suhteliselt

ruttu aktsepteerima madalakvaliteedilisi võib olla selle hinna vältimise väljendus. Tegime katse (VI) selgitamaks sellise mehhanismi toimimise võimalikkust vaksikuliigil, kellel kirjeldatud akstepteerimisläve langus tõepoolest esineb (I, II). Ilmnes, et munakvaliteet tõepoolest langeb elu jooksul. Samuti, munemise edasilükkamine tõi kaasa munade koorumisedukuse languse. Tõenäoliselt väheneb edasilükkamise jooksul juba eelnevalt küpsete munade kvaliteet. Seega, munakvaliteedi muutus võib tõesti toimida munemise selektiivsuse hinnana ja seeläbi mõjutada aktsepteerimisotsuseid uuritud liigil.

Kokkuvõtvalt hindan, et käesolevas väitekirjas esitatud uurimused on lisanud empiirilisi andmeid ja täpsustanud arusaama kogemuse mõju kohta munemissubstraadi aktsepteerimise strateegiatele putukatel. Peamiselt on selgitatud aja- ja munalimitatsiooni skaala mõju aktsepteerimisotsustele. Samuti on selgitatud vastseaa kogemuse mõju elupaiga kvaliteedi kohta ning munakvaliteedi dünaamika mõju. Lisaks on selgitatud aktsepteerimisstrateegia võimalikku mõju populatsioonidünaamikale.

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THE EFFECT OF EGG LOAD ON MOTIVATION TO OVIPOSIT IS WEAK AND INCONSISTENT IN A GEOMETRID MOTH

Juhan Javoš & Toomas Tammaru

ABSTRACT

1. Most of empirical and theoretical studies treat egg load as a major determinant of insect oviposition behaviour, and predict a positive link between egg load and motivation to oviposit.
2. In the current study, the effect of egg load on the probability of laying eggs on a low-ranked host was examined in a moth *Scotopteryx chenopodiata* L.
3. The overall effect of egg load on oviposition behaviour was weak and inconsistent. As dependent on the date of catching and moth age, the effect of egg load was found either positive, absent, or negative.
4. These findings emphasize that the conventional assumption of higher egg load being related to higher motivation to oviposit needs not always to be met. The possibility that the effect of egg load may change in the course of adult life calls for caution in interpreting empirical results.

INTRODUCTION

Numerous empirical studies have shown that egg load, i.e. the number of mature eggs in the abdomen, increases an insect's motivation (*sensu* Singer et al., 1992) to oviposit. The high motivation is reflected by high oviposition rate, low selectivity towards hosts, large clutches, high host searching activity etc. (Minkenberg et al., 1992). The accumulation of the empirical evidence has been paralleled by several theoretical models (e.g. Jaenike, 1978; Iwasa et al., 1984; Mangel, 1987; Sirot et al., 1997). These models explain the phenomenon by increased risk of time limitation on laying all eggs, and increased pessimism about chances to find high-quality hosts in future, both of which accompany the accumulation of egg load.

Nevertheless, these models do not justify the expectation of the positive correlation between egg load and motivation be present universally. There are good reasons to assume adaptive mechanisms which could obscure, or even reverse the direction of this correlation. In particular, as in many species egg-supply decreases throughout lifetime (e.g. Boggs, 1997; Dixon & Agarwala

2002), individuals with high egg load tend to have a high life expectancy. High life expectancy, in turn, has been shown both theoretically (Mangel, 1987; Sirot et al., 1997), and empirically (Roitberg et al., 1993; Javoiš & Tammaru, 2004) to decrease oviposition motivation. Indeed, experimental studies are emerging that question the straightforward and universal effect of egg load on oviposition motivation (Barton Browne et al., 1990; Rojas, 1999; Agnew & Singer, 2000; Babendreier & Hoffmeister, 2002).

Our previous results with the geometrid moth *Scotopteryx chenopodiata* L. have provided circumstantial evidence against the proposed major role of egg load in determining oviposition selectivity, and the suggested invariably positive link between egg load and motivation. In particular experiments, these insects have manifested both positive (Javoiš & Tammaru, 2004) and negative (Tammaru & Javoiš, 2000) effect of egg load on the probability to accept low-ranked hosts for oviposition. In both cases the effect of egg load remained limited. However, these studies did not measure egg load directly, but rather estimated this variable basing on weight and winglength, or feeding status of the insects.

The current note presents an experiment in which the effect of egg load on the motivation to oviposit was measured directly. In particular, the probability of wild-caught insects to lay eggs on a low-ranked host was recorded, and egg loads were determined by dissection thereafter. The effect of initial egg load (eggs laid+residual egg load) on motivation was found to be weak and not invariably positive, it varied considerably in different samples .

MATERIALS AND METHODS

Scotopteryx chenopodiata L. is an oligophagous geometrid moth (see Tammaru & Javoiš, 2000 or Javoiš & Tammaru, 2004, for more details on biology). For the experiment, female moths were caught by netting in the field, near Tartu, Estonia (58° 24' N, 26° 44' E). The insects were assumed to be mated and involved in oviposition behaviour (Tammaru & Javoiš, 2000). Within one month, four samples were caught (see Fig. 1, for catching dates and sample sizes), 177 females in total. All the females were obtained from the same 25 ha area of homogenous seminatural grassland. Being captured, the moths were preserved overnight at 4°C.

A single-substrate oviposition experiment (e.g. Singer, 1986) was set up to measure the effect of the moths' initial egg load on the probability of laying eggs on a low-quality host within one day. We had an a-priori knowledge (Javoiš & Tammaru, 2004) that less than 50% of the moths start to oviposit on the used low-ranked hostplant, the Siberian pea-tree (*Caragana arborescens* Lam.) within one day, while a clear majority would do so in the presence of a higher ranked host. More motivated individuals were assumed to start to lay eggs earlier (Ward, 1987; Courtney et al., 1989; Singer et al., 1992; Tammaru &

Javoiš, 2000), and hence more probably within the one-day trial (Javoiš & Tammaru, 2004).

The moths were placed singly in 50 ml transparent plastic vials with a branch of pea-tree as the oviposition substrate. Drinking-water was provided soaked into a piece of porous paper. Light regime was maintained at 18/6 L/D, and temperature at +18°C. In the beginning of the experiment, the wear of the wings of each moth was visually estimated on a four-grade scale (grade 4 meaning the most worn wings). The purpose was to use insect age (reflected by the wingwear: Heimpel et al., 1996; Javoiš & Tammaru, 2004) as an additional factor in the statistical analyses.

A day (24 hours) after the beginning of the experiment, the eggs laid were counted, and the moths were killed by rapid freezing. Thereafter, residual egg loads (the amounts of chorionated eggs in the abdomens) were determined at dissection. The sum of the eggs laid and found on dissection served as the estimate of the moths' initial egg load. The effect of this variable on the probability of oviposition was analyzed by logistic regression (SAS, proc GENMOD: SAS Institute Inc., 2000). Wingwear grade and subsample identity (the date of capture) were included as additional nominal factors in the analyses. Additionally, to characterize the strength of the effect of egg load, the generalized coefficient of determination was calculated (SAS, proc LOGISTIC).

RESULTS AND DISCUSSION

In total, 28% (50 out of 177) of the moths started oviposition during the 24 hour trial, while egg loads varied from 4 to 129 eggs (mean \pm SD: 62.2 \pm 25.1). In the total sample, the effect of egg load on the probability of oviposition was nonsignificant ($\chi^2_1=0.81$, $P=0.37$; this qualitative result did not change if one or both of the additional factors were excluded from the model). The overall effect of egg load on motivation to oviposit was minimal (the generalized $r^2=0.013$, model concordance 56.9%). Both interactions between the factors (egg load*wingwear, egg load*subsample identity) were nonsignificant when simultaneously added to the model, but significant when included one at a time in alternative models (Table 1, Models A and B).

The character of the interactions was further clarified. Separate analyses of the four wingwear classes showed the effect of egg load disappearing at older ages (Fig. 2). Intriguing differences were found also between the subsamples caught on different days (Fig. 1). In the earliest sample (Jul. 20), higher egg load tended to lead to higher probability of oviposition. In the second sample (Jul. 20, i.e. caught only one day later), the result was reverse: the layers turned out to be with lower egg load. In the third sample (Aug. 4), egg load did not affect oviposition probability. In the fourth sample (Aug. 13), again, the layers tended to have lower egg loads.

The contrast in the effect of egg load between the two earliest subsamples can be explained by the age (wingwear) differences between the subsamples: the moths of the second subsample (Jul. 21), in which the negative effect of egg load on oviposition was found, had significantly more worn wings (grade 3–4 without exception) than those of the first subsample (t-test treating wingwear as a continuous variable: $t_{97}=4.29$, $P<0.0001$; Fig. 1).

Along with our previous results with *S. chenopodiata* (Javoiš & Tammaru, 2004, Tammaru & Javoiš, 2000), the experiment reported here showed that the overall effect of egg load on motivation to lay eggs is weak and inconsistent. In this species, egg load appears thus not to be a major factor of readiness to oviposit. This is in contrast with the majority of relevant empirical studies which are consistent with the simple “mainstream” viewpoint, reporting clear positive effect of egg load on motivation (Minkenberg et al., 1992; but see Barton Browne et al., 1990; Rojas, 1999; Babendreier & Hoffmeister, 2002). It may be possible, however, that such a concordant overall picture is affected by a publication bias: results where no effect is found, as well as “puzzling” results, find submission and publication less frequently than positive ones. In any case, generalisations over species should be drawn with caution, because the effect of egg load on motivation to oviposit can result from different selective pressures in different ecological groups of insects (e.g. pro-ovigenic vs synovigenic insects; Jaenike, 1978; Iwasa et al., 1984; Mangel, 1987), and can therefore have a largely different character.

In *S. chenopodiata*, the effect of egg load on motivation depended on adult age of the insect, being positive at younger ages but negligible later on. To our knowledge, age differences in the effect of egg load on oviposition behaviour have not been reported before. The variation in the relationship between egg load and oviposition motivation may well have an adaptive basis. For instance, throughout the adult life of an insect, the diminishing egg load is typically accompanied by decreasing life expectancy (also in *S. chenopodiata* older individuals have lower egg loads, on average: J. Javoiš, unpublished data). As these two factors should affect oviposition motivation in opposite directions, their net outcome effect is not straightforward. The relative importance of these two factors might also change with age, which could explain the complex pattern recorded in this study. At earlier ages, the effect of egg load (egg-limitation risk) could be the dominant determinant of motivation, while at higher ages the effect of life expectancy (time-limitation risk) could counterbalance its effect.

There was a “puzzling” but perhaps instructive controversy in our results: the effect of egg load on oviposition was inconsistent between different subsamples. The qualitative difference in the effect of egg load on oviposition between subsamples caught in only one day interval could at least partly be attributed to the wingwear differences between the subsamples. The latter could result from the microhabitat differences between the catching places of different subsamples – although within the same relatively little grassland area, the

places were apart from each other up to few hundred meters, and the age-structure of the *S. chenopodiata* adult population probably varied between microhabitats. In any case, this finding cautions against drawing too far-reaching conclusions from individual oviposition trials: the effect of eggload may well vary within species and populations, in interaction with other state variables of the insects.

ACKNOWLEDGEMENTS

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Table 1. The effects of the studied factors on the probability to oviposit on the low-ranked host (type 3 logistic regression).

Model A

Source	d.f.	χ^2	<i>P</i>
egg load	1	1.3	0.25
subsample	3	10.9	0.012
wingwear	3	18.1	0.0004
egg load* wingwear	3	12.4	0.0060

Model B

Source	d.f.	χ^2	<i>P</i>
egg load	1	2.7	0.098
subsample	3	6.7	0.082
wingwear	3	11.2	0.010
egg load* subsample	3	13.4	0.0038

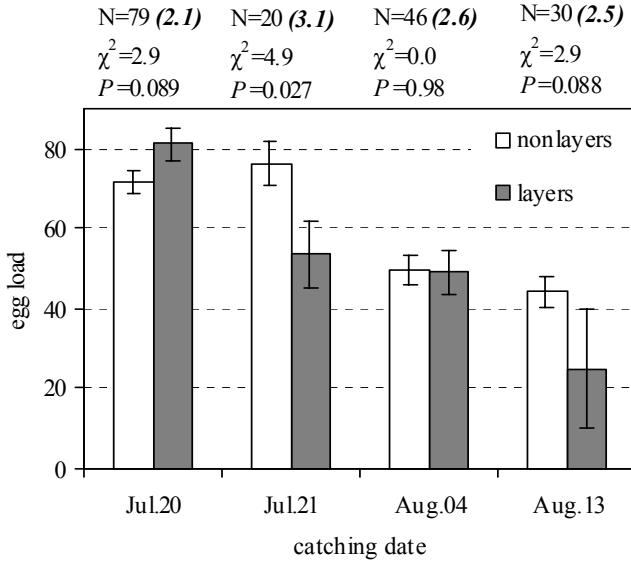


Fig. 1. Egg loads (\pm SE) of the moths that laid eggs and those that did not, presented by different subsamples. The effect of egg load on the probability of oviposition is tested separately for each subsample. The mean wingwear values for each subsample are given in brackets, next to sample sizes.

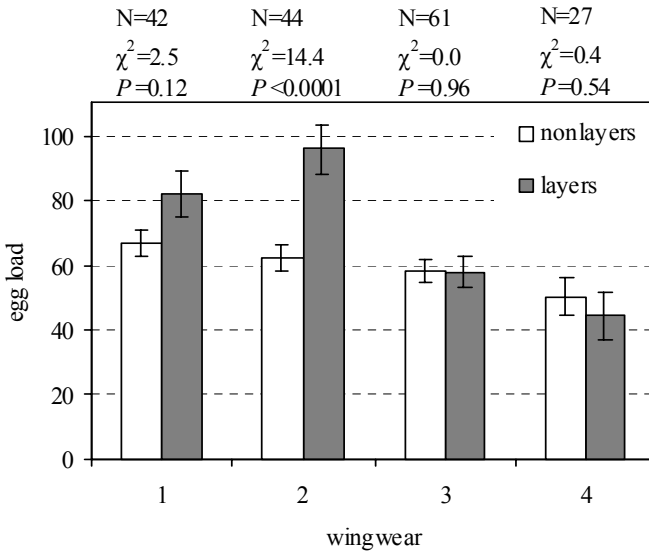


Fig. 2. Egg loads (\pm SE) of the moths that laid eggs and those that did not, presented by different wingwear classes (the lower wingwear values represent less worn wings). The effect of egg load on the probability of oviposition is tested separately for each wingwear class.

DECREASING EGG QUALITY AS A COST OF OVIPOSITION SPECIFICITY IN INSECTS

Juhan Javoiš & Toomas Tammaru

ABSTRACT

Various insects are known to start laying eggs on low-quality substrates if high quality substrates are not available. According to the conventional theory, such a behaviour is caused by the risk of time limitation on realizing potential fecundity. We hypothesized that another evolutionary constraint on oviposition specificity could be set by temporal decrease of the quality of eggs laid. In the geometrid moth *Scotopteryx chenopodiata* L., we found that both hatching success and the size of eggs, indeed, decreased with the age of the mother, (and not merely with the progressive number of eggs laid). Moreover, moths which were manipulated to delay oviposition by host deprivation showed reduced hatching success of the eggs laid immediately after the delay. However, we failed to detect lower lifetime average quality of eggs in response to a single few-days host deprivation period, while lifetime restriction to a low quality host caused only a minor tendency towards smaller eggs. It is plausible that deterioration of mature eggs in the abdomens is responsible for the found short-term decrease of egg quality, and thereby constrains oviposition specificity in the studied species.

INTRODUCTION

It is well documented in various insects that, favourable substrates being in short supply, females soon lower their acceptance thresholds, i.e. they start to lay eggs on substrates which they ignored previously (e.g. Rausher 1983, Singer et al. 1992, Courtney et al. 1989, Roberts & Schmidt 2004, Wang & Horng 2004). As the reason for such a behaviour, optimality models see the risk of time limitation (e.g. Mangel 1987, Ward 1987, McGregor 1997, Sirot et al. 1997, Burger et al. 2004). Under conditions of poor availability of substrates, an ovipositing female should relax its choosiness to avoid the risk of dying with too few eggs laid, and facing low fitness thereby. As accidental deaths occur commonly in insects, the risk of time limitation is, indeed, a plausible evolutionary cause behind the sensitive adjustment of oviposition selectivity to substrate availability.

Admitting the role of time limitation does not, however, exclude other evolutionary constraints on host specificity (expressed as the delay of oviposition on a low-quality host, *sensu* Singer 1982). In particular, we are

proposing here that a decrease in the quality of eggs with time progressing can contribute to the cost of specificity. If the quality of eggs laid decreases as a consequence of a delay in oviposition, insects are selected to lay their eggs faster. This should be manifested in lowered oviposition selectivity under conditions of poor host availability.

On the first glance, the assumptions of such a scenario appear to be met: decrease in egg quality throughout the mother's lifetime has been shown in various insects (e.g. Wiklund & Persson 1983, Forrest 1986, Fox 1993, Torres-Vila & Rodriguez-Molina 2002). Such a pattern *per se* does not, however, prove the existence of the cost of delayed oviposition in terms of decreased egg quality. This is because the decreasing pattern can be caused by two different proximate mechanisms: the quality of an egg may depend either on mother's absolute age, or on the number of eggs laid by the mother earlier in her life (i.e. *egg rank*). Only the first of these two mechanisms can form the basis for the cost of oviposition delay: egg rank is not affected by postponing oviposition. We are unaware of attempts to separate these two mechanisms, or to directly demonstrate the decrease in egg quality as a response to delayed oviposition. However, a related phenomenon has been shown in several lepidopterans: postponed mating adversely affects hatching success of eggs (e.g. Leather & Burnand 1987, Lingren et al. 1988, Unnithan & Paye 1991, Proshold 1996, Fraser & Trimble 2001).

In the present study, we experimentally tested the possibility that delayed oviposition (as an expression of host specificity) entails a cost in terms of decreased egg quality. We manipulated females of a geometrid moth to postpone oviposition by depriving them of favoured host plant for different periods. As the response, we measured both the hatching success and size of the eggs laid. We studied if the manipulative delay affected egg quality. Moreover, we analyzed lifetime patterns of egg quality of the experimental moths in an attempt to separate the effects of mother's absolute age, and egg rank statistically.

MATERIAL AND METHODS

Study species. *Scotopteryx chenopodiata* L. (Lepidoptera: Geometridae) is an oligophagous moth which feeds on various *Fabaceae* as larva, and inhabits various open landscapes. The insect is synovigenic, i.e. new eggs are matured during adult life (Tammaru & Javoiš 2000). However, a few dozens of mature eggs is usually carried in the abdomen (Tammaru & Javoiš 2000, J. Javoiš unpubl.). In the lab, total fecundity may reach about 300 eggs, and adult life may last up to one month (J. Javoiš unpubl.). The eggs are laid singly on or near the plants (but not attached to them) where the larvae would hatch and start to feed on about two weeks later.

The experiment. Female moths were collected by netting in the field in Tartu, Estonia (58°N, 26°E) and preserved under 4°C overnight. The actively flying moths were assumed to be mated (Tammaru & Javoiš 2000). Next morning, the insects were placed individually in transparent 50 ml vials. They were randomly allocated to four oviposition treatments, 50 insects in each. In the control group, a branch of a high ranked (Javoiš & Tammaru 2004) host, the white melilot (*Melilotus albus* Med.) was provided as oviposition substrate since the beginning of the experiment. Three treatments were aimed to simulate low availability or quality of hosts in nature. In one treatment, a nonhost plant, white birch (*Betula pendula* Roth) was provided for the two first days of the experiment, and the white melilot thereafter (the *2-day-delay* treatment henceforth). In the second treatment, such host deprivation lasted for four days (the *4-day-delay* treatment). In the third treatment, a low-ranked (Javoiš & Tammaru 2004) host, the Siberian pea-tree (*Caragana arborescens* Lam.) was provided throughout a moth's life (the *low-ranked-host* treatment).

Restriction to a non-host plant for a limited period was aimed to mimic a natural situation in which hosts are scarce, and ovipositing moths have to search for them for a considerable time. It was known from our previous studies that most individuals delay oviposition for at least four days if provided a non-host plant as a substrate (Tammaru & Javoiš 2000). However, most individuals initiate oviposition on the first day if provided with a favoured host plant.

Every second day the eggs laid were counted and removed, and the plant branches and sources of adult food (10% sugar solution soaked in porous paper) were relieved. The experiment (18°C, 18/6 L/D) was run until the death of the insects.

After each removal of the eggs, samples of approximately ten eggs (or less if less were laid) per insect were retained and allowed to hatch in controlled conditions (18°C, 80% rel. hum.). The hatching success (i.e. the proportion of eggs hatched) of each such replicate was recorded. Because egg quality is likely to be positively correlated to egg size (Fox & Czesak 2000), we additionally measured egg sizes (widths of hatched egg-shells) in 386 replicates, chosen randomly between all the individuals, treatments, and days of oviposition. From each replicate, three eggshells were measured, and the mean of these three was taken as the value of the response variable *egg size*.

DATA ANALYSIS

Analysis of lifetime dynamics of egg quality. This analysis was aimed to reveal the effect of manipulative delay in oviposition on the quality of eggs laid throughout a moth's life. Moreover, the data allowed us to separate the effects of egg rank and mother age on egg quality.

Hatching success and egg size served as two alternative indices of egg quality, and were compared between the four treatments. Egg size was a

continuous variable and was subjected to ordinary repeated measures analysis of general linear models (SAS, PROC MIXED; Littell et al 1996). For hatching success, logistic regression for repeated measures (SAS, PROC GENMOD; SAS Institute Inc. 2000) was applied to facilitate a similar analysis of this binary response variable.

In addition to detecting the effect of manipulations, we addressed the question about the presence of a unique effect of mother age on egg quality, i.e. we tested for an effect of age which were independent of the effect of egg rank. It was natural to assume that the rank of an egg laid and the age of the mother are strongly correlated. To take a conservative approach, we therefore included both of these factors simultaneously in type 3 models (which conceal the joint effect of any intercorrelated factors). As the used moths were wild-caught, their absolute adult ages in the beginning of the experiment were not known. Similarly, we were not aware of the number of eggs each female had laid prior to the experiment. For this reason, both egg rank and mother age were counted backwards, starting from the death of a female. This was done, respectively, by counting the remaining days until death, and by summing the eggs laid later in the experiment plus half of the eggs laid within the analysed replicate.

When testing the effect of mother age, our intention was to eliminate also any influence of the different background of the experimental individuals. Accordingly, two covariates, *total fecundity* and *mother longevity*, were included in the models. As, in this case, it is reasonable to expect non-linear relationships, also the effects of second and third grades of egg rank and the covariates were included in alternative models.

Analysis of short-term effects of oviposition delay. In another analysis, we investigated the effect of oviposition delay on the hatching success of eggs laid immediately after the delay period. We used logistic regression (SAS, PROC GENMOD; SAS Institute Inc. 2000) to compare the eggs between the treatments as follows: (a) *2-day-delay* treatment vs control: the eggs of the four first days of the experiment pooled; (b) *4-day-delay* treatment vs control: the eggs of the six first days of the experiment pooled; (c) *low-ranked-host* treatment vs control: the eggs of the six first days of the experiment pooled. Fecundity during the analysed time-periods was included in the analyses as a covariate.

RESULTS

Effect of the treatments on oviposition schedules. As compared to control, all three manipulations lead to a delay in oviposition (Figure 1). However, the manipulated moths relatively quickly compensated for most of the fecundity lag caused by the initial delay in oviposition: in all three manipulated groups, mean total fecundity approximated 80% of that of the control by the eighth day of the experiment, and by the end of the experiment the figure exceeded 90% (Figure

1). Lifespan of the moths was longer in the *low-ranked-host* treatment than in the control (mean longevity: 16.5 vs 14.0 days; the effect of treatment with total fecundity as a covariate: $F_{3,189}=4.44$, $p=0.0049$; Scheffe-adjusted pairwise comparison: $t=3.53$, $df=96$, $p=0.0070$), but was not significantly affected by the two host deprivation treatments.

Lifetime dynamics of egg quality. Hatching success over lifetime egg-complements was not affected by the treatments ($\chi^2=3.32$, $df=3$, $p=0.3$; Figure 2). Pairwise comparisons of single treatments with the control confirmed the lack of significant effect (in all cases $p>0.05$).

Hatching success of eggs decreased considerably with time progressing: eggs laid later were less probable to hatch (Table 1, Figure 2). Importantly, although egg rank and mother age were strongly correlated ($r=0.78$, $p<0.0001$), the independent role of mother age in causing the temporal decrease of hatching success was convincingly shown: the decrease could not be solely ascribed to the progressive rank number of eggs (Table 1).

Similarly to hatching success, size of the (hatched) eggs was not affected by treatment in the general analysis ($F_{3,150}=1.54$, $p=0.2$), although pairwise comparisons revealed marginally smaller eggs in the *low-ranked-host* treatment than in controls ($F_{1,78}=4.20$, $p=0.044$).

Egg size decreased throughout lifetime of the mother (Table 1, Figure 3). Again, mother age had a clear independent effect on this decrease (Table 1).

Short-term effects of oviposition delay. The four-day deprivation of host significantly reduced the hatching success of eggs laid immediately after the delay (mean: 0.78, vs 0.86 in controls; Table 2, Figure 2). The effects of the 0 2-day-delay and *low-ranked-host* treatments remained non-significant (Table 2, Figure 2).

DISCUSSION

Both hatching success and size of the eggs laid decreased with time progressing: eggs laid later were smaller and showed a considerably lower hatching success. Importantly, this effect was not only related to the progressive rank of the eggs laid, but also, independently, to the aging of the mother. A female's n -th egg is thus smaller and has a lower probability to hatch if more time has passed from the adult's eclosion. This implies that a delay in oviposition has, indeed, a potential to cause a lower quality of eggs laid. The critical assumption of the proposed scenario is thus met: decreasing egg-quality can act as a cost of host specificity, and may thus contribute to the evolution of lower specificity in insects.

In accordance, the egg-quality cost of host specificity was detected directly: the moths which were manipulated to delay oviposition for the longest time (four days on a nonhost) showed, as compared to controls, lower hatching success of eggs laid immediately after the deprivation period. However, lifetime

quality of eggs was not different between the treatments. It is possible that this difference was caused by the relatively rapid compensation of the fecundity lag caused by the oviposition delay: the average age of the mother at each oviposition event was only minutely altered between treatment groups. Even when restricted to a low-quality host until death, the moths were apparently “wise” enough to accept the host in time, and not to let a considerable egg-quality cost to be expressed, although a minor tendency towards smaller eggs in this treatment was detected.

Nevertheless, it is most likely that in a natural situation the moths would die younger than they did in the lab, primarily due to predation. Few days could often constitute a whole lifetime in nature. Therefore even a single few-days delay in oviposition could strongly affect average lifetime egg-quality, and should be avoided by lowering acceptance threshold and laying eggs on low-quality hosts when the high-quality ones are not available. Moreover, because, on average, 50% of the total fecundity was realized already by the 6th–8th day of the experiment (Fig.1), the found significant decrease of hatching success during four-day host deprivation actually affected half of the eggs laid during the whole experiment, even though the moths were allowed to die of senescence.

Temporal decrease of the quality of eggs laid can be caused by two mechanisms. First, it is possible that lower-quality (e.g. smaller: Fox & Czesak 2000) oocytes are matured at higher ages of the mother. For instance, in *Lobesia botrana* moths, delayed mating causes resorption of basal oocytes, and replacement of those by younger ones, which are smaller and have lower hatching success (Torres-Vila & Rodriguez-Molina 2002). As an alternative mechanism, it could be that mature eggs deteriorate in the abdomen if they are not laid “in time”, i.e. stay there too long. We suppose that in our experiment the latter mechanism was primarily responsible for the low hatching success of eggs laid immediately after the four-days host deprivation, because, on average, the amount of eggs laid within the six days roughly approximates the amount usually mature carried by females, and the species is apparently not able for oosorption (Tammaru & Javoiš 2000).

Acceptance of low-quality hosts, or even nonhosts, after some period of deprivation of high-quality substrates hosts has been shown in numerous insects (e.g. Rausher 1983, Singer et al. 1992, Courtney et al. 1989, Roberts & Schmidt 2004, Wang & Horng 2004). Usually, such behaviour has been explained by the risk of time limitation at laying enough eggs. The results of the current study show that the risk of decreased egg quality is another plausible evolutionary constraint on host specificity. It remains to be studied, how generally over different taxa and ecological groups of insects this constraint operates. Basing on the presented results, it can be hypothesized that deterioration of mature eggs in abdomens form a cost of specificity in species which usually carry a considerable load of mature eggs and are not able for oosorption, proovigenic insects in the first place.

ACKNOWLEDGEMENTS

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Table 1. The effects of mother age and other factors (see text for details) on hatching success (proportion of eggs hatched) and size of the hatched eggs, in a type 3 analysis. All the factors in the initial model are shown, however, the nonsignificant effects (NS) were sequentially omitted from the final model.

Effect	Hatching success			Egg size			
	DF	χ^2	P	Num DF	Den DF	F	P
treatment			NS				NS
total fecundity	1	48.1	<0.0001				NS
mother longevity	1	38.4	<0.0001	1	151	48.3	<0.000
egg rank	1	44.4	<0.0001				NS
mother age	1	44.5	<0.0001*	1	231	187.3	<0.0001*

* the effect remained highly significant (p<0.0001) in an alternative model, where also second and third grades of total fecundity, mother longevity and egg rank were included, and nonsignificant effects thereafter sequentially omitted.

Table 2. The effect of oviposition delay caused by different periods of host deprivation (2- and 4-day-delay treatments) or stay on a low-ranked host (low-ranked-host treatment) on hatching success of eggs laid immediately after the delay (see text for details), in a type 1 analysis. Fecundity during the analysed periods is taken as a covariate.

Effect	2-day-delay vs control				4-day-delay vs control				low-ranked-host vs control			
	Num DF	Den DF	F	P	Num DF	Den DF	F	P	Num DF	Den DF	F	P
treatment	1	83	1.5	0.2	1	88	7.3	0.0085	1	88	0.2	0.6
fecundity	1	83	15.3	0.0002	1	88	27.6	<0.0001	1	88	34.9	<0.0001

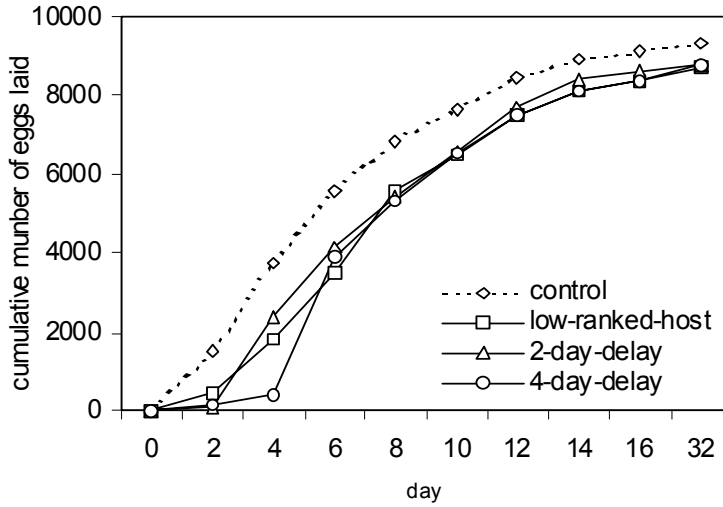


Figure 1. Cumulative oviposition schedules in different treatments. Each point is attained by summing up the eggs laid by all the moths in the respective treatment by the respective day of the experiment.

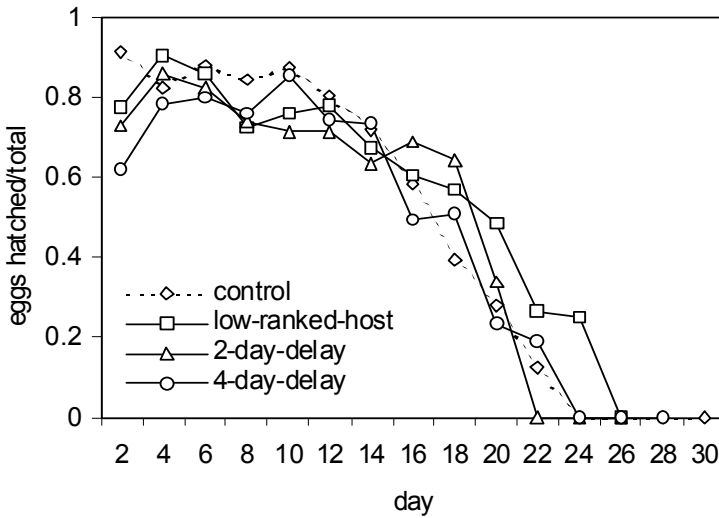


Figure 2. Mean hatching success of eggs (the proportion of hatched eggs), laid on progressive days of the experiment.

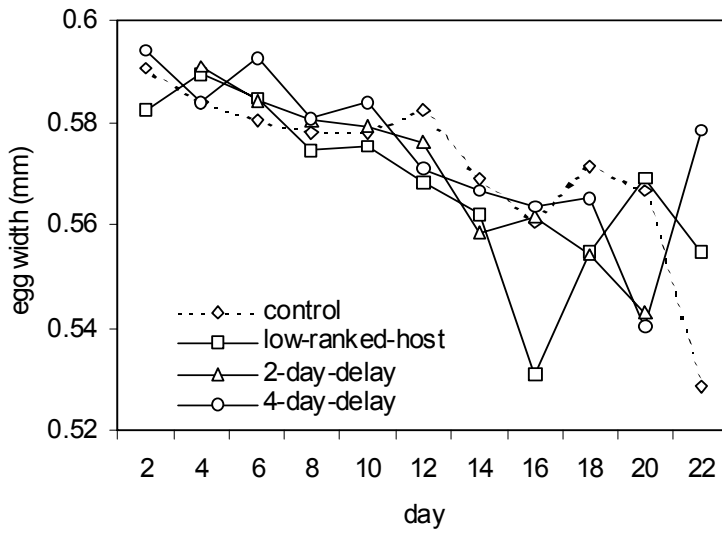


Figure 3. Mean size of the (hatched) eggs, laid on progressive days of the experiment.

CURRICULUM VITAE

I. General

- 1. Name:** Juhan Javoiš
2. Date and place of birth: 15.03.1975, Tartu
3. Citizenship: Estonian
4. Marital status: married
5. Address: Vikerkaare 10, Tartu;
phone: 7422880;
e-mail: juku@ut.ee
6. Position: Tartu University, Institute of Zoology and
Hydrobiology, *PhD* student
7. Educational history: Tartu 2. Secondary School: 1993
Tartu University, *baccalaureus scientiarum* in
zoology: 1998
Tartu University, *magister scientiarum* in animal
ecology: 2001
8. Languages spoken: Estonian, English
9. Working experience: since 2001: Tartu University, Institute of Zoology
and Hydrobiology, *PhD* student

II. Research history

- 1. Research interests:** ecology of reproduction in insects

2. Publications:

- Tammaru T Javoiš J 2000 Responses of ovipositing moths (Lepidoptera: Geometridae) to host plant deprivation: life-history aspects and implications for population dynamics. *Environmental Entomology* 29: 1002–1010
- Smits MJA, van Duinen GA, Bosman J, Brock AMT, Javoiš J, Kuper JT, Peeters TMJ, Peeters MAJ, Esselink H 2002 Species richness in a species poor system: aquatic macroinvertebrates of Nigula Raba, an intact raised bog system in Estonia. *Proceedings of the International Peat Symposium, Pärnu, Estonia* 3.–6. Sept. 2002
- Javoiš J, Tammaru T 2004 Reproductive decisions are sensitive to cues of life expectancy: the case of a moth. *Animal Behaviour* 68: 249–255
- Javoiš J, Tammaru T, Käär M 2005 Oviposition in an eruptive moth species, *Yponomeuta evonymellus*, is insensitive to the population density experienced during larval period. *Entomologia Experimentalis et Applicata* 115: 379–386

Tammaru T, Javoiš J 2005 When being alive implies being safe: variation in mortality rates can cause oviposition selectivity to increase with age. *Oikos*, in press.

3. Grants and scholarships:

Tartu University scholarship for doctoral students DBGZH 2329

CIMO scholarship, 2003

4. Conference theses:

“Oviposition selectivity in *Scotopteryx chenopodiata* L. (Lepidoptera: Geometridae): links to physiological state and population dynamics” (poster presentation), 11th International Symposium of Insect-Plant Relationships, Helsingør, 4.–10. Aug. 2001.

“Reproductive decisions are sensitive to cues of life expectancy: the case of a moth” (oral presentation, co-author T. Tammaru), 10th International Behavioral Ecology Congress, Jyväskylä, 10.–15. Aug. 2004.

III. Improvement of skills

Scientific research in Nijmegen Catholic University (the Netherlands): Sept.–Dec.2001.

NorFA course: “Individual-based population models: current use, future prospects, and limitations”. 24.–29.08.2002 Holbaek, Denmark.

Scientific research in Turku University (Finland): May – Jul. 2003.

CURRICULUM VITAE

I. Üldandmed

- 1. Ees- ja perekonnanimi:** Juhan Javoiš
2. Sünniaeg ja koht: 15.03.1975, Tartu
3. Kodakondsus: Eesti
4. Perekonnaseis: abielus
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e-mail: juku@ut.ee
6. Praegune töökoht, amet: Tartu Ülikool, Zooloogia ja Hüdrobioloogia Instituut, doktorant
7. Haridus: Tartu 2. Keskkool: 1993
Tartu Ülikool, *baccalaureus scientiarum* zooloogia erialal: 1998
Tartu Ülikool, *magister scientiarum* loomaökoloogia erialal: 2001
8. Keelteoskus: eesti, inglise
9. Töökogemus: alates 2001: Tartu Ülikool, Zooloogia ja Hüdrobioloogia Instituut, doktorant

II. Teaduslik ja arendustegevus

1. Peamised uurimisvaldkonnad: putukate sigimisökoloogia

2. Publikatsioonide loetelu:

- Tammaru T Javoiš J 2000 Responses of ovipositing moths (Lepidoptera: Geometridae) to host plant deprivation: life-history aspects and implications for population dynamics. *Environmental Entomology* 29: 1002–1010
- Smits MJA, van Duinen GA, Bosman J, Brock AMT, Javoiš J, Kuper JT, Peeters TMJ, Peeters MAJ, Esselink H 2002 Species richness in a species poor system: aquatic macroinvertebrates of Nigula Raba, an intact raised bog system in Estonia. *Proceedings of the International Peat Symposium, Pärnu, Estonia* 3.–6. Sept. 2002
- Javoiš J, Tammaru T 2004 Reproductive decisions are sensitive to cues of life expectancy: the case of a moth. *Animal Behaviour* 68: 249–255
- Javoiš J, Tammaru T, Käär M 2005 Oviposition in an eruptive moth species, *Yponomeuta evonymellus*, is insensitive to the population density experienced during larval period. *Entomologia Experimentalis et Applicata* 115: 379–386

Tammaru T, Javoiš J 2005 When being alive implies being safe: variation in mortality rates can cause oviposition selectivity to increase with age. *Oikos*, in press.

3. Saadud uurimistoetused ja stipendiumid:

Tartu Ülikooli doktorandi teadustöö stipendium DBGZH 2329

CIMO stipendium: 2003

4. Konverentside ettekanded:

“Oviposition selectivity in *Scotopteryx chenopodiata* L. (Lepidoptera: Geometridae): links to physiological state and population dynamics” (stend-ettkanne), 11th International Symposium of Insect-Plant Relationships, Helsingør, 4.–10. Aug. 2001.

“Reproductive decisions are sensitive to cues of life expectancy: the case of a moth” (suuline ettkanne, kaasautor T. Tammaru), 10th International Behavioral Ecology Congress, Jyväskylä, 10.–15. Aug. 2004.

III. Erialane enesetäiendus

Teadustöö Nijmegeni Katolikus Ülikoolis, Hollandis: 09.–12.2001.

NorFA kursus: “Individual-based population models: current use, future prospects, and limitations”. 24.–29.08.2002 Holbaek'is, Taanis.

Teadustöö Turu Ülikoolis, Soomes: 05.–07.2003.