

Integrating optimal foraging and optimal oviposition theory in plant–insect research

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The current approach for studying host selection by phytophagous insects is mainly based on optimal oviposition theory, i.e. the preference–performance hypothesis. Almost no attention has been given to optimal foraging theory. However, recent papers and additional evidence given in this work illustrate that also optimal foraging may shape host preference patterns of phytophagous insects. Therefore and because optimal foraging and optimal oviposition may oppose conflicting needs to phytophagous insects, we plea for an integration of optimal foraging and optimal oviposition in plant–insect research. We argue how this may improve our understanding of plant–insect interactions.

Optimal oviposition theory, i.e. the preference–performance hypothesis, has been central in the approach for studying host selection by phytophagous insects for most of the history of plant–insect research. The preference–performance hypothesis (Jaenike 1978) predicts that oviposition preference should correlate with host suitability for offspring development (= survival offspring and later adult potential fecundity) because females are assumed to maximise their fitness by ovipositing on high quality hosts. Although some studies reported strong, positive correlations between host preference and offspring performance, many studies found poor correlations (reviewed by Mayhew 1997). Despite a recently broadened approach in which more attention is devoted to the effect of top-down forces (e.g. Bernays and Graham 1988, Dyer 1995, Berdegué et al. 1996, Björkman et al. 1997, Camara 1997, Gratton and Welter 1999, Stamp 2001), physiological state of the animal (Minkenbergh et al. 1992), information processing (Bernays 2001), and learning processes (Dukas and Bernays 2000, Egas and Sabelis 2001) on oviposition preference, still many studies keep reporting large amounts of unexplained variation in host choice

(e.g. Berdegué et al. 1998, Price et al. 1999, Pires et al. 2000, Cronin and Abrahamson 2001). This observation leaves two alternatives, i.e. either optimality theory is not applicable on host selection or the approach is wrong (see also Mayhew 2001).

Optimal foraging has the potential to influence host plant choice because many phytophagous insects do not only use plants for larval feeding but also as adult resources (Stephens and Krebs 1986). This theory predicts that phytophagous adults should prefer to feed on those hosts that give the highest adult performance (=realised fecundity) (Stephens and Krebs 1986). The quality of the host for adult performance is hereby determined by bottom-up forces (i.e. food quality and competition) and top-down forces (i.e. parasites, predators, and diseases) (Stephens and Krebs 1986). Intriguingly, optimal foraging has been rarely addressed in plant–insect research despite the wealth of literature on this topic in other, sometimes closely related (host–parasitoid), fields (Stephens and Krebs 1986). That optimal foraging may indeed be important in shaping host preference patterns of phytophagous insects was illustrated recently by Scheirs et al. (2000). They showed that females of the grass miner *Chromatomyia nigra* (Meigen) (Diptera: Agromyzidae) oviposit where they feed, and that they feed on the hosts which best enhance adult, not offspring, performance. Results from a second study confirm this for a related species (Scheirs 2000).

We searched the ISI database “Science Citation Index Expanded” which covers all main ecological journals from 1973 on, for studies that investigated the optimal foraging and optimal oviposition hypothesis or studies that contain the necessary data to test both hypotheses. A study on the omnivorous bug *Orius*

Table 1. Mean preference and performance of *Altica carduorum* (data from Wan et al. 1996).

Host plant	Host preference		Adult perfor- mance	Offspring performance	
	Feeding (no. feeding holes)	Oviposition (no. eggs)	Realised fecundity	Survival (%)	Development time (d)
<i>C. arvensis</i>	255.0	2.50	70.1	62	24.2
<i>C. flodmanii</i>	3.3	0.00	5.1	27	26.8
<i>C. fontinale</i>	3.0	0.07	1.5	48	25.3
<i>C. japonicum</i>	50.9	0.00	4.8	59	25.8
<i>C. occidentale</i>	8.9	0.00	4.6	55	25.6
<i>C. scariosum</i>	8.3	0.60	19.8	52	25.5
<i>C. undulatum</i>	10.2	0.00	1.8	47	27.1
<i>S. marianum</i>	2.0	0.00	2.4	36	26.7

insidiosus (Say) (Heteroptera: Anthocoridae) (Coll 1996) is besides Scheirs et al. (2000) and Scheirs (2000) probably the only other work available that has explicitly tested whether optimal foraging shapes host preference patterns. Coll (1996) found no proof for the latter hypothesis, nor for the hypothesis that optimal oviposition shapes host preference. We found only one study, i.e. Wan et al. (1996) on the thistle-feeding beetle *Altica carduorum* Guer. (Coleoptera: Chrysomelidae), that contained the necessary data (i.e. feeding preference, oviposition preference, and host specific variation in adult and offspring performance) in order to test both hypotheses. From the data of the latter study (Table 1), we calculated the correlation between host preference of this beetle and its adult and offspring performance characteristics on the different host plants (Table 2). This analysis shows that the correlations between host preference (feeding and oviposition preference) and adult performance (realised fecundity) were nearly perfect, while those between host preference and the offspring performance measures (survival and development time) were always weaker. The latter observation strongly suggest that *A. carduorum* feeds and oviposits on the hosts that best enhance adult performance, not offspring performance.

Optimal foraging and optimal oviposition can most probably not be seen as independent processes. Ideally, females should try to maximise their fitness by optimising adult and offspring performance (Krebs and Davies 1997). However, optimal adult and offspring resources may be separated in space or time (e.g. Panizzi et al. 1996, Miller and Ware 2001), and search time constraints may then prevent the optimisation of both strategies causing a parent-offspring conflict (Nylin et al. 1996, Krebs and Davies 1997). The best indication for the existence of such a conflict is the observation that oviposition site selection of a number of insects is influenced by the proximity of adult resources. The latter was observed in several taxonomically distinct insect groups ranging from butterflies (Murphy et al. 1984, Grossmueller and Lederhouse 1987), over Coleoptera (Johnson and Siemens 1991), to Diptera

(Vacek et al. 1985, Averill and Prokopy 1993, Prokopy et al. 1996), which suggests that a parent-offspring conflict among phytophagous insects is potentially widespread.

A conflict of interest among different life stages has already been postulated as an explanation for the many poor correlations between oviposition preference and offspring performance by several researchers (Reavey and Lawton 1991, Nylin and Janz 1996, Mayhew 1997). Now that evidence is available (Scheirs 2000, Scheirs et al. 2000, this study), we urge for an integration of optimal foraging and optimal oviposition in plant-insect research. We do not want to polarise the discussion in favour of optimal foraging because it is beyond doubt that optimal oviposition shapes host preference patterns also (e.g. Price 1994). The successful integration of optimal foraging and optimal oviposition in host-parasitoid research illustrates that such an approach may work (Takasu and Lewis 1993, Weisser et al. 1994, Sirot and Bernstein 1996, Lewis et al. 1998).

It may be misleading that we have only presented examples relating foraging and oviposition patterns to host food quality because many other selection pressures and processes may determine host choice (Thompson 1988, Mayhew 2001). We want to stress that optimality theory considers all selection pressures and processes that shape behavioural processes (Stephens and Krebs 1986, Parker and Maynard Smith 1990). Despite the fact that the latter definition is

Table 2. Correlation matrix between host preference and performance of *Altica carduorum*.

Preference	Performance	<i>r</i>	<i>P</i>
Feeding	Adult realised fecundity	0.951	0.0003
	Offspring survival	0.562	0.1470
	Offspring development time	-0.721	0.0435
Oviposition	Adult realised fecundity	0.996	0.0001
	Offspring survival	0.508	0.1983
	Offspring development time	-0.761	0.0284

generally accepted and used in various fields (e.g. Stephens and Krebs 1986, Parker and Maynard Smith 1990, Weisser et al. 1994), plant–insect researchers frequently have a more restricted view on what is meant by optimal foraging and oviposition theory. We treat the concept of optimal foraging and optimal oviposition in its broadest sense throughout this paper as we believe that optimal behaviour can only be understood if all selection pressures and processes influencing this behaviour like bottom-up forces, top-down forces, temporal and spatial distribution of resources, physiological state of the animal, etc, are considered.

Integrating optimal foraging and optimal oviposition may improve our understanding of plant–insect interactions in several ways. First, we may be able to show that host selection of phytophagous insects is truly adaptive. Optimality theory assumes that an animal will try to maximise its lifetime fitness (Parker and Maynard Smith 1990). For this, all fitness parameters contributing to lifetime fitness, or at least those that show variation among hosts, should be investigated in order to test whether host choice is adaptive. The reductionist approach which considers only a subset of fitness parameters related to offspring performance is therefore not correct. The important thing we did learn from the latter approach is that many phytophagous insects seem to be poor mothers. We firmly believe that a trade-off between optimal foraging and optimal oviposition most likely explains this bad motherhood of many species.

Second, we may get a better understanding of the selection pressures that drive the evolution of host choice. Chemically mediated host plant suitability for offspring development has been considered as the major selective force in the evolution of the diet of plant-feeding insects for most of the history of plant–insect research, until several researchers began to doubt this predominant position during the last decade (see paper of Bernays and Graham 1988 and resulting discussion in a special issue of *Ecology* 69[4] which was devoted to this topic, Thompson 1988, Courtney and Kibota 1990, Mayhew 1997, Dicke 2000, Stamp 2001, Walker and Jones 2001). Some of the latter researchers concluded from the frequently observed poor correlations between chemically mediated host plant suitability for offspring development and actual host use that additional ecological selection pressures like predation, parasitism, and diseases also drive the evolution of host choice and should receive more attention. Recent studies confirm that top-down forces are important determinants of host choice (see Berdegué et al. 1996, Dicke 2000). Nevertheless, the argument used to question the predominant position of host chemistry is not genuine as host chemistry may also influence adult performance.

Third, the reductionist “optimal oviposition” approach has also resulted in a reductionist view of ecological geneticists on host choice. For instance, a popular hypothesis to explain the high degree of host

specialisation among phytophagous insects and mites is the existence of host associated fitness trade-offs caused by antagonistic pleiotropy (Via 1990). Evidence for this hypothesis is ambiguous which may be explained by the fact that 31% of the studies on this topic focus on host specific variation in offspring performance only (Scheirs and De Bruyn unpubl.). Furthermore, divergent evolution in host choice can also be facilitated when host plant preference and herbivore performance are genetically correlated due to antagonistic pleiotropy or linkage disequilibrium (Via 1990). Evidence for the latter hypothesis is however scarce, perhaps because host specific variation in adult performance is not always considered (e.g. Jaenike 1989, Fox 1993, Gu et al. 2001).

Finally, a better understanding of the mechanisms that underlie host plant choice, the selection pressures that drive host plant choice, and its genetic basis will automatically result in a better understanding of the evolution of host plant choice. A popular and elegant approach to study the (co-)evolution of plant–insect systems is to reconstruct the evolutionary history of a group of phytophagous insects and to compare it with the phylogeny of potential host plants, and the distribution of certain plant traits like secondary chemistry or plant growth form (e.g. Futuyma and McCafferty 1990, Funk et al. 1995, Dobler et al. 1996, Janz and Nylin 1998, Wahlberg 2001). Many studies using this approach assume that host range evolution is determined by host plant quality for offspring performance. We believe that also in this type of analysis it may bear fruit to consider optimal foraging as a genuine mechanism driving the evolution of host choice.

The fact that optimal foraging may influence host preference patterns of phytophagous insects could have consequences for sub-disciplines in plant–insect research that do not focus on host selection in se. For instance, the basis for studying habitat selection by phytophagous insects is also formed by optimal oviposition theory. Rausher (1979) hypothesised that phytophagous insects will select those habitats for oviposition in which their larvae perform best. Since Rausher proposed his hypothesis, many researchers studying habitat preference of phytophagous insects followed the same approach (e.g. Valladares and Lawton 1991, Kopper et al. 2000, Sipura and Tahvanainen 2000). Yet, Whitham (1978, 1980) showed clearly that it is relevant to consider also adult performance in this context. Last but not least, applied fields dealing with the development of plant resistance traits to phytophagous insects or biological control may develop more efficient control measures if they also focus on reducing adult performance (see also Lewis et al. 1998).

The need for a more general, unified theory to understand complex behavioural processes as argued in this paper was already recognised by a number of authors in different contexts (Pianka 1976, Mangel and Clark

1986). Mangel and Clark (1986) have presented a method called ‘‘Unified theory of animal behaviour’’ that applies optimality thinking to complex situations like foraging problems. Extending their model for phytophagous insects facing the problem of choosing a host optimal for adult or offspring performance may present a unique opportunity to actually integrate optimal foraging and optimal oviposition theory in plant–insect research.

In conclusion, we recommend the integration of optimal foraging and optimal oviposition in plant–insect research as a new tool to help disentangle the complex interactions between plant and insects. We hope this paper will stimulate plant–insect researchers to routinely carry out measurements of host-specific variation in both adult and offspring performance in order to reveal under which conditions that host preference patterns are shaped by optimal foraging and/or oviposition. For instance, host choice of synovigenic insects is more likely to be determined by optimal foraging than in protoovigenic insects or insects that do not feed during the adult stage. The same may hold for insects that can not predict future plant quality for offspring development or species that do not oviposit on plants like many Orthoptera and Phasmida (Price 1994). On the other hand, optimal oviposition is more likely to determine host preference in insects of which larval development depends on plant growth processes like in gallers (see Price 1994), or in insects with sedentary larval stages (Thompson 1988, but see Scheirs 2000, Scheirs et al. 2000). Also plant traits may be important in determining the magnitude of the parent–offspring conflict. For instance, the parent–offspring conflict may be greater on plants with inducible defences compared to plants with constitutive defences as adult feeding may affect the quality of the larval food resource in the first group. An approach that may be fruitful while it is thought provoking and may serve as an ideal basis for experimental work, is to model the parent–offspring conflict under varying conditions. Host–parasitoid models (e.g. Weisser et al. 1994, Sirot and Bernstein 1996) can hereby serve as an example as they can easily be extrapolated to plant–insect systems.

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