

SHORT COMMUNICATION

Optimal foraging shapes host preference of a polyphagous leafminer

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Abstract. 1. Most research on host selection by arthropods is based on optimal oviposition theory. This theory, also called the oviposition preference–offspring performance hypothesis, predicts that a female will choose those hosts for oviposition on which larvae perform best. Recent studies suggested, however, that optimal foraging by adults, or the quality of the host for adult performance, might also influence host choice.

2. This study investigated whether host preference of the polyphagous leafminer *Liriomyza trifolii* is determined by optimal foraging and/or optimal oviposition.

3. Female realised fecundity correlated nearly perfectly with feeding and oviposition preference of *L. trifolii*. The relationships between host preference and the offspring performance measures were always weaker. Hosts optimal for adult nutrition were also optimal for offspring performance but not *vice versa*. Hence, it was concluded that optimal foraging shapes feeding and oviposition preference of *L. trifolii* as this is the best strategy in order to maximise female fitness.

Key words. Feeding preference, host choice, *Liriomyza*, optimality theory, oviposition preference–offspring performance, plant–animal interactions, realised fecundity.

Introduction

Much of the theoretical and empirical research on host choice by arthropods is based on optimal oviposition theory (Scheirs *et al.*, 2000; Mayhew, 2001; Scheirs & De Bruyn, 2002). This theory, also called the oviposition preference–offspring performance hypothesis, predicts that a female will choose those hosts for oviposition on which larvae perform best, as this will maximise her own fitness (Jaenike, 1978). Ever since Jaenike proposed his hypothesis, the literature has been dominated by studies that look at larval performance traits only (offspring survival, development time, and size or mass) in order to explain host preference patterns of phytophagous (reviewed by Mayhew, 1997), mycophagous (e.g. Pawlitz & Bultman, 2000), saprophagous (e.g. Ruiz & Heed, 1988; Kibota & Courtney, 1991; Krebs

et al., 1992), algivorous (e.g. Poore & Steinberg, 1999), and predatory arthropods (e.g. Tauber & Tauber, 1987; Sadeghi & Gilbert, 1999). However, many insects have been shown to make poor oviposition choices (Thompson, 1988; Courtney & Kibota, 1989; Price, 1994; Mayhew, 1997). Therefore, host choice seems, at least in some instances, to make little adaptive sense or optimal oviposition theory may be inadequate for predicting host choice (Mayhew, 2001).

Jaenike (1986) was the first to realise that optimal foraging may determine host choice, as female insects can maximise fitness through the optimisation of adult performance (realised fecundity). He hypothesised that females may select those hosts that are optimal for adult nutrition instead of those that are optimal for their offspring. Yet, this paper received almost no attention compared to his optimal oviposition paper. Only recently have host–parasitoid and plant–insect researchers started to pay more attention to the role of optimal foraging in host choice (Weisser *et al.*, 1994; Jervis & Kidd, 1995; Sirot & Bernstein, 1996; Lewis *et al.*, 1998; Scheirs *et al.*, 2000; Scheirs & De Bruyn, 2002). Scheirs *et al.* (2000) and Scheirs and De Bruyn (2002) provided the first evidence that optimal foraging might be more important than optimal oviposition in shaping host choice by phytophagous

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insects. They showed that the grass miner, *Chromatomyia nigra* (Meigen) (Diptera: Agromyzidae) (Scheirs *et al.*, 2000), and the thistle-feeding beetle, *Altica carduorum* Guer. (Coleoptera: Chrysomelidae) (Scheirs & De Bruyn, 2002), oviposit where they feed, and they feed on the hosts that best enhance adult rather than offspring performance. Some herbivorous insects seem therefore to be bad mothers (Mayhew, 2001).

Despite the vast amount of literature on host choice, there still exists little evidence for a role of optimal foraging in host selection. This is mainly due to the fact that very few studies measure adult performance (see also Awmack & Leather, 2002). Zoebisch and Schuster (1987) studied oviposition preference and larval development (offspring performance) of the polyphagous leafminer, *Liriomyza trifolii* (Burgess) (Diptera: Agromyzidae), on four host plant species. Fortunately, adult performance and adult feeding preference also were assessed, which provides the opportunity to test the optimal foraging and optimal oviposition hypothesis with *L. trifolii*.

Liriomyza trifolii is a polyphagous, leafmining species with an exceptionally wide host range. It is an important pest of vegetables and ornamental plants (Spencer, 1973). Females feed on leaf saps exuding from feeding punctures made with their ovipositor in the leaves of the host. They also use their ovipositor to lay eggs under the epidermis of leaves. The larvae mine plant foliage (Spencer, 1973; Parrella, 1987). Thus, *L. trifolii* is a good candidate for comparing optimal oviposition and optimal foraging theories.

Materials and methods

Zoebisch and Schuster (1987) studied host preference of *L. trifolii* among tomatoes (*Lycopersicon esculentum* Mill. cv. Walter), American black nightshade (*Solanum americanum* Mill.), common beggar-tick (*Bidens alba* (L.) DC.), and downy groundcherry (*Physalis pubescens* L.). Flies from a field-grown tomatoes population were used to initiate laboratory colonies on tomatoes, common beggar-tick, and nightshade. These flies were used in the experiments after the colonies had been maintained in the laboratory for at least five generations. Only data from the tomatoes colony was used in the analysis as host-specific performance of the beggar-tick and the nightshade-reared flies was not available for all hosts (only tomatoes). Host preference of *L. trifolii* was determined by four-way choice experiments. Excised plant leaves of every plant species were offered simultaneously during a choice trial to five pairs of newly emerged adults. The petioles of the excised plant leaves were placed in a plastic cup with water in order to prevent desiccation. The choice trials lasted 24 h. Twelve trials were carried out. Host preference was established by counting the number of feeding punctures and eggs as measures of adult feeding and oviposition preference respectively. Preference was expressed as the number of feeding punctures and eggs per leaf surface (cm²) in order to correct for differences in leaf size among plant species.

Adult performance (adult fecundity and longevity) was determined by placing one pair of newly emerged *L. trifolii*

of the tomatoes colony in a clip cage. One leaf was inserted in the clip cage. The leaf was replaced two times a day by a leaf of the same plant species until the female died. Males were replaced as they died. Female longevity (days) and fecundity (number of eggs laid) were recorded as measures of adult performance. Twenty females were tested per plant species.

Offspring performance (larval development time, pupal development time, pupal mass, and larval survival) was determined by offering two leaves of the same plant species in a clip cage to two pairs of newly emerged *L. trifolii* adults. After 24 h, the flies were removed. To prevent overcrowding, the first three larvae per leaflet were allowed to survive, and the rest were killed with an insect pin. Larvae were observed daily. Leaflets were excised before the larvae vacated their mines. These leaflets were put into small transparent plastic cups to obtain pupae. Pupae were weighed to the nearest 0.01 mg 2 or 3 days after pupation and were placed in rearing cups until adults emerged. Fifty-five, fifty, forty-six, and thirty-seven larvae were reared on tomatoes, nightshade, common beggar-tick, and downy groundcherry, respectively. For more details regarding the design of these experiments, refer to Zoebisch and Schuster (1987).

The relation between preference and performance was studied using Pearson's correlation analyses (Statsoft, 1994). Mean preference and mean performance on the different hosts were correlated, which resulted in three degrees of freedom for every correlation.

Results and discussion

Zoebisch and Schuster (1987) showed that *L. trifolii* females of the tomatoes colony clearly preferred tomatoes and American nightshade for feeding and oviposition (Table 1). Fecundity was also clearly higher on these plants. Adult longevity was lower on downy groundcherry compared to the other three hosts. Larval development was shorter on tomatoes and American nightshade compared to common beggar-tick and downy groundcherry. Pupal development time did not differ among the hosts. Pupal mass was higher on common beggar-tick than on the other three hosts. Larval survival did not differ significantly among tomatoes, American nightshade and common beggar-tick, but was lower on downy groundcherry.

Host preference (feeding and oviposition) was nearly perfectly and significantly correlated with female realised fecundity (Table 2). Adult longevity did not correlate as well to host preference and the relationship was not significant. The correlations between host preference and the offspring performance measures (survival, larval, and pupal development time) were always weaker than the host preference–realised fecundity relationship. Feeding and oviposition preference were also strongly correlated ($r = 0.99$, $P = 0.010$).

It is clear from the analyses that optimal foraging shapes host preference of *L. trifolii*. The perfect correlation between feeding preference and realised fecundity and

Table 1. Mean preference and performance of *Liriomyza trifolii*. Means in the columns followed by the same letter do not differ significantly by Duncan's multiple range test (from Zoebisch & Schuster, 1987).

Host plant	Host preference		Adult performance		Offspring performance			
	Feeding (punctures/cm ²)	Oviposition (eggs/cm ²)	Fecundity (eggs/female)	Longevity (days)	Larval time (days)	Pupal time (days)	Pupal mass (mg)	Survival (%)
Tomatoes	15.6a	1.0a	34.6a	4.3a	4.6a	8.8a	0.28b	80.0a
American nightshade	14.3a	0.8a	31.8a	3.8a	4.1a	8.9a	0.33b	80.7a
Common beggar-tick	5.2b	0.2b	14.1b	3.9a	5.4b	9.5a	0.40a	83.8a
Downy groundcherry	2.2b	0.1b	9.1b	2.9b	5.6b	8.6a	0.28b	41.8b

the weaker correlations between host preference and the offspring performance measures indicate that females maximise their fitness by selecting high quality hosts for feeding in order to optimise the number of eggs laid. The high correlation between feeding and oviposition preference shows that eggs are laid at the feeding site. This is in line with previous work (Scheirs *et al.*, 2000; Scheirs & De Bruyn, 2002). Hosts optimal for adult performance of *L. trifolii* like tomatoes and American nightshade are also good for offspring performance, which indicates that there exists no large trade-off between host suitability for adult and offspring performance. However, hosts good for offspring performance are not always good for adult performance. Offspring performance is excellent on common beggar-tick as indicated by the high pupal mass and larval survival, while adult fecundity is considerably lower on this host compared to tomatoes and American nightshade. Hence, optimal foraging is the best strategy for females of *L. trifolii* to maximise fitness.

Several fitness parameters of *L. trifolii* did not co-vary among hosts, which is probably due to the fact that fitness components are at least partially under separate genetic control (Thompson *et al.*, 1990; Thompson, 1996) and environmental influence (Scheirs *et al.*, 2003). As a consequence, there exists no single unequivocal fitness parameter. All fitness components of phytophagous insects should therefore be considered when testing hypotheses related to optimality theory.

Table 2. Correlation matrix between host preference and performance of *Liriomyza trifolii*.

Preference	Performance	<i>r</i>	<i>P</i>
Feeding	Adult fecundity	1.000	< 0.001
	Adult longevity	0.777	= 0.223
	Larval development time	-0.928	= 0.072
	Pupal development time	-0.125	= 0.875
	Pupal mass	-0.218	= 0.782
	Offspring survival	0.656	= 0.344
Oviposition	Adult fecundity	0.993	= 0.007
	Adult longevity	0.749	= 0.251
	Larval development time	-0.889	= 0.114
	Pupal development time	-0.224	= 0.776
	Pupal mass	-0.335	= 0.665
	Offspring survival	0.575	= 0.425

It is important to know the history of the flies that are used in host preference experiments as local adaptation (Hawthorne, 1999) and experience (e.g. Dukas & Bernays, 2000; Egas & Sabelis, 2001) have been shown to influence host selection of phytophagous insects. Zoebisch and Schuster (1987) collected flies from field-grown tomatoes in order to initiate laboratory colonies on tomatoes, common beggar-tick, and nightshade. Experiments were performed when the laboratory colonies had been maintained for at least five generations on the different plant species. Only data from the tomatoes colony was used in the analysis as host-specific performance of the beggar-tick and the nightshade-reared flies was not available for all hosts (only tomatoes). Host preference of the beggar-tick and the nightshade colonies was, however, determined by Zoebisch and Schuster (1987). Oviposition preference of the beggar-tick-reared *L. trifolii* was significantly higher on tomatoes and nightshade than on the other plants. However, feeding preference of the beggar-tick line was higher for common beggar-tick and nightshade. Furthermore, nightshade-reared *L. trifolii* oviposited significantly more on nightshade than on the other plants. Stippling of flies from the nightshade colony was higher on nightshade and common beggar-tick. These observations suggested that host preference differed among colonies and that preference was relatively higher for the plant on which the colony had been maintained. Unfortunately, the preference-adult performance and the preference-offspring performance relationships for the beggar-tick and the nightshade colonies could not be investigated here as performance of these flies was not measured on all four hosts (Zoebisch & Schuster, 1987). Little can therefore be concluded about the adaptive nature of the host selection behaviour of the flies from the beggar-tick and nightshade colonies. Two possible hypotheses may explain the differences in preference among the colonies. First, *L. trifolii* adapts quickly to a new host. Hawthorne (1999) has shown that larval survivorship increases linearly over 10 generations of *L. trifolii* on a novel host. The relatively higher preference of the flies for the colony host plant may therefore be the result of an increase in performance on the colony host plant. The flies from the tomatoes colony were probably already adapted for living on tomatoes before the start of the experiment, as the colonies were initiated from flies from field-grown tomatoes. This long period of adaptation may provide an

explanation for the high preference for and performance on tomatoes, and the tight link between host preference and performance that was observed for the tomatoes-reared flies. Second, experience or learning may affect host choice of phytophagous insects (e.g. Papaj & Prokopy, 1989; Szentesi & Jermy, 1990; Dukas & Bernays, 2000; Egas & Sabelis, 2001). Insects that have been in contact with a particular host may show a biased preference towards that host (e.g. Papaj & Prokopy, 1989; Szentesi & Jermy, 1990). The relative higher preference for the colony hosts may therefore be the result of the past experience of the flies. Future studies should investigate whether herbivores from the same population but with a different experience still behave according to the predictions of the optimal foraging hypothesis. Finally, it must be stressed that host-specific performance is not only determined by bottom-up forces like plant quality, but also by top-down forces (Bernays & Graham, 1988; Thompson, 1988; Sih, 1993). Future studies should therefore investigate whether selection pressures that were absent in the experimental set-up of Zoebisch and Schuster (1987), such as natural enemies, have additional influences on host preference of *L. trifolii*.

In conclusion, this study adds to the growing belief that host-specific variation in adult performance has an important role in shaping host preference of phytophagous insects. Studies on host choice, therefore, must consider both host-specific variation in adult and offspring performance instead of focussing only on offspring performance. Evidence in favour of the optimal foraging hypothesis now comes mainly from holometabolous species like flies and beetles. Future studies should investigate whether this hypothesis also holds in other groups like hemimetabolous insects or species like parasitoids, and mycophagous or saprophagous arthropods that exploit resources other than plants.

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