

Optimization of adult performance determines host choice in a grass miner

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Models and empirical studies on host selection in plant–insect, algae–amphipod, host–parasite and prey–predator systems assume that oviposition preference is determined by the quality of the oviposition site for offspring development. According to the oviposition-preference–offspring-performance hypothesis, oviposition-preference hierarchy should correspond to host suitability for offspring development because females maximize their fitness by optimizing offspring performance. We show, we believe for the first time, that adult feeding site and related adult performance may explain most of the variation in adult feeding and oviposition site selection of an oligophagous grass miner, *Chromatomyia nigra* (Diptera). This study advances our understanding of the complex interactions between plants and herbivores because it shows that host-preference patterns are not only shaped by the optimization of offspring performance, as previously assumed, but also by the optimization of adult performance.

Keywords: plant–insect interactions; oviposition-preference–offspring-performance hypothesis; host plant selection; optimization of adult performance; optimization of offspring performance

1. INTRODUCTION

Oviposition site selection in plant–insect (e.g. Jaenike 1978; Ng 1988; Thompson 1988; Courtney & Kibota 1989; Thompson *et al.* 1990; Fox 1993; Price 1994; Mayhew 1997; Rank *et al.* 1998), algae–amphipod (Poore & Steinberg 1999), host–parasite (Vinson & Iwantsch 1980; Godfray 1994) and prey–predator (Tauber & Tauber 1987; Sadeghi & Gilbert 1999) systems is assumed, both in ecological and evolutionary time, to be determined by the quality of the oviposition site for offspring development. According to the oviposition-preference–offspring-performance hypothesis, which was originally formulated in plant–insect research (Jaenike 1978) and recently also applied in other fields (Tauber & Tauber 1987; Poore & Steinberg 1999; Sadeghi & Gilbert 1999), oviposition-preference patterns of insects are supposed to correspond to host suitability for offspring development because females are assumed to maximize their fitness by ovipositing on high-quality hosts. However, evidence for a positive correlation between oviposition preference and offspring performance ranges from excellent to poor, at least in phytophagous insects (Thompson 1988; Courtney & Kibota 1989; Price 1994; Mayhew 1997). The surprisingly large number of poor correlations (reviewed by Mayhew (1997)) has led to the formulation of several alternative hypotheses considering various ecological and behavioural selection pressures on host selection (Thompson 1988). Nevertheless, a strong oviposition-preference–offspring-performance relationship is still the basic assumption of most models describing the evolution of host plant choice (Mayhew 1997).

Most empirical studies and optimality models on the evolution of host plant range and preference hierarchy are based on offspring-performance characteristics only (e.g. Ng 1988; Thompson 1988; Courtney & Kibota 1989; Price 1994; Mayhew 1997; Poore & Steinberg 1999). However, female fitness is not only a function of the

survival and fecundity of her offspring (offspring performance), but is also determined by the number of eggs she lays (adult performance) (Reavey & Lawton 1991; Nylin & Janz 1996; Krebs & Davies 1997). Variation in the quality of adult food resources has, for instance, been shown to cause considerable variation in adult performance of phytophagous insects (Murphy *et al.* 1983; Zoenisch & Schuster 1987; Minkenberg & Ottenheim 1990; Janz *et al.* 1994; Leather 1994; Coll 1996; Nagata *et al.* 1998). Female fitness may therefore not only be maximized by ovipositing on high-quality hosts but also by feeding on high-quality hosts. Yet, optimal adult and optimal offspring resources are often separated in space and/or time, and search-time constraints will prevent the optimization of both strategies causing trade-offs between the two life stages (Nylin & Janz 1996; Krebs & Davies 1997). Several studies have already postulated that the optimization of female performance may influence oviposition-preference hierarchy (Nylin & Janz 1996; Price *et al.* 1999) but evidence is lacking at the moment.

Here we report upon the preference–performance relationship in an oligophagous grass miner, *Chromatomyia nigra* (Meigen 1830) (Diptera: Agromyzidae). Both adults and larvae of *C. nigra* are phytophagous and feed on the same hosts. We addressed the following questions in this study: first, does *C. nigra* exhibit a feeding-and/or an oviposition-preference hierarchy among grasses? Second, are there differences in offspring and/or adult performance among the different grasses? Third, does the optimization of adult and/or offspring performance shape the preference hierarchies of *C. nigra*?

2. MATERIAL AND METHODS

(a) *Life history*

C. nigra is an oligophagous leaf miner that is common throughout Europe. It is recorded from most C₃ grass genera (Griffiths 1980; Scheirs *et al.* 2001). Females insert their eggs directly into the mesophyll layer between two veins of a grass

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leaf. Larvae emerge within one week and immediately eat their way through the internal leaf tissues. Larvae pupate within their mines and adults emerge through the leaf surface. Females feed on leaf saps exuding from feeding punctures made by their ovipositor in the leaf blade of host grasses. Potential additional food resources of Agromyzidae are dew, nectar and aphid honeydew (Zoebisch & Schuster 1987; Nagata *et al.* 1998) but whether *C. nigra* uses these resources under natural conditions is unknown.

(b) *Experimental conditions*

Four grass species were used in the experiments: *Agrostis tenuis* Sibth., *Dactylis glomerata* L., *Lolium perenne* L. and *Poa trivialis* L. Grasses were sown in 10 cm × 10 cm × 11 cm pots containing a soil mixture of 50% white sand and 50% vermiculite. Grasses were grown in a greenhouse under controlled conditions (16:8 h light:dark, 20 ± 1 °C, 70% relative humidity in the light and 100% relative humidity in the dark) and were watered weekly with 150 ml half-strength Hoagland solution per pot (Hoagland & Arnon 1950). Grasses were used in the experiments when they were 12 weeks old.

The *C. nigra* females used in the experiments were collected from a field population living on *Holcus lanatus* L. at Hoboken, Belgium. All four grasses used in these experiments occurred in the vicinity of the field population. *H. lanatus* was not included in the experiments to avoid biased female preference and female performance due to past experience and to mitigate maternal effects on offspring performance. We used only gravid females, which were easily recognized by their swollen abdomens. Flies and grasses were used only once in an experiment to avoid pseudo-replication. All experiments were set up in a greenhouse under controlled conditions (16:8 h light:dark, 20 ± 1 °C, 70% relative humidity in the light and 100% relative humidity in the dark).

(c) *Preference hierarchy*

The preference hierarchy of *C. nigra* was determined by multiple-choice experiments (six replicates). This type of experimentation gave the same results as binary and no-choice experiments (Scheirs *et al.* 2001; J. Scheirs, unpublished data) and is therefore considered to give reliable estimates of host preference. One pot of each grass species was offered simultaneously to five females during a trial. All grasses in a trial were of the same age and had a comparable amount of biomass. Pots were randomly positioned in a rectangle in a flight cage (50 cm × 75 cm × 75 cm). Flies were observed to move freely among the four grass pots. A trial lasted 48 h, after which the number of eggs and feeding punctures per grass species were recorded as a measure of adult oviposition and feeding preference, respectively. Feeding punctures and eggs were counted by examining each individual leaf under a microscope with light projecting through the leaf.

(d) *Adult and offspring performance*

Adult performance was determined by no-choice trials in which a single grass species was offered to individual females (15–16 replicates per grass species). Females were placed in small plastic vials (10 cm diameter × 10 cm high) with slits in their side through which grass leaves were offered to the female. Leaves were replaced every 24 h. No extra water or food was offered to the females, as in the multiple-choice experiments, in order to study the direct effect of host quality on female choice and performance. As measures of adult performance, we recorded adult longevity and fecundity (number of eggs laid).

Offspring performance was determined by raising the eggs that were laid in the multiple-choice experiments (*A. tenuis*, 82 eggs; *D. glomerata*, 29 eggs; *L. perenne*, 64 eggs; *P. trivialis*, 98 eggs). Pots were censused daily for pupated and dead larvae. All pupated larvae were dissected from the leaves and put into individual rearing containers, which were checked daily for emerging adults. The positions of the larval host plants and the rearing containers of the pupae were randomized daily within the environmental chamber to avoid position effects. The length of the puparium was assessed with an ocular micrometer fitted to a dissection microscope (to the nearest 0.05 mm). In this way we determined three measures of offspring performance: offspring survival, developmental time and pupal size. Only larvae that completed their development in the absence of competition were considered in the analyses, because intraspecific competition decreases offspring performance of Agromyzidae (Parrella 1983; Quiring & McNeil 1984; Pettitt & Wietlisbach 1992). We considered intraspecific competition to be present when the mine of the larva was crossed or used by one or more other mining larvae and/or the mine crossed a batch of feeding punctures.

(e) *Statistical methods*

The results of the multiple-choice experiments (feeding preference and oviposition preference) were analysed using Quade tests (Quade 1979; Conover 1980). This non-parametric test takes the lack of independence among the simultaneously offered food types into account (Roa 1992). Exact Quade-test statistics were calculated with StatXact 3 (Metha & Pattel 1995).

Adult longevity was analysed using the Kaplan–Meier method and the log-rank test in the PROC LIFETEST module of SAS 6.12 (Allison 1995). Adult fecundity was analysed with a mixed-model regression analysis with log link and Poisson error. Offspring survival was analysed using mixed-model logistic regression with logit link and binomial errors. Choice trial was added to the model as a random variable. Total development time and pupal size were analysed with mixed-model regression with normally distributed errors. We used pot nested within choice trial as random variables. Grass species and sex were considered as fixed variables. The interaction between grass species and sex was never significant and was therefore excluded from the model. Mixed-model regressions were calculated with the PROC MIXED module in SAS in the case of normal errors, and with the GLIMMIX macro in the case of binomial or Poisson errors. The degrees of freedom of the fixed-effects *F*-test were adjusted for statistical dependence using Satterthwaite formulae. Variance components were estimated by restricted maximum likelihood (REML) (Littell *et al.* 1996).

The relation between preference and performance was studied by correlation analyses; we calculated Pearson's correlations using STATISTICA (Statsoft 1994). Only those offspring- and adult-performance characteristics that differed significantly among grasses were included in the analyses. Mean preference and mean performance were compared in all analyses, resulting in three degrees of freedom.

3. RESULTS

The number of feeding punctures ($Q = 13.93$, $p < 0.001$) and eggs ($Q = 5.62$, $p < 0.01$) differed significantly among grasses (figure 1) and were highly correlated ($r = 0.996$, $t = 16.00$, $p = 0.0039$). *P. trivialis* was the most preferred

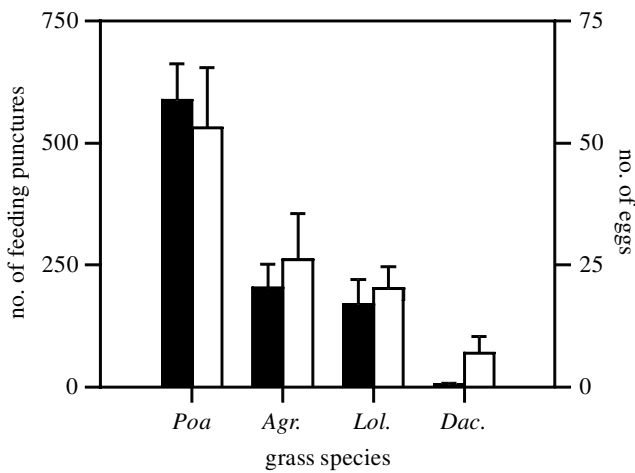


Figure 1. Feeding and oviposition preference (mean \pm s.e.m.) of *Chromatomyia nigra* in the multiple-choice experiments. Abbreviations used: *Poa trivialis* (*Poa*), *Lolium perenne* (*Lol.*), *Agrostis tenuis* (*Agr.*) and *Dactylis glomerata* (*Dac.*).

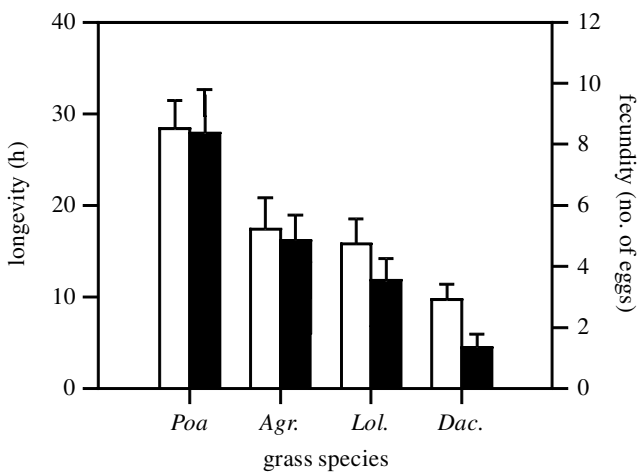


Figure 2. Adult performance (mean \pm s.e.m.) of *Chromatomyia nigra* on the different grass species. For abbreviations see figure 1.

host of *C. nigra*, and preference decreased in the order *A. tenuis*, *L. perenne*, *D. glomerata*.

Both measures of adult performance differed among grasses (longevity: $\chi^2 = 17.69$, d.f. = 3, $p < 0.001$; fecundity: $F_{3,61} = 9.71$, $p < 0.001$) (figure 2). Adult longevity and fecundity were clearly highest on *P. trivialis*, and decreased in the order *A. tenuis*, *L. perenne*, *D. glomerata*.

Offspring performance also differed among grasses (figure 3). Offspring survival was the highest on *P. trivialis* and gradually decreased in the order *L. perenne*, *A. tenuis*, *D. glomerata* ($F_{3,10} = 23.43$, $p < 0.0001$). Pupal size was higher on *P. trivialis* and *L. perenne* than on *A. tenuis* and *D. glomerata* (grass species effect: $F_{3,12.9} = 3.98$, $p = 0.0327$; sex effect: $F_{1,176} = 179.67$, $p < 0.0001$). We found no differences in total development time (grass species effect: $F_{3,114} = 1.48$, $p = 0.2715$; sex effect: $F_{1,175} = 5.20$, $p = 0.0238$).

Both oviposition and feeding preference were highly and significantly correlated with the adult-performance characteristics (table 1); only the relationship between feeding preference and adult fecundity became insignificant after sequential Bonferroni correction. The correlations between

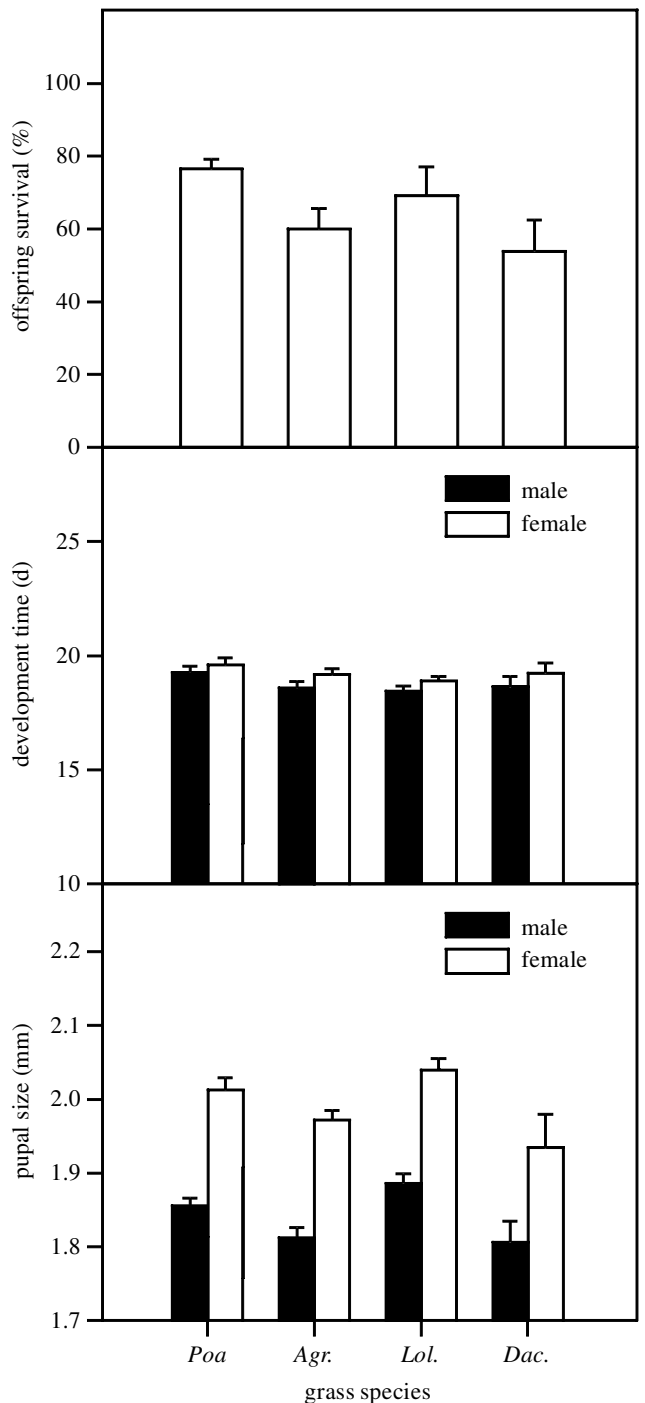


Figure 3. Offspring performance (mean \pm s.e.m.) of *Chromatomyia nigra* on the different grass species. For abbreviations see figure 1.

preference hierarchy and the offspring-performance characteristics were always weaker than the host-preference-adult-performance relationships and never significant.

4. DISCUSSION

Feeding and oviposition preference were nearly perfectly correlated with adult performance, while their relationships with the different offspring-performance measures were always weaker. The high correlation between feeding and oviposition preference further indicated that eggs are deposited near the adult feeding site.

Table 1. *Correlation matrix between preference hierarchy and performance*

preference	performance	<i>r</i>	<i>p</i>
feeding	adult longevity	0.996	0.0036 ^a
	adult fecundity	0.984	0.0158
	offspring survival	0.879	0.1215
	pupal size, male	0.398	0.6028
	pupal size, female	0.527	0.4729
oviposition	adult longevity	0.999	0.0013 ^a
	adult fecundity	0.996	0.0041 ^a
	offspring survival	0.859	0.1411
	pupal size, male	0.362	0.6376
	pupal size, female	0.514	0.4865

^aProbabilities significant after sequential Bonferroni correction.

These results show that *C. nigra* females maximize their fitness by selecting high-quality hosts for feeding, and consequently optimize the number of eggs laid, rather than optimizing offspring performance as assumed by the oviposition-preference-offspring-performance hypothesis.

This study advances our understanding of the complex interactions between plants and herbivores because it is, to our knowledge, the first study to illustrate that feeding- and oviposition-preference patterns of phytophagous insects are shaped by the optimization of adult performance. The only comparable study where both adult and offspring performance were taken into account found no proof of any preference-performance relationship (Coll 1996). However, this was probably because the study species was an omnivore, switching between plant and prey feeding, and only host plant quality, not prey distribution, was taken into account.

As female fitness is determined by both adult and offspring performance (Reavey & Lawton 1991; Nylin & Janz 1996; Krebs & Davies 1997), we argue that the variation in adult performance among hosts relative to the variation in offspring performance will determine which strategy will be used in order to maximize female fitness when search-time constraints prevent the optimization of both adult and offspring performance. For *C. nigra*, it is clear that females benefit more by optimizing adult performance in this experimental set-up because of the large variation in adult fecundity among hosts relative to the variation in offspring performance. For instance, feeding on *L. perenne* reduces adult fecundity by ca. 44% relative to *P. trivialis* (the host with the highest performance) while offspring performance is only reduced by ca. 9%.

Many studies have already reported large variations in adult performance among hosts (e.g. Murphy *et al.* 1983; Zoebisch & Schuster 1987; Minkenberg & Ottenheim 1990; Janz *et al.* 1994; Leather 1994; Coll 1996; Nagata *et al.* 1998), which suggests that the optimization of adult performance may shape host-preference patterns in other phytophagous insects. However, few studies consider the potential influence of adult feeding site and related performance on host plant selection (but see Coll (1996)). Most studies take a unilateral approach by considering the optimization of offspring performance only as the mechanism driving the evolution of host plant ranges and

host-preference patterns (Jaenike 1978; Ng 1988; Thompson 1988; Courtney & Kibota 1989; Price 1994; Mayhew 1997). It is beyond doubt that the optimization of offspring performance is important in shaping host-preference patterns of phytophagous insects as many studies have reported very tight oviposition-preference-offspring-performance relationships (Price 1994). However, this approach has at the same time resulted in a large number of studies in which the optimization of offspring performance could not explain all the variation in host preference (Thompson 1988; Courtney & Kibota 1989; Price 1994; Mayhew 1997). Because of the potential influence of the optimization of adult performance, we argue that future studies may yield a far better understanding of host plant selection if both strategies are considered.

We want to stress that host-specific performance need not be the consequence of intrinsic plant quality only, but can also be caused by various other selection pressures (Thompson 1988; Bernays & Graham 1988; Sih 1993). Therefore, future studies should consider whether extrinsic selection pressures on adult and offspring performance, which were absent in our experimental set-up, such as natural enemies or the distribution of alternative adult food resources, have an additional influence on host preference of *C. nigra*. These studies should also determine whether the same mechanisms underlie host preference under controlled conditions and field conditions. We also do not rule out the possibility that the motivational or physiological state of a phytophagous insect (e.g. hunger or egg load) may influence the strategy of the insect in a plastic way.

The preference-performance hypothesis was originally formulated for plant-insect systems, but has also been applied to explain oviposition-preference patterns within algae-amphipod (Poore & Steinberg 1999) and prey-predator systems (Tauber & Tauber 1987; Sadeghi & Gilbert 1999). Recent research in host-parasite systems illustrated a trade-off in the time budgets invested in feeding and oviposition (Weisser *et al.* 1994; Jervis & Kidd 1995; Sirot & Bernstein 1996; Lewis *et al.* 1998), which suggests that the optimization of adult performance may shape host-preference patterns in other systems besides plant-insect interactions.

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