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Host preference and performance of lichenivorous *Eilema* spp. larvae in relation to lichen secondary metabolites

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Summary

1. We compared the larval host preference of four lichenivorous *Eilema* (Lepidoptera, Arctiidae) species on four common epiphytic lichen species including *Hypogymnia physodes*, *Melanelia exasperata*, *Vulpicida pinastri* and *Xanthoria parietina*. Survival and growth of larvae on different species were monitored and correlation to qualitative and quantitative variation in lichen secondary compounds was analysed.
2. All moth species preferred *M. exasperata*, which does not contain polyphenolic substances, over other lichens, but also foraged on other lichens in the food preference experiment. All larvae reared on *V. pinastri* and *H. physodes* died during the growth and survival experiment. Survival of larvae on *X. parietina* and *M. exasperata* were equal. Larvae grew faster and and bigger on *M. exasperata* than on other lichens.
3. Consumption and utilization measurements also revealed that *M. exasperata* was of the highest quality, although the relative consumption rate was highest on *X. parietina*. Our results indicate that different secondary chemicals have different effect against lichenivores or that larvae are either well adapted to certain chemicals or that these chemicals may have other roles than antiherbivore function for lichens.
4. It is suggested that lichenivorous lepidopteran species may have different adaptations, such as dietary mixing to receive nutrients in optimal proportions or compensatory feeding ability to ensure the maximal growth efficiency on a suboptimal host.

Key-words: growth, host use, Lithosiinae, secondary chemical, survival.

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Introduction

Ecological and evolutionary factors that determine diet breadth, host use and host specialization have fascinated researchers for decades, since Ehrlich & Raven (1964) proposed that plant secondary chemistry is the driving force behind coevolution in phytophagous butterflies and plants. Host use of phytophagous insects is determined, first, by evolutionary factors, such as life history characters and enemy-free space (Price *et al.* 1980; Bernays & Graham 1988; Scheirs, De Bruyn & Verhagen 2001) and secondly, by several more proximate factors that include, for example, secondary chemistry (Rosenthal & Berenbaum 1992), nutritional value (Mattson 1980; Scriber & Slansky 1981), toughness (Pennings *et al.* 1998), prior experience of the herbivore (Papaj & Prokopy 1989) and interspecific interactions (Rieske & Raffa 1995; Cronin & Abrahamson 2001). Although in Lepidoptera host-selection and, thus, the rank of preference is determined in most cases by adult oviposition (Thompson & Pellmyr 1991; Renwick & Chew 1994), there are species (e.g. in Arctiidae) with relatively mobile larvae with grazing feeding habits that are able to locate and select host plants themselves (Dethier 1988; Thompson 1988).

Plant–herbivore studies have dealt mainly with insects feeding on higher plants while interactions between other primary producers, such as algae and lichens, and their herbivores have been less studied. Lichenivores are relatively common in nature ranging from small invertebrates such as springtails, mites, slugs and lepidopteran larvae to big ungulate grazers such as reindeer (Lawrey 1987). Lichen–invertebrate associations have been studied since Zukal (1895) proposed that secondary compounds may protect lichens from herbivory. This was opposed by Zopf (1896), who argued that such compounds afford lichens little protection. Subsequently, there have been several studies of lichen–invertebrate associations, of which most have concentrated on the role of lichen secondary chemicals as antiherbivore compounds (e.g. Stahl 1904; Slansky 1979; Lawrey 1980, 1983a, 1983b; Reutimann & Scheidegger 1987; Blewitt & Cooper-Driver 1990; Emmerich *et al.* 1993; Fröberg, Baur & Baur 1993).

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Although lichen secondary compounds obviously have a significant role in host selection and host use of lichen feeders, additional factors such as lichen growth form, surface toughness and nutrient content may influence the food choice of lichen feeders (Mattson 1980; Lawrey 1983a; Baur, Baur & Fröberg 1994). However, general chemical properties of a host plant may play a more important role in the host selection of lichen feeders than with other herbivores, because the availability of lichens is not limited by phenology or mechanical defence, as is often the case with higher plants. Moreover, the nutritional quality of lichens is low compared to higher plants (Lawrey 1987) and, in lichens, secondary chemicals often occur in relatively high concentrations (Fahselt 1994; Hyvärinen *et al*. 2000). For example, in *V. pinastri* the concentration of secondary chemicals exceed 3% of dry mass (Hyvärinen *et al*. 2000).

In Lepidoptera lichenivory occurs in several families, but the largest radiation of lepidopteran lichenivores occurs in the Arctiidae, subfamily Lithosiinae, whose larvae feed on lichens, algae, liverworts or mosses (Rawlins 1984). *Eilema complanum* (L.), *E. depressum* (Esper), *E. lurideolum* (Zincken) and *E. lutarellum* (L.) are common and abundant Arctiid species found in southern Finland. *Eilema* larvae begin foraging in October, overwinter as small larvae and resume feeding in spring. The caterpillars feed on lichens and algae, and some species also feed on mosses and dead plant material (Lepidopterologen arbeitsgruppe 2000). Several lichen secondary chemicals have been sequestered from individual adult moths of *Eilema* species (Hesbacher *et al*. 1995). In our study we compare larval host preference, growth, survival, consumption and utilization of *E. complanum*, *E. depressum*, *E. lurideolum* and *E. lutarellum* on different lichen species in relation to the nutritional quality and secondary chemistry. We hypothesized that lichens lacking or with low concentrations of secondary chemicals and with high nutritional quality are the most preferred, and will provide the best performance as measured by survival, growth and host utilization ability of larvae.

Materials and methods

STUDY SPECIES

Female moths of *Eilema* species were collected at the end of July and the beginning of August 2000 from different localities in southern Finland. Females were placed individually in small photographic film containers, where they laid their eggs on the ceiling or on the wall of containers within a few days. Eggs in containers were stored at room temperature until hatching. The offspring of two females of *E. lutarellum*, five females of *E. depressum* and *E. complanum* and six females of *E. lurideolum* were used in subsequent experiments.

In all experiments three lichen species containing the following secondary chemicals (in parentheses) were offered as food: *Xanthoria parietina* (L.) Th. Fr. (parietin), *Vulpicida pinastri* (Scop.) J.-E. Mattsson & M. J. Lai (vulpinic and pinastric acids) and *Hypogymnia physodes* (L.) Nyl. (atranorin and physodic acid). *Melanelia exasperata* (De Not.) Essl., which does not contain polyphenolic secondary substances (Culberson, Culberson & Johnson 1977), was used as a control species. *X. parietina* and *H. physodes* were collected from *Populus tremula* (L.) and *Picea abies* (L.) H. Karst., respectively, growing in our study area in the south-eastern part of the city of Oulu (64°45′N, 26°00′E). *V. pinastri* was collected from branches of *Betula nana* (L.) and *M. exasperata* from *Sorbus aucuparia* (L.).

FOOD PREFERENCE EXPERIMENT

In the food preference experiment 10 neonate larvae of one species in each dish were allowed to feed on the four lichen species for 2 weeks in Petri dishes (Ø = 9 cm, a dish was used as a replicate in statistical analysis). The positions of lichens were randomized in each dish. The experiment was carried out in the laboratory at 21 °C and 16 : 8 light : dark photoperiod with a 60-W incandescent lamp 1 m above the dishes.

Before being given to the larvae the lichens were air-dried for 2 days in the laboratory and 2 days in a desiccator prior to weighing. Thalli were then moistened overnight in a chamber with 100% relative humidity and sprayed with deionized water before placing on dishes. Spraying was repeated three times a week during the experiment. When about 50% of the thalli were consumed, thalli were replaced with new thalli. All thalli in a dish were replaced after the first week. After the experiment, thalli were dried and weighed as before the experiment. The food preference was calculated as the mass of lichen consumed.

GROWTH AND SURVIVAL EXPERIMENT

Sixteen neonate larvae of *E. complanum* and *E. depressum* were reared individually on each of four lichen species in a climate chamber with 16 light : 8 dark photoperiod and 20 °C : 16 °C temperature. One larva with a thallus of one lichen species was placed in a plastic cup (0·1 L) and covered by a veiling. A total number of 64 larvae of both moth species were used in the experiment. Because larvae overwinter in their early instars as a part of their natural annual rhythm larvae were reared for 80 days in chambers in autumn and during the last 2 weeks the temperature were lowered to 7 °C : 4 °C and the photoperiod changed to 6 : 18 light : dark. Larvae were then stored in dark at 4 °C for 75 days before being returned to climate chambers with the same conditions as before overwintering. Thalli were sprayed daily with deionized water and replaced once in 2 weeks before overwintering and once a week after overwintering. Larval developmental period (hibernating time excluded) and pupal mass 3 days after pupating were measured at the end of the experiment.

CONSUMPTION AND UTILIZATION OF LICHENS

Relative growth rate (RGR), relative consumption rate (RCR), assimilation efficiency (AE) and efficiency of conversion of digested food (ECD) were also calculated to see if there are differences in food consumption and utilization. Measurements were calculated according to Slansky & Scriber (1985) as follows:

$$RGR = \frac{B}{\bar{B} \times T}$$

$$RCR = \frac{I}{\bar{B} \times T}$$

$$AE = \frac{I - F}{I}$$

$$ECD = \frac{B}{I - F}$$

where B = larval mass gained, $\bar{B}$= average larval mass, T = days, I = mass of food ingested and F = mass of frass. Overwintered larvae (which were reared earlier on *Parmelia sulcata* Taylor) of *E. complanum* (n = 9 for each lichen species) and *E. depressum* (n = 8 for each lichen species) were reared for 4 days and the dry weight of thalli before and after the experiment, dry weight of faeces and the gain of fresh weight of larva were measured. To measure the air-dry weight of thalli and faecal pellets we dried them 2 days at room temperature, followed by 2 days in a desiccator. *V. pinastri* was not used in this experiment, because the larvae died when reared on that lichen.

CHEMICAL ANALYSIS OF LICHENS

Lichens were rehydrated overnight in water-saturated air and then sprayed with deionized water. One 3–4-mm-wide peripheral strip and one 1-cm^2 area from the central part of thallus were cut from each thallus by a razor blade. The pieces were air-dried overnight and oven-dried 1 night more and then ground in a mortar. Total N concentration was analysed by dynamic flash combustion method with Element Analyser EA 1110 CHSN 0 (Fisons Instruments, Rodano, Italy). The number of thalli for N analysis varied between four and nine (*M. exasperata* n = 9, *X. parietina* n = 7, *H. physodes* n = 4 and *V. pinastri* n = 6). N concentration of a thallus was calculated as a mean (% dry weight) of N concentration in peripheral strips and central part of the thallus. Total phenol concentration was calculated as a mean of phenol concentration in somatic and reproductive parts for a lichen species from Fig. 1 in Hyvärinen *et al.* (2000), where lichens from the same area were used.

STATISTICAL ANALYSIS

Differences in food preference were tested with the ANOVA model with lichen species, moth species (female nested within moth species) and moth × lichen species interaction term as explanatory factors. Tukey's HSD were used as a *post-hoc* test for food preferences within moth species. Pearson's correlation was used to compare the host preference with N concentration and total phenol concentration. Naturally, these two tests are not independent of each others and hence the P-values in Table 2 should be compared to Dunn–Šidák-corrected P-limits (see, e.g. Sokal & Rohlf 1995). Consumption and utilization of different lichens as a food were analysed using one-way ANOVA on the amount of consumed lichen biomass. If the variances were unequal we used Kruskall–Wallis non-parametric test instead of one-way ANOVA. To compare the pupal masses and the length of development between larvae reared on different lichen species we used ANOVA, with lichen species, sex, moth species and their interactions as explanatory factors. The impact of lichen and moth species on the survival of larvae was tested with linear logit-models using *R* statistical software (Ihaka & Gentleman 1996). Akaike information criteria (AIC, Venables & Ripley 1999) was used for stepwise model

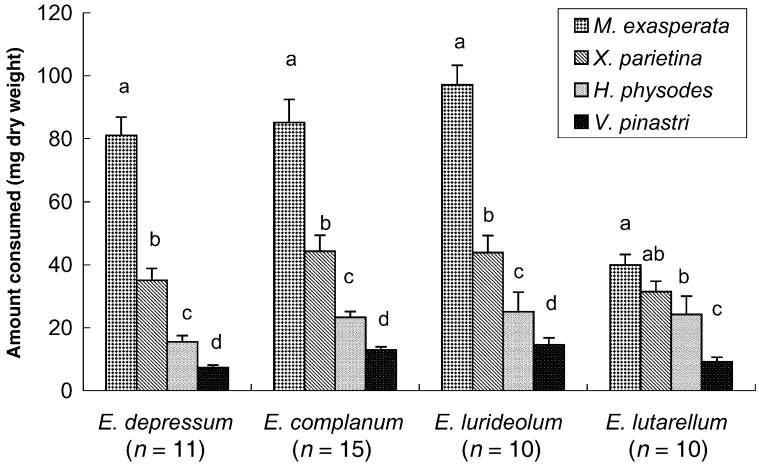

Fig. 1. Total consumption of lichen dry mass by *Eilema* spp. (± 1 SE). Letters above bars indicate signficant differences between lichens (Tukey's HSD). n = number of replicates. Results of two-way ANOVA: lichen species, $F_{3,9} = 26{\cdot}6$, $P < 0{\cdot}001$; moth species (female), $F_{14,154} = 1{\cdot}1$, NS, lichen × moth species (female) $F_{9,154} = 6{\cdot}0$, $P < 0{\cdot}001$.

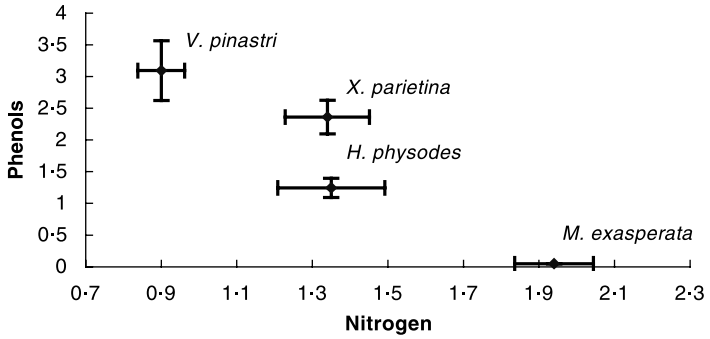

Fig. 2. Mean concentrations of phenols and total N in lichens ± 1 SE (% dry weight).

Table 1. Pearson correlation coefficients of total consumption of lichen dry mass with total nitrogen and phenol concentrations ($n = 4$)

Species	Nitrogen	*P*	Phenols	*P*
E. lurideolum	0·945	0·055	–0·839	0·161
E. complanum	0·945	0·055	–0·834	0·166
E. depressum	0·940	0·060	–0·840	0·160
E. lutarellum	0·941	0·059	–0·820	0·180

*Note that Dunn–Šidák corrected *P*-limits equal 0·051†, 0·025*, 0·005**, 0·0005***.

reduction starting from a saturated model that contained the main effects of lichen and moth species and their interaction.

Results

FOOD PREFERENCE EXPERIMENT

Lichen species had a significant effect on the host preference of *Eilema* species (Fig. 1) and all four moth species showed the same preference sequence from the most preferred lichen to the least preferred: *M. exasperata*, *X. parietina*, *H. physodes* and *V. pinastri* (Fig. 1). However, with *E. lutarellum* the differences in the amount of consumed lichen biomass between lichen species were not as significant as with other moth species, which is reflected in significant lichen species × moth species interaction (Fig. 1). The differences in the amount of lichen consumed between lichen species were significant for all moth species (Fig. 1). There was a slight trend for host preference to be correlated positively with N concentration and correlated negatively with total phenol concentration (Fig. 2; Table 1).

GROWTH AND SURVIVAL EXPERIMENT

All larvae of both moth species reared on *V. pinastri* and *H. physodes* died during the first two instars (on *V. pinastri*), or just after hibernation (on *H. physodes*) (Fig. 3). The results of linear logit models show that lichen species had a major influence on the survival of moths (Table 2). Moreover, there was a clear difference in the survival between the moth species. The lack of lichen species × moth species interaction showed that both moth species responded in similar ways to different lichen species. When survival of larvae only on *X. parietina* and *M. exasperata* where tested (Table 2) only the moth species proved to be a significant factor for survival.

Larvae on *M. exasperata* received pupal stage earlier and grew bigger than larvae on *X. parietina* (Table 3). Only sex of moth × moth species interaction in developmental period was significant and almost significant on pupal mass, which means that differences between sexes both in pupal mass and duration of larval time were greater in *E. depressum* (Table 3). Female pupae were always heavier than male ones, but this difference was greater in *E. depressum* than in *E. complanum* (Table 3).

CONSUMPTION AND UTILIZATION OF LICHENS

In consumption and utilization measurements larvae of both moths had highest RGR values on *M. exasperata*, but RCR values were highest on *X. parietina* (Table 4). There were significant differences in RCR between larvae reared on three different lichen species

Table 2. Final linear logit model for the survival of *Eilema* moths, first when all lichen species are tested and secondly when only *X. parietina* and *M. exasperata* are tested

	Variable	d.f.	Change in deviance*	*P*
All lichen	Moth species	1	10·60	0·0011
species	Lichen species	3	86·20	< 0·001
Only *X. parietina* and *M. exasperata*	Moth species	1	10·393	0·0013

*Indicates change when variable is omitted from the final model.

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Table 3. Three-way ANOVA of pupal masses (mg ± SE) and length of larval times (days ± SE) of larvae on *X. parietina* and on *M. exasperata*

			M. exasperata	*X. parietina*	SS	*F*	d.f.	*P*
Pupal mass	Lichen species				293·251	3·396	1	0·074
	Moth species				1160·097	13·436	1	< 0·001
		E. complanum						
		females	76·57 ± 2·65 (n = 8)	73·19 ± 3·72 (n = 9)				
		males	76·60 ± 5·02 (n = 5)	74·35 ± 2·12 (n = 4)				
		E. depressum						
		females	73·71 ± 4·30 (n = 3)	64·27 ± 4·04 (n = 7)				
		males	61·87 ± 4·13 (n = 3)	52·75 ± 1·65 (n = 2)				
	Sex of moth				246·484	2·855	1	0·101
	Lichen species × moth species				83·634	0·969	1	0·332
	Lichen species × sex of moth				1·065	0·012	1	0·912
	Sex of moth × moth species				302·032	3·498	1	0·070
	Lichen × moth × sex				0·332	0·004	1	0·951
	Error				86·343		33	
Developmental period	Lichen species				6941·094	11·328	1	0·002
	Moth species				1514·299	2·471	1	0·125
		E. complanum						
		females	160·13 ± 7·70 (n = 8)	176·00 ± 7·43 (n = 9)				
		males	130·80 ± 4·57 (n = 5)	145·00 ± 10·11 (n = 4)				
		E. depressum						
		females	93·00 ± 17·56 (n = 3)	155·29 ± 11·63 (n = 7)				
		males	141·67 ± 24·23 (n = 3)	167·00 ± 10·00 (n = 2)				
	Sex of moth				0·002	0·000	1	0·999
	Lichen species × moth species				1659·280	2·708	1	0·109
	Lichen species × sex of moth				747·669	1·220	1	0·277
	Sex of moth × moth species				7300·898	11·916	1	0·002
	Lichen × moth × sex				623·608	1·018	1	0·320
	Error				612·720		33	

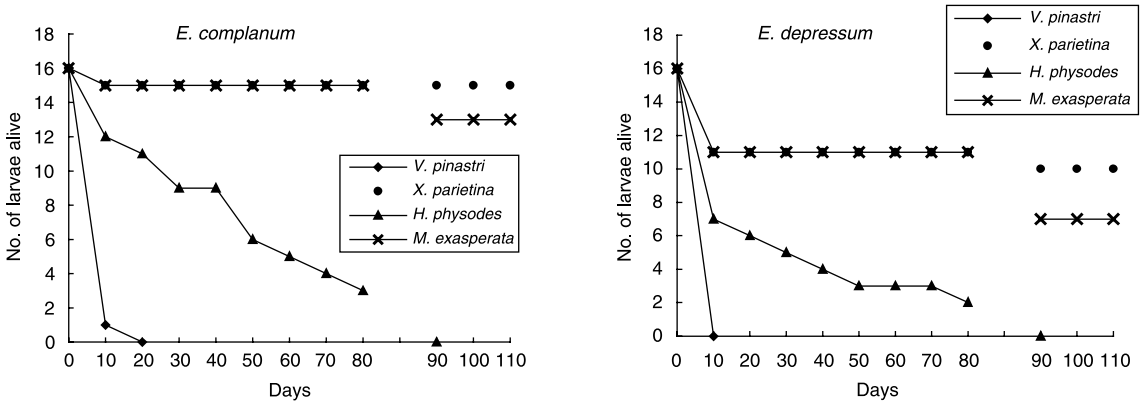

Fig. 3. Survival of *E. complanum* and *E. depressum* on different lichens from the beginning of the experiment. The gap between days 80 and 90 indicates overwintering time.

Table 4. ANOVA of consumption and utilizaton of lichens by *E. complanum* and *E. depressum*. RGR = relative growth rate, RCR = relative consumption rate, AE = assimilation efficiency and ECD = efficiency of conversion of digested food, with the rates expressed in mg day^{-1} mg^{-1} and the efficiences expressed in percentages. Numbers are means ± 1 SE. Tukey's HSD was used as a *post-hoc* test. Letters indicate significant differences between lichens: [a]between *H. physodes* and *X. parietina*, [b]between *X. parietina* and *M exasperata*, and [c]between *H. physodes* and *M. exasperata*

	H. physodes	*X. parietina*	*M. exasperata*	Source of variation	d.f.	MS (*χ^2)	*F*	*P*
E. complanum								
AE*	17·7 ± 24·2	28·7 ± 3·9	54·7 ± 4·2	Lichen	2	6·617*		0·037
ECD	76·3 ± 135·1	269·2 ± 43·2	183·8 ± 26·9	Lichen	2	0·326	1·753	0·195
				Residual	24	0·186		
RGR	0·044 ± 0·019	0·164 ± 0·034	0·178 ± 0·066	Lichen[a,c]	2	0·049	24·987	< 0·001
				Residual	24	0·002		
RCR	0·067 ± 0·016	0·255 ± 0·014	0·183 ± 0·115	Lichen[a,b,c]	2	0·081	46·535	< 0·001
				Residual	24	0·002		
E. depressum								
AE*	–18·0 ± 43·7	26·1 ± 5·8	38·3 ± 6·5	Lichen	2	1·755*		0·416
ECD	39·2 ± 39·8	178·7 ± 70·6	216·4 ± 55·9	Lichen	2	6·974	2·700	0·090
				Residual	21	2·583		
RGR	–0·018 ± 0·010	0·078 ± 0·019	0·109 ± 0·012	Lichen[a,c]	2	0·035	21·646	< 0·001
				Residual	21	0·002		
RCR	0·016 ± 0·018	0·279 ± 0·030	0·178 ± 0·018	Lichen[a,b,c]	2	0·141	34·229	< 0·001
				Residual	21	0·001		

*Kruskall–Wallis was used instead of one-way ANOVA.

and RGR of larvae reared on *H. physodes* was lower than on other lichens. There were no differences in RGR between larvae reared on *M. exasperata* or on *X. parietina*, although larvae consumed *X. parietina* significantly more than *M. exasperata*. Both moth species had the highest AE value on *M. exasperata*. *E. complanum* larvae were able to use *H. physodes* as a food and gained a slight increase in biomass, but larvae of *E. depressum* even lost their weight on that lichen (Table 4).

Discussion

All moth species performed most optimal and preferred to *M. exasperata*, the lichen species with highest N concentration and without polyphenolic compounds. Larvae also used *M. exasperata* as a food most effectively, since assimilation efficiency was highest on that lichen (Table 4). In spite of the fact that larvae reared on *X. parietina* consumed more lichen biomass than those on *M. exasperata*, they failed to reach the same pupal mass and needed more time for development compared to larvae feeding on *M. exasperata*. Grazing larvae, which largely locate and select the host themselves, probably benefit from compensatory feeding on suboptimal hosts if the costs of searching a higher quality food exceeds the costs of using more time in feeding on suboptimal host.

M. exasperata was the best food source for both species in all measurements. However, the host use of herbivores is not always determined by the nutritional value of food, as sequestration of secondary chemicals from host plants for defence is very common among butterflies and moths (Nishida 2002). It has been suggested by several authors (Hesbacher *et al*. 1995; Wink & von Nickisch-Rosenegk 1997; Weller, Jacobson & Conner 1999) that Lithosiinae have adapted to sequester lichen secondary compounds from their hosts and that these chemicals may have defensive role for these

moths. Whether larvae benefit from this kind of sequestration of lichen substances by decreased parasitism or palatability to predators remains a matter of speculation.

Larvae of *E. complanum* and *E. depressum* were not able to survive on *V. pinastri* and *H. physodes* throughout their larval period, although in preference experiments they consumed small amounts of both lichens, and survived for a while on *H. physodes*. This is caused probably by secondary chemicals, rather than the poorer nutritional quality of these two lichens, because larvae of both species were able to partially compensate lower nutritional quality of *X. parietina* compared to nutritionally better *M. exasperata* by increased feeding. Hence, if the secondary chemicals in *V. pinastri* and *H. physodes* were ineffective against larvae, one should see similar compensatory increase in intake.

V. pinastri contains vulpinic and pinastric acids, and *H. physodes* atranorin and physodic acid. The antiherbivore function of vulpinic acid has been demonstrated (Slansky 1979; Stephenson & Rundel 1979; Emmerich *et al*. 1993). According to Slansky (1979) this acid deterred feeding activity of yellow-striped armyworm (*Spodoptera ornithogallii*) at relatively low concentrations, but did not reduce growth when larvae were forced to feed on vulpinic acid-treated leaves treated. In other experiments with *Spodoptera littoralis* vulpinic acid demonstrated pronounced acute toxicity and feeding deterrency (Emmerich *et al*. 1993). However, it should be kept in mind that such experiments were all performed with generalist caterpillars whose natural diet does not include lichens, and the applicability of those results to specialist lichen-feeders may be limited.

In lichen–lichenivore studies the potential antiherbivore role of parietin has been demonstrated only circumstantially. Yom-Tov & Galun (1971) observed two desert snails that fed on several lichen species, but always avoided the ones containing parietin despite the fact that those species were the most common in the habitats they studied. Although larvae in our experiments preferred *M. exasperata* over *X. parietina*, they consumed parietin-containing lichen more than *M. exasperata*. The present results, together with the results of Hesbacher *et al*. (1995), who found that parietin (together with atranorin) was the most common lichen secondary chemical to be found sequestred in dead Lithosiinae specimens, seem to point to the conclusion that *Eilema* moths are either well adapted to parietin and that it may have some role for increasing the fitness of *Eilema* species or that parietin may have other ecological roles than antiherbivore functions for the lichen.

It has been suggested by Rawlins (1984) that lichenivory is essentially nothing more but feeding on algae. Hesbacher *et al*. (1995) observed that *E. complanum* larvae fed on cortical and algal layers of *Cladonia pyxidata* (L.) Hoffm. and they concluded that larvae avoid the medullary hyphae which are rich in fumarprotocetraric acid. Our own casual observations during the experiment support the hypothesis that the algal layer is an essential part of the lichen thallus for Lithosiinae nutrition, because small larvae in particular avoided medullary hyphae. However, after hibernating, in most cases larvae consumed a whole thallus. This may be due partially to their bigger mandibles that will not allow them to select only the algal layer, and consequently they are forced to consume the whole thallus, or that larvae gradually gain resistance against lichen secondary metabolites and switch to consume the whole lichen, as the handling costs of selecting algae overrides benefits.

In our experiments larvae survived only on two lichen species, but in the food preference experiment they were also able to ingest small amounts of other species (Fig. 1). This pattern may indicate several things. First, larvae may be able to select those parts of a lichen thallus which contain only small amounts of secondary chemicals or larvae may be able to tolerate or detoxify moderate amounts of secondary chemicals or that larvae actively search for small amounts of secondary metabolites. Secondly, larvae may benefit from dietary mixing. Although many Lepidopteran larvae are sedentary and are restricted to one or few foodplants due to the oviposition site selection by a female (Thompson & Pellmyr 1991), in some species (e.g. many Arctiidae) caterpillars are relatively mobile and perform some or all host location and selection (Dethier 1988; Thompson 1988). For a lichenivorous larva feeding on tree trunks and branches or on the ground, where several lichen species from several families are available within short distances, dietary mixing may be even more common than on Lepidopteran species in general. The benefits of dietary mixing for polyphagous *Eilema* species might arise either from avoiding harmful amounts of a single polyphenolic substance (Freeland & Janzen 1974) or, as lichens are in general nutritionally poor food for herbivores (Lawrey 1987), from receiving nutrients in better balanced proportions (Rapport 1980; see also Bernays *et al*. 1994).

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