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Nutritional Plasticity of the Predatory Ladybeetle *Harmonia axyridis* (Coleoptera: Coccinellidae): Comparison Between Natural and Substitution Prey

Olivier Specty,[1] Gérard Febvay,[1] Simon Grenier,[1*] Bernard Delobel,[1] Christine Piotte,[2] Jean-François Pageaux,[3] André Ferran,[2] and Josette Guillaud[1]

The predatory coccinellid *Harmonia axyridis* is a polyphagous species, efficient at controlling certain aphid species and already commercialized in Europe for that purpose. The complete development of this predator can be accomplished using the aphid *Acyrthosiphon pisum* or *Ephestia kuehniella* eggs as substitution prey. Biochemical analyses were conducted on the proteins, lipids, and carbohydrates of these two different prey species. *E. kuehniella* eggs were 2 times richer in amino acids than *A. pisum* adults (12% of the fresh weight vs. 6%). *E. kuehniella* eggs were 3 times richer in lipids than the aphids but, on the contrary, the aphids were 1.5 times richer in glycogen. The impact of these two kinds of food on the body composition of the coccinellid was evaluated to appreciate the degree of nutritional plasticity of the coccinellid. The composition of the coccinellids feeding either on *E. kuehniella* eggs or on aphids was compared for amino acid, fatty acid and glycogen contents, revealing a good capability of *H. axyridis* to develop on foods that are very different in their biochemical composition. Nevertheless, when fed on aphids, the crude protein content of the predator was reduced and the lipid content decreased by a factor of two, with a change in amino and fatty acid patterns. Some biological parameters, such as larval mortality, adult weight, and fecundity, were modified according to the food eaten. Arch. Insect Biochem. Physiol. 52:81–91, 2003.

KEYWORDS: *Harmonia; Ephestia; Acyrthosiphon;* entomophagous insect; predator; nutrition

INTRODUCTION

The coccinellid beetles have been closely linked to the biological control concept for over 130 years, since the famous use of *Rodolia* (*Novius*) *cardinalis* (Mulsant) to control the scale pest *Icerya purchasi* Maskell, introduced from Australia into California. Many of these coccidophagous as well as aphidophagous beneficials were released in inoculative or inundative biological control strategies (De Bach and Rosen, 1991). *Harmonia axyridis* Pallas is an aphidophagous Asiatic coccinellid introduced into France in the 1980s. This polyphagous coccinellid, feeding on many aphid species, was used in the 1990s in the biological control of aphids, such as *Macrosiphum rosae* (L.), through inundative release on rose bushes (Ferran et al., 1996), and it has also been tested against *Phorodon humuli* (Schrank) on hops (Trouve et al., 1996, 1997). A methodology has been developed where lepidopterous eggs

[1]UMR INRA/INSA de Lyon, Biologie Fonctionnelle Insectes et Interactions, Villeurbanne, France

[2]Entomologie et Lutte Biologique, UMR ROSE, INRA, Antibes, France

[3]Laboratoire de Biochimie et Pharmacologie, INSA, Villeurbanne, France

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*Correspondence to: Simon Grenier, UMR INRA/INSA de Lyon, Biologie Fonctionnelle Insectes et Interactions, INSA Bâtiment Louis Pasteur, 20 av. A. Einstein, 69621 Villeurbanne Cedex, France. E-mail: sgrenier@jouy.inra.fr

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(*Ephestia kuehniella* Zeller) are used as substitution prey (Schanderl et al., 1988), and the mass production of this coccinellid is performed on these eggs. Nevertheless, the main problem limiting its commercial use remains the cost of the current multiplication procedure. Artificial diets have been developed for different coccinellid species, including *H. axyridis*, but none are available at an industrial or commercial level (Obrycki and Kring, 1998). Taking into account the wide spectrum of its prey, for the development of an efficient diet in further studies, it was interesting to evaluate the adaptability of this predator. In a first approach, this evaluation could be performed by comparing the composition of the prey and of the predator itself grown on different kinds of prey. These carcass analyses of the coccinellid are of interest in providing both complementary information about the nutritional needs of the predator and the necessary references for the evaluations of artificial diets and of the quality of the predators produced.

The purpose of this work is an investigation of the biochemical analysis of a natural prey, the aphid *Acyrthosiphon pisum* (Harris), and the substitution prey *E. kuehniella* eggs, then of the predator itself. Subsequent analyses concern the body content in amino acids, fatty acids, and glycogen. We also compare some of the biological parameters of *H. axyridis* reared either on aphids or on *E. kuehniella* eggs.

The good flight ability of adult aphidophagous coccinellids restricts their potential for controlling pests because they frequently leave the treated areas. To increase their efficiency in biological control, a natural flightless mutation was selected in a laboratory population of *H. axyridis* (Ferran et al., 1998; Tourniaire et al., 2000). We used this strain to conduct the research described in this study.

MATERIALS AND METHODS

Insect Culture

A parthenogenetic clone of *A. pisum* (Lusignan strain, Ap-LL01) was maintained in the laboratory on broad bean seedlings (*Vicia faba* L., var. Aquadulce) in Plexiglas cages at 21 ± 0.5°C, 70 ± 5% RH, and a 16:8 (L:D) photoperiod. Mass-reared adults were allowed to lay progeny overnight (16 h) at a low density on young *V. faba* plants. Young apterous adults (approximately 7 days after larviposition) were used for lipid, protein, and glycogen analyses.

A natural flightless strain of *H. axyridis* (Tourniaire et al., 2000) was maintained on *E. kuehniella* eggs as described by Schanderl et al. (1988). For experiments, adults and immature stages were reared in Plexiglas cages at 23.5 ± 0.5°C, 75 ± 5% RH, and a 16:8 (L:D) photoperiod, and fed daily ad libitum, either with *A. pisum* adults or with *E. kuehniella* eggs.

The *E. kuehniella* eggs, purchased from Biotop (Valbonne, France), were UV irradiated. Prior to use, they were stored at –20°C for stock culture of *H. axyridis*, and at 4°C for all biochemical and biological studies.

Biological Parameters

Immature development. For the study of the larval development of the coccinellid, 40 individuals were singly reared either on *A. pisum* or on *E. kuehniella* eggs. For each immature stage, from first instar to pupa, the duration of the development was determined by monitoring moulting events twice a day. The individual weight was determined on a 10-µg-sensitive Mettler microbalance for each larval instar within a couple of hours after moultings and for newly emerged adult of both sexes. The mortality was recorded twice a day along the immature development, and expressed as a percentage for each stage.

Fecundity and fertility. The fecundity and fertility of the coccinellid were determined on 30 isolated couples (at emergence) obtained from stock cultures conducted on each kind of prey. The fecundity was evaluated by the number of eggs laid during the 10 days following the first egg laying, and the fertility by the percentage of egg hatching.

Water Content

The water content of different instars of *H. axyridis* tested was evaluated by weighing individu-

als before and after desiccation by freeze-drying (Usifroid SMH15, Boulogne, France). The water content of approximately 5 mg of prey (*A. pisum* or *E. kuehniella* eggs) was estimated by dehydration at 80°C for 20 h. The results were expressed as a percentage of water related to the fresh weight.

Coccinellid Food Intake

The experiments of food intake were conducted on young fourth instars (less than 12 h old) reared on *E. kuehniella* eggs. After weighing, the larvae were confined in individual boxes and fed either *A. pisum* or *E. kuehniella* eggs. The water content of the prey was estimated at the beginning of the experiment. After 24 h, the coccinellid larvae were weighed and the difference between the final weight at the end of the experiment and their initial weight provided an estimation of the weight gain (B) expressed in mg of fresh weight per day. To take into account the changes in the water content, the remaining prey were desiccated to estimate their dry weight at the end of the experiment. The ingested food (I) was estimated by the difference between the weight of provided and remaining prey expressed in mg of fresh or dry weight per day. The ratio B/I measured the efficiency of conversion of ingested food to body substance, in other words the weight gain of larvae per mg of ingested food.

Amino Acid Analyses

The analyses were performed either on prey (batches of about 1 mg of *E. kuehniella* eggs and individual young adults of *A. pisum*) or on coccinellid adults (individual newly emerged females). All these samples were hydrolysed, under nitrogen, in HCl vapour at 120°C for 24 h using a Pico-Tag work station (Waters, St. Quentin Les Yvelines, France). Along with 2-β-mercaptoethanol (4%), to preserve sulphur-containing amino acids, 200 µl of 6N HCl were placed in the hydrolysis tank. After hydrolysis, 10 nmol of glucosaminic acid per mg of sample were added as an internal standard. The samples were dried under vacuum in a Speedvac apparatus (Savant Instrument Inc., Farmingdale, NY) and taken up with 0.05 M lithium-citrate buffer, pH 2.2. The samples were submitted to ion exchange chromatography on an automatic amino acid analyser (Beckman 6300, Roissy, France). Amino acids were detected by the ninhydrin reaction, identified by their retention time and wavelength ratio, and quantified by their absorption at 570 nm (440 nm for proline).

Lipid Analyses

The analyses were performed on samples similar to those used for amino acid analyses. Total lipids were extracted from the whole insect body according to the modified method of Folch et al. (1957). An internal standard (consisting of triheptadecanoin, Sigma, St. Louis, MO) was added during lipid extraction for the determination of recovery yields (natural heptadecanoic acid, C17:0, was never detected in previously analysed samples).

Methyl esters of fatty acids were prepared in tubes stoppered with Teflon-lined caps. Lipids of total extracts were transmethylated with 1 ml of 5% sulphuric acid in methanol for 75 min at 90°C to yield methyl esters of the corresponding fatty acids. Methyl esters were extracted twice with pentane after adding 0.5 ml of 10% K_2CO_3 to each tube. Analysis of the methyl esters was performed using gas chromatography (Hewlett Packard 5890 Series II, Wilmington, DE) equipped with a SP2380 column (30 m × 0.32 mm, Supelco, Bellefonte, PA), a flame ionization detector and a split/splitless injector. The temperatures of the injector and of the detector were 200° and 230°C, respectively. The oven temperature was programmed from 55 to 210°C at 3°C/min until 130°C, then at 1.5°C/min until 210°C. Quantification was obtained from electronic integration of the peak areas, using an external standard (methyl pentadecanoate, Sigma) added at a known amount (20–50 µg) to each assay. Results were corrected for recovery deduced from the C17:0 internal standard.

Glycogen Analyses

The glycogen content was quantified either on prey (batches of *E. kuehniella* eggs and individual

young adults of *A. pisum*) or individual coccinellids (late fourth instar and mature females) using a Bioquant kit 10638 starch (Merck), with the protocol recommended for this kit. All samples (maximum weight 40 mg) were weighed and ground in 1 ml of distilled water. The results were expressed in μg of glycogen per mg of fresh weight.

Statistical Analyses

All results from biochemical analyses were expressed per mg of fresh weight. The ANOVA test with contrast method was used to compare the compositions between aphids and *E. kuehniella* eggs and between *H. axyridis* grown on these two prey. The Student's *t*-test was used to compare the biological parameters between *H. axyridis* grown on the two prey. Percentage data were arcsine transformed prior to statistical analyses.

RESULTS

Biological Parameters of *H. axyridis*

The developmental times of different larval instars and pupae, together with the time from hatching of the first instar to the adult emergence of *H. axyridis,* reared either on *A. pisum* or on *E. kuehniella* eggs, are all reported in Table 1, as well as the mortality rate of each stage. The weights at moulting are also given for the larval instars, the adult female and the male of *H. axyridis* reared on the two kinds of prey.

There was no significant difference between the total developmental times from first instar to adult emergence grown on the two kinds of prey, although we observed some small differences for the durations of instars 2 and 3. However, there was a significant difference for total mortality during larval and pupal development, the coccinellids grown on aphids showing a higher mortality than those grown on *E. kuehniella* eggs. The mortality on aphids mainly appeared during first and second larval instars (15.8%).

During larval development, there were no differences in weights between the coccinellids grown on the two kinds of prey, except slight differences in the opposite direction for instars 2 and 3, leading to similar weights at moulting up to the fourth instar. The maximum weights attained by prepupae were not significantly different ($P > 0.05$) for coccinellids reared on *A. pisum* and *E. kuehniella* eggs, i.e., 40.5 ± 0.9 and 39.2 ± 0.8 mg, respectively. However, the newly emerged adult coccinellids reared on *E. kuehniella* eggs were significantly heavier than those reared on *A. pisum*, for females (36.1 ± 0.7 vs. 29.4 ± 0.4 mg) and males (29.7 ± 0.5 vs. 25.8 ± 0.6 mg). These differences appeared during the pupal stage.

Water contents were significantly different ($P < 0.01$) between females (75.6 ± 0.5 and 69.7 ± 1.5%) and not significantly different between males (72.9 ± 0.2 and 71.1 ± 0.8%), reared on *A. pisum* and *E. kuehniella* eggs, respectively.

The fecundity, assessed for 10 days, of *H. axyridis* reared on *A. pisum* averaged 154 ± 79 eggs, with a 67.5% hatch rate, while on *E. kuehniella* eggs the

TABLE 1. Developmental Time (Day), Mortality Rate (%), and Weight at Moulting (mg) for Larval Instars and Pupa of *Harmonia axyridis* Reared Either on Adults of *Acyrthosiphon pisum* or on Eggs of *Ephestia kuehniella**

		Stage					
	Prey	1st instar	2nd instar	3rd instar	4th instar	Pupa	Total
Developmental time (day)	*A. pisum*	1.79 ± 0.03[a]	1.87 ± 0.03[b]	2.28 ± 0.05[a]	3.62 ± 0.09[a]	4.90 ± 0.10[a]	14.46 ± 0.13[a]
	E. kuehniella	1.70 ± 0.07[a]	1.58 ± 0.05[a]	2.48 ± 0.06[b]	3.50 ± 0.01[a]	4.85 ± 0.08[a]	14.12 ± 0.11[a]
Mortality rate (%)	*A. pisum*	12.5	3.3	0	6.7	3.5	23.8[b]
	E. kuehniella	0	0	0	3.3	0	3.3[a]
	Prey	1st instar	2nd instar	3rd instar	4th instar	Adult female	Adult male
Weight at moulting (mg)	*A. pisum*	0.22 ± 0.01[a]	0.76 ± 0.01[a]	2.93 ± 0.07[b]	9.90 ± 0.23[a]	29.40 ± 0.41[a]	25.84 ± 0.60[a]
	E. kuehniella	0.21 ± 0.01[a]	0.89 ± 0.02[b]	2.71 ± 0.06[a]	9.62 ± 0.18[a]	36.06 ± 0.72[b]	29.69 ± 0.48[b]

*Values are means ± SE from 40 individuals. For developmental time, mortality rate, and weight at moulting, respectively, means with the same letter in the same column do not differ significantly, using the Student's *t*-test ($P < 0.05$). "Total" represents the complete developmental time from the hatching of the first instar to the adult emergence.

fecundity was 393 ± 43 eggs, with 67.6% hatch rate. The difference between the two kinds of prey was highly significant for fecundity (n = 30, P = 0.05), showing that the eggs of *E. kuehniella* seem to be an efficient prey for the expression of the biological potential of the coccinellid.

Composition of the Prey

The total amount of amino acids resulting from complete hydrolysis was 521 ± 16 nmol/mg in *A. pisum* and twofold higher in *E. kuehniella* eggs, i.e., 1,135 ± 17 nmol/mg (n = 5 and 4, $P < 0.01$). The same differences were observed for each amino acid (Fig. 1). Thus, the patterns of amino acids expressed in % of total amino acids were similar for the two kinds of prey, with only slight differences for some of them (Fig. 1, inset). The main amino acids are Glx (13.2%), Gly (10.8%), Leu (10.4%), and Ala (10.3%) in *E. kuehniella* eggs. In *A. pisum*, Glx (20.4%), Asx (12.2%), and Ala (11.2%) represent the main amino acids. The protein content, calculated from these amino acid quantifications, was 5.7 and 12.2% in *A. pisum* and in *E. kuehniella* eggs, respectively.

The total amount of fatty acids was 33.1 ± 4.0

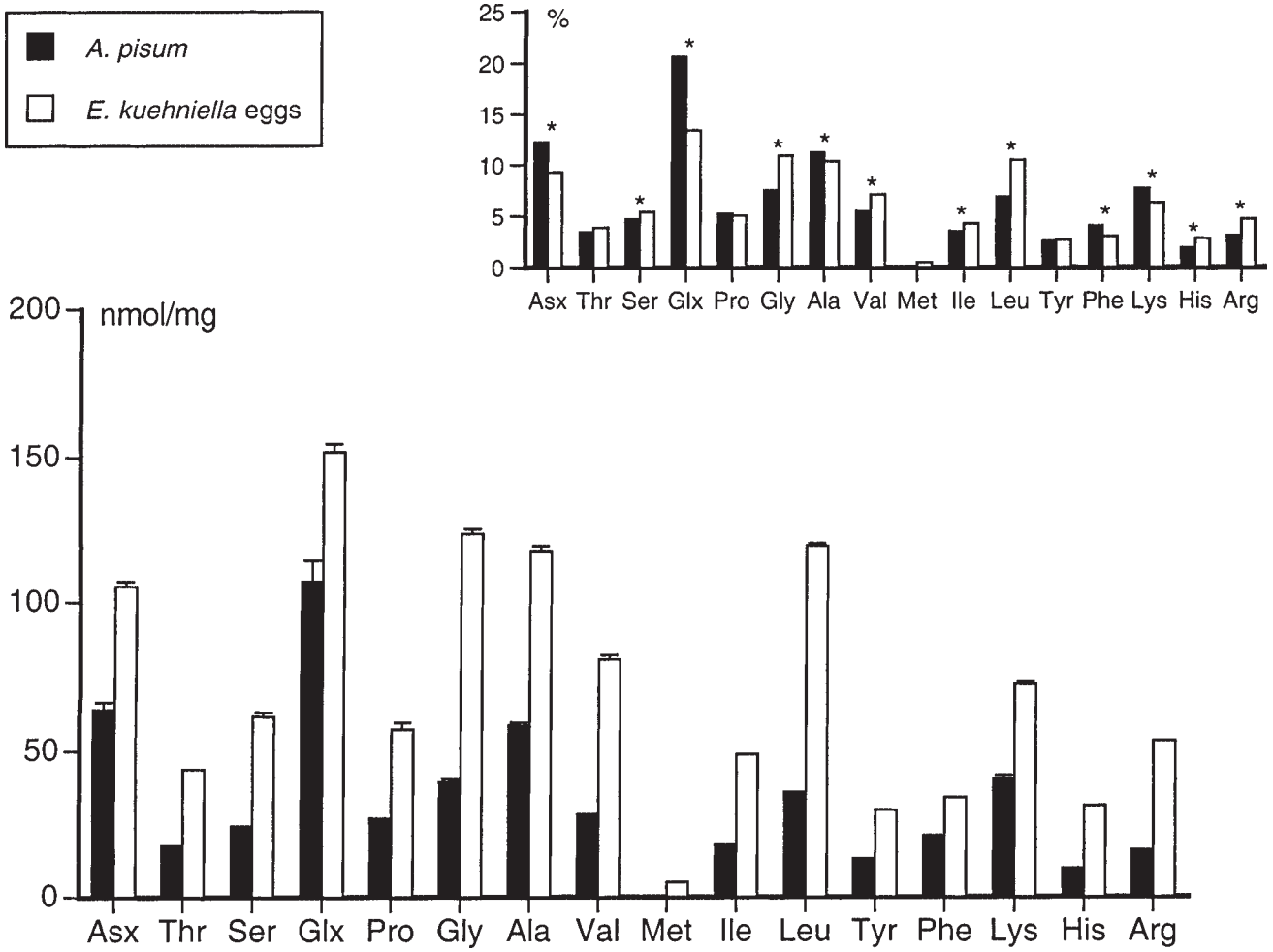

Fig. 1. Total amino acid contents (nmol/mg of fresh weight) of *Acyrthosiphon pisum* adults and *Ephestia kuehniella* eggs. The mean values of 5 and 4 independent analyses are given, together with their Standard Error. There were significant differences, using the ANOVA contrast method ($P < 0.05$), for all the amino acids. **Inset:** Relative amino acid contents (% of total amino acids) of *Acyrthosiphon pisum* adults and *Ephestia kuehniella* eggs. The asterisk represents a significant difference shown by the ANOVA contrast method ($P < 0.05$).

µg/mg in *A. pisum* and about threefold higher in *E. kuehniella* eggs, i.e., 95.4 ± 0.9 µg/mg (n = 4 and 5, $P < 0.01$). The patterns were completely different for the two kinds of prey, with higher quantities of C14:0 in aphids than in *E. kuehniella* eggs but the contrary for C16:0, C16:1, C18:0, C18:1, C18:2, C18:3 (Fig. 2). The presence of C6:0, C10:0 as traces (< 0.5 µg/mg), C12:0, and C18:3n-1 was observed only in aphids. The presence of traces of C20:0 and C22:0 was observed only in *E. kuehniella* eggs.

Contrary to the results obtained for lipids, *A. pisum* was richer in glycogen than *E. kuehniella* eggs: 24.4 ± 2.7 and 15.7 ± 1.2 µg/mg, respectively (n = 4 and 3, $P < 0.01$).

The water content of *E. kuehniella* eggs is low (72%) and similar to that observed in *Sitotroga cerealella* (Olivier) eggs (66%) and in *Eurygaster integriceps* (Putton) eggs (70%), but the total amount of amino acids in *E. kuehniella* eggs (12.2%), appears to be lower than that in *S. cerealella* (15.6%) (Yazlovetsky, 1992). Adult aphid water content is 80%.

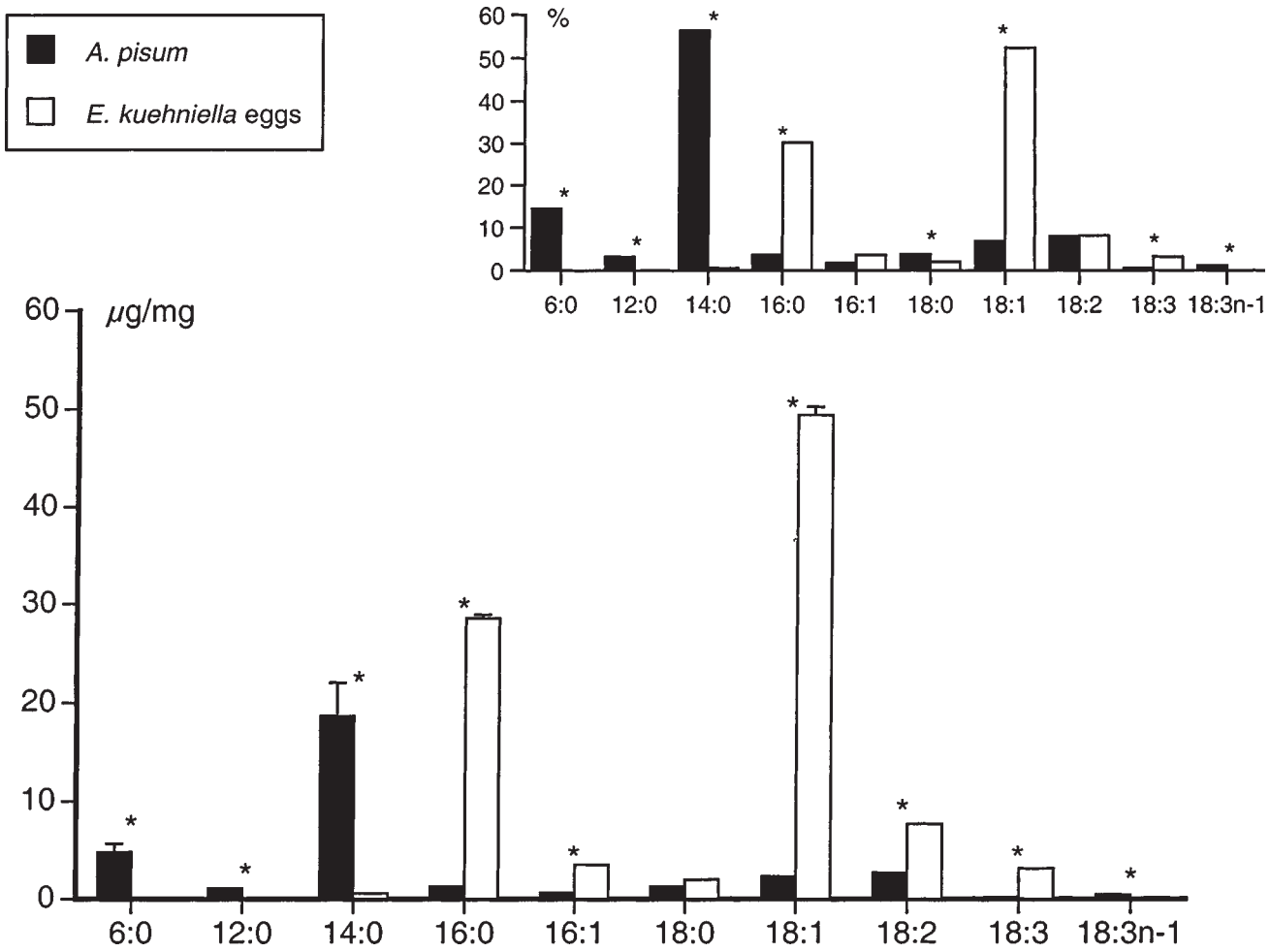

Fig. 2. Total fatty acid contents (µg/mg of fresh weight) of *Acyrthosiphon pisum* adults and *Ephestia kuehniella* eggs. The mean values of 4 and 5 independent analyses are given, together with their Standard Error. The asterisk represents a significant difference shown by the ANOVA contrast method ($P < 0.05$). **Inset:** Relative fatty acid contents (% of total fatty acids) of *Acyrthosiphon pisum* adults and *Ephestia kuehniella* eggs. The asterisk represents a significant difference using the ANOVA contrast method ($P < 0.05$). Abbreviations for fatty acids: 6:0 = caproic acid, 10:0 = capric acid, 12:0 = lauric acid, 14:0 = myristic acid, 16:0 = palmitic acid, 16:1 = palmitoleic acid, 18:0 = stearic acid, 18:1 = oleic acid, 18:2 = linoleic acid, 18:3 = linolenic acid, 18:3n-1 = (Z, Z)-9, 12, 17-octadecatrienoic acid, 20:0 = arachidic acid, 22:0 = behenic acid.

Food Intake And Weight Gain

The quantity of fresh food ingested over a 24-h period was significantly higher when larvae were fed on *A. pisum* rather than on *E. kuehniella* eggs: 104.0 ± 8.0 vs. 31.5 ± 1.8 mg per larva, but the fresh weight gains were similar on both prey (11.4 ± 1.9 vs. 14.7 ± 1.0 mg per larva). Therefore, the efficiency of the conversion of ingested food to body substance (ratio of biomass to amount of ingested food) was significantly higher with *E. kuehniella* eggs (0.47) than with *A. pisum* (0.11). The difference in water content of the prey (80 vs. 72%) correlated with a similar difference in the water content of the predators developed on each kind of prey (77 and 69% for early fourth larval instar reared on *A. pisum* or *E. kuehniella* eggs, respectively), cannot explain the difference in the efficiency of the food conversion (B/I calculated from dry weight = 0.45 and 0.11).

Composition of the Coccinellids Grown on the Two Kinds of Prey

The total amount of amino acids was 1,404 ± 166 nmol/mg in *H. axyridis* grown on *A. pisum* and

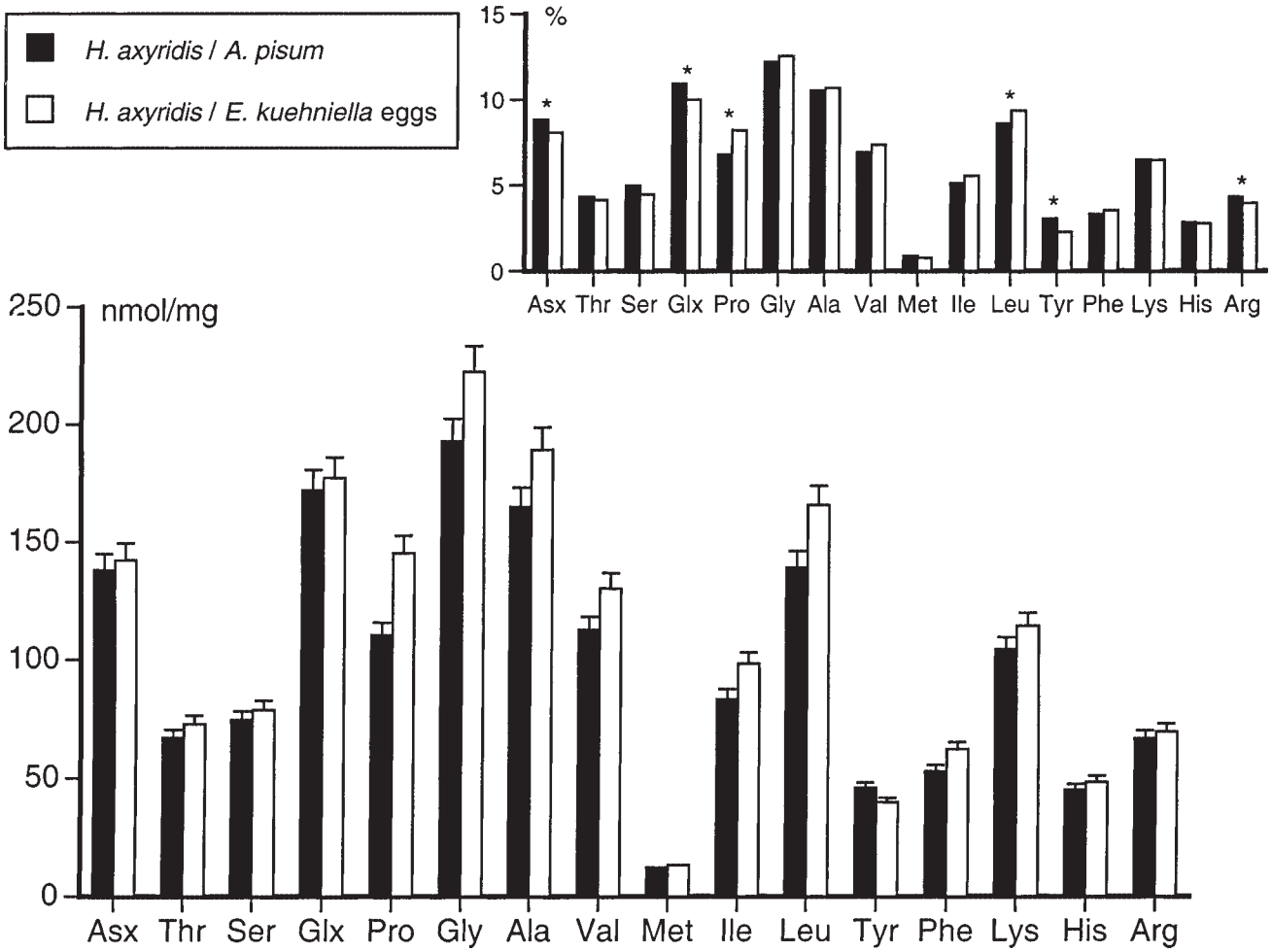

Fig. 3. Total amino acid contents (nmol/mg of fresh weight) of *Harmonia axyridis* reared either on adults of *Acyrthosiphon pisum* or on eggs of *Ephestia kuehniella*. The mean values of 4 and 5 independent analyses are given, together with their Standard Error. There are no significant differences shown by the ANOVA contrast method ($P < 0.05$). **Inset:** Relative amino acid contents (% of total amino acids) of *Harmonia axyridis* reared either on adults of *Acyrthosiphon pisum* or on eggs of *Ephestia kuehniella*. The asterisk represents a significant difference using the ANOVA contrast method ($P < 0.05$).

1,771 ± 79 nmol/mg in *H. axyridis* grown on *E. kuehniella* eggs (n = 4 and 5, $P = 0.40$). The concentrations of each amino acid were not significantly different between the two kinds of predators grown on aphids or on *E. kuehniella* eggs (Fig. 3). When the results were expressed as percentages, there were some significant differences ($P < 0.05$) for Asx, Glx, Pro, Leu, Tyr, and Arg. These compositions expressed as protein lead to apparent protein contents of 16.8 and 18.6% in *H. axyridis* females grown on *A. pisum* and on *E. kuehniella* eggs, respectively.

The total amount of fatty acids was 89 µg/mg in *H. axyridis* grown on *A. pisum* and about two-fold higher in *H. axyridis* grown on *E. kuehniella* eggs, i.e., 176 µg/mg. The patterns of fatty acids of the two kinds of predators were also very different (Fig. 4), especially for myristic (C14:0), linolenic (C18:1), and arachidic (C20:0) acids. The differences observed were in concordance with those observed for the composition of their food.

The glycogen content of the late fourth larval instar (prepupa) of *H. axyridis* was higher (25.5 ± 1.2 µg/mg) when reared on *A. pisum* than on *E. kuehniella* eggs (13.7 ± 2.9 µg/mg) (n = 3, $P = 0.01$). On the contrary, no difference was apparent in mature females: 2.1 ± 0.5 on *A. pisum* vs. 1.0 ± 0.6 µg/mg on *E. kuehniella* eggs (n =2 and 3, $P = 0.47$).

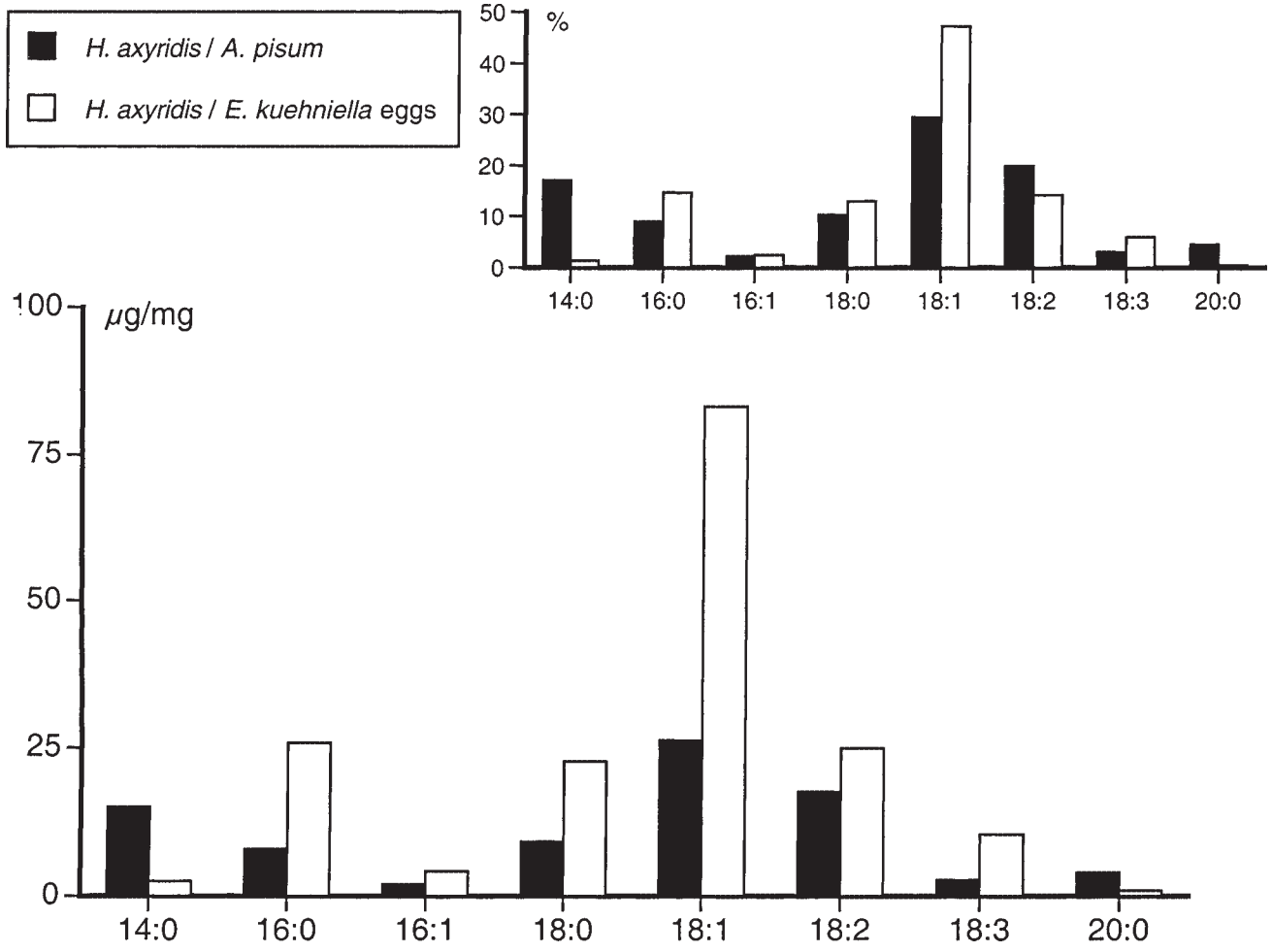

Fig. 4. Total fatty acid contents (µg/mg of fresh weight) of *Harmonia axyridis* reared either on adults of *Acyrthosiphon pisum* or on eggs of *Ephestia kuehniella* (one determination for each condition). **Inset:** Relative fatty acid contents (% of total fatty acids) of *Harmonia axyridis* reared either on adults of *Acyrthosiphon pisum* or on eggs of *Ephestia kuehniella*. See Figure 2 for abbreviations of fatty acids.

DISCUSSION

The larval developments of *H. axyridis* reared on the two kinds of prey, the natural food *A. pisum* or the substitution food *E. kuehniella* eggs, are very similar. Indeed, the weights of the ladybeetles at the beginning of each larval instar are not significantly different and the larval development times are equal, with 14.5 vs. 14.1 days for larvae reared either on aphids or on *E. kuehniella* eggs, respectively. Even if the weights and the total development times of the larval stages were similar on both prey, the higher mortality rate of coccinellid larvae reared on *A. pisum* vs. on *E. kuehniella* eggs (24 vs. 3%) could be due to differences in the nutritional quality of these two kinds of food as shown by biochemical results.

Moreover, important differences in weight appear at the adult stage. At moulting, male and female adults reared on aphids are lighter than those reared on *E. kuehniella* eggs; this difference is more noticeable between females. The differences between young adults were not apparent at the end of the larval development (prepupae) and this can only be explained by a difference in biochemical conversions during the pupal stage and a subsequent greater weight loss at ecdysis (exuvia plus meconium). This weight difference may be related to a difference in fecundity (154 vs. 393 eggs).

The biological differences observed in females are in relation to the biochemical analyses of *H. axyridis*. The ladybeetles reared on *E. kuehniella* eggs have a higher protein content than those reared on *A. pisum* (18.6 vs. 16.8%) with the same pattern of amino acids. These values are not significantly different but when expressed in µmol per female, instead of concentration, a significant difference (41.3 vs. 63.8 µmol per female) is revealed for ladybeetles reared on *A. pisum* or on *E. kuehniella* eggs, respectively. This difference in protein amount could partially explain the fecundity results. The other reason could be the lipid content, with 8.9 vs. 17.6% of fatty acids for ladybeetles reared on *A. pisum* or on *E. kuehniella* eggs, which means 3.6 vs. 6.9 mg per female, respectively. In addition to this difference in concentration, the fatty acid pattern is quite different, with a lower amount of unsaturated fatty acids of 57.2 vs. 70.0%. The lipid composition of *A. pisum* described here is similar to that given by Febvay et al. (1992, 1993), with the presence of the singular fatty acid C18:3n-1. The lower total amount of fatty acids in Febvay et al. (27.6 vs. 33.1 µg/mg of fresh weight) is explained by the quantification of only long chain fatty acids (≥12 C) by these authors. The total fatty acids for *E. kuehniella* eggs observed in the present study (9.5% fresh weight) is similar to the amounts found in *S. cerealella* eggs (8.5%) (Yazlovetsky, 1992) and *E. integriceps* eggs (8.8%) (Daskalova and Dimitrova, 1994). In *E. kuehniella* eggs, the three main fatty acids are the oleic, palmitic, and linoleic acids representing 52.0, 30.0, and 8.1% of total fatty acids, respectively, as in *S. cerealella* (43.1, 41.1, and 4.0%) (Yazlovetsky, 1992).

The differences in these biochemical parameters of ladybeetles are important but the differences observed between the two types of food are drastic and appear in all the nutrient classes, such as protein contents, as well as lipid contents and the patterns of fatty acids. These two kinds of prey represent different physiological stages (egg and larva) of insects belonging to different orders (Homoptera and Lepidoptera), and showing very different feeding habits, explaining the biochemical differences detected.

So, whatever the prey, the ladybeetles undertake considerable metabolic conversions in order to fulfill, as much as possible, their own growth needs. The food intake of ladybeetles reared on *A. pisum* is 3-fold greater than those reared on *E. kuehniella* eggs. This major difference in food intake should satisfy the nutritional requirements of ladybeetles reared on *A. pisum* but a low efficiency of the conversion of the ingested food for *A. pisum* (0.11), in comparison with *E. kuehniella* eggs (0.47), justifies the differential composition in *H. axyridis*. This difference in efficiency of the food conversion is a consequence of an inadequate quality of *A. pisum*, with a differential pattern in amino acids and fatty acids in comparison to *E. kuehniella* eggs. So, high metabolic costs are required from

the predator to synthesise amino and fatty acids fitting to its own pattern. For example, the ladybeetles reared on *A. pisum* must convert some of the short chain fatty acids (including myristic acid) to 18 carbon fatty acids, which seem to be crucial components for *H. axyridis*. The value of efficiency of the food conversion for *A. pisum* is low for carnivorous predators, which are characterised by a range of between 0.13 and 0.75 (Slansky and Scriber, 1985).

In conclusion, the polyphagous ladybeetle *H. axyridis* shows a good ability to adapt to various foods at a biological level, as described previously with different aphid species (Hukusima and Kamei, 1970) and as described also in other entomophagous insects (Delobel and Pageaux, 1981; Delobel et al., 1981; Thompson, 1999; Thompson and Hagen, 1999). However, these capabilities of adaptation to non-optimal food have a negative effect on some of the biological parameters of the ladybeetles. The same results were obtained with the ladybeetle *Coleomegilla maculata* DeGeer reared on *Ostrinia nubilalis* (Hübner) eggs and *A. pisum* (Phoofolo and Obrycki, 1997), with no effect of the larval prey regime on the preimaginal development but a much higher larval mortality on *A. pisum* (80%) than on *O. nubilalis* eggs (28%) or on *A. pisum* alternated daily with *O. nubilalis* eggs (22%). In the field, *H. axyridis* is not restricted to one single food and may modulate its regime with alternating food (aphids, eggs, and pollen) leading to improved biological parameters.

It will be advisable to use the data reported in this work to elaborate an artificial diet suitable for *H. axyridis*. Taking into account the biological results and the efficiency of the food conversion, the composition of this diet could be preferably based on *E. kuehniella* egg analyses. The ability of *H. axyridis* to adapt to various species of prey should be an advantage for the future elaboration of artificial diets. Thanks to this plasticity, the coccinellid would be expected to be more easily reared even on a non-optimum diet, since most successes in this field concerned polyphagous predators and parasitoids (Yazlovetsky, 1992).

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