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RESEARCH ARTICLE

Influence of plant, animal and mixed resources on development of the zoophytophagous plant bug *Campylomma verbasci* (Hemiptera: Miridae)

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The mullein bug, *Campylomma verbasci* (Meyer-Dür) (Hemiptera: Miridae), exploits both plant and animal resources. The aim of this study was (1) to evaluate the quality of different plant, animal and mixed diets (i.e. plant material or prey from the overwintering host, the summer host or the laboratory rearing) for the development and survival of mullein bug, and (2) to evaluate if the suitability of the resource changes according to the nymphal instar of *C. verbasci*. Mullein bug nymphs were reared individually in Petri dishes containing different diets and observed daily until reaching adulthood or dying. The rearing diet (living potato aphids + potato leaf + *Ephestia* eggs + apple pollen) was a *high-quality* diet. The *medium-quality* diets were apple fruit + apple pollen, *Ephestia* eggs and *Sitotroga* eggs. The *low-quality* diets included mullein leaf, frozen aphids, living aphids + potato leaf and apple fruit + living aphids + potato leaf. Finally, the *inappropriate* diets (when no nymphs reached adulthood) were agar gel, apple fruit, apple pollen, apple leaf, potato leaf, frozen spider mites and frozen conspecifics. When comparing the value of the diets for different instars, living aphids + potato leaf was a *high-quality* diet for third instar. Apple pollen and frozen conspecifics were *low-quality* diets for third instar. ‘Red Delicious’ fruit was a *high-quality* diet for fifth instar and *low-quality* for third instar. ‘Honeycrisp’ fruit constituted an *inappropriate* diet whatever the instar. Thus, a whole mixed diet maximises development and survival of *C. verbasci* nymphs.

Keywords: Heteroptera; mullein bug; omnivory; diet quality; survival; apple

Introduction

The mullein bug, *Campylomma verbasci* (Meyer-Dür) (Hemiptera: Miridae), is a palaeartic zoophytophagous insect common in Canada and in US apple orchards (Thistlewood, Borden, Smith, Pierce, & McMullen, 1989). It feeds on both plant and animal materials (Thistlewood & Smith, 1996). As zoophagous, this mirid is considered as a biocontrol agent of economically important pests in some areas, because it is an important predator of several pest species including: the European red mite *Panonychus ulmi* (Koch) (Acari: Tetranychidae), the two-spotted spider mite *Tetranychus urticae* Koch (Acari: Tetranychidae), the green apple aphid *Aphis pomi* De Geer (Hemiptera: Aphididae), the pear psylla *Cacopsylla pyricola* (Foerster) (Hemiptera: Psyllidae), the pear rust mite *Epitrimerus pyri* (Nalepa) (Acari: Eriophyidae),

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the apple rust mite *Aculus schlechtendali* (Nalepa) (Acari: Eriophyidae) and various thrips (Thysanoptera) (Arnoldi, Stewart, & Boivin, 1992; McMullen & Jong, 1970; Niemczyk, 1978; Reding, Beers, Brunner, & Dunley, 2001; Smith, 1989; Thistlewood, 1986). As phytophagous, newly emerged nymphs damage apples by puncturing the flowers and fruitlets while feeding, inducing a physiological reaction in sensitive cultivars that damages and often downgrades the apples (MacPhee, 1976; Thistlewood, McMullen, & Borden, 1989). Nymphs and adults of mullein bugs can be found in North American orchards throughout the growing season, but generally in higher numbers during spring (McMullen & Jong, 1970; Reding et al., 2001) when they can puncture apple fruitlets. The greatest proportion of the second generation occurs on herbaceous weed hosts, especially mullein, *Verbascum thapsus* L. (Scrophulariaceae) (McMullen & Jong, 1970; Thistlewood, Borden, & McMullen, 1990).

True omnivory is the fact of feeding on both plant and animal resources (Coll & Guershon, 2002). Among omnivorous heteropterans, distinction must be made between phytozoophagous or zoophytophagous according to the prevalence of feeding on plant or animal resources (Alomar, 2007; Coll & Guershon, 2002; Lucas, Frechette, & Alomar, 2009; Strawinski, 1964). Past studies suggest that the mullein bug prefers arthropod prey to plant material and is considered as zoophytophagous (Fauvel, 1999; Stigter, 1996), while Strawinski (1964) classifies it as phytozoophagous. Lord (1971) observed that *C. verbasci* damage is rare in orchards with high mite populations. Thereby, Thistlewood and Smith (1996) suggested a novel management technique by manipulating prey densities (e.g. low densities of prey in fall and high densities of prey in spring) to reduce and prevent fruit injury by the mullein bug.

Zoophytophagous insects such as *C. verbasci* derive nutrients not only from prey but also from plants (Coll, 1996; Naranjo & Gibson, 1996; Smith, 1965). The dietary requirements of the mullein bug are not fully understood, although this knowledge is crucial to determine its ecological status. McMullen and Jong (1970) found in laboratory tests that survival is enhanced when *C. verbasci* consumes animal prey and that this resource is necessary for the complete development of the early instars. However, Bartlett (1996) found in laboratory that *C. verbasci* still uses plant food sources even in the presence of prey, and that pollen is sufficient for nymphs to complete their development in absence of prey. Therefore, a better comprehension of the quality of the different plant and animal resources for the predator is necessary to understand its tendency to behave as a noxious phytophagous or a useful zoophagous insect.

The quality of food sources may vary during the insect development. Many species consume different foods and/or change habitat as they grow from hatching to adulthood (Cisneros & Rosenheim, 1997; Ebenman, 1987; Keast, 1997; Mittelbach, Osenberg, & Leibold, 1988; Muotka, 1990; Polis, 1984; Wissinger, 1988). Changes in prey preference associated with the age of the predator are well documented among insects including Nematocera (Diptera: Chaoboridae) (Fedorenko, 1975), damselflies (Odonata: Coenagrionidae) (Johannsson, 1978; Rowe, 1992; Thompson, 1975), grasshoppers (Orthoptera: Acrididae) (Lockwood, 1989) and the hemipterous *Zelus renardii* Kolenati (Hemiptera: Reduviidae) (Cisneros & Rosenheim, 1997) and *Notonecta glauca* (Hemiptera: Notonectidae) (McArdle & Lawton, 1979). If nutritional requirements change with the age of *C. verbasci*, it will greatly influence its status.

The aim of this study was (1) to evaluate the quality of different plant, animal and mixed diets (i.e. plant material or prey from the overwintering host, the summer host or the laboratory rearing) for the development and survival of mullein bug, and (2) to evaluate if the suitability of the resource changes according to the nymphal instar of *C. verbasici*. Our first hypothesis was that mixed diets constitute the optimal diet for nymph's development, followed by animal diets and plant diets. Our second hypothesis was that older instars have a better development and higher survival than younger instars on *low-quality* diets.

Material and methods

Arthropod and plant material

Mullein bugs came from a permanent rearing, initiated during the summer 2007, on potato plants *Solanum tuberosum* L. ('Norland') infested with potato aphids *Macrosiphum euphorbiae* (Thomas) (Hemiptera: Aphididae) and provided with pollen, Mediterranean flour moth *Ephesia kuehniella* Zeller (Lepidoptera: Pyralidae) eggs and honey + water solution (Uiterdijk, Vaal, & Bloomers, 1997). Rearing was conducted in growth chambers maintained at 23°C, 16 L:8 D and 60% RH. Aphids (*M. euphorbiae*) were collected from permanent laboratory rearing. Spider mites (*P. ulmi*) were collected from a pesticide-free orchard. Lepidopteran eggs were bought from Anatis Bioprotection, Inc. (Saint-Jacques-le-Mineur, Quebec, Canada).

Apple fruits, mature apple leaves and apple pollen were collected in pesticide-free 'Red Delicious' apple trees. Mature potato leaves and mature mullein leaves were collected from plants grown under laboratory conditions.

Plant, animal and mixed diets

The plant diets were composed of plant resources from the overwintering/spring host (apple fruits, leaves and pollen), the summer host (mullein leaves) and the laboratory rearing host (potato leaves). The animal diets consisted of resources collected in orchards (spider mites) or reared in the laboratory (lepidopteran eggs, potato aphids, conspecifics). The mixed diets consisted of resources collected in orchards (apple fruits and pollen) and reared or grown in the laboratory (living potato aphids, potato leaves, lepidopteran eggs). The diets tested as part of the second objective were composed of plant resources from the overwintering/spring host (apple pollen and fruits of two cultivars) and resources reared or grown in the laboratory (potato aphids, potato leaves and conspecifics).

Experimental units and assessment of immature survivorship and development

In this study, each experimental unit consisted of one *C. verbasici* nymph reared in Petri dish (diam. = 10 cm) with one diet + agar gel + water freely available (chimney Petri). All diets were placed on agar gel to prevent dehydration and were renewed every two days to prevent mouldiness. Each treatment (diet) was repeated 20 times. Experimental units were placed in growth chambers at 23°C, 16 L:8 D and 60% RH. The nymphal instars were identified by shape, size, colour and setigerous spots (Leonard, 1915). The stage of the nymphs and their survival were determined every 24 h until they reached adulthood or died. The presence of exuvia indicated successful

moulting. Survival and developmental time were measured for the nymphs. Adults were sexed and weighed. The diets were provided *ad libitum*. According to Arnoldi et al. (1992), one *C. verbasci* adult has a daily consumption of 1.20 green apple aphid or 2.87 European red mite.

Evaluation of diet quality

In this experiment, first nymphal instars from the permanent rearing were placed individually in Petri dishes with different diets. A diet composed of agar gel only was tested as a negative control.

Six plant diets were tested: one apple fruit ('Red Delicious'; diam. = 7–9 mm), one apple leaf (length = 6 cm), one potato leaf (length = 6 cm), one mullein leaf (length = 6 cm), apple pollen (5–10 mg) and one apple fruit + apple pollen.

Five animal diets were tested: eggs of the Mediterranean flour moth *E. kuehniella* (5–10 mg), eggs of the Angoumois grain moth *Sitotroga cerealella* Olivier (Lepidoptera: Pyralidae) (5–10 mg), 10 frozen spider mite (*P. ulmi*) adults, five frozen aphids (*M. euphorbiae*) of various instars and five frozen mullein bug nymphs of various instars (to evaluate cannibalism). Animal prey were frozen in order to avoid the presence of plant material in the test (to maintain them alive). Frozen insects were killed by keeping them at -10°C for a few days.

Three mixed diets were also evaluated: five living aphids (*M. euphorbiae*) + one potato leaf, one apple fruit ('Red Delicious'; diam. = 7–9 mm) + five living aphids (*M. euphorbiae*) + one potato leaf, and rearing diet (potato leaf + living aphids *M. euphorbiae* + *Ephestia* eggs + apple pollen) as a positive control.

Influence of the nymphal instar

In this experiment, mullein bug nymphs of first, third or fifth instar from the permanent rearing were placed individually in Petri dishes to compare the effect of selected diets on the different instars.

Six diets were tested: one 'Red Delicious' fruit (diam. = 7–9 mm; cultivar susceptible to damage) for first, third and fifth nymphal instars; one 'Honeycrisp' fruit (diam. = 7–9 mm; cultivar less susceptible to damage) for first and third nymphal instars; apple pollen (5–10 mg) for first and third nymphal instars; five living aphids (*M. euphorbiae*) + one potato leaf for first and third nymphal instars; five frozen mullein bug nymphs of various instars (cannibalism) for first and third nymphal instars; the rearing diet (potato leaf + living aphids *M. euphorbiae* + *Ephestia* eggs + apple pollen) as a control for first, third and fifth nymphal instar.

Data analysis

All analyses were carried out with the statistical software JMP® for Windows, version 11 (SAS Institute, 2013).

Survival of nymphal instars and adults were compared with a likelihood ratio *G*-test followed by multiple comparisons (Sokal & Rohlf, 1981). Since multiple tests were involved with this research design, a correction using the Holm–Bonferroni procedure has been completed to obtain a more conservative α ($p < \alpha/(m - 1)$) (Holm, 1979). The mean developmental time per diet for each nymphal instar (not including

the individuals who died before reaching the next stage) was analysed by the non-parametric Kruskal–Wallis test followed by the Dunn multiple comparison test (unequal group sizes). The survival duration, defined by the number of days an individual survived independently of the stage reached, was analysed by the non-parametric Kruskal–Wallis test followed by the Steel–Dwass pairwise multiple comparison test (equal group sizes). Adult weight and developmental time by sex were analysed using a non-parametric Wilcoxon test. Female and male weight and developmental time per diet were analysed by a non-parametric Kruskal–Wallis test followed by the Dunn multiple comparison test.

A development index was calculated by averaging a number attributed at each stage of death (1 = first instar, 2 = second instar, 3 = third instar, 4 = fourth instar, 5 = fifth instar, 6 = adult). It allows for a specific diet to evaluate the average stage reached by the individuals. Development index per diet was analysed by a non-parametric Kruskal–Wallis test followed by the Steel–Dwass pairwise multiple comparison test.

Percentage of survival to next instar and percentage of survival to adulthood by nymphal instar (first, third or fifth) for each diet were analysed using a χ^2 test and a Bonferroni correction. Development index per nymphal instar were analysed by a non-parametric Kruskal–Wallis test followed by the Steel–Dwass pairwise multiple comparison test.

Results

Evaluation of diet quality

Adult survival (% reached), weight and developmental time

Adult survival (Table 1). Only eight diets of 15 allowed at least one nymph to reach adulthood: mullein leaf, apple fruit + apple pollen, *Ephestia* eggs, *Sitotroga* eggs, frozen aphids, living aphids + potato leaf, apple fruit + living aphids + potato leaf and rearing diet. Frozen aphids and living aphids + potato leaf had significantly less adult survival compared with rearing diet, but not apple fruit + apple pollen, mullein leaf, *Ephestia* eggs, *Sitotroga* eggs and apple fruit + living aphids + potato leaf (*G*-test: $\chi^2 = 100.136$; *df* = 14; *p* < .0001).

Adult weight (Table 2). For all diets, adult weight was not different for males and females (Wilcoxon test: $\chi^2 = 3.5418$; *df* = 1; *p* = .0598). Females were heavier when reared on *Ephestia* eggs than on apple fruit + apple pollen, mullein leaf and frozen aphids (Kruskal–Wallis test: $\chi^2 = 26.5368$; *df* = 7; *p* = .0004) (Table 2). Males were heavier when produced on rearing diet than on apple fruit + apple pollen and mullein leaf (Kruskal–Wallis test: $\chi^2 = 17.2721$; *df* = 5; *p* = .0040) (Table 2).

Adult developmental time (Table 2). For all diets, adult developmental time was not different for males and females (Wilcoxon test: $\chi^2 = .1613$; *df* = 1; *p* = .6880). Female developmental time was lower when produced on rearing diet and *Ephestia* eggs than on apple fruit + apple pollen (Kruskal–Wallis test: $\chi^2 = 24.9189$; *df* = 7; *p* = .0008) (Table 2). Male developmental time was not different when comparing all diets (Kruskal–Wallis test: $\chi^2 = 24.9189$; *df* = 7; *p* = .0008) (Table 2).

Nymphal instars survival (% reached) (Table 1)

Agar gel, apple fruit, apple leaf and potato leaf allowed mullein bugs to reach the second nymphal instar, but not the third instar. Mullein leaf sustained development

Table 1. Mean percentage of first nymphal instar mullein bugs that reached each instar during their development on respective diets.

Diet	Treatment	% survival				
		N2	N3	N4	N5	Adult
Control	Agar gel	15 ^{de}	0 ^d	0 ^d	0 ^c	0 ^c
Plant	Apple fruit	10 ^e	0 ^d	0 ^d	0 ^c	0 ^c
	Apple leaf	15 ^{de}	0 ^d	0 ^d	0 ^c	0 ^c
	Potato leaf	20 ^{de}	0 ^d	0 ^d	0 ^c	0 ^c
	Mullein leaf	80 ^{abc}	45 ^{abcd}	35 ^{bcd}	30 ^{bc}	25 ^{abc}
	Apple pollen	90 ^{ab}	60 ^{ab}	10 ^{bcd}	0 ^c	0 ^c
Animal	Apple fruit + apple pollen	90 ^{ab}	65 ^{ab}	55 ^{abc}	50 ^{ab}	50 ^{ab}
	<i>Ephestia</i> eggs	70 ^{abcd}	50 ^{abc}	50 ^{abc}	45 ^{abc}	40 ^{abc}
	<i>Sitotroga</i> eggs	90 ^{ab}	70 ^{ab}	60 ^{ab}	50 ^{ab}	45 ^{abc}
	Frozen spider mites	30 ^{cde}	0 ^d	0 ^d	0 ^c	0 ^c
	Frozen aphids	55 ^{abcde}	45 ^{abcd}	35 ^{bcd}	30 ^{bc}	10 ^{bc}
Mixed	Frozen conspecifics	60 ^{abcde}	5 ^{cd}	5 ^{cd}	0 ^c	0 ^c
	Living aphids + potato leaf	35 ^{bcde}	25 ^{bcd}	20 ^{bcd}	10 ^{bc}	10 ^{bc}
	Apple fruit + living aphids + potato leaf	45 ^{abcde}	30 ^{bcd}	30 ^{bcd}	20 ^{bc}	20 ^{abc}
	Rearing diet	95 ^a	95 ^a	95 ^a	90 ^a	70 ^a

Numbers within a column followed by the same letter do not differ significantly (*G*-test; $p < .05/(m - 1)$).

Table 2. Mean (\pm SE) weight and developmental time for male and female adults (from first nymphal instar).

Sex	Diet	Treatment	<i>n</i>	Weight (μ g)	Developmental time (days)
Female	Plant	Mullein leaf	2	535 (\pm 5) ^b	18 (\pm 0) ^{ab}
		Apple fruit + apple pollen	6	635 (\pm 18) ^b	18.8 (\pm 0.8) ^b
	Animal	<i>Ephestia</i> eggs	6	995 (\pm 43) ^a	12.5 (\pm 0.3) ^a
		<i>Sitotroga</i> eggs	4	860 (\pm 24) ^{ab}	14.5 (\pm 0.9) ^{ab}
		Frozen aphids	2	515 (\pm 45) ^b	16 (\pm 1) ^{ab}
	Mixed	Living aphids + potato leaf	2	745 (\pm 65) ^{ab}	18 (\pm 1) ^{ab}
		Apple fruit + living aphids + potato leaf	2	695 (\pm 25) ^{ab}	19.5 (\pm 1.5) ^{ab}
		Rearing diet	9	822 (\pm 28) ^{ab}	13.7 (\pm 0.6) ^a
Male	Plant	Mullein leaf	3	530 (\pm 47) ^{b'}	17.3 (\pm 1.2) ^{a'}
		Apple fruit + apple pollen	4	565 (\pm 45) ^{b'}	17 (\pm 1.1) ^{a'}
	Animal	<i>Ephestia</i> eggs	2	825 (\pm 5) ^{ab'}	13 (\pm 3) ^{a'}
		<i>Sitotroga</i> eggs	5	730 (\pm 17) ^{ab'}	15.8 (\pm 0.9) ^{a'}
		Frozen aphids	0	–	–
	Mixed	Living aphids + potato leaf	0	–	–
		Apple fruits + living aphids + potato leaf	2	620 (\pm 0) ^{ab'}	20.5 (\pm 1.5) ^{a'}
		Rearing diet	5	804 (\pm 21) ^{a'}	13 (\pm 0.6) ^{a'}

Numbers within a column followed by the same letter do not differ significantly (Kruskal–Wallis test, $p < .05$; Dunn test, $p < .05$); males and females were analysed separately.

of mullein bugs until adulthood. Apple pollen allowed development to fourth nymphal instar, but not the fifth instar. Apple fruit + apple pollen, *Ephestia* eggs and *Sitotroga* eggs permitted mullein bugs to reach adulthood. Frozen spider mites allowed nymphs to reach the second instar, but not the third instar. Frozen aphids sustained development of mullein bugs until adulthood. Frozen conspecifics permitted nymphs to reach the fourth instar, but not the fifth instar. Living aphids + potato leaf, apple fruit + living aphids + potato leaf and rearing diet allowed mullein bugs to reach adulthood.

Nymphal instar developmental time and survival duration

Second instar developmental time (Table 3) was significantly lower on rearing diet than on mullein leaf, apple pollen, apple fruit + apple pollen, and apple fruit + living aphids + potato leaf (Kruskal–Wallis test: $\chi^2 = 30.1039$; $df = 9$; $p = .0004$), but not different from *Ephestia* eggs, *Sitotroga* eggs, frozen aphids, frozen conspecifics and living aphids + potato leaf.

Third instar developmental time (Table 3) was significantly lower on *Ephestia* eggs than on apple fruit + apple pollen (Kruskal–Wallis test: $\chi^2 = 23.2690$; $df = 9$; $p = .0056$), but not different from mullein leaf, apple pollen, *Sitotroga* eggs, frozen aphids, frozen conspecifics, living aphids + potato leaf, apple fruit + living aphids + potato leaf and rearing diet.

Fourth instar developmental time (Table 3) was significantly lower on rearing diet and *Ephestia* eggs than on mullein leaf and apple fruit + apple pollen (Kruskal–Wallis test: $\chi^2 = 34.7114$; $df = 7$; $p < .0001$), but not different on *Sitotroga* eggs, frozen aphids, living aphids + potato leaf and apple fruit + living aphids + potato leaf.

Fifth instar developmental time (Table 3) was significantly lower on rearing diet and *Ephestia* eggs than on mullein leaf and apple fruit + apple pollen (Kruskal–Wallis test: $\chi^2 = 33.3057$; $df = 7$; $p < .0001$), but not different on *Sitotroga* eggs, frozen aphids, living aphids + potato leaf and apple fruit + living aphids + potato leaf.

Survival duration (Table 3) was significantly longer on rearing diet than on agar gel, apple fruit, apple leaf, potato leaf, apple pollen, frozen spider mites, frozen aphids, frozen conspecifics and living aphids + potato leaf (Kruskal–Wallis test: $\chi^2 = 145.3841$; $df = 14$; $p < .0001$), but not different on the other diets. Survival was significantly shorter on agar gel than on mullein leaf, apple pollen, apple fruit + apple pollen, *Ephestia* eggs, *Sitotroga* eggs, frozen aphids, frozen conspecifics, apple fruit + living aphids + potato leaf and rearing diet, but not different on the other diets.

Development index (Figure 1)

Development index was significantly different depending of the diet (Kruskal–Wallis test: $\chi^2 = 135.5601$; $df = 14$; $p < .0001$). Development index was significantly higher on rearing diet than on other diets, except apple fruit + apple pollen, *Ephestia* eggs and *Sitotroga* eggs. Development index was significantly smaller on agar gel, apple fruit, apple leaf, potato leaf, frozen spider mites, frozen aphids, frozen conspecifics, living aphids + potato leaf and apple fruit + living aphids + potato leaf than on other diets. Development indexes on apple pollen and mullein leaf were intermediate.

Table 3. Mean developmental time (days) for each nymphal instar (\pm SE) and survival duration (\pm SE).

Diet	Treatment	Developmental time (days)				Survival duration
		N2	N3	N4	N5	
Control	Agar gel	–	–	–	–	1.0 (\pm 0.1) ^g
Plant	Apple fruit	–	–	–	–	1.6 (\pm 0.2) ^{defg}
	Apple leaf	–	–	–	–	1.2 (\pm 0.2) ^{fg}
	Potato leaf	–	–	–	–	1.5 (\pm 0.3) ^{efg}
	Mullein leaf	3.6 (\pm 0.4) ^b	2.4 (\pm 0.4) ^{ab}	4.3 (\pm 0.4) ^b	5.2 (\pm 0.2) ^b	9.7 (\pm 1.7) ^{abc}
	Apple pollen	3.3 (\pm 0.3) ^b	3.5 (\pm 0.5) ^{ab}	–	–	6.8 (\pm 0.6) ^{bc}
	Apple fruit + apple pollen	3.3 (\pm 0.2) ^b	3.4 (\pm 0.3) ^b	3.9 (\pm 0.3) ^b	5.2 (\pm 0.2) ^b	11.8 (\pm 1.5) ^{ab}
Animal	<i>Ephestia</i> eggs	2.5 (\pm 0.2) ^{ab}	1.8 (\pm 0.2) ^a	2.3 (\pm 0.2) ^a	3.9 (\pm 0.2) ^a	7.1 (\pm 1.2) ^{abcd}
	<i>Sitotroga</i> eggs	2.9 (\pm 0.1) ^{ab}	2.9 (\pm 0.2) ^{ab}	3.0 (\pm 0.1) ^{ab}	4.4 (\pm 0.2) ^{ab}	10.8 (\pm 1.1) ^{ab}
	Frozen spider mites	–	–	–	–	2.1 (\pm 0.3) ^{cdefg}
	Frozen aphids	2.8 (\pm 0.3) ^{ab}	2.6 (\pm 0.4) ^{ab}	3.7 (\pm 0.3) ^{ab}	4.0 (\pm 0) ^{ab}	6.1 (1.3) ^{bcdef}
	Frozen conspecifics	3 (\pm 0) ^{ab}	2.0 (\pm 0) ^{ab}	–	–	3.3 (\pm 0.5) ^{cdef}
Mixed	Living aphids + potato leaf	2.6 (\pm 0.2) ^{ab}	2.0 (\pm 0.6) ^{ab}	3.0 (\pm 0) ^{ab}	4.0 (\pm 0) ^{ab}	4.7 (\pm 1.2) ^{bcdefg}
	Apple fruit + living aphids + potato leaf	3.8 (\pm 0.6) ^b	3.0 (\pm 0.4) ^{ab}	3.5 (\pm 0.3) ^{ab}	4.8 (\pm 0.3) ^{ab}	6.7 (\pm 1.6) ^{abcde}
	Rearing diet	2.1 (\pm 0.1) ^a	2.2 (\pm 0.2) ^{ab}	2.6 (\pm 0.1) ^a	3.9 (\pm 0.1) ^a	12.6 (\pm 0.7) ^a

Numbers within a column followed by the same letter do not differ significantly (Kruskal–Wallis test, $p < .05$; Dunn test, $p < .05$; Steel–Dwass test, $p < .05$).

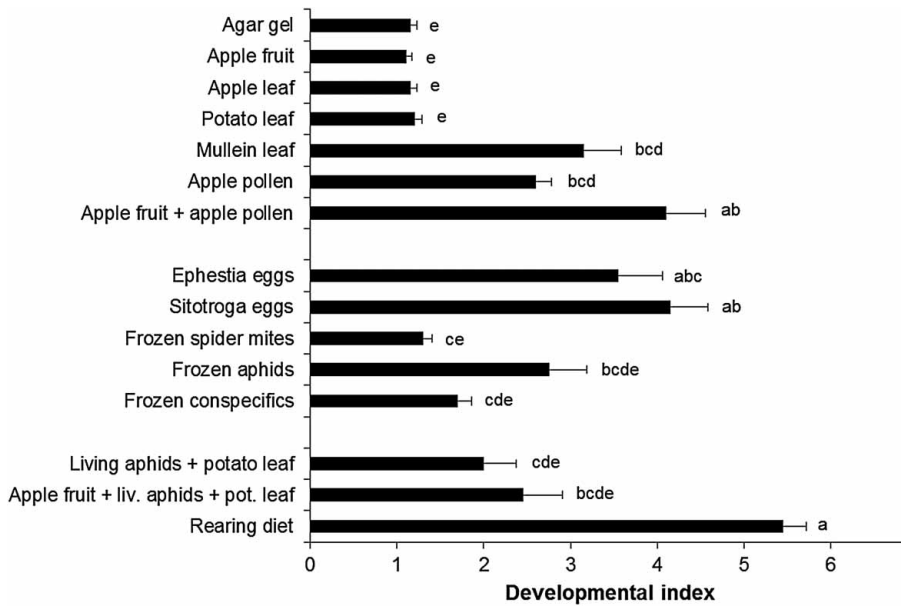


Figure 1. Developmental index (\pm SE) of mullein bugs per (a) plant diets, (b) animal diets and (c) mixed diets. Diets with the same letters are not significantly different (Kruskal–Wallis test, $p < .05$; Steel–Dwass test, $p < .05$).

Influence of the nymphal instar

Survival to the next instar (depending of the starting instar) (Figure 2(a))

Survival to the next instar on rearing diet was not different when nymphs were reared from the first, third or fifth instar (χ^2 -test: $\chi^2 = 6.252$; $df = 2$; $p = .0439$). Survival of the mullein bug to the next nymphal instar on ‘Red Delicious’ fruit was significantly higher when reared from the third instar or fifth instar than when reared from first instar nymphs (χ^2 -test: $\chi^2 = 31.667$; $df = 2$; $p < .0001$), but not different between third instar and fifth instar. Survival to the next nymphal instar on ‘Honeycrisp’ fruit was not different when reared from the third instar (χ^2 -test: $\chi^2 = 1.758$; $df = 1$; $p = .1848$) than nymphs reared from first instar nymphs. Survival to the next nymphal instar on frozen conspecifics was not different when reared from the third instar (χ^2 -test: $\chi^2 = 1.905$; $df = 1$; $p = .1675$) than nymphs reared from first instar nymphs. Survival to the next nymphal instar on living aphids + potato leaf was significantly higher when reared from the third instar (χ^2 -test: $\chi^2 = 12.907$; $df = 1$; $p = .0003$) than nymphs reared from first instar nymphs. Survival to the next nymphal instar on apple pollen was not different when reared from the third instar (χ^2 -test: $\chi^2 = 2.105$; $df = 1$; $p = .1468$) than nymphs reared from first instar nymph.

Survival to adulthood (depending of the starting instar) (Figure 2(b))

Apple pollen and frozen conspecifics allowed at least one nymph to reach adulthood when reared from the third nymphal instar, but not when reared from the first nymphal instar. Adult survival on living aphids + potato leaf was significantly higher when reared from the third instar (χ^2 -test: $\chi^2 = 19.798$; $df = 1$; $p < .0001$) than nymphs

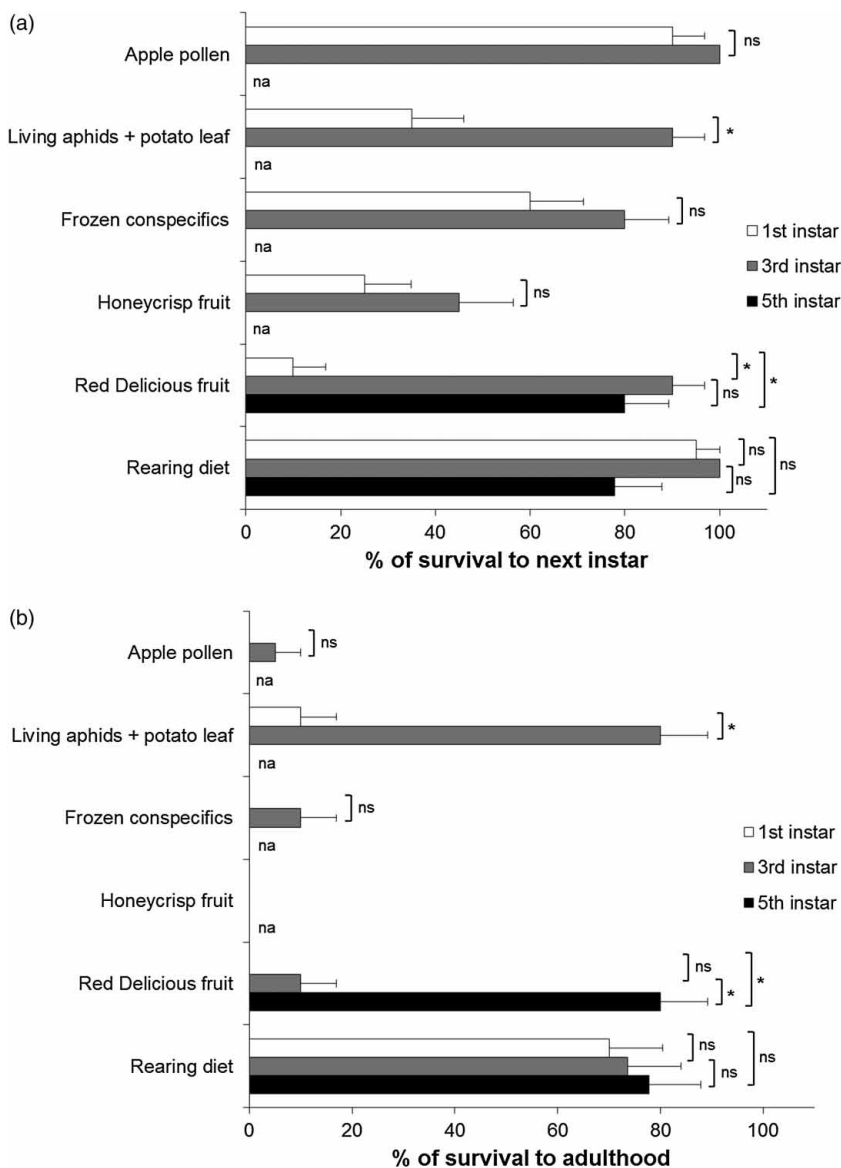


Figure 2. (a) Percentage of nymphs surviving and reaching the next nymphal instar (experiments began with first, third or fifth nymphal instar from the permanent rearing). For each diet, an asterisk indicates that the percentage survival to the next instar for nymphs reared from the first, third and/or fifth instar was significantly different (χ^2 -test, $p > .05/m$). (b) Percentage of nymphs surviving to adulthood (experiments began with first, third or fifth nymphal instar from the permanent rearing). For each diet, an asterisk indicates that the percentage of adults reared from first, third and/or fifth nymphal instars was significantly different (χ^2 -test, $p > .05/m$). The fifth nymphal instar was only been tested for ‘Red Delicious’ fruit and rearing diet.

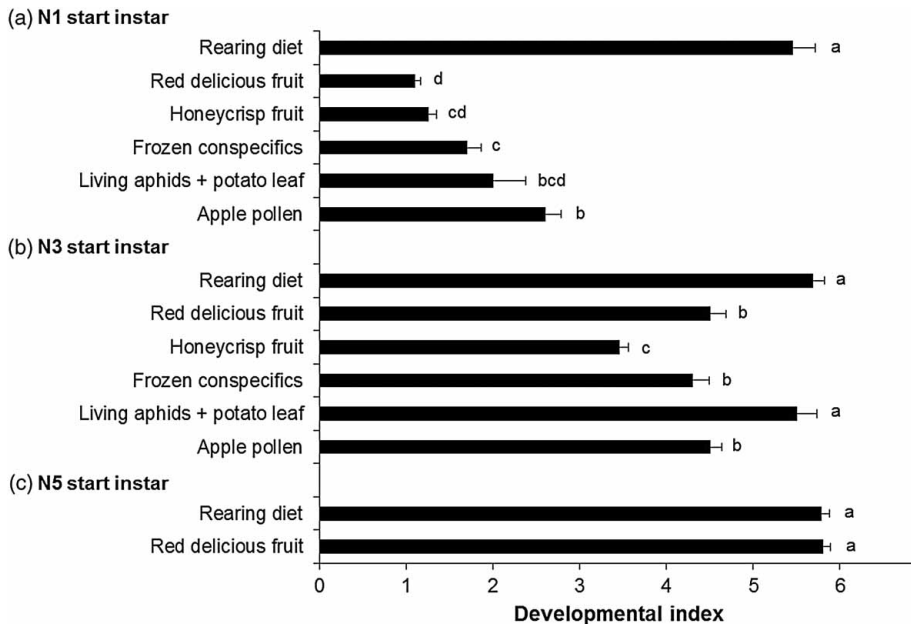


Figure 3. Developmental index (\pm SE) of mullein bugs reared from (a) first nymphal instar, (b) third nymphal instar and (c) fifth nymphal instar using different diets. For each instar, diets with the same letters are not significantly different (Wilcoxon/Kruskal–Wallis test, $p < .05$; Steel–Dwass test, $p < .05$).

reared from first instar nymphs. ‘Honeycrisp’ fruit was unable to sustain development of adults when reared from the first nor the third nymphal instar. Adult survival on ‘Red Delicious’ fruit was significantly lower when reared from the first instar or third instar than when reared from fifth instar nymphs (χ^2 -test: $\chi^2 = 36,190$; $df = 2$; $p < .0001$). Adult survival on rearing diet was not different when nymphs were reared from the first, third or fifth instar (χ^2 -test: $\chi^2 = 0,296$; $df = 2$; $p = .8626$).

Development index (Figure 3)

For the first nymphal instar (Figure 3(a)), development index was significantly higher on rearing diet than on other diets (Kruskal–Wallis test: $\chi^2 = 68.6814$; $df = 5$; $p < .0001$).

For the third nymphal instar (Figure 3(b)), the index was significantly higher on rearing diet and living aphids + potato leaf, than on ‘Red Delicious’ fruit, frozen conspecifics and apple pollen, and was smaller on ‘Honeycrisp’ fruit (Kruskal–Wallis test: $\chi^2 = 59.1311$; $df = 5$; $p < .0001$).

For the fifth nymphal instar (Figure 3(c)), the index was not different on rearing diet than on ‘Red Delicious’ fruit (Wilcoxon test: $\chi^2 = .0274$; $df = 1$; $p < .8685$).

Discussion

The different diets had different values for the zoophytophagous mullein bug. The diets could be classified either as *high-quality* diets (>50% adults, shorter

developmental time, bigger adults and higher development index), *medium-quality* diets (30–50% adults, high development index), *low-quality* diets (<30% adults, longer developmental time and medium development index) or *inappropriate* diets (when no nymphs reached adulthood). The first hypothesis that mixed diets constitute the optimal diet for nymph's development, followed by animal diets and plant diets was not confirmed.

Concerning the plant diets, apple fruit, apple leaf and potato leaf were *inappropriate* diets and had the same value as that of agar gel (control). Aubry, Cormier, Chouinard, and Lucas (2011) also found that first instar nymphs of *C. verbasci* were unable to develop on apple fruit regardless of the cultivar. Similar results have been found with other zoophytophagous insects (Hemiptera: Miridae) on tomato leaves: *Dicyphus tamaninii* Wagner (Lucas & Alomar, 2001), *Dicyphus hesperus* Knight (Gillespie, McGregor, Qiring, & Foisy, 1999) and *Macrolophus melanotoma* Costa (Gillespie et al., 1999; Kaspar, 1982). However, Perdakis and Lykouressis (2000) reported that *Macrolophus pygmaeus* (Rambur) (Hemiptera: Miridae) survived on different plant leaves, including tomato leaves. Nevertheless, 10–20% nymphs were able to moult to the second instar without any food source. It is therefore possible that first instar nymphs had either enough reserves to moult to the following instar or could survive on water only, as hypothesised by Lucas and Alomar (2001) with *D. tamaninii*. Mullein leaf (summer host) was a *low-quality* diet to reach adulthood but was an excellent diet for younger nymphs as 80% reached the second instar compared with 15% on apple leaf (spring host). Similarly, *D. hesperus* nymphs were able to complete their development on mullein alone, but not on the leaves of several other plant species (McGregor, Gillespie, Qiring, & Mitch, 1999; Sanchez, Gillespie, & McGregor, 2004). The mullein leaf may contain some nutrients unavailable in the potato leaf (laboratory rearing host) and the apple leaf and fruit (spring host). Apple pollen was an *inappropriate* diet and all nymphs died before reaching the fifth instar. Pollen is rich in proteins, lipids, carbohydrates and minerals, and consequently it is one of the most nutritious non-prey food sources for omnivorous predators (Jervis, Hawkins, & Kidd, 1996; Lundgren, 2009). However, a supplemental source of water is necessary for maximum fitness when pollen is the sole nutriment (De Clercq, Bonte, van Speybroeck, Bolckmans, & Deforce, 2005; Michaud & Grant, 2005). No nymphs reached adulthood when reared on apple pollen only, although water was provided. On the other hand, apple fruit + apple pollen was a *medium-quality* diet. Bartlett (1996) found that 95% of nymphs reached adulthood when fed on apple pollen + apple leaf, but used young nymphs collected in orchards that were probably older than first instar nymphs (24–48 h). Nymphs probably found water and other nutrients in plant tissue (e.g. apple fruit or apple leaf) to supplement apple pollen.

Concerning the animal diets, lepidopteran eggs constituted a *medium-quality* diet. In the literature, eggs of *E. kuehniella* constitute a high-quality food source for different insect predators (De Puyseleir, De Man, Höfte, & De Clercq, 2013). However, a diet composed of lepidopteran eggs must be supplemented with other resources to maximise development to adulthood. For example, only 6% of the mirid *D. hesperus* developed to adults when fed solely on *E. kuehniella* eggs; if both *E. kuehniella* eggs and tomato leaves were provided, 97% of nymphs reached adulthood (Gillespie & McGregor, 2000). In our study, frozen aphids were a *low-quality* diet. Similar results were obtained when nymphs were reared on living aphids, despite the presence of plant support. Frozen spider mites (natural prey in the

orchard) were an *inappropriate* diet. Our observations indicate that live motile forms were consumed more often by nymphs than frozen spider mites (personal observations). Moreover, Smith and Borden (1991) reared *C. verbasci* with living *T. urticae* on seedlings. Furthermore, Provost, Lucas, Coderre, and Chouinard (2006) showed that prey suitability was affected by prey mobility for a coccinellid. In our study, frozen conspecifics were an *inappropriate* diet. However, food quality has been identified as a significant factor in the occurrence of cannibalism (Fox, 1975; Joyner & Gould, 1987; Polis, 1981). Castane, Iriarte, and Lucas (2002) suggested that if cannibalism is a response to some deficiency, it may disappear once the necessary nutrients are acquired.

The *high-quality* rearing diet was composed of water, plant tissues (potato leaf), protein-rich components (apple pollen and *Ephestia* eggs) and prey (living *M. euphorbiae*). Uiterdijk et al. (1997) showed that mullein bug development was slower when *Sitotroga* eggs were removed from the rearing diet because younger instars handle these eggs much more easily than prey. In our mixed diet composed of living aphids + potato leaf, only 10% of nymphs reached adulthood and most mortality occurred at the first nymphal instar. Uiterdijk et al. (1997) observed that young *C. verbasci* nymphs had some difficulty to survive in the presence of living aphids on potato plants. The authors noted that some aphids kicked away mullein bug nymphs. This could explain our results although *C. verbasci* is a predator of aphids. All three mixed diets sustained the development to adulthood. Moreover, apple fruit + apple pollen being a *medium-quality* diet, apple pollen could be used as a substitute for preys when these are scarce.

The second hypothesis – that older instars have a better development and higher survival than younger instars on low-quality diets – was validated with most diets. The suitability of the different diets tested increased as the nymphal instars increased. Apple pollen and frozen conspecifics, *inappropriate* diets for the first nymphal instar, were *low-quality* diets for the third instar. Living aphids + potato leaf, a *low-quality* diet for the first nymphal instar, became a *high-quality* diet for the third nymphal instar. ‘Red Delicious’ fruit constituted an *inappropriate* diet for the first instar, but a *low-quality* diet for the third instar and a *high-quality* diet for the fifth nymphal instar. ‘Honeycrisp’ fruit constituted an *inappropriate* diet regardless of nymphal instar (first or third). The *high-quality* value of the rearing diet did not change when nymphs were reared starting with first, third or fifth instars. Our results suggest that older nymphs will develop and survive on ‘Red Delicious’ fruit in the field, when pollen or prey are unavailable, but not on ‘Honeycrisp’ fruit. It is possible that older nymphs had some nutritional reserves, as they had been reared on the same diet in the laboratory during previous instars. However, ‘Honeycrisp’ fruit, which has low susceptibility to mullein bug damage, did not allow development to adulthood despite the fact that previous instars have been reared in the same conditions. ‘Red Delicious’ is not only a susceptible cultivar to damage (Thistlewood, McMullen, & Borden, 1989) but can also sustain development of older instars to adulthood. Previous studies showed that arthropod preys are necessary for younger mullein bug nymphs, but not for older instars that have been fed prey in their early instars (McMullen & Jong, 1970; Niemczyk, 1978). Similarly, our results showed that third instar nymphs can reach adulthood when fed on a plant diet without animal resources (e.g. apple pollen or ‘Red Delicious’ fruit). However, adult survival is higher when prey are present as living aphids + potato leaf was a *high-quality* diet for third instar.

Among omnivorous insect species, phytophagy or zoophagy can be opportunistic (e.g. compensation for nutritional deficiencies), or necessary (e.g. essential nutrients for development) (Alomar, 2007). The poor development of mullein bug fed with *low-quality* diets may be explained by the lack or the insufficient levels of some nutritional components in each diet, or by an inefficient use of the nutrients in the food source. All of the animal diets included in our study (except frozen spider mites) provided more than 50% survival of the second instar, suggesting that a basal level of plant feeding is required to sustain vital functions in younger *C. verbasci* nymphs. According to our results demonstrating that phytophagy is associated with lesser performance for nymphal development (e.g. longer developmental time, smaller adults), *C. verbasci* may be considered as zoophytophagous (according to Fauvel, 1999) rather than phytozoophagous (Strawinski, 1964). However, even if plant diets are of *low-quality* (except apple fruit + apple pollen), they can function as an egg-laying substrate and can also serve as a source of moisture and supplementary nutrients for predatory heteropterans (Coll, 1998; Coll & Guershon, 2002; Dolling, 1991; Riudavets & Castane, 1998; Wheeler, 2001).

This study provides new information on the nutritional ecology of the mullein bug. In apple orchards, the first generation hatches in the spring on apple trees and nymphs have the opportunity to feed on apple fruit supplemented by apple pollen or prey to reach adulthood. In the summer, the nymphs of the subsequent generations live on mullein plant and can only consume mullein leaves to reach adulthood. In laboratory rearing conditions, nymphs can reach adulthood on diets composed of lepidopteran eggs or aphids only. However, a whole mixed diet (composed of water, plant tissues, protein-rich components and preys) is required to maximise the developmental success of the insect. Finally, assessing the value of the different resources for *C. verbasci* has direct implications for the potential use of food supplements in biological control programmes or in laboratory rearing (e.g. replacement of potato plants by mullein).

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