

ECOLOGY, BEHAVIOR AND BIONOMICS

Influence of Previous Experience on the Preference, Food Utilization and Performance of *Ascia monuste orseis* Wild Larvae (Godart) (Lepidoptera: Pieridae) for Three Different Hosts

AF K SANTANA, FS ZUCOLOTO

Lab de Nutrição e Comportamento Alimentar de Insetos, Depto de Biologia, FFCLRP, Univ de São Paulo, Ribeirão Preto, SP, Brasil

Keywords

Brassica oleraceae, Brassicaceae, *Eruca sativa*, feeding behavior, specialist larva

Correspondence

FERNANDO S ZUCOLOTO, Lab de Nutrição e Comportamento Alimentar de Insetos, Depto de Biologia, FFCLRP, USP, 14049-901, Av. Bandeirantes, 3900, Ribeirão Preto, SP, Brasil; zucoloto@ffclrp.usp.br

Edited by Ângelo Pallini – UFV

Received 28 October de 2010 and accepted 20 August 2011

Abstract

The exhaustion of food resources which occurs during the ontogenetic growth of *Ascia monuste orseis* (Godart) results in the dispersion of older larvae to nearby plants in order to complete their development, which might expose these animals to the nutritional variation of the hosts found. This study aimed to verify whether the food ingested in the beginning of the development influences the larvae host preference and whether the shift to a new host can affect the digestion and performance of *A. monuste orseis*, using two natural hosts: kale (*Brassica oleracea* var. *acephala*) and rocket (*Eruca sativa*), or kale and cabbage (*B. oleracea* var. *capitata*). Larvae were reared throughout their larval development on a single host or on two different hosts. When a host change was tested, larvae were reared for four instars on a host, and offered the other host plant in the fifth instar. Development time, percentage of pupation and emergence, pupal weight, fecundity and digestive indices were evaluated. The change in feeding preference for kale and for rocket in the fourth instar, when those were the original hosts, respectively, shows that prior experience plays a major role in food preference of immature *A. monuste orseis*. The shift can be beneficial for larval development, depending on the order of the hosts; in general, larvae fed on kale at the end of the development showed better performance. Our results presented strong evidence of a considerable phenotypic plasticity in *A. monuste orseis* for host preferences.

Introduction

The use of different species of host plants with varied physical characteristics and nutritional contents can influence the survival, growth, development time and reproduction of herbivorous insects, as well as their host choice behavior (Scriber & Slansky 1981, Awmack & Leather 2002). The initial exposure to a certain host allows for the access to information by the insects and may result in a change in their preference (Grabstein &

Scriber 1982, Saxena & Schoonhoven 1982). Previous experience, therefore, may play an important role in the process of plant recognition and in the host preference by insects (Dethier 1982).

The term preference involves a choice situation which relates a hierarchy of species of plants that can be used as hosts (Thompson & Pellmyr 1991). In addition to the substances of recognition (secondary substances), other conditions provide a choice among viable hosts, such as the nitrogen content (White 1984, Bittencourt-Rodrigues

& Zucoloto 2005), the plant physical characteristics (Bittencourt-Rodrigues & Zucoloto 2005), and the amount of attractive volatile substances (Chew & Renwick 1995) among others. The preference for a previously experienced food (i.e. induction) has been reported in some species of phytophagous insects, such as *Manduca sexta* (L.) (Lepidoptera: Sphingidae) and *Anastrepha obliqua* (Macquart) (Diptera: Tephritidae) (Saxena & Schoonhoven 1982, Leal & Zucoloto 2008).

Previous experience can influence both decision and performance of the insect in a subsequent encounter (Dethier 1982). The type of food consumed, the quantity, and the efficiency with which it is used by the insect are factors that determine the availability of nutrients for their growth during a certain period of development (Browne & Raubenheimer 2003). Some studies have shown deleterious effects of host shift on the performance of immature insects (e.g., Scriber 1981, Cunningham & West 2001), such as the increase in the development time, temporary decrease in food consumption, suppression of growth rate, reduced use of food, lower pupal weight, and even mortality (Bernays & Bright 2001). However, other studies have demonstrated that the variability of resources may increase the biomass incorporation (Pfisterer *et al* 2003) or, depending on the sequence of hosts, that the immature may even be benefited (Stoyenoff *et al* 1994a, Moreau *et al* 2003). A diversified diet can improve the balance of nutrients and can increase the dilution of any host-derived secondary compound which is possibly toxic for the insect (Bernays *et al* 1994).

Larvae of *Ascia monuste orseis* (Godart) are crucifer specialists and important herbivores of Brassicaceae in the Neotropical region (Chew 1988). The first instars feed exactly in the place where the mother oviposited (Catta-Preta & Zucoloto 2003). For this reason, the selection of the host plant by females is crucial to the survival and adequate performance of the larvae. Field observations made it clear that last instars (4th and 5th) are able to move reasonably in the field and can even move from one cultivation to another (Catta-Preta & Zucoloto 2003). The increase in ingestion and the exhaustion of food resources which occur during larval development often result in larval dispersion to nearby plants in order to complete their development (Chew 1975, Barros-Bellanda & Zucoloto 2003). This behavior may expose larvae to the leaves with a varied nutritional value (Catta-Preta & Zucoloto 2003), which may differ in relation to the age (Bittencourt-Rodrigues & Zucoloto 2005), variety, and species.

Therefore, our main objectives were 1) to verify whether previous experience influences the preference of older larvae for different hosts, and 2) to assess whether the shift to leaves of different hosts, in a same ontogenetic stage, can affect the digestion and performance of *A. monuste orseis*. Our hypothesis is that larvae of *A. monuste*

orseis can modify the selection of the feeding host, depending on their recent feeding experiences and on the effect of this experience in their development.

Material and Methods

Eggs of *A. monuste orseis* were collected on kale leaves (*B. oleracea* var. *acephala*) deriving from a pesticide-free vegetable garden, located 100 m away from the Departamento de Biologia building (21° 05'S, 47°50'W), USP, Ribeirão Preto, Brazil. Leaves were taken to the laboratory and larvae were transferred to acrylic boxes (10 x 10 x 4 cm) lined with paper towel upon hatching (Felipe & Zucoloto 1993), and kept under controlled conditions (29°C ± 2°C; 75 ± 5% RH; and photophase of 14h) (Felipe & Zucoloto 1993, Barros & Zucoloto 1999). Only one of the following hosts was made available to the newly-hatched larvae: kale, rocket (*Eruca sativa*) or cabbage (*B. oleracea* var. *capitata*). Rocket has higher amounts of protein than kale, but cabbage and kale have similar amounts of protein (dry weight/mg) (Franco 2002). Plants were cultivated in separate pots in the same period and at the same substrate and only mature leaves (middle region of the plant) were offered to the larvae.

Effect of previous experience in the preference for different hosts

Newly-hatched larvae (NHL). Naïve, newly-hatched larvae were separated in groups: a) NHL placed to choose between kale and rocket (n = 10) and b) NHL placed to choose between kale and cabbage (n = 10). Ten NHL (10 larvae = one replicate) were placed in the center of the previously described acrylic boxes with two pieces of kale leaves and two of rocket leaves (or cabbage) of similar sizes (≈ 3.14 cm²) distributed in alternate corners in the boxes. After 24h, the pieces of food were removed and the number of larvae present in each one was counted. Data obtained were analyzed by Wilcoxon signed rank test with a significance level of 5%.

Larvae previously fed on kale, rocket or cabbage. Fourth instars were used in order to test the effect of prior food experience. Only one caterpillar per box was used in order to make sure that the food choice would reflect the host quality and not be due to a disturbance by other larvae (Dussutour *et al* 2007). Four experimental groups were set up: a) larvae fed on kale up to the end of the 3rd instar and then offered a choice between kale or rocket leaves (n = 10); b) larvae fed on rocket up to the end of the 3rd instar and then offered a choice between kale or rocket leaves (n = 10); c) larvae fed on kale up to the end of the 3rd instar and then offered a choice between kale or cabbage leaves (n = 10); and d) larvae fed on cabbage up to the end of the 3rd instar and then offered a choice between kale or cabbage

leaves ($n = 10$). The choice assays were carried out only after larvae molted to the 4th instar. Pieces of each host plant were placed in the corners of the boxes as early described. Pieces of similar sizes were placed in an incubator in order to obtain the original dry weight.

Larvae were observed in the beginning of the experiment and after 9h. The recorded variables were: the first leaf visited by the larva and the total amount of leaf consumed during the proposed time period (preference *sensu* Singer 2000). Additionally, the number of larvae which ingested only one type of host was observed. After the experimental period, the remaining pieces of leaves were dried at 80°C for 24h, and then compared to the dry weight of the original leaves for the calculation of the amount of food ingested by the larvae. The boxes were kept in incubators during all the experimental period, under the previously described condition.

The same experiment was run but with 5th instars instead. But as larvae at this age are faster and take a smaller period to choose their food, the experimental period used in this case was 6h. The data related to the first visit by the larvae were analyzed by the sign test and the ones concerning preferences were analyzed by the Wilcoxon signed rank test, both with significance level of 5%.

Effect of previous experience in food utilization. In order to test the effect of previous experience in *A. monuste orseis*, the food efficiency and the digestion indices obtained by the Slansky and Scriber method (1985) were measured: *approximate digestibility* (DA), *efficiency in the conversion of the ingested food* (ECI) and *efficiency in the conversion of the digested food* (ECD) were: $AD = [(ingested\ food - feces) / ingested\ food] \times 100$, $ECI = (incorporated\ biomass / ingested\ food) \times 100$, $ECD = [incorporated\ biomass / (ingested\ food - feces)] \times 100$. The experimental groups consisted of larvae fed with: a) kale throughout development (*k*), b) kale up to the end of the 4th instar, then rocket (*k-r*), c) rocket throughout development (*r*) and d) rocket up to the end of the 4th instar, then kale (*r-k*). The same procedure was used for the kale and cabbage hosts (*k*, *k-c*, *c* and *c-k*). Each group consisted of 10 boxes with seven larvae in each. One leaf/box (~150 cm²) was enough to feed larvae for 24h without competition (Barros-Bellanda & Zucoloto 2003). Leaves were renewed daily and treatments that required a shift in host plant were made on the first day of the 4th or 5th instar. For each instar, a new group of larvae was used.

Food consumption, production of feces and incorporated biomass were measured in the first 24h after host shift. Each measure was correspondent to one larvae individualized in standard glasses (5.5 cm diameter and 7 cm height) with the correspondent food. Experiments were conducted on the same conditions as earlier described.

The initial weight for each instar was calculated

by using the mean dry weight of three larvae in each box, separated at random, soon after food shift. The remaining larvae were individualized in the described glasses and were subjected to the treatments. Each leaf was folded lengthwise and had their edges jagged, so that the two halves of the leaf were nearly identical. One half was used as control to determine the initial weight and the other half was made available as food to the larva. Twenty-four hours later, the remaining leaf was weighed (Felipe & Zucoloto 1993), and food intake was correspondent to the difference between the initial and the final weight of the leaf offered to the larva. The excreted feces were collected and weighed, and the larva was frozen and weighed. The incorporated biomass corresponds to the difference between the initial and final weight of each larva. All vegetal and animal material was calculated based on the dry weight (mg), kept in incubators at 80°C for 24h (Felipe & Zucoloto 1993). The data were analyzed by the Kruskal-Wallis test with 5% of significance.

Effect of previous experience in larval performance. The development indices were used as performance parameters. The treatments described in the previous experiment were kept. When the focal individual went to the next instar, the duration of its phase was noted. The focal individual was the first larva of each box to molt. The development indices were: days up to the 4th instar, days from the fourth instar up to pupation, larval survival (number of pupae obtained as compared to the initial number of larvae), pupae development time (days), emergence rate (%), pupal weight (mg) and potential fecundity (number of oocytes). The boxes were checked twice daily (8 am and 5 pm). Ten young pupae (one per box, $n = 10$ /group) were separated immediately after pupation to determine the dry weight (mg); gender was not taken into account, as *A. monuste orseis* do not present sexual dimorphism in the pupal stage. In order to get the potential fecundity, female butterflies (one per box, $n = 10$ /group) were frozen after their emergence, dissected in saline solution (0.09%) for the removal of the ovarioles and their oocytes were counted under a stereomicroscope (Zago-Braga & Zucoloto 2004). These data were analyzed by the Mann-Whitney test with 5% of significance.

Results

Effect of previous experience in the preference for different hosts

Newly hatched larvae. NHL chose rocket instead of kale ($P = 0.04$) and in the test with kale and cabbage, NHL did not present any preference ($P = 0.8$) (Fig 1).

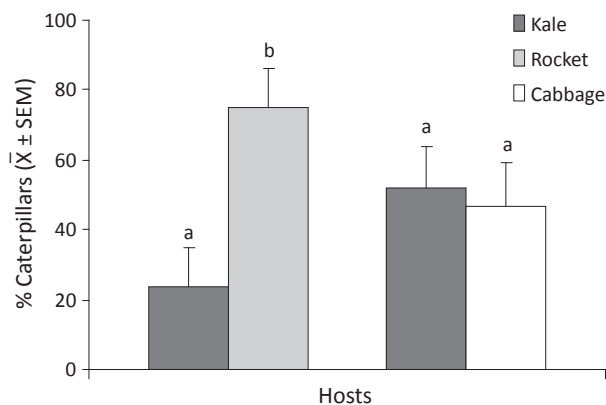


Fig 1 Feeding preference of newly hatched *Ascia monuste orseis* for different hosts. Bars pairs followed by different letters represent significant difference (Wilcoxon signed rank test, $P < 0.05$).

Larvae previously fed on kale, rocket or cabbage. There was no significant difference among the number of 4th instars which visited first kale or rocket ($P = 0.5$, kale as previous food; $P = 0.1$, rocket as previous food) (Fig 2a). However, a significant number of 5th instars visited rocket first, independently of their prior experience ($P = 0.005$, kale as previous food; $P < 0.001$, rocket as previous food) (Fig 2a).

In relation to the total intake of each host, 4th instars always chose for the initial host when offered a choice of different hosts (Fig 2b), but no preference was observed for 5th instars (Fig 2b). The percentages of larvae that ingested only kale were 5% and 0% for 4th and 5th instars, respectively, whereas those which ingested only rocket were 25% and 15%. Fourth instars experienced on kale visited kale first instead of cabbage ($P = 0.03$), and no such preference was observed for 5th instars. However, when larvae were experienced with cabbage, both 4th and 5th instars visited kale first on a free-choice assay ($P = 0.03$, $P = 0.03$) (Fig 3a). Similar results were obtained for the total food ingested when larvae were experienced with kale for both 4th and 5th instars. Fourth instars experienced on kale ingested more kale than cabbage ($P = 0.02$), and no difference was observed for 5th instars. Larvae experienced on cabbage showed no difference in the amount of ingested hosts (kale or cabbage) regardless of their instar (Fig 3b). The percentages of larvae that ingested only kale were 15% and 25% in the 4th and 5th instars, respectively, whereas those who ingested just cabbage were only 10% and 20%.

Effect of previous experience in food utilization. In the 4th instar, group k ingested more food than group r (45.2 ± 3.2 mg and 31.9 ± 3.0 mg, respectively, $P = 0.002$). However, group r accumulated a larger amount of biomass (11.9 ± 1.0 mg versus 9.1 ± 0.9 mg from group k, $P = 0.02$). Group r values for AD, ECI and ECD (%) were also higher than group k (58.1 ± 1.9 vs 49.9 ± 2.8 , 38.3 ± 1.3 vs 21.1 ± 1.8

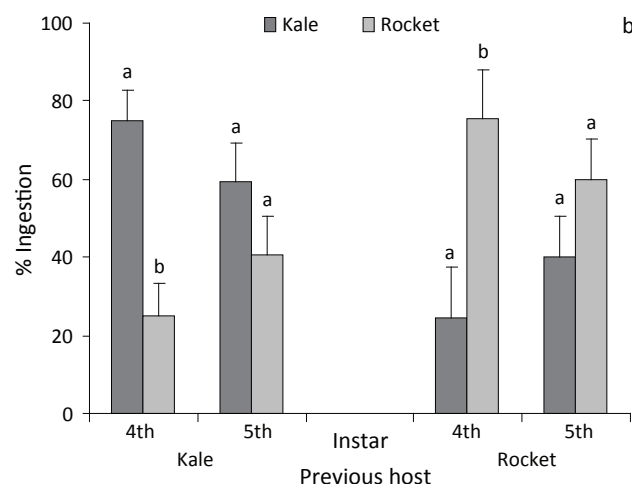
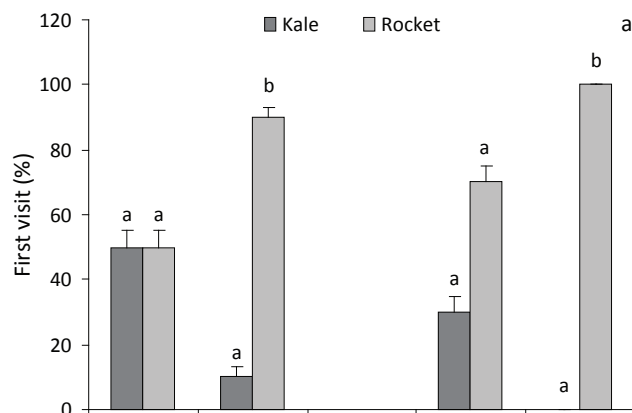


Fig 2 Feeding preference ($\bar{X} \pm \text{SEM}$) of 4th ($n = 10$) and 5th ($n = 10$) instars of *Ascia monuste orseis* for different hosts determined by (a) the first visited host and (b) the total intake of each leaf. Larvae had a prior feeding experience on kale or rocket. Bars pairs followed by different letters represent significant difference when compared to previous food on a particular instar (a = sign test and b = Wilcoxon signed rank test, $P < 0.05$).

and 66.6 ± 2.7 vs 46.4 ± 5.3 ; $P = 0.005$, $P < 0.001$ and $P = 0.003$, respectively). The group which was previously fed on kale and started to feed on rocket in the 5th instar (k-r) accumulated significantly less biomass (31.8 ± 0.4 mg) than the group which remained on kale (k-k) (49.9 ± 0.5 mg; $P = 0.01$). The other parameters did not differ between the groups previously fed on kale (food intake, $P = 0.06$; AD, $P = 0.1$; ECI, $P = 0.9$; ECD, $P = 0.7$).

The group which was previously fed on rocket and switched to kale in the 5th instar (r-k) presented the greatest food intake (219.1 ± 37.4 mg vs 105.1 ± 15.9 mg; $P = 0.006$) and the highest increase in biomass (53.5 ± 0.5 mg vs 26.8 ± 0.3 mg; $P = 0.03$), despite a smaller AD (52.6 ± 5.6 vs 69.0 ± 3.9 ; $P = 0.02$). ECI and ECD did not differ among treatments ($P = 0.9$, $P = 0.2$, respectively). For kale and cabbage in the 4th instar, the only parameter that significantly differed between the groups was the biomass incorporation, which was higher in the group

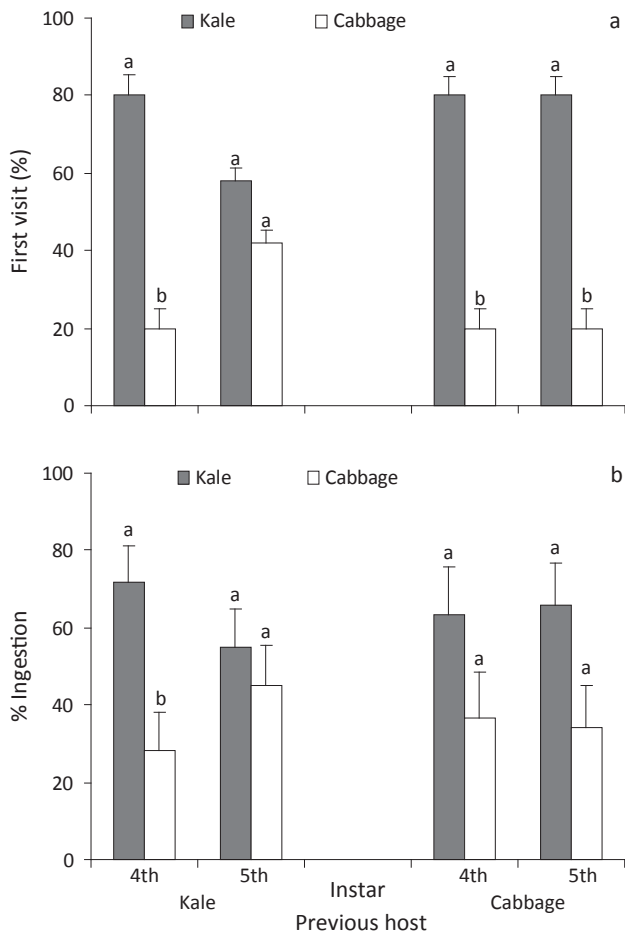


Fig 3 Feeding preference ($\bar{X} \pm \text{SEM}$) of 4th (n = 10) and 5th (n = 10) instars of *Ascia monuste orseis* larvae on for different hosts determined by (a) the first visited host and (b) the total intake of each leaf. Larvae had a prior feeding experience on kale or cabbage. Bars pairs followed by different letters represent significant difference when compared to previous food on a particular instar (a = sign test and b = Wilcoxon signed rank test, P < 0.05).

fed on cabbage (13.8 ± 1.0 mg vs 8.9 ± 1.8 mg from kale group, P = 0.02; food intake, P = 0.1; AD, P = 0.7; ECI, P = 0.2; ECD, P = 0.1). However, the group which was previously fed on kale and switched to cabbage in the 5th

instar (k-c) accumulated significantly less biomass (25.6 ± 5.1 mg) than the k-k group (43.6 ± 3.2 mg; P = 0.01), this last group also presenting higher ECI (25.5 ± 1.6 vs 17.1 ± 2.4 ; P = 0.01). The other parameters did not differ among treatments (food intake, P = 0.4; AD, P = 0.4; ECD, P = 0.05). Larvae initially fed on cabbage did not show any significant difference in the 5th instar (food intake, P = 0.07; biomass, P = 0.5; AD, P = 0.6; ECI, P = 0.06; ECD, P = 0.1) regardless if fed on cabbage or kale (c-c or c-k groups).

Effect of previous experience in the performance. The group which was fed on kale up to the 4th instar presented a delay in development in relation to the group fed on rocket (P = 0.01) (Table 1). In relation to the host shift from the 5th instar, a significant difference was detected in the mortality of larvae fed exclusively on rocket (r-r) as compared to those that switched from rocket to kale (r-k) (P = 0.001). Food shift from kale to rocket also affected the pupal weight if compared to those that fed exclusively on kale (k-k) (P = 0.02).

There was no difference in the development time between groups fed on kale or cabbage up to the 4th instar (P = 0.6) (Table 2). The group which was previously fed on cabbage and switched to kale (c-k) showed a better performance, verified by the shorter development time required to pupation (P = 0.03) and lower mortality (P = 0.02).

Discussion

The preference of 4th instars for the food source they were initially experienced (kale or rocket) clearly shows that previous experience plays a major role in the preference for host feeding by immature *A. monuste orseis*. For many insect species, the induction of preference usually develops after one or more instars remain on a particular host, with a complex chemical stimuli(us) participating in this process, involving the central and peripheral nervous system (Hsiao 1985). The induction was not evident

Table 1 Developmental parameters of *Ascia monuste orseis* fed on: kale only (k), kale until the 4th instar and then on rocket (k-r), rocket only (r) and rocket until the 4th instar and then on kale (r-k).

Groups	Development until the 4 th instar (days)	Development 4 th instar until pupation (days) ^{ns}	Pupation (days) ^{ns}	Total development (days) ^{ns}	Emergence (%) ^{ns}	Mortality (%)	Pupal weight (mg)	Potential fecundity ^{ns}
k	6.7 ± 0.37 a	3.2 ± 0.14	5.8 ± 0.15	15.5 ± 0.32	83.8 ± 4.71	26.7 ± 5.90 a	77.9 ± 3.23 a	390.4 ± 21.17
k-r		3.0 ± 0.13	5.7 ± 0.12	15.4 ± 0.16	67.1 ± 11.70	40.8 ± 10.3 a	64.3 ± 3.10 b	363.5 ± 22.73
r	6.4 ± 0.44 b	3.3 ± 0.18	5.6 ± 0.12	15.3 ± 0.19	86.3 ± 6.96	30.2 ± 7.06 a	71.7 ± 3.84 a	311.0 ± 24.09
r-k		3.1 ± 0.09	5.9 ± 0.15	15.4 ± 0.20	77.3 ± 7.11	15.0 ± 4.34 b	76.6 ± 4.75 a	361.3 ± 15.94

Data represent the mean \pm SEM of 10 replicates, except for *Development until the 4th instar* parameter, n = 20. Means followed by different letters on the same column indicate significant difference (Mann-Whitney test, P < 0.05); ^{ns}Non significant.

Table 2 Developmental parameters of *Ascia monuste orseis* fed on: kale only (k), kale until the 4th instar and then cabbage (k-c), cabbage only (c) and cabbage until the 4th instar and then kale (c-k).

Groups	Development until the 4 th instar (days) ^{ns}	Development 4 th instar until pupation(days)	Pupation (days) ^{ns}	Total development (days) ^{ns}	Emergence (%) ^{ns}	Mortality (%)	Pupal weight (mg) ^{ns}	Potential fecundity ^{ns}
k	6.6 ± 0.39	3.2 ± 0.14 a	5.8 ± 0.15	15.5 ± 0.32	83.8 ± 15.60	26.7 ± 5.90 a	77.9 ± 3.23	390.4 ± 21.17
k-c		3.3 ± 0.18 a	5.8 ± 0.18	15.8 ± 0.20	88.7 ± 15.70	14.3 ± 7.97 a	67.5 ± 3.78	357.5 ± 20.23
c	6.5 ± 0.54	3.5 ± 0.20 a	5.8 ± 0.10	15.9 ± 0.32	77.6 ± 21.40	33.8 ± 5.45 a	74.6 ± 3.16	306.3 ± 23.60
c-k		3.0 ± 0.04 b	5.7 ± 0.11	15.3 ± 0.21	88.3 ± 22.20	12.7 ± 5.37 b	73.8 ± 4.92	341.7 ± 27.56

Data represent the mean ± SEM of 10 replicates, except for *Development until the 4th instar* parameter, n = 20. Means followed by different letters on the same column indicate significant difference (Mann-Whitney test, P < 0.05); ^{ns}Non significant.

between kale and cabbage. The preference for kale in the 4th instar, when kale was the initial food source ceased when cabbage was previously ingested. Therefore, there was also a change in preference, since prior feeding on cabbage annulled the preference for kale.

Host plants with the best nutritional value are not always chosen by species in the field, as other variables, such as predation, may influence host choice. In general, Lepidoptera larvae have better performance on diets containing protein and carbohydrate in similar amounts or, in some cases, with a high protein content (Waldbauer *et al* 1984). Rocket is richer in protein (1.60 g/100 g of food) when compared to kale (1.40 g/100 g) and poorer in carbohydrates (2.03 g/100 g) than kale (4.50 g/100 g) (Franco 2002), resulting in a much higher rate of protein to carbohydrate for rocket (0.79) than for kale (0.31). The better biomass incorporation of larvae fed on rocket probably resulted from its high protein value and the lowest food intake of these ones compared to larvae fed on kale, could be a result of lower phagostimulant effect, due to the rocket lower carbohydrate content.

Greater digestive efficiency enables the larvae to satisfy their nutritional needs while minimizing the time spent on food, reducing the risk of attack by natural enemies in a field situation. The risk of predation is higher during the larvae feeding period (Bernays 1997). Taking into account that a better diet decreases the time that the caterpillar spends feeding, the consumption of rocket instead of kale is thus advantageous because it maximizes the incorporation of biomass and minimizes exposure to natural enemies.

Better digested and used in the 4th instar, rocket became comparatively less appropriate in the 5th instar: besides lower food intake, the groups fed on rocket showed lower biomass incorporation than the groups fed on kale. The assimilation rate of nutrients by larvae which ingested kale in the last instar may have been further optimized by removing the effects of the cell wall (Clissord *et al* 2006), in addition to its higher amount of carbohydrates compared to rocket.

Depending on the order, the host shift negatively affected the performance of *A. monuste orseis*, by increasing mortality and decreasing pupal weight. Besides the differences in chemical constituents, rocket also have morphological features that may facilitate nutrient use by the herbivore if compared to kale, as rocket leaves are much softer than the ones from kale. The reduced size of rocket leaves, in relation to the ones of kale and cabbage, may exert additional selective pressure on *A. monuste orseis* larvae when they develop in this species due to their smaller area and foliar mass. Rocket plants do not bear the same number of larvae as kale and cabbage plants. As these larvae behavior is gregarious in the early instars, these factors eventually force a greater dispersion of larvae that feed on this host. Besides a higher risk of death (Bernays 1997), the increased time for pupation and a lower emergence rate (Barros-Bellanda & Zucoloto 2003) are other risks which are inherent to dispersion.

Generally, the larvae demonstrated better performance in kale, probably as a result of an adaptation to this host during many generations (see Barros & Zucoloto 1999). This contact with a single host is a strong selective pressure, which can lead to a tendency of female larvae to oviposit on this plant and/or the ability of immature ones to grow well in it (Rossiter 1991, Fox *et al* 1995). It is clear that *A. monuste orseis* larvae do not immediately realize the quality of the ingested host, but prior host feeding may influence their consumption and, therefore, their preferences.

The adaptive significance of the induction in the insects food preference can reflect an adaptation, where frequent changes in the type of food decrease the efficiency of its use (Grabstein & Scriber 1982). Feeding on one single host during larval development can, therefore, be physiologically less costly to the insect. The permanence in cabbage incurred in a very high physiological cost for the larvae, highlighted by the delay in the development and larger larval mortality. In this case, the absence of induction allied to the capacity of the larvae to select the

best food for their development (Barros & Zucoloto 1999) are highly adaptive mechanisms for this species.

The absence of preference in newly hatched larvae in the pair kale/cabbage may implicitly indicate that these hosts' leaves are indeed nutritionally similar. The presence of secondary compounds cannot be neglected either, as it can influence the insects' activity (Bernays & Chapman 2000). Certain compounds of some Brassicaceae plants, for example, are not acceptable for some *Pieris* species, although they have glucosinolates (van Loon & Schoonhoven 1999). It is possible that the reduced performance of the larvae in cabbage and its relatively low attractiveness and consumption in the experiments of preference have occurred due to the presence or to the concentration of some repellent and/or deterrent allelochemical.

Changes in larval food preferences are a strong evidence of a considerable phenotypic plasticity in host plant selection in *A. monuste orseis*. The switch of *A. monuste orseis* between different hosts probably contributes in a significant way to several aspects in their biology, reducing the inherent risks to the larval dispersion. If the original food source is a limiting resource, the survival in another host does not severely affect the immature development, and may even improve their performance depending on the found host. It is therefore clear that the food preferences may change according to the experience, and that the consumption of a certain food source may occasionally decline or increase with previous experience.

Acknowledgments

The authors would like to thank Laércio Massocato for technical assistance, and CAPES and CNPq for financial support.

References

- Awmack CS, Leather SR (2002) Host plant quality and fecundity in herbivorous insects. *Annu Rev Entomol* 47: 817-44.
- Barros HCH, Zucoloto FS (1999) Performance and host preference of *Ascia monuste* (Lepidoptera, Pieridae). *J Insect Physiol* 45: 7-14.
- Barros-Bellanda HCH, Zucoloto FS (2003) Importance of larval migration (dispersal) for the survival of *Ascia monuste* (Godart) (Lepidoptera: Pieridae). *Neotrop Entomol* 32: 11-17.
- Bernays EA (1997) Feeding by caterpillars is dangerous. *Ecol Entomol* 22: 121-123.
- Bernays EA, Bright KL (2001) Food choice causes interrupted feeding in the generalist grasshopper *Schistocera americana*: further evidence for inefficient decision-making. *J Insect Physiol* 47: 63-71.
- Bernays EA, Bright KL, Gonzalez N, Angel J (1994) Dietary mixing in a generalist herbivore: tests of two hypotheses. *Ecology* 75: 1997-2000.
- Bernays EA, Chapman RF (2000) Plant secondary compounds and grasshoppers: beyond plant defenses. *J Chem Ecol* 26: 1773-1793.
- Bittencourt-Rodrigues R, Zucoloto FS (2005) Effect of host age on the oviposition and performance of *Ascia monuste* Godart (Lepidoptera: Pieridae). *Neotrop Entomol* 34: 169-175.
- Browne LB, Raubenheimer D (2003) Ontogenetic changes in the rate of ingestion and estimates of food consumption in fourth and fifth instar *Helicoverpa armigera* caterpillars. *J Insect Physiol* 49: 63-71.
- Catta-Preta PD, Zucoloto FS (2003) Oviposition behaviour and performance aspects of *Ascia monuste* (Godart, 1919) (Lepidoptera: Pieridae) on kale (*Brassica oleracea* var. *acephala*). *Revta Bras Entomol* 47: 169-74.
- Chew FS (1975) Coevolution of pierid butterflies and their cruciferous foodplants. *Oecologia* 20: 117-127.
- Chew FS (1988) Biological effects of glicosinolates. *ACS Symp. Ser.* 380: 155-181.
- Chew FS, Renwick JAA (1995) Chemical ecology of host-plant choice in *Pieris* butterflies, p. 214-238. In Cardé RT, Bell WJ (eds) *Chemical ecology of insects*, 2nd ed., New York, Chapman & Hall, 433p.
- Cunningham JP, West SA (2001) Host selection in phytophagous insects: a new explanation for learning in adults. *Oikos* 95: 537-43.
- Dethier VG (1982) Mechanism of host-plant recognition. *Entomol Exp Appl* 31: 49-56.
- Dussutour A, Simpson SJ, Despland E, Colasurdo N (2007) When the group denies individual wisdom. *Anim Behav* 74: 931-939.
- Felipe MC, Zucoloto FS (1993) Estudos de alguns aspectos da alimentação de *Ascia monuste* Godart (Lepidoptera, Pieridae). *Revta Bras Zool* 10: 333-341.
- Franco G (2002) Tabela de composição química dos alimentos. 9^a ed. São Paulo. Editora Atheneu, 103p.
- Fox CW, Waddell KJ, Mousseau TA (1995) Parental host plant affects offspring life histories in a seed beetle. *Ecology* 76: 402-411.
- Grabstein EM, Scriber JM (1982) Host plant utilization by *Hyalophora cercropia* as affected by prior feeding experience. *Entomol Exp Appl* 32:262-268.
- Hsiao TH (1985) Feeding behaviour, p.471-512. In Kerkut GA, Gilbert LI (eds) *Comprehensive insect physiology, biochemistry and pharmacology*, Vol. 9. Oxford, Pergamon Press, 734p.
- Leal TABS, Zucoloto FS (2008) Selection of artificial hosts for oviposition by wild *Anastrepha obliqua* (Macquart) (Diptera, Tephritidae): influence of adult food and effect of experience. *Revta Bras Entomol* 52: 467-471.
- Lee KP, Behmer ST, Simpson SJ (2006) Nutrient regulation in relation to diet breadth: a comparison of *Heliothis* sister species and a hybrid. *J Exp Biol* 209: 2076-2084.

- Moreau G, Quiring DT, Eveleigh ES, Bauce E (2003) Advantages of mixed diet: feeding on several foliar age classes increases the performance of a specialist insect herbivore. *Oecologia* 135: 391-99.
- Pfisterer AB, Diemer M, Schmid B (2003) Dietary shift and lower biomass gain of a generalist herbivore in species-poor experimental plant communities. *Oecologia* 135: 243-241.
- Rossiter MC (1991) Environmentally-based maternal effects – a hidden force in insect population dynamics. *Oecologia* 87: 288-294.
- Saxena KN, Schoonhoven LM (1982) Induction of orientational and feeding preferences in *Manduca sexta* larvae for different food sources. *Entomol Exp Appl* 32: 173-180.
- Scriber JM (1981) Sequential diets, metabolic costs and growth of *Spodoptera eridantia* (Lepidoptera: Noctuidae) feeding upon dill lima bean and cabbage. *Oecologia* 51: 175-180.
- Scriber JM, Slansky Jr F (1981) Nutritional ecology of immature insects. *Annu Rev Entomol* 26: 183-211.
- Singer MC (2000) Reducing ambiguity in describing plant-insect interactions: “preference”, “acceptability” and “electivity”. *Ecol Lett* 3: 159-162.
- Slansky F Jr, Scriber JM (1985) Food consumption and utilization, p.87-164. In Kerkut GA, Gilbert LI (eds) *Comprehensive insect physiology, biochemistry and pharmacology*, v.4. Oxford, Pergamon Press, 373p.
- Stoyenoff JL, Witter JA, Montgomery M, Chilcote CA (1994a) Effects of host switching on gypsy moth (*Lymantria dispar* (L.)) under field conditions. *Oecologia* 97: 143-157.
- Thompson JN, Pellmyr O (1991) Evolution of oviposition behavior and host preference in Lepidoptera. *Annu Rev Entomol* 36: 65-89.
- van Loon JJA, Schoonhoven LM (1999) Specialists chemoreceptors deterrence in able *Pieris* caterpillars to discriminate between different chemical deterrents. *Entomol Exp Appl* 914: 29-35.
- Waldbauer GP, Cohen RW, Friedman S (1984) Self-selection of an optimal nutrient mix from defined diets by larvae of the corn earworm, *Heliothis zea* (Boddie). *Physiol Zool* 57: 590-597.
- White TCR (1984) The abundance of invertebrate herbivores in relation to the availability of nitrogen in stressed food plants. *Oecologia* 63: 90-105.
- Zago-Braga RC, Zucoloto FS (2004) Cannibalism studies on eggs and newly hatched caterpillars in a wild population of *Ascia monuste* (Godart) (Lepidoptera, Pieridae). *Revta Bras Entomol* 48: 415-420.
-