ECOLOGY, BEHAVIOR AND BIONOMICS

Importance of Larval Migration (Dispersal) for the Survival of *Ascia monuste* (Godart) (Lepidoptera: Pieridae)

HELEN C.H. BARROS-BELLANDA AND FERNANDO S. ZUCOLOTO

Depto. Biologia, Faculdade de Filosofia Ciências e Letras de Ribeirão Preto, Universidade de São Paulo
Av. Bandeirantes 3900, 14049-901, Ribeirão Preto, SP
e-mail: hbarros@usp.br, zucoloto@ffclrp.usp.br

Neotropical Entomology 32(1):011-017 (2003)

Importância da Migração Larval (Dispersão) para a Sobrevivência de *Ascia monuste* (Godart) (Lepidoptera: Pieridae)

RESUMO - Espécies de insetos com larvas que têm alta mobilidade, como por exemplo *Ascia monuste* (Godart), mostram comportamento de oviposição pouco discriminatório com relação à quantidade de alimento. Nesta espécie, tal comportamento é influenciado pela abundância espacial e temporal na horta de seu principal hospedeiro, a couve (*Brassica oleracea* Var. *acephala*), condição que facilita a migração larval. As lagartas de *A. monuste* freqüentemente migram para outro hospedeiro em busca de alimento de modo a completarem seu desenvolvimento, e mesmo as agregações larvais menores com até 20 indivíduos não foram suportadas por plantas de couve de tamanho-médio. A migração larval no início do 5º ínstar ocorreu tanto nos grupos que se alimentaram de plantas confinadas em gaiolas como em plantas distribuídas na natureza. Durante a migração, as lagartas de *A. monuste* mostraram baixa capacidade de detectar seu hospedeiro. As fêmeas de *A. monuste* colocaram posturas em plantas isoladas na natureza de forma semelhante às posturas feitas em plantas agregadas. Porém, as posturas em plantas isoladas contribuíram para reduzir a sobrevivência dos imaturos, uma vez que o sucesso da migração larval ficou prejudicado por não haver plantas-hospedeiras próximas (condição experimental). A predação de lagartas que se alimentavam em suas plantas de origem foi a principal causa da mortalidade de *A. monuste* na natureza.

PALAVRAS-CHAVE: *Brassica oleracea*, comportamento de oviposição, lagarta-da-couve, postura, predação

ABSTRACT - Insect species whose larvae have high mobility, such as *Ascia monuste* (Godart), show a poor discriminatory oviposition behavior with respect to the quantity of food. Such behavior in *A. monuste* is influenced positively by the spatial and temporal abundance of kale (*Brassica oleracea* Var. *acephala*), its main host, in nature. *A. monuste* caterpillars frequently migrate in search of food to complete their development and even smaller larval clusters at about 20 individuals are not supported by the resources provided by a medium-size kale plant. Migration (dispersal) of 5th-instar larvae was necessary both in groups feeding on plants confined in cages and on plants growing in nature, and migration was successful when the plants were close to one another. The oviposition of *A. monuste* females on isolated plants was similar to the oviposition in clustered plants in nature. Ovipositing on isolated plants reduced the survival of immatures since larval migration was impaired by the absence of nearby host plants (experimental condition). Predation of larvae on the plant of origin was the major cause of *A. monuste* mortality in nature.

KEY WORDS: *Brassica oleracea*, egg-cluster, larval group, oviposition behavior, predation

Food resources generate some of the most powerful selective forces shaping insect life history traits (Rhoades 1985). The degree of specificity and adaptation between animals and their food depends on the food resource most extensively used. If, for example, the resource used has high nutritional quality and is highly persistent and available, the selective pressure that interacts with the feeding behavior of the animal will be weak (Tallamy & Wood 1986).

The fitness function is built either from the perspective of a mother insect or from her offspring. One such situation is when offspring can move from plant to plant (Mayhew 1997). This will lead to weaker selection on oviposition behavior (Thompson 1983).

Insects that lay more than one egg per resource patch [eg. *Ascia monuste* (Godart)] not only choose an oviposition site but may also determine how many eggs to lay. This "decision" represents a compromise between factors favouring large group size and the number of offspring that the patch can support (Damman 1991). Larval migration (dispersal) is presumably an adaptive behavior aimed at enhancing survival of larval with limited food resources and is common when there are more larvae than a single plant can sustain (Chapman *et al.* 1983, Berger 1992).

A. monuste, known as the kale caterpillar, is one of the most important consumers of Brassicaceae in Brazil and frequently migrates in search of food to complete its development. The family Brassicaceae is characterized by the presence of glycosinolates and there is ample evidence that these compounds are the major factors responsible for recognition of viable hosts on the part of these butterflies (Chew 1988). Kale leaves (*Brassica oleracea* var. a*cephala*), the main host of the species under study, are of low nutritional quality, but their persistence and availability are high (Barros & Zucoloto 1999). On this basis, *A. monuste* probably faces a weak selective pressure by using kale as a food resource for the immatures.

The work reported here investigated the number of *A. monuste* eggs in the clutches on plants placed in cages and also on plants in nature (isolated and clustered), and the larval group behavior from egg-clutches on plants in cages and in nature. How is the importance of larval migration for the survival of *A. monuste*?

Materials and Methods

Eggs were collected from kale leaves in a garden to which no pesticide had been applied, located 100 m from the Departamento de Biologia, Faculdade de Filosofia Ciências e Letras de Ribeirão Preto (21°05'S, 47°50'W), São Paulo State, Brazil.

Seven newly hatched caterpillars were placed on plastic boxes (10x10x4 cm) lined with paper towel (Felipe & Zucoloto 1993) and the food, one leaf per box (» 150 cm^2), was changed daily. The boxes were placed in an incubator at 29 ± 2°C; luminosity was provided by a fluorescent lamp (400 lux) for 10h per day and humidity was maintained at » 80% (Barros & Zucoloto 1999).

Number of *A. monuste* Eggs per Clutch on Kale

A. In Cages. Adults emerged were placed in cages (1x1x1 m) with a side opening used to introduce the animals and food. The cage contained a pot with kale and a glass plate 4 cm in diameter with a 10% sucrose solution and a blue dye (Felipe & Zucoloto 1993) lined with cotton to facilitate feeding (Huang & Renwick 1993). The cages were left in a protected site in the field and exposed to sunlight from 10:00h to 14:00h for the butterflies to mate and oviposit (Barros & Zucoloto 1999).

Kale seedlings were planted in pots measuring 15 cm in diameter by 15 cm in height, with the mean height of the plant being 30-40 cm and containing approximately nine leaves with different sizes. These plants were similar with plants grown in vegetable gardens (medium-size kale plant). Care was taken to use plants of similar appearance that were not old (with dark and rigid leaves). The plants were inspected daily and the leaves containing eggs were removed and taken to the laboratory for egg counts per clutch. The plants containing many eggs were replaced with others of similar characteristic.

The total number of eggs laid by each of the 20 females and the number of eggs per female per day (up to the death of the butterfly) were also recorded.

B. In Nature (Isolated and Clustered). Six kale pots were separated from the others at a distance of 3 m to 5 m. The number of eggs per clutch laid on these plants was recorded for 30 days. The number of eggs per clutch on plants clustered in the same area and used as controls (a plot with 12 plants close to one another by a distance of 30 cm) was also recorded.

The number of *A. monuste* eggs per clutch on plants in cages and in nature (isolated and clustered) were analyzed statistically by Kruskal – Wallis test (Sigma Stat for Windows, 1994 – Jandel Corporation, San Rafael, California),with μ = 0.05.

Larval Cluster Behaviour of *A. monuste* on Kale

A. In Cages. The behavior of a mean larval cluster of 20 caterpillars in pots with kale (30-40 cm high) was observed in a rearing cage. Offspring survival was evaluated up to adult emergence, with emphasis on the occurrence and characterization of larval migration. Twenty caterpillars were placed on each plant since this was the mean number of caterpillars obtained per clutch in 1A experiment.

Another kale pot was also placed in each cage in contact with the pot containing the caterpillars. This second pot served as a complementary source of food and was also used to evaluate the success and the characteristics of migration.

The parameters measured were: larval migration day, number of caterpillars that reached a new host-plant (after 24h), number of caterpillars dead, time for pupation (days), number of emergent adults and imago weight (male and female).

The parameters of the performance of caterpillars submitted to a situation of possible migration were compared with the data obtained for larvae that were transported one by one to another host- plant, i.e., caterpillars that did not need to migrate. The experimental conditions for this group (No Migration Group – NMG) were the same as those described above for the Migrating Group (MG).

The statistical test was t-test (Sigma Stat for Windows, 1994 – Jandel Corporation, San Rafael, California), with μ = 0.05.

B. In Nature. The behavior of larvae in nature was also observed (in the presence of parasites, predators, rain, sunshine etc.) and the survival of larval clusters from eggs laid by wild females on these plants was evaluated.

The parameters measured were: number of caterpillars before migration, larval mortality caused from predation (caterpillars that disappeared from the plants that contained some leaves), larval mortality caused from migration (caterpillars that disappeared from the plants without leaves and that were not found in another plant after 24h), total larval mortality, larval migration day and number of caterpillars on final 5th instar.

The statistical tests were t-test or Mann-Whitney test (Sigma Stat for Windows, 1994 – Jandel Corporation, San Rafael, California), with $\mu = 0.05$. Each value of percentages was transformed to its arcsine.

The behavior of each larval cluster was analyzed individually and plants - that were found suffering with high predation - were replaced with a pot containing another one.

- Isolated Plants. Six pots containing kale plants were separated from one another by a distance of 3 m to 5 m. The larval clusters obtained on these isolated plants would already be considered unviable due to the total number of caterpillars since the distance between plants hampers larval migration, a behavior that may be necessary for the caterpillar to complete their development. Immature behavior was analyzed in 10 distinct egg batches tested at random on the six kale plants mentioned above.

- Clustered Plants. Some pots containing one kale plant each were placed quite close to one another by a distance of 30 cm (1 set of 12 pots), and the larval clusters obtained on the plants were observed. Immature behavior was analyzed in 10 distinct egg batches tested at random on each of the 12 kale plants mentioned above.

Results

Number of *A. monuste* Eggs per Clutch on Kale

A. In Cages. Each female laid on average a total of 138.1 ± 54.12 eggs and the 4th day was the main one for the oviposition of most females (Fig. 1). Under the present experimental conditions, the approximate number of eggs per clutch on kale plants was 19.9 ± 5.45 eggs (Fig. 2). Mean female longevity was 7.1 ± 0.90 days.

B. In Nature (Isolated and Clustered). On the spaced plants, the number of eggs per oviposition ranged from 27 to 48. A total of 40 egg-clutches were obtained during the 30 days of the experiments, with a total number of 1688 eggs. The mean number of eggs per clutch was 42.0 ± 16.00 on isolated plants and 43.7 ± 17.51 on clustered plants (Fig. 2). Thirty-six ovipositions and a total of 1574 eggs were obtained on the clustered plants over the 30 days of the experiment. It can be seen that the number of egg-clutches was closely similar on isolated and clustered plants, but much higher than that obtained in the experiment conducted in cages (Fig. 2).

Larval Cluster Behavior of *A. monuste* on Kale

A. In Cages. In summary, we observed that the plants supported the development of 20 caterpillars up to 8th day (early 5th instar), after which migration was necessary. In the group in which migration of the 20 caterpillars was permitted (MG), seven of them, on average, did not reach a new host-plants after 24h (35%) and 13 of them did (65%) (Table 1).

The caterpillars that did not reach the new plant within the 24h of migration usually died and, at the end of this period of time, only a few pupated with a greatly reduced size and did not reach emergence.

The migration of 5th instar *A. monuste* caterpillars was of a random type, i.e., the caterpillars moved to search for food in different directions. Some climbed down the stem of the plant and moved around in circles for a while, but then chose a direction and moved away. There was a new plant quite close to the initial one (30 cm), but not all caterpillars found it. The main reason was that they chose the wrong direction in which to move, sometimes opposite to the right one and did not reach the new plant even after a 24h search (Table 1).

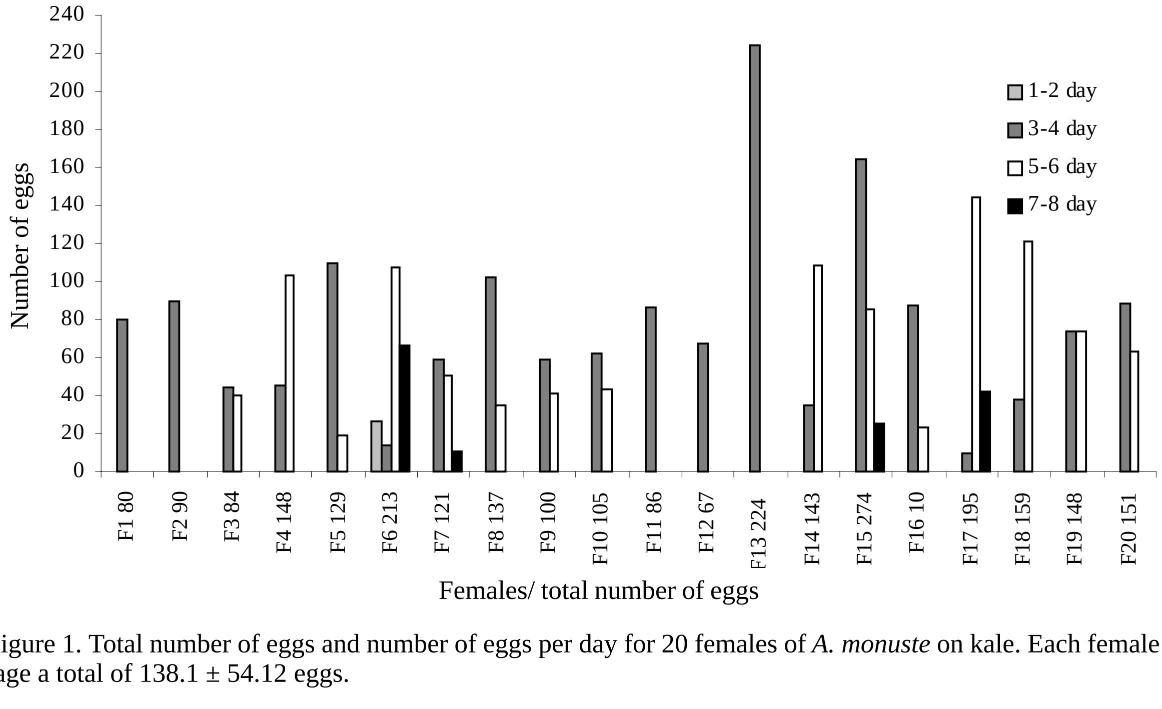

Figure 1. Total number of eggs and number of eggs per day for 20 females of *A. monuste* on kale. Each female laid on average a total of 138.1 ± 54.12 eggs.

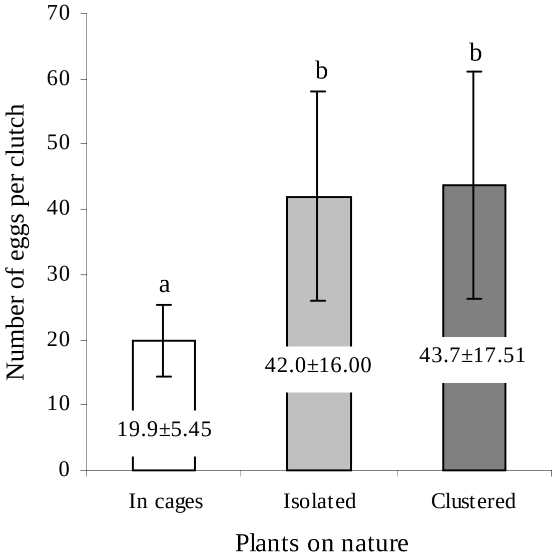

Figure 2. The number of eggs in the clutches on plants confined in cages and on plants growing in nature (isolated and clustered). Means ± SD followed by different letters differed significantly (Kruskal – Wallis test, P > 0.05). d. f. = 2.0 and H = 42.7.

B. In Nature

- Isolated Plants. In this experiment, the total survival of larvae on isolated plants was only 12.7% (53/416). Larval mortality was high due to problems such as predation and also due to the impossibility of migration (Table 2).

Only one caterpillar was found to be parasitized and in most cases in which the caterpillars "disappeared" from the leaves and the plants, markings (cuttings) were observed on the leaves, probably due to predation by birds. Predation was high, but did not fully exclude the possibility that the caterpillars preyed upon were also parasitized.

Despite the difficulty in migrating to a new plant, 5th-instar caterpillars move rapidly and most are resistant to a period of food deprivation, with some of them actually being able to reach distant plants (more than 3 m). This occurred on plants 1, 3, 4, 5 and 8 (Table 2). The rate of successful migration under these conditions was only 28.2%.

It can be seen that on plant nº 2 there was no migration and the 10 caterpillars that survived predation completed their development on the plant itself (Table 2).

- Clustered plants. In the present experiment, the total survival rate of immatures in the 10 ovipositions studied was 32% (116/371). The major cause of mortality was also predation by birds (Table 3), a fact that does not fully exclude the possibility that caterpillars preyed upon are also parasitized.

Table 1. Comparative behavior of 20 caterpillars per group on plants confined in cages. NMG, immature group where the caterpillars were transported one by one to another plant on the beginning of 5th instar, i. e. caterpillars that did not migrate. MG, immature group where migration to a new host-plant was permitted.

Group	Larval migration (days)	N. of caterpillars on the new host	N. of caterpillars dead	Time for pupation (days)	Number of emergent adults	Imago weight	
						Male	Female
NMG	-	-	2.0 ± 1.22 a	10.0 ± 0.32 a	16.5 ± 0.62 a	57.9 ± 7.01 a	69.2 ± 6.42 a
MG	8.3 ± 0.53	13.0 ± 1.13	6.0 ± 1.64b	10.5 ± 0.20 b	12.2 ± 0.83 b	55.0 ± 4.82 a	70.1 ± 4.50 a
t value			-5.1	-3.2	9.8	0.8	-0.05

n = 6, means ± SD followed by different letters differed significantly (t-test, P > 0.05). d. f. = 10.0.

Table 2. Larval behavior of *A. monuste* in nature from egg clutches on 10 isolated plants. Each larval cluster was analyzed individually. The number on parenthesis on the last column is the number of caterpillars that found a new host-plant (migration).

Egg-clutches	N. of eggs hatched	N. of caterpillars before migration	Larval mortality (predation) [1]	Larval mortality (migration) [1]	Total larval mortality [1]	Larval migration (day and age)	N. of caterpillars on final 5th instar
1	49/47	38	25.9	59.1	62.5	8th day, 5th instar	10
2	46/41	No	60.4	-	60.4	No	10
3	37/35	34	3.0	69.9	70.3	9th day, 5th instar	4
4	46/43	30	33.3	63.4	68.0	7th day, 5th instar	6
5	36/30	24	26.5	57.3	61.1	10th day, 5th instar	7
6	53/47	0	90.0	-	90.0	No	0
7	31/27	0	90.0	-	90.0	No	0
8	56/50	26	43,8	38.3	55.5	8th day, 5th instar	16
9	60/55	0	90.0	-	90.0	No	0
10	43/41	0	90.0	-	90.0	No	0
Total	457/416	152					53 (43)
Mean			*55.3 ± 33.10a	57.6 ± 11.83a	*73.8 ± 14.51a		
				t = -4.8			
				d.f. = 10.0			

[1] Value of percentages was transformed to arcsine. Means ± SD followed by different letters between columns differed significantly (t-test or *Mann-Whitney test, P > 0.05).

Table 3. Larval behaviour of *A. monuste* in nature from egg clutches on 10 clustered plants. Each larval cluster was analyzed individually.

Egg-clutches	N. of eggs and hatched	N. of caterpillar before migration	Larval mortality (predation)[1]	Larval mortality (migration) [1]	Total larval mortality[1]	Larval migration (day and age)	N. of caterpillars at final 5th instar
1	45/40	35	20.7	26.6	33.2	9th day, 5th instar	28
2	51/48	0	90.0	-	90.0	No	0
3	38/36	36	0	21.7	21.7	9th day, 5th instar	31
4	43/39	0	90.0	-	90.0	No	0
5	36/30	20	35.2	30.0	45.0	9th day, 5 th instar	15
6	55/51	25	45.6	5.1	47.8	10th day, 5th instar	23
7	33/33	0	90.0	-	90.0	No	0
8	28/28	22	27.5	-	34.5	10th day , 5th instar	19
9	27/26	0	90.0	-	90.0	No	0
10	41/40	0	90.0	-	90.0	No	0
Total	397/371	138					116
Mean			*57.9 ± 35.74a	21.0 ± 9.53 b	*63.2 ± 29.00 a		
				t = -4.8			
				d.f. = 10.0			

[1] Value of percentages was transformed to arcsine. Means ± SD followed by different letters between columns differed significantly (t-test or *Mann-Whitney test, P > 0.05).

The success of migration in this experiment with clustered plants was 84% (116/ 138), with migration being facilitated by the fact that the plants were close to one another.

Larval mortality due to migration was significantly higher on isolated plants but mortality due to predation was similar on isolated and clustered plants (Tables 2 e 3).

Discussion

A. monuste caterpillars frequently migrate in search of food to complete their development and even smaller larval clusters (20 individuals) are not supported by the resources provided by a medium-size kale plant. Larval migration (dispersal) was successfully performed by 5th-instar caterpillars.

Predation occurred at high frequency during the feeding of *A. monuste* caterpillars on their leaves of origin, confirming that natural enemies represent the greatest risk of mortality for the larval stage of insects (Feeny *et al.* 1985, Damman 1987).

Species with mobile larvae always showed a more indiscriminate oviposition with respect, for instance, to the quantity of resources (e. g. Marques *et al.* 1994, Tammaru *et al.* 1995). However, it seems more logical that the characteristics of the females precede and cause the characteristics of the caterpillars, since females are often better equipped to choose between potential host plants (Price 1994 *apud* Janz & Nylin 1997) and the preference for oviposition seems to be evolutionarily more plastic than larval performance (Wasserman & Futuyma 1981, Janz *et al.* 1994). It seems that evolution, when it turns oviposition more indiscriminate, leads to selection for greater larval mobility, which in turn pre-adapts the females that lay eggs in a more indiscriminate manner (Janz & Nylin 1997).

During migration, *A. monuste* caterpillars did not show a high capacity to detect their host in experiments with plants in cages or in nature. Species such as *Charidryas harrissi* Scudder, *Battus philenor* L. and *Pieris rapae* L. need to be located at a distance of a few millimeters from the host plant to be able to detect it as a source of food (Dethier 1959, Rausher 1979, Cain *et al.* 1985). In *A. monuste*, for a successful larval migration it is indispensable that the plants be close to one another, since this behaviour occurs in a random manner.

Migration was always necessary in nature and has been well studied in *Chilo partellus* Swinhoe, a corn caterpillar, and is due to the fact that the size of the larval cluster is larger than what a plant can support, thus being a density-dependent behaviour (van Hamburg 1980 *apud* Berger 1992, Chapman *et al.* 1983). Fifth-instar larvae, which move rapidly and keep their mobility even in the absence of food, have a better chance to escape predators than smaller caterpillars (Berger 1992). We believe that this also applies to *A. monuste* caterpillars, also because kale gardens occupy extensive areas in the region studied (Barros & Zucoloto 1999).

A. monuste females laid eggs on isolated plants in nature. This behaviour greatly reduced immature survival since larval migration was impaired by the lack of nearby plants. The limitation of the time spent by females looking for a host is a reasonable explanation for this type of oviposition since, as the time for choice becomes scarce, it is a risk to leave the host plant without laying eggs on it, since another, more adequate plant may not be found (Jaenike 1978 *apud* Mayhew 1997; Ward 1987). In the present experiment, perhaps it was easier for the females to find spaced plants (a total of 6 plants) than the group of clustered plants (a set of 12 plants), even though they all were in the same area (close to the Department of Biology).

Another experiment carried out with *A. monuste* in a natural garden (Diniz & Zucoloto unpl. data) showed that the females of this species oviposited more on plants peripherally distributed in the garden than in those located centrally, i.e., there was a preference for more isolated plants.

In the present study, the oviposition of *A. monuste* females on isolated plants was similar to the oviposition in clustered plants in nature.

It was found a difference in clutch size between plants confined to cages and plants growing in nature, with females confined to cages facing some factors that limited their ovipositing rate, with fewer eggs being laid. Even in the experiment of offspring behavior in rearing cages, in which only 20 caterpillars were present, larval migration was also necessary, because the food was not sufficient. The larval performance of the group of caterpillars artificially transported to another plant differed in terms of larval mortality and time for pupation from the group in which migration occurred, with both parameters being higher in the latter group.

Insect species whose larvae have high mobility, such as *A. monuste*, show a poorly discriminatory oviposition behavior with respect to the quantity of food, i. e., females frequently place more eggs than a kale plant can support and do not show preference for clustered plants. Furthermore, larval migration of *A. monuste* is influenced positively by the abundance of kale in space and time, and because kale plants are quite close to one another in most gardens.

Under the conditions of the present study, predation was the major cause of mortality of *A. monuste* caterpillars in nature. The feeding activity of larvae on the plants is quite dangerous since its movements, the chewing sounds and the odors released by the plants can be stimuli evaluated by predators to locate their prey. Feeding time must also be an important factor, with the caterpillars being vulnerable during this period (Bernays 1997).

Some insects are often observed on kale leaves, such as the caterpillar *Trichoplusia ni* (Hübner) and the aphid *Brevicoryne brassicae* (Figueira 1982). The level of parasitism of *A. monuste* caterpillars in the first instars by *Cortesia ayerzai* Bréthes can also be high (Gobbi *et al*. 1990); perhaps parasitism was not often observed in the present study because the caterpillars were preyed upon before it could manifest. Wasps are important predators of medium-sized *Manduca sexta* (L.) caterpillars (Tautz & Markl 1978), and it may also occur with *A. monuste* immatures. There is also the risk of predation by spiders and birds, including adults.

Acknowledgments

Helen C. H. Barros-Bellanda held a Ph.D. studentship in Entomology, FFLC-USPRP, and FAPESP fellowship.

Literature Cited

Barros, H.C.H. & F.S. Zucoloto. 1999. Performance and host preference of *Ascia monuste* (Lepidoptera, Pieridae). J. Insect Physiol. 45: 7-14.

Berger, A. 1992. Larval movements of *Chilo partellus* (Lepidoptera: Pyralidae) within and between plants: timing, density responses and survival. Bull. Entomol. Res. 82: 441-448.

Bernays, E.A. 1997. Feeding by caterpillars is dangerous. Ecol. Entomol. 22: 121-123.

Cain, M.L., J. Eccleston & P.M. Kareiva. 1985. The influence of food plant dispersion on caterpillar searching success. Ecol. Entomol. 10: 1-7.

Chapman, R.F., S. Woodhead & E.A. Bernays. 1983. Survival and dispersal of young larvae of *Chilo partellus* (Swinhoe) (Lepidoptera: Pyralidae) in two cultivars of sorghum. Bull. Entomol. Res. 73: 65-74.

Chew, F.S. 1988. Searching for defensive chemistry in the cruciferae, or, do glucosinolates always control interactions of cruciferae with their potential herbivores and symbionts? No!, p. 81-112. In K.C. Spencer (ed.), Chemical mediation of coevolution. Academic Press, San Diego, 417p.

Damman, H. 1987. Leaf quality and enemy avoidance by the larvae of a pyralid moth. Ecology 68: 88-97.

Damman, H. 1991. Oviposition behaviour and clutch size in a group-feeding pyralid moth, *Omphalocera munroei*. J. Animal Ecol. 60: 193-204.

Dethier, V. 1959. Food plant distribution and density and larval dispersal as factors affecting insect populations. Can. Entomol. 91: 581-596.

Felipe, M.C. & F.S. Zucoloto. 1993. Estudos de alguns aspectos da alimentação em *Ascia monuste* Godart (Lepidoptera, Pieridae). Rev. Bras. Zool. 10: 333-341.

Feeny, P., W.S. Blau & P.M. Kareiva. 1986. Larval growth and survivorship of the black swallowtail butterfly in central New York. Ecol. Monogr. 55: 167-187.

Figueira, F.A.R. 1982. Brassicáceas, p. 34-75. In Figueira, F.A.R., Manual de olericultura. São Paulo, Editora Agronômica Ceres Ltda, 357p.

Gobbi, N., M.C.A. Cunha, R. Zucchi & H.G. Fowler. 1990. Ovipositon pattern by *Cotesia auerzai* (Hym: Braconidae) on *Ascia monuste* (Lep.: Pieridae) under laboratory conditions. Entomophaga 35: 195-202.

Huang, X. & J.A.A. Renwick. 1993. Differential selection of host plants by two *Pieris* species: the role of oviposition stimulants and deterrents. Entomol. Exp. Appl. 68: 59-69.

Janz, N. & S. Nylin. 1997. The role of female search behaviour in determining host plant range in plant feeding insects: a test of the information processing hypothesis. Proc. R. Soc. Lond. B. 264: 701-707.

Janz, N., S. Nylin & N. Wedell. 1994. Host plant utilization in the comma butterfly: sources of variation and evolutionary implications. Oecologia 99: 132-140.

Marques, R.S.A., E.S.A Marques & P.W. Price. 1994. Female behavior and oviposition choices by an eruptive herbivore, *Disnycha pluriligata* (Coleoptera: Chysomelida). Environ. Entomol. 23: 887-892.

Mayhew, P.J. 1997. Adaptive patterns of host-plant selection by phytophagous insects. Oikos 79: 417- 428.

Rausher, M.D. 1979. Larval habitat suitablity and oviposition preference in three related butterflies. Ecology 60: 503-511.

Rhoades, A.F. 1985. Offensive-defensive interactions between herbivores and plants: Their relevance in herbivores and plants: Their relevance in herbivore population dynamics and ecological theory. Amer. Natur. 125: 205-238.

Tallamy, D.W. & T.K. Wood. 1986. Convergence patterns in subsocial insects Annu. Rev. Entomol. 31: 369-390.

Tammaru, T., P. Kaitaniemi & K. Ruohomaki. 1995. Oviposition choices of *Epirrita cutumnata* (Lepidoptera: Geometridae) in relation to its eruptive population dynamics. Oikos 74: 296-304.

Tautz, J. & H. Markl. 1978. Caterpillars cetect flying wasps by hairs sensitive to airborne vibration. Behav. Ecol. Sociobiol. 4: 101-110.

Thompson, J.N. 1983. Selection pressures on phytophagous insects on small plants. Oikos 40: 438-444.

Ward, S.A. 1987. Optimal habitat selection in time-limited dispersers. Amer. Natur. 129: 568-579.

Wasserman, S.S. & D.J. Futuyma. 1981. Evolution of host plant utilization in laboratory populations of the southern cowpea weevil, *Callosobruchus maculatus* Fabricus (Coleoptera: Bruchidae). Evolution 35: 605-617.

Received 01/04/02. Accepted 12/02/03.