

Life cycle of *Agrotis malefida* (Lepidoptera: Noctuidae): a diapausing cutworm

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ABSTRACT. This study describes the life cycle of *Agrotis malefida* Guenée, 1852 (Noctuidae: Noctuinae) under laboratory conditions. The insects were reared in a controlled environment ($25 \pm 1^\circ\text{C}$, $70 \pm 10\%$ RH and 14 hours photo phase) and observed daily. The larvae were fed Greene's artificial diet and adults were offered a 10% sucrose solution. The viability and duration of immature stages were assessed. The experiment initiated with 2,410 eggs. Larvae were isolated shortly after hatching. Longevity, pre-, post- and oviposition, fecundity and fertility of 13 adult couples were also evaluated. The viability of eggs, larvae, pupae and pre-pupae was 96.72, 91.25, 78.37 and 95.26%, respectively. The average duration of egg, larva, pre-pupa, pupa and adult was 7.93, 54.26, 61.61, 37.43 and 12.85 days, respectively. The immature stage of *A. malefida* lasted an average of 161.29 days, ranging from 102 to 227 days. The life cycle of *A. malefida* is much longer than that of congeners. The mean fecundity was 1,696.77 eggs and fertility 1,641.15 larvae per female. Under the conditions in which the study was conducted, the biotic potential of *A. malefida* was of 606,666.59 individuals/female/year. The results also indicated that this species goes through larval (pre-pupae) and pupal diapause.

KEY WORDS. Bionomy; caterpillar; development; diapause.

Agrotis Ochsenheimer, 1816 (Noctuidae: Noctuinae: Noctuini) (LAFONTAINE & SCHMIDT 2010) is a cosmopolitan genus with 317 species (POOLE 1989). All *Agrotis* larvae are voracious and are able to feed on a variety of hosts (KITCHING & RAWLINS 1998, POGUE 2006). They have underground habits, coming to the surface at night to feed. While feeding, they cut the stems of their food plants, causing severe damage and rapid crop loss. When disturbed, *Agrotis* larvae roll up in a very characteristic behavior (BAUDINO 2004, LAFONTAINE 2004, ANGULO *et al.* 2008).

Agrotis malefida Guenée, 1852 has been recorded from most of the Americas (PASTRANA & HERNANDES 1979, RIZZO *et al.* 1995, LAFONTAINE 2004) and is likely to occur worldwide (ANGULO & QUEZADA 1975). The species has been widely documented in the United States and Mexico (LAFONTAINE 2004, POGUE 2006), Chile (ANGULO & QUEZADA 1975, ANGULO *et al.* 2008), Argentina (MARGHERITIS & RIZZO 1965, IGARZÁBAL *et al.* 1994, RIZZO *et al.* 1995, BAUDINO 2004, PASTRANA 2004), Brazil (SILVA *et al.* 1968, SPECHT & CORSEUIL 1996, 2002, SPECHT *et al.* 2004) and Uruguay (BENTANCOURT & SCATONI 2006). Larvae of *A. malefida* are known in North America as Pale-Sided Cutworms; in Latin America as "gusano áspero", "oruga áspera" or "oruga cortadora áspera" (LAFONTAINE 2004); and in Brazil as "lagarta-rosca" (SILVA *et al.* 1968).

Larvae of *A. malefida* are polyphagous, attacking various herbaceous, native and cultivated plants, including economically relevant crops such as alfalfa, barley, bean, beet, cabbage, cauliflower, clover, coffee, collard, corn, cotton, cowpea, cucumber, flax, garlic, lettuce, melon, oat, onion, pea, pepper, potato, rice, rye, sorghum, soybean, squash, strawberry, sunflower, Swiss chard, tobacco, tomato and wheat (SILVA *et al.* 1968, VILLATA *et al.* 1988, COTTO *et al.* 1995, RIZZO *et al.* 1995, PASTRANA 2004, SPECHT *et al.* 2004, BAUDINO & VILLARREAL 2007, ANGULO *et al.* 2008). Larvae often build a subterranean tunnel which is used as a hiding place during the day, and as a place to eat the host plants cut during the night (LAFONTAINE 2004).

The economic relevance of *A. malefida* has motivated various studies on the morphology of the adult (ANGULO & QUEZADA 1975) and of immature stages (RIZZO *et al.* 1995, ANGULO *et al.* 2008), along with biological studies (VILLATA *et al.* 1988, RIZZO *et al.* 1995, BAUDINO 2004, BAUDINO & VILLARREAL 2007). Despite the morphological similarities of the adults and the sympatry of *Agrotis ipsilon* (Hufnagel, 1766) and *A. malefida* in the American continent (ANGULO & QUEZADA 1975), previous studies indicate several biological differences, especially in the immature stages of *A. malefida* (VILLATA *et al.* 1988, RIZZO *et al.* 1995, BAUDINO 2004, BAUDINO & VILLARREAL 2007). In view of the

importance of the species, and its large intraspecific variability (VILLATA *et al.* 1988, RIZZO *et al.* 1995), we have endeavored to describe the biological parameters and to estimate the biotic potential of *A. malefida* in the laboratory, using individual observations on thousands of specimens.

MATERIAL AND METHODS

Our laboratory rearing experiment initiated with 13 couples obtained from a mass rearing colony maintained by the Laboratório de Biologia, Campus Universitário da Região dos Vinhedos (CARVI), Universidade de Caxias do Sul (UCS). The mass rearing itself originated from individuals collected in the Vale dos Vinhedos, Bento Gonçalves, state of Rio Grande do Sul. Our experiments were conducted in a controlled environment ($25 \pm 1^\circ\text{C}$, $70 \pm 10\%$ UR and 14 hours photo phase), with daily observations.

Each adult couple ($n = 13$) was maintained inside a cylindrical plastic container (10 cm diameter, 15 cm height). In order to stimulate oviposition, strings of filter-paper of the same length as the plastic vial were inserted into each container and attached using a plastic film cover. The moths were fed an aqueous sucrose solution (10%), made available in hydrophilic cotton inside a 10 mL glass Erlenmeyer flask. The following parameters were evaluated: fecundity (number of eggs per female), fertility (number of hatched larvae per female), longevity and duration of pre-oviposition, post-oviposition and oviposition periods.

During the egg stage, we assessed the viability and duration of the incubation period of five random ovipositions from each couple (including first and last ovipositions), totaling 2,410 eggs. Each egg mass was individually placed in a Petri dish, where it remained until the larvae hatched. The bottom of each Petri dish was lined using filter paper moistened with distilled water, in order to avoid desiccation.

After hatching, neonate larvae were separately placed in 150 ml plastic cups, covered with a lid, and fed an artificial diet (GREENE *et al.* 1976), previously used successfully by RIZZO *et al.* (1995) for the same species. We evaluated the survival and the duration of the larval period of 2,331 individuals. The pre-pupal period was considered separately, and its onset was recorded when the larva stopped feeding and decreased in size. We added expanded vermiculite, moistened with distilled water, to each cup, in order to allow the pre-pupae to build a pupal chamber.

Pupae were kept in the same containers as pre-pupae. On the second day after pupation, when the cuticle had hardened, we ascertained the sex of each individual using sketches from ANGULO *et al.* (2008). Besides ascertaining the duration of the pupal period, we measured the weight, the greater width between pterotectae, and the total length of each pupa.

We calculated the biological potential from the biological variables, considering the environmental resistance to be null. The fertility life table was calculated using the equations of

SILVEIRA NETO *et al.* (1976) and the following parameters were determined: net reproductive rate (R_0), mean generation time (T), natural intrinsic growth rate (r_m), and infinite growth rate (λ).

Monthly collections of *A. malefida* moths were made within the CARVI ($29^\circ08'99''\text{S}$; $51^\circ31'39''\text{W}$, 675 m a.s.l.), from January 2007 to December 2008, four nights during each new moon, using light traps as described in SPECHT *et al.* (2005), in order to obtain information on the period of adult occurrence.

The temporal and morphometric parameters were analyzed using descriptive statistics to calculate the means and standard errors. When necessary, the means were compared using a t-test assuming unequal variances, at a significance level of 95%.

Voucher specimens (10 couples) were deposited in the collection of the CARVI-UCS.

RESULTS

Adult stage

The longevity of *A. malefida* did not significantly differ between the sexes ($p = 0.076$), and represented 7.38% of the developmental cycle (Fig. 1, Table I). Under the conditions of this study, adults of *A. malefida* reach sexual maturation soon after emergence (Table II). The egg laying period occurs from the second to the tenth day after sexual maturation, and the highest fecundity was observed between the seventh and the tenth day (Fig. 2). The fecundity of *A. malefida* varied greatly between individuals resulting in approximately 1,700 eggs per female (Table II).

Table I. Survival and duration of the life cycle of *Agrotis malefida* during different stages of development, under controlled conditions ($25 \pm 1^\circ\text{C}$, $70 \pm 10\%$ RH and 14 hours photo phase).

Developmental stage	Inicial-final N	Survival (%)	Duration (days)	Range
Adult	26	–	12.85 ± 3.78	5-22
Egg	2,410-2,331	96.72	7.93 ± 1.22	6-10
Larvae	2,331-2,127	91.25	54.25 ± 6.39	44-77
Pre-pupae	2,127-1,667	78.37	61.61 ± 17.56	10-131
Pupae	1,667-1,588	95.26	37.43 ± 4.13	11-99
Total immature	1,588	–	161.29 ± 17.35	102-227
Total	–	65.89	174.08	–

Table II. Mean fecundity and duration of the pre-, post-, and oviposition periods (days) of *Agrotis malefida* reared under controlled conditions ($25 \pm 1^\circ\text{C}$, $70 \pm 10\%$ RH and 14 hours photo phase). (N = 13 couples).

Parameter	Mean \pm SE	Range
Fecundity (eggs/female)	1696.77 ± 412.73	992-2170
Periods (days)		
Pre-oviposition	2.54 ± 1.05	1-4
Post-oviposition	0.15 ± 0.38	0-1
Oviposition	9.69 ± 3.04	5-15

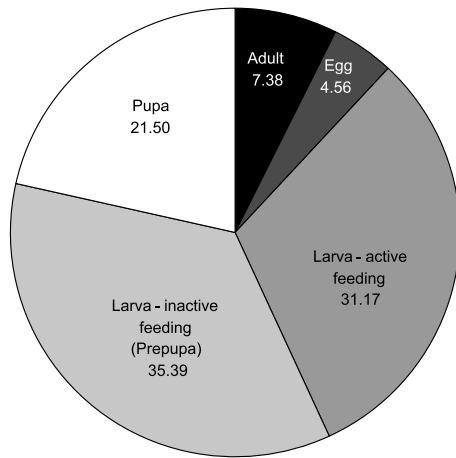


Figure 1. Duration (%) of each developmental period for *Agrotis malefida* reared at 25 ± 1°C, 70 ± 10% RH and 14 hours photo phase.

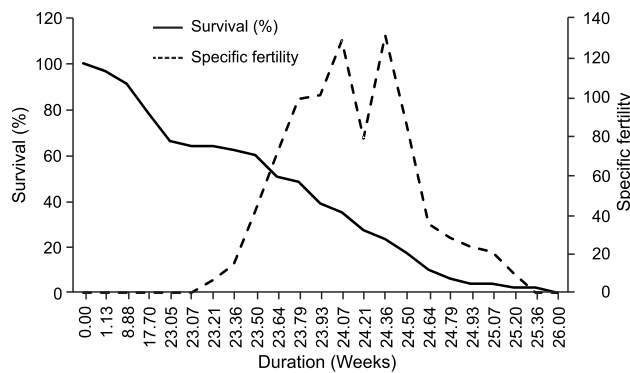


Figure 2. Relationship between specific fertility (mx) and survival rate (lx) during the development of *Agrotis malefida* reared on an artificial diet at 25 ± 1°C, 70 ± 10% RH and 14 hours photo phase.

Adults of *A. malefida* were collected during most of the year, except in November and December, with the largest numbers being collected between April and July (Fig. 3).

Egg stage

The average duration of the embryonic period corresponded to 4.557% of the life cycle (Fig. 1, Table I). We observed a high viability of *A. malefida* eggs (Table I), including those from the first oviposition.

Larval stage

In our experiment, the average duration of the larval stage (including the pre-pupa) of *A. malefida* was almost four months (Table I), accounting for two-thirds of the entire life cycle (Fig. 1).

Females spent more time in the larval stage than males (Table III). Despite the large difference between sexes in the duration of the larval period, not including the pre-pupal period, the variation in the duration of this phase was similar,

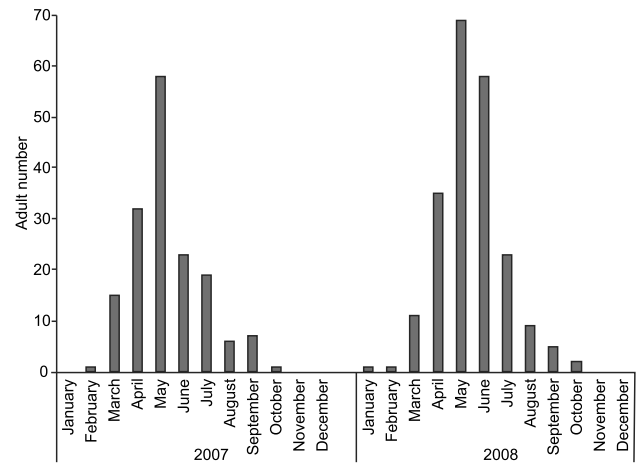


Figure 3. Number of *Agrotis malefida* adults collected by light traps, during four nights per month, in the Bento Gonçalves municipality, state of Rio Grande do Sul, Brazil.

and did not exceed 33 days for either sex (Table III). Most females (81.43%) developed between 40 and 59 days, and only 41 (5.04%) took longer than 70 days (Table IV). Similarly, most males (74.06%) completed their larval phase between 50 and 59 days, and only 30 individuals (3.89%) took more than 70 days.

Table III. *Agrotis malefida* reared under controlled conditions (25 ± 1°C, 70 ± 10% RH and 14 hours photophase). Mean duration (days), and standard errors, of larval and pupal periods, considering males and females separately. The prepupal period is separated from the larval period. The mean values of both sexes were compared using a t-test, at a confidence level of 95%.

	Females (n = 813)		Males (n = 775)	
	Mean ± SE	Range	Mean ± SE	Range
Larvae	54.77 ± 6.64*	44-77	53.70 ± 6.05	46-77
Pre-pupae	62.23 ± 17.28 ns	10-128	60.93 ± 17.83	18-131
Pupae	37.78 ± 4.24*	16-99	37.05 ± 3.98	11-71
Total*	162.81 ± 17.34*	117-227	159.68 ± 17.23	102-225

* p < 0.001, ns = p > 0.05.

The duration of the pre-pupal period of *A. malefida* was longer for females (without statistical significance) than for males (Table III) and was greatly variable (Table IV). The highest frequencies (above 15%) of males and females which completed the pre-pupal period occurred between 40 and 80 days. A few pre-pupae were observed between days 0-20 (n = 4 ~ 0.25%), and also after day 100 (n = 32 ~ 2.02%) (Table IV). The regression analysis (n = 1,583, r² = 0.066, p < 0.001) indicated a direct correlation between the number of days a larva remained active, and the duration of the pre-pupal stage.

Table IV. Number of immature females and males of *Agrotis malefida*, at ten day intervals, indicating larval feeding activity, pre-pupae and pupae, maintained under controlled conditions ($25 \pm 1^\circ\text{C}$, $70 \pm 10\%$ RH and 14 hours photo phase).

Interval (days)	Larvae								Pupae			
	Active feeding				Inactive feeding (prepupae)				Female		Male	
	Female		Male		Female		Male		N	%	N	%
	N	%	N	%	N	%	N	%				
10-19	-	-	-	-	1	0.12	3	0.39	3	0.37	3	0.39
20-29	-	-	-	-	13	1.60	22	2.84	5	0.62	5	0.64
30-39	-	-	-	-	59	7.26	49	6.32	579	71.22	611	78.84
40-49	190	23.37	92	11.87	143	17.59	166	21.42	222	27.31	151	19.48
50-59	473	58.18	574	74.07	144	17.71	133	17.16	-	-	2	0.26
60-69	109	13.41	76	10.19	178	21.89	161	20.77	3	0.37	1	0.13
70-79	41	5.04	30	3.87	148	18.20	124	16.00	-	-	2	0.26
80-89	-	-	-	-	85	10.46	79	10.19	-	-	-	-
90-99	-	-	-	-	27	3.32	21	2.71	1	0.12	-	-
100-109	-	-	-	-	7	0.86	11	1.42	-	-	-	-
110-119	-	-	-	-	7	0.86	4	0.52	-	-	-	-
120-129	-	-	-	-	1	0.12	1	0.13	-	-	-	-
130-139	-	-	-	-	-	-	1	0.13	-	-	-	-
Total	813	100.00	775	100.00	813	100.00	775	100.00	813	100.00	775	100.00

Despite our precautions, 28.48% of the larvae died in our experiment, with higher mortality (71.19%) of the larval stage being observed during the pre-pupal period (Table I).

Pupal stage

The pupal stage of *A. malefida* accounted for 21.501% of the development cycle (Fig. 1, Table I) However, the variation in the duration of this stage was very large, where 98.423% of specimens had a larval period lasting from 31 to 50 days and the others lasted from 11 to 99 days (Tables I, III and IV).

The survival of *A. malefida* pupae was relatively high (Table I). The female pupae were significantly larger and heavier than their male counterparts (Table V).

Table V. Weight, width and length of *Agrotis malefida* pupae (means and standard errors), reared under controlled conditions ($25 \pm 1^\circ\text{C}$, $70 \pm 10\%$ RH and 14 hours photo phase), including comparisons on females and males using a t-test, at a confidence level of 95%.

	Weight (g)	Width (mm)	Length (mm)
Females (n = 194)	0.89 ± 0.15	8.04 ± 0.51	26.39 ± 1.80
Males (n = 131)	0.81 ± 0.11	7.68 ± 0.42	25.92 ± 1.56
	**	**	*

*p < 0.01, **p < 0.001.

Biotic potential

The sex ratio (sr) calculated for the 1,588 pupae (813 females and 775 males) was 0.512. Each female oviposited, on average, 1,696.769 eggs; the overall egg survival was 65.892%, yielding 1,118.035 viable individuals per female (d). The average duration of the life cycle (174.075 days) corresponded to

2.097 generations per year (n). Thus, considering the environmental resistance (er) as null, we obtained the following result for the equation $BP = (sr * d)^n - er$. $BP = (0.512 * 1118.035)^{2.097} - 0 = 6.067 * 10^5$ individuals per female. In other words, each female could generate more than half a million offspring.

Life and fertility tables

The net reproductive rate (Ro) was 322.6 times per generation, and the mean generation time (T) was 23.97 weeks. The intrinsic rate of increase (rm) was 0.24, with a finite rate of increase (Λ) – the number of females added to the population per female that will generate another female – of 1.27. The maximum rates of population increase occurred between days 168 and 170, during the 24th week of development (Fig. 2).

DISCUSSION

Adult stage

In our experiment, the longevity of *A. malefida* (Table I) was higher than in the results obtained by VILLATA *et al.* (1988) (4.86 days) and RIZZO *et al.* (1995) (3-9 days). When reared at temperatures near those used in our experiment, the longevity of the congener *A. ipsilon* was equivalent to that of *A. malefida* (BENTO *et al.* 2007 ~ 13 days). However, in our experiment, *A. malefida* spent more time in the larval stage (66.56% – Fig. 1) with respect to *A. ipsilon* individuals (SANTOS & NAKANO 1982 ~ 24.3%, BENTO *et al.* 2007 ~ 24.5%), which spent relatively more time in the adult stage.

The relatively short pre-oviposition period (Table II) indicates that, under the conditions of this study, adults of *A. malefida* reach sexual maturation soon after emergence. Females of *A. malefida*, as those of *A. ipsilon*, are able to lay eggs two

days after emergence (HARRIS *et al.* 1962, SWIER *et al.* 1976, SANTOS & NAKANO 1982, BENTO *et al.* 2007). The duration of the egg laying period and the highest fecundity, between the seventh and the tenth day (Fig. 2), also resemble the values obtained for *A. ipsilon* (HARRIS *et al.* 1962, SWIER *et al.* 1976, SANTOS & NAKANO 1982, BENTO *et al.* 2007).

The mean fecundity of *A. malefida* (Table II) resembles that obtained by RIZZO *et al.* (1995), who reported between 1,000 and 1,600 eggs per female. However, it differs from the results of VILLATA *et al.* (1988), who reported an average of only 474.5 eggs per fertile female. Our results are also consistent with values obtained for other Noctuidae, such as for *A. ipsilon* (SWIER *et al.* 1976 – 1,423.53, ARCHER *et al.* 1980 – maximum average 1,984, SANTOS & NAKANO 1982 – 1,263, BENTO *et al.* 2007 – 1,806 eggs), *Agrotis ignicans* (Guenée, 1852) (FOESTER & MELLO 1996 – 1,807) and *Agrotis mahalpa* Schaus, 1898 (SPECHT *et al.* 2008 – 2,014).

Despite the greater abundance of individuals per collection, our field results resembled observations made by TARRAGÓ *et al.* (1975), in Santa Maria, Rio Grande do Sul, and by S. Silveira Neto (unpublished data) in various localities of São Paulo, indicating collections of adults during virtually all the year, with highest numbers between April and June. On the other hand, the same species is only reported from April to July in south and southeastern Rio Grande do Sul by SPECHT *et al.* (2004). Similar behavior is recorded in various localities of Argentina with a population peak in April (RIZZO *et al.* 1995, BAUDINO 2004, BAUDINO & VILLARREAL 2007). Such data indicate that despite being considered a univoltine species (VILLATA *et al.* 1988, RIZZO *et al.* 1995, BENTANCOURT & SCATONI 2006), under field conditions adults of *A. malefida* may emerge at different times of the year, peaking in winter. Similar flight behavior is recorded in the northern part of USA where adults begin emerging in late January (LAFONTAINE 2004). Nevertheless, *A. malefida* flies throughout the year in the southern United States (LAFONTAINE 2004) and within the xerophilic zone in the island of Guadeloupe (ZAGATTI *et al.* 2006).

These observations indicate that in higher latitudes larvae of *A. malefida* are sensitive to the daily increase of the photoperiod culminating in aestival diapause, a mechanism described for several insects, especially from temperate regions (SCHNEIDER 2009). In fact, despite the non-variable photoperiod used in our experiment (14 hours of light), it corresponded to the maximum observed at latitude 30°, which triggered the initiation of diapause, at least in part of the population.

Egg stage

The embryonic period (Table I) of *A. malefida* was longer than previously reported by RIZZO *et al.* (1995), who found that this stage lasts five to six days under lower temperatures (22–23°C). Our results, however, resemble those of VILLATA *et al.* (1988), who reported that the embryonic period in *A. malefida* lasted eight days when experiments were conducted at 25°C and a relative humidity of 60%. The embryonic period of *A. malefida* is relatively long when compared with that of several

other representatives of Noctuidae reared under similar temperatures, such as in *A. ipsilon* (HARRIS *et al.* 1962 – 4 days, SANTOS & NAKANO 1982 – 4 days, BENTO *et al.* 2007 – 3.3 days) and *Agrotis infecta* (Ochsenheimer, 1816) (TESTON *et al.* 2001 – 3.2 days).

The high viability of *A. malefida* eggs (Table I), including those from the first oviposition, suggests that females were fertilized soon after emergence. These results differ from those obtained for *A. ipsilon* females, which are less attractive to males during the first few days after emergence (SWIER *et al.* 1976), resulting in infertile first ovipositions, and consequently low average values of relative viability (SANTOS & NAKANO 1982 to 64.45%, BENTO *et al.* 2007 to 81.00%).

Larval stage

In our experiment, the long duration of the larval stage (including the pre-pupa) of *A. malefida* was similar to the 93.2 days reported for the same species when reared at 25°C and 60% humidity, but very different from the 36.14 days found for specimens reared under the same temperature and 50% relative humidity (VILLATA *et al.* 1988). In the present study, larvae remained in separate plastic cups inside an incubator with a relative humidity of 70 ± 10%. They were fed an artificial diet rich in water. After the third or fourth instars, larvae dug a tunnel in their food, where they remained. Therefore, the effective experimental humidity was above 50 and 60% used by VILLATA *et al.* (1988) and the added moisture was likely responsible for increasing the duration of the larval phase. The direct relationship between increased moisture and increased duration of the larval period in *A. malefida* (VILLATA *et al.* 1988) contrasts with results described for *A. ipsilon*. Moisture generally did not influence the duration of the developmental phases of *A. ipsilon*, except during the first five instars, when it significantly accelerates the larval stage (ARCHER *et al.* 1980).

The larval stage of *A. malefida*, corresponding to 66.56% of the species' entire life cycle, lasted longer than in other Noctuidae representatives such as *A. ipsilon* (HARRIS *et al.* 1962 – 48.99%; SANTOS & NAKANO 1982 – 43.42%, BENTO *et al.* 2007 – 46.65%), *Peridroma saucia* (Hübner, [1808]) (MORENO FAJARDO & SERNA CARDONA 2006 – 43.15%), *A. infecta* (TESTON *et al.* 2001 – 44.09%) and *A. mahalpa* (SPECHT *et al.* 2008 – 48.18%). Furthermore, the larval phase of *A. malefida* showed greater variability (Tables I and III), a fact that had also been mentioned by VILLATA *et al.* (1988) and RIZZO *et al.* (1995), though to a lesser extent. However, the period in which the larvae are active and feeding (Table I, Fig. 1) (31.17%) is similar among *A. malefida* and *A. ipsilon* (HARRIS *et al.* 1962 – 45.37%, SANTOS & NAKANO 1982 – 38.82%), *P. saucia* (MORENO FAJARDO & SERNA CARDONA 2006 – 40.06%), *A. infecta* (TESTON *et al.* 2001 – 37.48%) and *A. mahalpa* (SPECHT *et al.* 2008 – 42.14%).

The longer larval period of *A. malefida* females (Table III) can be explained by the fact that females are on average larger (see pupal stage). For this reason, in species which are sexually dimorphic such as *Spodoptera albula* (Walker, 1857) (Noctuidae: Noctuidae: Prodeniini) (MONTEZANO *et al.* 2013) and in other

Lepidoptera, females can have additional instars (ALLEN *et al.* 2011).

The great variation of the pre-pupal period (Table IV) can be considered a specific characteristic of *A. malefida*, already described for Lepidoptera of temperate regions in which individuals in the population emerge at different times (SCHNEIDER 2009). Additionally, *A. malefida* males are smaller, have faster development during larval and pupal periods, emerging before the females as a form of sexual competition (ALLEN *et al.* 2011), like other species of the same group, such as *Sesamia nonagrioides* (Lefebvre, 1827) (LÓPEZ *et al.* 2003).

After rearing the same species under four different temperature regimes and humidity between 50 and 60%, VILLATA *et al.* (1988) found that individuals remained in the pre-pupal stage between 3-25 days. However, in their study the last instar (presumably the pre-pupa) lasted longer on average when temperatures were set between 19 and 25°C and the relative humidity was highest. Their results corroborate our findings that higher humidity levels lengthen the larval period of *A. malefida*. The occurrence of prepupal diapause in *A. malefida* (BENTANCOURT & SCATONI 2006) has already been reported for some noctuid species in other genera, such as in *Xestia c-nigrum* (Linnaeus, 1758) (HONIK 1979, OKU 1984), *Helicoverpa armigera* (Hübner, [1809]) (WILSON *et al.* 1979, QURESHI *et al.* 2000, FENG *et al.* 2010), and *S. nonagrioides* (FANTINOU *et al.* 1996, GADENNE *et al.* 1997, EIZAGUIRRE *et al.* 2008). However, larval and pupal diapause were not expected to occur in *A. malefida* under the rearing conditions of our experiment ($25 \pm 1^\circ\text{C}$, $70 \pm 10\%$ RH and 14 hours photoperiod). Nevertheless, EIZAGUIRRE *et al.* (2008) mention a few individuals of *S. nonagrioides* expressing diapause when reared under similar environmental conditions.

The direct correlation between the number of days a larva remained active and the duration of the prepupal stage may be related to the number of larval instars. Even though we have not investigated the number of larval instars of our specimens, VILLATA *et al.* (1988) reported that *A. malefida* may have from seven to 11 instars. Additionally, according to them, the greater number of instars occurs when the larval phase is longer. In view of the fact that the number of instars is greater in noctuids that undergo diapause (ESPERK *et al.* 2007, GADENNE *et al.* 1997), and given the results found in our study combined with those of VILLATA *et al.* (1988), we have confirmed that *A. malefida* larvae undergo larval diapause.

The lower larval survival rate of *A. malefida*, especially in the prepupal stage (Table I), may be associated with the longer duration of the larval period in this species. A similar observation was made by EIZAGUIRRE *et al.* (2008), who noted that diapausing larvae of *S. nonagrioides* had low survival rates.

Pupal stage

In this study, the variation in the duration of the pupal stage of *A. malefida* (Tables I, III and IV) was much higher than the range reported for the same species by RIZZO *et al.* (1995) (29 to 44 days) and BAUDINO (2004) (41.0 ± 20 days). These re-

sults demonstrate that, like other noctuids such as *H. armigera* (WILSON *et al.* 1979, QURESHI *et al.* 2000), the pupa of *A. malefida* may also go through diapause.

The high survival of *A. malefida* pupae (Table I) was similar to that of most noctuids reared in the laboratory, such as *A. ipsilon* (REESE *et al.* 1972, BENTO *et al.* 2007) and *A. mahalpa* (SPECHT *et al.* 2008).

The length and width of *A. malefida* pupae (Table V) were similar to those obtained by RIZZO *et al.* (1995) and greater than those described by ANGULO *et al.* (2008). The fact that female pupae were significantly larger and heavier than their male counterparts (Table V) was previously described as sexual dimorphism (e.g., ANGULO *et al.* 2008).

Biotic potential

The biotic potential of *A. malefida*, 6.067×10^5 individuals per female, is very low when compared to the biotic potential of *A. ipsilon*, approximately 4.120×10^{18} (calculated using the data from BENTO *et al.* 2007). Whereas, the fecundity and fertility of *A. malefida* is similar to *A. ipsilon*, the difference in the biotic potential of these two species was primarily a function of the difference between the life cycle and survival. The total duration of the life cycle of *A. malefida* (Table I) was three times longer than that of *A. ipsilon* (SANTOS & NAKANO 1982, BENTO *et al.* 2007). Moreover, the total survival, especially of the prepupal stage of *A. malefida* (Table I), was much lower than described for *A. ipsilon* (HARRIS *et al.* 1962, SWIER *et al.* 1976, SANTOS & NAKANO 1982, BENTO *et al.* 2007).

Life and fertility tables

The net reproductive rate ($R_0 = 322.6$), the intrinsic rate of increase ($r_m = 0.24$) and the finite rate of increase ($\Lambda = 1.27$) are lower than those obtained for *A. ipsilon* by BENTO *et al.* (2007), who reported a R_0 of 616.9, a r_m of 0.94 and a Λ of 2.55. Similar to what was observed in biotic potential, and considering the high fertility of *A. malefida* obtained in this study, the discrepancy between our results and those mentioned above can be explained by the shorter generation time of *A. ipsilon* ($T = 6.86$ weeks), when compared to *A. malefida* ($T = 23.97$ weeks).

Final considerations

Although ANGULO & QUEZADA (1975) observed morphological and behavioral similarities between adults of *A. malefida* and *A. ipsilon*, our results demonstrated that the life cycle of both species are very different, being longer in *A. malefida*.

Our results demonstrated that in warmer regions, especially at lower latitudes, *A. malefida* develops more than one generation per year, and adults can be collected throughout the year (LAFONTAINE 2004). However, as mentioned by BENTANCOURT & SCATONI (2006), in temperate regions and at higher latitudes, this species, like other representatives of Noctuidae, goes through larval (prepupa) and pupal diapause (HONIK 1979, WILSON *et al.* 1979, OKU 1984, FANTINOU *et al.* 1996, GADENNE *et al.* 1997, QURESHI *et al.* 2000, FENG *et al.* 2010, EIZAGUIRRE *et al.* 2008). The occurrence of larval and/or pupal diapause highlights the need to

develop further studies in order to assess the response of *A. malefida* to environmental variations such as photoperiod, humidity, temperature or combinations thereof.

The observation that *A. malefida* goes through diapause indicates that other species with similar distribution and occurrence such as *Agrotis brachystris* (Hampson, 1903) and *Agrotis gypaetina* Guenée, 1852 (SPECHT *et al.* 2004, BENTANCOURT & SCATONI 2006) may also present this type of physiological behavior.

Considering the widespread distribution and its easy development in the laboratory, *A. malefida* could be a good model for biological studies, especially for comparing species that exhibit different behaviors depending on the latitude in which they live.

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