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Influence of larval crowding and mating on lifespan and fecundity of *Mamestra brassicae* (Lepidoptera: Noctuidae)

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***Mamestra brassicae*, population density, pupal weight, mating, reproduction, weight-related fecundity**

Abstract. Lifespan, preoviposition and oviposition periods of *Mamestra brassicae* were unaffected by larval rearing densities and the group effect. Fecundity of both mated and unmated females was correlated significantly with pupal weight. Weight-related fecundity was not influenced by larval phase variation. Mated females lived, on average, 2 days longer and had 2.2–3.8 times greater potential fecundity than unmated females. Positive fecundity/oviposition period and fecundity/lifespan relationships existed in mated and unmated females, respectively.

INTRODUCTION

In common with some other Noctuidae, *Mamestra brassicae* L. shows a density-related phase variation of juvenile stages as well as a pupal weight reduction at larval crowding (Hirata, 1954; Kazimírová, 1992). In a large number of Lepidoptera, larval crowding has been correlated with changes in adult physiological and behavioural characteristics (Rivnay & Meisner, 1966; Hill & Hirai, 1986; Gunn & Gatehouse, 1987; Hammond & Fescemyer, 1987; Lewis & Keaster, 1989). Some noctuid moths, derived from gregarious-phase larvae, have been suggested to be specifically adapted for migration (Iwao, 1968; Woodrow et al., 1987).

In general, development of smaller and less fecund adults can be considered among the mean consequences of larval crowding in insects (Peters & Barbosa, 1977). Fecundity is positively related to size in several insect species (Honěk, 1993). However, the fecundity/size relationships can often be masked by other factors of the environment (Leather, 1988).

Food, diapause, population density and various abiotic factors have been shown to influence the cabbage moth reproductive performance (Bonnemaison, 1961, 1962; Noll, 1963). However, the impact of crowding and that of larval phase variation on adult lifespan and reproduction of this species have not been studied in detail.

The main objective of this study was to determine, if crowding and the group effect, inducing larval phase variation in *M. brassicae*, lead to subsequent changes in the lifespan and reproduction potential of both mated and unmated females. Mechanical separation of crowded larvae and the reduction of rearing space have been evaluated as possible factors changing adult reproduction performance. Pupal weight-related fecundity and lifespan, as well as fecundity/oviposition period and fecundity/lifespan relationships are reported on.

MATERIAL AND METHODS

Eggs of *M. brassicae* (Lepidoptera: Noctuidae) were derived from a laboratory stock, reared on Brussels sprout leaves, in an outdoor cage. Experiments were performed at 23 ± 1°C, 65 ± 5% RH and long day conditions (16L : 8D). The first two larval instars were fed on Brussels sprout leaves and those following by a semi-synthetic diet (Podmanická & Weismann, 1975). Larvae were provided with excess food throughout their development. From the fourth instar to pupation, larvae were reared in three experimental conditions:

Experiment A. The effect of population density was investigated by rearing larvae at 1, 2, 4, 6 and 8 individuals in a petri dish (100 x 15 mm).

Experiment B. Larvae were reared as in experiment A, but they were separated from each other by means of plastic barriers. In this way the influence of mechanical separation and rearing space reduction was studied.

Experiment C. The influence of "group effect" was studied by rearing 1, 2, 4, 8 and 12 larvae in petri dishes of 50 x 15, 70 x 15, 100 x 15, 120 x 20 and 150 x 25 mm, respectively (for details see Kazimírová, 1992).

Pupae were weighed and sexed one day after pupation. In female pupae, taken at random from each treatment A group, length was measured and moth weights were recorded after eclosion and voiding of the meconium.

Just after emergence, the moths were placed in pairs (1 male, 1 female) into 600 cm^3 plastic containers with paper as a substrate for oviposition. Moths were provided with a cotton wool bud soaked with a 10% honey solution. The cotton wool was moistened daily with distilled water and renewed once every 5 days. The containers were checked daily for oviposition and dead moths. The paper sheets were removed and egg masses cut out and counted. Dead females were dissected and the number of mature chorionate eggs in their ovarioles was recorded. Another male was introduced into any container in which one had died before the female. A group of females was maintained singly in the same manner. Females kept with males and laying unfertile eggs were considered as unmated.

Data were analysed using one-way ANOVA, the Duncan multiple range test, two-sample analysis (t-test) and simple linear regression.

RESULTS

Effect of larval density

Significant reduction of pupal weight of both sexes was found at increasing larval density, as well as under the influence of the group effect. However, these factors did not affect considerably the lifespan, preoviposition and oviposition periods and fecundity of mated females (Table 1). In unmated females the increase in larval population density from 1 to 4 individuals per dish caused a significant decrease in potential fecundity. The opposite was found in "the group effect" treatment, where the average fecundity of unmated females increased with the number of larvae per dish (Table 2). Rearing larvae in reduced space did not show any effect on female life characteristics. In each experimental group, the incidence of sterile females was observed. However, their proportion, ranging between 0.86–19.56%, did not show any density-dependence. Male lifespan was not influenced by larval rearing conditions (Table 2).

Effect of mating

In most experimental groups (except for experiment B, group of 4 individuals) mated females lived longer than those unmated. These differences were significant in 8 out of 15 groups (t-test, Table 1). The potential fecundity of mated females was significantly higher than in unmated females in all groups (Table 1, 2). On average, mated and unmated females laid 94.6% and 11.1% of their egg complement, respectively.

TABLE 1. Pupal weight and some life characteristics in mated *Mamestra brassicae* females originating from different larval rearing conditions.

	N	n	Pupal weight (mg)	Lifespan (days)	Preoviposition period (days)	Oviposition period (days)	Fecundity	
							potential (No. of eggs)	actual (%)
A	1	69	405.3 ± 9.0^{a}	11.7 ± 0.4	4.7 ± 0.3	6.7 ± 0.3	1222 ± 72	93.5
	2	78	374.6 ± 8.6^{b}	11.5 ± 0.4	4.5 ± 0.3	6.9 ± 0.3	1182 ± 57	96.9
	4	63	366.5 ± 6.8^{b}	11.8 ± 0.5*	4.8 ± 0.4	6.8 ± 0.3	1171 ± 68	97.9
	6	68	373.6 ± 8.7^{b}	11.5 ± 0.4*	4.2 ± 0.3	6.8 ± 0.4	1124 ± 65	93.8
	8	99	373.3 ± 6.2^{b}	11.9 ± 0.3	4.4 ± 0.3	7.2 ± 0.3	1247 ± 45	95.4
B	1	19	442.4 ± 17.5^{a}	9.8 ± 0.4	3.5 ± 0.5	6.2 ± 0.5	1313 ± 129	95.8
	2	47	392.8 ± 7.9^{c}	11.2 ± 0.6*	4.3 ± 0.4	6.2 ± 0.5	1164 ± 73	98.5
	4	54	409.2 ± 7.2^{bc}	10.6 ± 0.4	4.1 ± 0.3	6.3 ± 0.4	1202 ± 76	95.7
	6	41	421.7 ± 9.7^{ab}	11.0 ± 0.6*	3.6 ± 0.3	6.5 ± 0.4	1354 ± 83	94.2
	8	27	430.8 ± 10.3^{ab}	10.1 ± 0.6*	3.6 ± 0.5	6.6 ± 0.5	1173 ± 80	96.8
C	1	36	463.8 ± 11.0^{a}	11.7 ± 0.6***	4.7 ± 0.5	5.9 ± 0.5	1073 ± 94	85.8
	2	31	425.6 ± 10.7^{b}	11.6 ± 0.6***	4.5 ± 0.5	5.8 ± 0.5	983 ± 64	91.9
	4	30	422.7 ± 8.5^{b}	11.3 ± 0.7***	3.7 ± 0.4	6.6 ± 0.5	1199 ± 86	92.5
	8	45	362.4 ± 8.7^{c}	10.9 ± 0.5	3.9 ± 0.3	6.3 ± 0.4	981 ± 73	95.8
	12	40	364.8 ± 7.6^{c}	11.4 ± 0.4	4.2 ± 0.4	6.7 ± 0.3	956 ± 60	95.1

Results are expressed as the mean ± standard error. Mean weights of pupae within the same experiment followed by the same letter are not significantly different (ANOVA, Duncan multiple range test). A: $F = 3.43$, $P < 0.01$; B: $F = 3.57$, $P < 0.01$; C: $F = 23.07$, $P < 0.001$. N – number of larvae in a dish, n – number of examined individuals. * $P < 0.05$, *** $P < 0.001$ (t-test for comparison of the lifespan of mated and unmated females, values for unmated females of the corresponding rearing groups are given in Table 2). Actual fecundity expressed as a percentage of potential fecundity. A, B, C refer to experimental designs (see material and methods).

Relationships between pupal weight, lifespan and reproductive performance

In cabbage moth females, the pupal weight depending on pupal length can be expressed by the formula: $Y = 48.44 X - 584.398$ ($R = 0.903$; $F = 2093.9$; $P < 0.001$). Female wet weight was calculated as 57.4% of pupal weight.

Joint evaluation of all data available for cabbage moth female lifespan and reproductive performance showed that the potential fecundity of both mated and unmated cabbage moth females was related significantly to pupal weight. However, the relationship was stronger in mated (Fig. 1A) than in unmated individuals (Fig. 1B). A significant positive relationship between lifespan and pupal weight was found in mated females only ($R = 0.147$; $F = 18.04$; $P < 0.01$; $Y = 0.01 X + 8.53$, $n = 814$; for unmated females $R = 0.048$, $n = 658$). Fecundity of mated and unmated females was most dependent on the duration of oviposition ($R = 0.571$; $F = 392.56$; $P < 0.001$; $Y = 107.49 X + 450.38$, $n = 814$) and lifespan ($R = 0.429$; $F = 148.43$; $P < 0.001$; $Y = 25.105 X + 165.8$, $n = 658$), respectively. For mated females the relationships between fecundity and lifespan ($R = 0.056$, $n = 814$) and oviposition period and pupal weight ($R = 0.022$, $n = 814$) were not significant. A positive correlation was confirmed between their oviposition period and lifespan ($R = 0.416$; $F = 170.49$; $P < 0.001$; $Y = 0.33 X + 2.75$, $n = 814$). There was no relationship between the lifespan and pupal weight of males ($R = 0.007$, $n = 1,672$).

TABLE 2. Pupal weight and some life characteristics in unmated females and males of *Mamestra brassicae* originating from different larval rearing conditions.

		Unmated females					Males		
					Fecundity				
	N	n	Pupal weight (mg)	Lifespan (days)	potential (No. of eggs)	actual (%)	n	Pupal weight (mg)	Lifespan (days)
A	1	43	415.9 ± 14.2^{a}	10.7 ± 0.7	484 ± 46^{a}	9.7	101	366.2 ± 6.8^{a}	9.2 ± 0.4
	2	27	408.4 ± 16.1^{ab}	11.0 ± 0.8	494 ± 42^{a}	6.1	122	345.3 ± 5.8^{b}	9.9 ± 0.3
	4	74	375.7 ± 8.8^{bc}	10.4 ± 0.4	405 ± 25^{b}	11.9	116	330.8 ± 5.1^{bc}	9.6 ± 0.3
	6	45	379.2 ± 9.7^{bc}	9.8 ± 0.6	391 ± 30^{b}	12.0	96	340.0 ± 6.3^{b}	9.7 ± 0.4
	8	42	370.2 ± 9.8^{c}	11.7 ± 0.7	360 ± 37^{b}	12.0	128	320.3 ± 4.8^{c}	9.9 ± 0.3
B	1	31	425.6 ± 13.6	9.1 ± 0.5	398 ± 45	9.1	71	373.3 ± 6.7^{a}	8.4 ± 0.5
	2	30	435.0 ± 8.3	9.3 ± 0.6	432 ± 42	8.6	66	348.0 ± 5.2^{b}	9.0 ± 0.4
	4	10	430.3 ± 26.3	10.9 ± 1.4	396 ± 54	16.6	63	372.0 ± 7.2^{a}	9.8 ± 0.5
	6	25	440.6 ± 12.3	7.4 ± 0.9	358 ± 56	17.0	67	367.5 ± 6.8^{a}	8.6 ± 0.6
	8	18	430.7 ± 17.3	7.7 ± 1.1	385 ± 57	10.7	54	377.1 ± 7.3^{a}	9.1 ± 0.6
C	1	33	479.3 ± 10.8^{a}	7.8 ± 0.7^{a}	311 ± 39	8.0	112	408.9 ± 4.9^{a}	7.2 ± 0.4
	2	36	462.1 ± 10.5^{ab}	7.4 ± 0.6^{a}	320 ± 38	10.9	89	391.4 ± 5.1^{b}	8.0 ± 0.4
	4	33	441.3 ± 8.4^{b}	7.8 ± 0.6^{a}	382 ± 44	11.0	94	370.3 ± 5.0^{c}	7.4 ± 0.4
	8	34	380.6 ± 8.8^{c}	10.2 ± 0.7^{b}	421 ± 41	7.1	85	337.8 ± 5.6^{d}	7.2 ± 0.5
	12	28	378.9 ± 8.8^{c}	9.9 ± 0.8^{b}	436 ± 46	15.6	70	320.9 ± 4.6^{e}	7.7 ± 0.4

ANOVA – A: pupal weight of females – $F = 3.11$, $P < 0.05$; fecundity – $F = 2.40$, $P < 0.05$; pupal weight of males – $F = 8.97$, $P < 0.001$; B: pupal weight of males – $F = 2.98$, $P < 0.01$; C: pupal weight of females – $F = 22.99$, $P < 0.001$; lifespan of females – $F = 3.68$, $P < 0.01$; pupal weight of males – $F = 49.17$, $P < 0.001$. For others see Table 1.

To determine, whether larval rearing conditions could affect weight-, oviposition period- and lifespan-related fecundity, separate regressions were performed for females from each of the 15 experimental groups. The results showed that the relationship between fecundity and pupal weight of mated females was not influenced by larval population density or the group effect. This relationship was altered to a negative one, though not

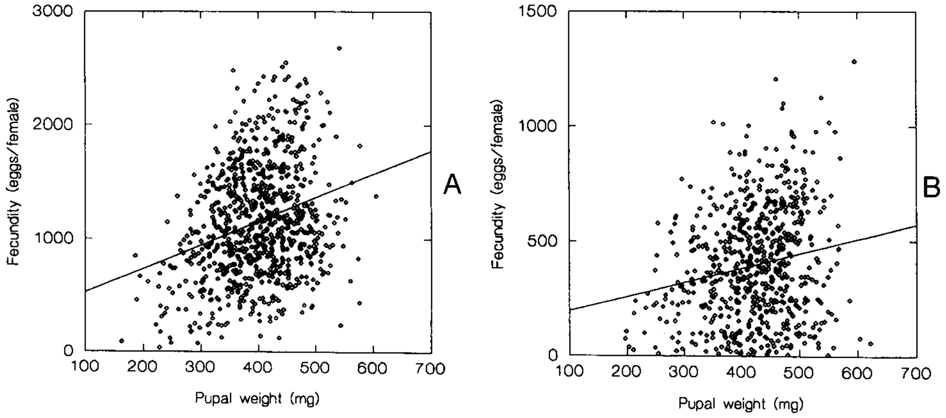

Fig. 1. Relationship between pupal weight and fecundity in *Mamestra brassicae* females. A – mated females. $R = 0.285$; $F = 72.03$; $P < 0.001$; $Y = 2.08X + 322.79$ ($n = 814$). B – unmated females. $R = 0.187$; $F = 23.78$; $P < 0.001$; $Y = 0.62X + 137.26$ ($n = 658$).

TABLE 3. Correlations (R) and probability of their significance for the relationships of: fecundity, lifespan with pupal weight; oviposition period with lifespan; fecundity with oviposition period in mated females; fecundity with pupal weight; fecundity with lifespan in unmated females of *Mamestra brassicae* reared at different conditions during larval development.

	N	n	Mated females				n	Unmated females	
			Pupal weight		Lifespan	Ovipos. period		Pupal weight	Lifespan
			Fecundity	Lifespan	Ovipos. period	Fecundity		Fecundity	Fecundity
A	1	69	0.474***	0.393***	0.427***	0.536***	43	0.587***	0.491***
	2	78	0.502***	0.200	0.599***	0.522***	27	0.429*	0.514**
	4	63	0.276*	0.277*	0.518***	0.600***	74	0.350**	0.381***
	6	68	0.397***	0.109	0.349**	0.596***	45	0.215	0.382**
	8	99	0.329***	0.338***	0.344***	0.570***	42	0.226	0.364*
B	1	19	0.521*	0.137	0.362	0.482*	31	0.240	0.287
	2	47	0.064	0.060	0.613***	0.660***	29	0.206	0.206
	4	54	0.134	0.025	0.579***	0.595***	10	0.063	–0.066
	6	41	0.133	0.119	0.300	0.584***	25	0.600**	0.487*
	8	27	–0.076	0.200	0.483*	0.374	18	0.386	0.377
C	1	36	0.266	–0.021	0.069	0.479**	33	–0.114	0.669***
	2	31	0.457**	–0.082	0.511**	0.515**	36	0.018	0.241
	4	30	0.367*	0.093	0.571***	0.700***	33	0.127	0.571***
	8	45	0.443**	0.357*	0.516***	0.861***	34	0.134	0.303
	12	40	0.244	–0.112	0.319*	0.560**	28	0.468*	0.544**

Significance of correlations: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$. For others see Table 1.

significantly, in females whose larvae lived in the smallest space (Table 3). Unmated female weight-related fecundity was affected positively by the group effect (females from individually reared larvae produced about 70% of the amount of eggs produced by those originating from gregarious larvae reared in group 12). Mated-female lifespan was related significantly to pupal weight in a few groups only. Conversely, their oviposition period showed a strong dependence on lifespan, irrespective of larval rearing conditions. Mated- and unmated-female fecundity was related most strongly to the duration of oviposition and lifespan, respectively, in almost all experimental groups. No effect of larval rearing conditions on the above relationships was noted.

DISCUSSION

Density-induced pupal and adult weight reduction has been reported in a number of insect species (Peters & Barbosa, 1977). Increasing population density and the group effect in *M. brassicae* are known to induce larval phase polyphenism and pupal weight reduction (Bonnemaison, 1962; Kazimírová, 1992). However, data upon the density-dependent response, in terms of adult life characteristics have been rather contradictory. Hirata (1956) reported an increase in egg number in *M. brassicae* ovaries and a prolongation of the oviposition period at larval crowding. However, Bonnemaison (1962) found that group rearing of larvae decreased fecundity of this species. Reduced fecundity as a result of larval crowding in Lepidoptera has also been reported, e.g. by Zaher & Long (1959) and Hill & Hirai (1986). Some lepidopteran insects have not shown any density-induced changes in their reproductive potential (Iwao, 1959; Sappington & Showers, 1992). Both lifespan and oviposition period of Lepidoptera can be either extended (Gunn & Gatehouse, 1987), shortened (Zaher & Long, 1959), or remain the same (Iwao, 1959) after subjection to crowding. This study did not provide evidence about density-induced changes in adult life characteristics and fecundity of the laboratory reared cabbage moth.

Physical disturbance in crowded populations is considered to affect development and reproduction of Lepidoptera more decisively than simple space reduction (Krishna & Mishra, 1985). These findings were supported by our study, showing that moth performance did not change considerably after mechanical separation of their larvae and rearing them in reduced space. Hovewer, rearing larvae in a very small space appeared to cause a negative weight-fecundity relationship, i.e., females originating from the heaviest pupae had lower fecundity than those coming from smaller pupae.

In this study, lifespan and fecundity of the cabbage moth females were affected most by their mating status. In comparison with other lepidopteran species in which unmated females lived longer than those mated (Steward & Philogène, 1983; Smith, 1986), mating in cabbage moth females appeared to extend their lifespan. Unmated females developed about three times fewer eggs in their ovaries than those mated and laid 11% of their egg complement only. This finding does not correspod with those of Wigglesworth (1966) who claimed that an equal number of ripe eggs develop in both mated and unmated females, but unmated females laid about one-third of their egg complement only.

Fecundity of insects was observed to correlate positively with female body size. Honěk (1993) generalised the relationship between size and fecundity in insects using data of 68 species, indicating the size of the female as a principal constraint on potential fecundity. This relationship in Lepidoptera can be influenced by genetic as well as different environmental factors and, in some species, fecundity also correlates positively with female lifespan, oviposition period and the factors influencing them (Cheng, 1972; Leather, 1988). Positive correlations between weight and fecundity and oviposition period and fecundity have been confirmed in the cabbage moth.

Gunn & Gatehouse (1987) found differences in lifespan and fecundity between two laboratory strains of *Spodoptera exempta* (Lepidoptera: Noctuidae) and a connection between phase variation and weight-related fecundity. When provided with distilled water, females originating from solitary-phase larvae laid about 50% of their egg number in comparison with those originating from gregarious-phase individuals. Moths provided with sucrose had comparable weight-related fecundities, irrespective of the larval phase. This suggested that, at least in some points, the density-induced response of adult *M. brassicae* might be similar to that observed in *S. exempta* and other noctuids displaying density-dependent polyphenism, in all of which an absence of an effect of larval phase on fecundity has been observed, when provided sucrose or honey solutions (Iwao, 1959; Hill & Hirai, 1986). However, to understand the significance of phase polyphenism in cabbage moth larvae, in relàtion to the population dynamics of this species, more laboratory and field investigations are required.

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REFERENCES

Bonnemaison L. 1961: Étude de quelques facteurs de la fécondité et de la fertilité chez la noctuelle du chou (Mamestra brassicae L.) (Lep.). III. – Influence de la diapause. *Bull. Soc. Entomol. Fr.* **66**: 128–133.

Bonnemaison L. 1962: Étude de quelques facteurs de la fécondité et de la fertilité chez la noctuelle du chou (Mamestra brassicae L.) (Lep.). V. – Influence de l'alimentation et de l'effet du groupe. *Bull. Soc. Entomol. Fr.* **67**: 15–24.

Cheng H.H. 1972: Oviposition and longevity of the dark-sided cutworm, Euxoa messoria (Lepidoptera: Noctuidae), in the laboratory. *Can. Entomol.* **104**: 919–925.

Gunn A. & Gatehouse A.G. 1987: The influence of larval phase on metabolic reserves, fecundity and lifespan of the African armyworm moth, Spodoptera exempta (Walker) (Lepidoptera: Noctuidae). *Bull. Entomol. Res.* **77**: 651–660.

Hammond A.M. & Fescemyer H.W. 1987: Physiological correlates in migratory noctuids: the velvetbean caterpillar as a model. *Insect Sci. Appl.* **8**: 581–589.

Hill M.G. & Hirai K. 1986: Adult responses to larval rearing density in Mythimna separata and Mythimna pallens (Lepidoptera: Noctuidae). *Appl. Entomol. Zool.* **21**: 191–202.

Hirata S. 1954: The phase variation observed in the armyworm, Barathra brassicae L. I. The relation between the rearing density and the variation of body colour of sixth-instar larva, weight of pupa, and rate of diapause. *Oyo-Dobuts. Zasshi.* **19**: 41–46. (In Japan., Engl. abstr.)

Hirata S. 1956: Phase variation observed in the armyworm, Barathra brassicae L. II. Influence of larval density upon variations observed in the adult stage. *Res. Popul. Ecol.* **3**: 79–92. (In Japan., Engl. abstr.)

Honěk A. 1993: Intraspecific variation in body size and fecundity in insects: a general relationship. *Oikos* **66**: 483–492.

Iwao S. 1959: Comparisons of the manifestation of density-dependent variabilities in Leucania unipuncta Haworth, L. loreyi Duponchel and L. placida Butler (Lepidoptera: Noctuidae). *Jpn. J. Ecol.* **9**: 32–38. (In Japan., Engl. abstr.)

Iwao S. 1968: Some effects of grouping in lepidopterous insects. *Colloq. Int. C.N.R.S.* **173**: 185–210.

Kazimírová M. 1992: The role of physical contact in the induction of phase polymorphism of Mamestra brassicae (Lepidoptera, Noctuidae). *Acta Entomol. Bohemoslov.* **89**: 87–95.

Krishna S.S. & Mishra S.N. 1985: A behavioral assessment of the impact of some environmental and physiological factors on the reproductive potential of Corcyra cephalonica (Stainton) (Lep., Pyralidae). *Proc. Indian Acad. Sci.* **94**: 249–264.

Leather S.R. 1988: Size, reproductive potential and fecundity in insects: things aren't as simple as they seem. *Oikos* **51**: 386–389.

Lewis E.E. & Keaster A.J. 1989: Effects of larval rearing conditions on size and flight behavior of adult black cutworm, Agrotis ipsilon (Lepidoptera: Noctuidae). *J. Kansas Entomol. Soc.* **62**: 542–547.

Noll J. 1963: Über den Einfluss der Temperatur auf die Lebensdauer der Imagines, auf Beginn, Verlauf und Dauer der Eiablage, sowie auf die Eizahlen (Eiproduktion) bei der Kohleule (Mamestra (Barathra) brassicae L.) und seine Bedeutung für den Massenwechsel des Schädlings. *NachrBl. Dt. PflSchutzdienst* **17**: 9–24.

Peters T.M. & Barbosa P. 1977: Influence of population density on size, fecundity, and developmental rate of insects in culture. *Annu. Rev. Entomol.* **22**: 431–451.

Podmanická D. & Weismann Ľ. 1975: Einfluss von Riboflavin auf die Fruchtbarkeit der Imagines von Scotia segetum Den. et Schiff. (Lepidoptera, Noctuidae). *Biológia (Bratislava)* **30**: 361–368.

Rivnay E. & Meisner J. 1966: The effects of rearing conditions on the immature stages and adults of Spodoptera littoralis (Boisd.). *Bull. Entomol. Res.* **56**: 623–634.

Sappington T.W. & Showers W.S. 1992: Lack of translation of density-induced morphological polyphenism to long-duration flight behavior of black cutworm (Lepidoptera: Noctuidae). *Ann. Entomol. Soc. Am.* **85**: 188–194.

Smith A.M. 1986: Fecundity and survival of the common armyworm, Mythimna convecta: effects of temperature and larval nutrition. *Entomol. Exp. Appl.* **42**: 31–37.

Steward J.G. & Philogène B.J.R. 1983: Reproductive potential of laboratory-reared Manduca sexta (Lepidoptera: Sphingidae) as affected by sex ratio. *Can. Entomol.* **115**: 295–298.

Wigglesworth V.P. 1966: *The Principles of Insect Physiology. 6th ed.* Dutton, New York, 544 pp.

Woodrow K.P., Gatehouse A.G. & Davies D.A. 1987: The effect of larval phase on flight performance of African armyworm moths, Spodoptera exempta (Walker) (Lepidoptera: Noctuidae). *Bull. Entomol. Res.* **77**: 113–122.

Zaher M.A. & Long D.B. 1959: Some effects of larval population density on the biology of Pieris brassicae L. and Plusia gamma L. *Proc. R. Entomol. Soc. Lond.* **34**: 97–109.

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