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THE BIOLOGY OF PALEXORISTA LAXA (CURRAN) (DIPTERA: TACHINIDAE), AN INTERNAL LARVAL PARASITOID OF HELIOTHIS ARMIGERA (HÜBNER) (LEPIDOPTERA: NOCTUIDAE).

THESIS

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CONTENTS

ABSTRACT

The Tachinid fly, Palexorista laxa (Curran) is an important parasitoid of Heliothis armigera (Hübner) in Africa and India. The biological characteristics of the parasitoid were studied with an emphasis on its host instar preference, host range, seasonality and percentage parasitism. The developmental stages were also studied and described.

A high host mortality (48%-100%) due to parasite attack occurred when small larvae were parasitised (2nd & 3rd instars). A preference for the 4th and 5th host instars was shown by the flies. P. laxa was found to be a non-specific parasitoid and parasitised a number of lepidopterous larvae in the laboratory including Busseola fusca (Fuller), Chilo partellus (Swinhoe) and Eldana saccharina Walker, but preferred H. armigera. The percentage parasitism on H. armigera in the field was variable peaking at 48% in 1988/89. Of the various parasitoids recorded from H. armigera on sunflower P. laxa was by far the most abundant.

Mating occurred immediately after emergence with the males emerging a day earlier than the females. Males were capable of multiple matings whereas females mated only once in a lifetime. P. laxa females produced incubated macrotype eggs which hatched almost immediately after oviposition. The duration of development of the incubated egg and larval stage was 6,7 days, the pupa 10,4 days for females and 9,4 days for males, and the adult lived up to 50 days at 25°C.

A reduction in pupal weight, an increase in the duration of the pupal stage and higher pupal mortality accompanied an increase in density of parasitoids per host.

A linear relationship was shown between adult mass and number of ovarioles and eggs in _P_. _laxa_ females. The oviposition period was 26,9 days with a high variation in daily progeny production. The total fertility per female was 126,3 puparia. "Inexperienced" females deposited incubated eggs on all parts of the host body while "experienced" females confined oviposition to the head and thorax. _P_. _laxa_ females did not discriminate between previously parasitised and non-parasitised hosts.

The effect of temperature on larval and pupal survival and development time was studied at 20°, 22°, 25°, 28°and 30°C. As expected, duration of development decreased with an increase in temperature, and there was a reduction in mortality.

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CHAPTER 1

INTRODUCTION

THE HOST, *Heliothis armigera*

The bollworm, *Heliothis armigera* (=*Helicoverpa armigera*) (Hübner) (Lepidoptera: Noctuidae) poses a major constraint on food and cash-crop production in Africa, attacking various crops including cotton, legumes, maize, grain sorghum, sunflower, tobacco and tomato (van den Berg *et al*. 1988). It also feeds and breeds on a wide variety of field crops (Pearson 1958). According to Annecke & Moran (1982), *H. armigera* has been identified as the most polyphagous and injurious pest in South Africa. It has been the subject of several studies and significant progress has been made in the development of integrated pest management strategies for cotton in South Africa (Mumford & van Hamburg 1985). Thus, this study is a component of a much wider research project on *H. armigera*.

The vernacular name "American bollworm" for *H. armigera* is an unfortunate misnomer which became entrenched because it was initially misidentified as conspecific with the North American "bollworm", *H. zea* Boddie. *H. armigera* occurs in the Old World, especially in Africa, Australia and India, but not in the New World, while the reverse is true for *H. zea*.

Generally *H. armigera* larvae live hidden within the fruiting parts of the plant during most of their development. Thus, large amounts of insecticide are needed if larvae are to ingest a lethal dose during their short period of contact with the foliage between hatching and entering the host plant. Moreover, *H. armigera* has a marked ability to develop resistance to insecticides and it also seems as if the impact of parasitoids on *H. armigera* populations in cotton has declined during the last decades with the escalating use of insecticides (Reed 1965). Biological control is a major component of integrated pest management which seeks to maximize the contribution of naturally occurring parasitoids, predators and pathogens to depress pest populations. There is a large number of parasitoid species that attack *H. armigera* in Africa (van den Berg *et al*. 1988). Only limited data exist on the role they play in controlling the pest and on their biology, behaviour and ecology. The subject of this thesis was the most important tachinid parasitoid, *Palexorista laxa* (Curran) of *H. armigera* on sunflower. Sunflower was the only crop investigated. No recoveries of *P. laxa* were made from any other potential insect hosts on this crop. The study was mainly concerned with the biology of *P. laxa* but comments on its taxonomy, distribution, alternative hosts and host plant association were also made.

THE PARASITOID - *Palexorista laxa* (DIPTERA: TACHINIDAE)

The Tachinidae is an exceedingly large family of cosmopolitan distribution. From an economic point of view it is by far the most important of the dipterous families of entomophagous habit (Clausen 1940). Tachinids are known to be of importance as parasitoids of crop pests with an extensive range in host preference, predominantly parasitoids of lepidopterous larvae of stalk- and wood-boring habits or which are otherwise concealed. A considerable number of species of Tachinidae are apparently specific in their host preference but at the other extreme are species that have a much wider host range than is known in any other group of parasitic insects (Clausen 1940). In general it may be said that the species of this family are less restricted in their host range than are the Hymenoptera. There are no recorded hyperparasites in the Tachinidae (Clausen 1940). A considerable number of species of the family have been successfully utilized in the biological control of crop pests (Bennett 1969; Clausen 1940).

According to Bennett (1969) tachinids are the most important larval parasitoids of sugar cane borers in the Americas, in sharp contrast to the Old World where hymenopterous parasitoids predominate. Great use has been made of tachinids in New World attempts to control cane moth borers biologically. Tachinid parasitoids have been largely responsible for the success of much of this biological control work. There has been less scope for use of tachinids in the Old World. However _P_. _laxa_ is an important indigenous natural enemy of _H_. _armigera_ in Africa (Old World).

TAXONOMIC REVIEW

Several *Palexorista* species are recorded as parasitoids of *H. armigera* in the Afrotropical Region. According to van den Berg *et al*. (1988), *P. laxa* has been confused with closely related species in the genus *Palexorista*. *P. laxa* has also been recorded as : *Drino* (*Prosturmia*) *imberbis* Wiedemann (Reed 1965; Robertson 1973), *D. munda* (Wied.) (Chauthani & Hamm 1967), *P. imberbis* (Wied.) (Chauthani & Hamm 1967; van den Berg *et al*. 1988), *P. munda* (Wied.) (Clement *et al*. 1983), *Sturmia* (*Prosturmia*) *imberbis* (Wied.) (Pearson 1958), *S.* (*Palexorista*) *inconspicua* Meigen (Jones 1939) and *S. laxa* Curran (synonym) (Cuthbertson & Munro 1941; Taylor 1932). But according to van den Berg *et al*. (1988) and Robertson (1973) the species *imberbis* and *inconspicua* do not occur in the Afrotropical Region.

These names probably belong to a complex of sibling or semi-sibling species and the group is currently being studied at the British Museum (Natural History) (Crosskey 1967; van den Berg *et al*. 1988).

DISTRIBUTION OF *Palexorista laxa* AND HOST PLANT ASSOCIATION

P. laxa was recorded from *H. armigera* in several countries in Africa, mainly on crops such as cotton and grain sorghum. *P. laxa* occurs in Botswana, Chad, Kenya, Malawi, Mali, Senegal, Somalia, South Africa, Sudan, Tanzania, Uganda, Zaire and Zimbabwe (Cuthbertson & Munro

1941; Greathead 1966; Jones 1939; Parsons 1940; Parsons & Ullyett 1934; Pearson 1958; Reed 1965; Robertson 1973; Roome 1971; Simmonds 1960, Taylor 1932; Tunstall 1958; van den Berg et al. 1988).

P. laxa was recorded also from India on cotton, lab-lab and tomatoes (Bryan et al. 1969; Divakar & Pawar 1983; Jackson et al. 1976; King & Coleman 1989).

This parasitoid was introduced to the USA (Arizona) from India for the biological control of H. virescens and H. zea and 51% parasitism was obtained during field-cage tests with this parasitoid in cotton (Jackson et al. 1970).

ALTERNATIVE HOSTS OF Palexorista laxa

The following Lepidoptera are recorded as hosts of P. laxa:

NOCTUIDAE

Busseola fusca (Fuller) (van den Berg et al. 1988)
Heliothis armigera (Hübner) (Crosskey 1967 & 1984; Roome 1971)
H. virescens (F.) (Bryan et al. 1969; Chauthani & Hamm 1967)
H. zea (Boddie) (Bryan et al. 1969; Chauthani & Hamm 1967)
Spodoptera exempta Walker (Crosskey 1984; van den Berg et al. 1988)
S. exigua (Hübner) (van den Berg et al. 1988)
S. frugiperda (Smith) (Chauthani & Hamm 1967)
S. littoralis Boisduval (Crosskey 1984; Gerling & Rotary 1973)
Taraché nitidula Fabricius (van den Berg et al. 1988)

PHALAENIDAE

Anomis auragoides (van den Berg *et al*. 1988)

Leocania leocosticha (van den Berg *et al*. 1988)

L. loreyi Duponchel (van den Berg *et al*. 1988)

Lycophotia oliveata Hampson (van den Berg *et al*. 1988)

Xanthodes graellsi Feisthamel (van den Berg *et al*. 1988)

Xylina exoleta Linnaeus (Tunstall 1958).

Crosskey (1967) regarded *H. armigera* as the only host of *P. laxa*. He argues that because *P. laxa* was confused with other species, these host records must be regarded as suspect.

CHAPTER 2

GENERAL MATERIALS AND METHODS

Only the general procedures are described here, specific details are given in each chapter.

FIELD COLLECTED MATERIAL

Field collections were made on sunflower at Towoomba Experimental Farm (Transvaal Region) near Warmbaths. Plots from different planting dates, cultivars and of different sizes were used. Fifty plants, randomly selected weekly per site were scouted. Sampling was done from March to June from 1988 to 1991. The field collected H. armigera larvae were placed singly in glass vials (100x25 cm) with artificial diet which was prepared according to a modified Shorey & Hale meridic larval diet in which dry powdered kidney beans were substituted for soaked pinto beans (van der Walt 1988). The larvae were kept in a controlled insectary at 25°C and 60% RH. Daily inspections were carried out and all parasitised, unparasitised, lost or dead larvae were recorded. The P. laxa adults were released into glass tapped wooden insect cages (45x30x32 cm) (Fig. 1a) and provided with water, raisins and sugar cubes. All unknown parasitoids that emerged from the collected larvae were sent to the National Collection of Insects (PPRI), for identification.

REARING PROCEDURE FOR Palexorista laxa

All experiments were carried out at 25°C and 60% RH. Fifth instar larvae of H. armigera were used as hosts. The larvae were obtained from a culture of H. armigera that had been maintained on the modified Shorey & Hale meridic larval diet, for about 15 years. The number of H. armigera instars was taken as five. Variations exist in the number of instars recorded; five, six and even more larval instars were recorded on various crops and under laboratory conditions (Abdul Nasr et al. 1976; Annecke & Moran 1982; Chaudhary & Sharma 1981; Mabbett et al. 1980; Poitout & Bues 1979; Toguebaye & Couilloud 1982). Possible explanations for the difference in number of larval instars is given by Nadgauda & Pitre (1983), who stated that additional moults were required due to low rates of food intake and in adverse conditions. Additional moults aid in extending the growth and development of the larvae.

The adult flies were housed and fed as described above. After a six-day mating and pre-oviposition period, 10-20 4th and 5th instar H. armigera were exposed to 25 P. laxa females for 60 minutes. The parasitised larvae were then placed singly in glass vials to prevent cannibalism. No artificial diet was provided as the parasitised larvae hardly feed. After about a week the fly maggots started to emerge from the cadavers and form puparia. After emergence the flies were sexed and released in new cages.

When longevity and sex ratio were measured, cylindrical

Perspex containers (20x18 cm) were used (Fig. 1b). In the Perspex containers only five 5th instar H. armigera were exposed to prevent overcrowding and cannibalism.

Chi-square analysis as done according to van Ark (1981) using 2x2 and 3x2 tables to determine the host instar preference of ovipositing P. laxa females in Chapter 3 and the effect of temperature on the duration of developmental stages in Chapter 6.

Student's t-test for independent samples and Mann-Whitney nonparametric U-test (van Ark 1981) were used to determine duration of development of the pupal stage (Chapter 4). These tests were also used to analyse longevity in adult flies(Chapter 5).

In Chaprers 4 and 5 the binomial test (van Ark 1981) was used to determine sex ratio.

Relationships between pupal and adult masses, adult mass and number of ovarioles, and adult mass and average number of eggs per female (Chapter 5) were analysed using linear regression according to the procedure outlined by van Ark (1981).

Where appropriate, results were given in the form $\bar{x}$ ± SE.

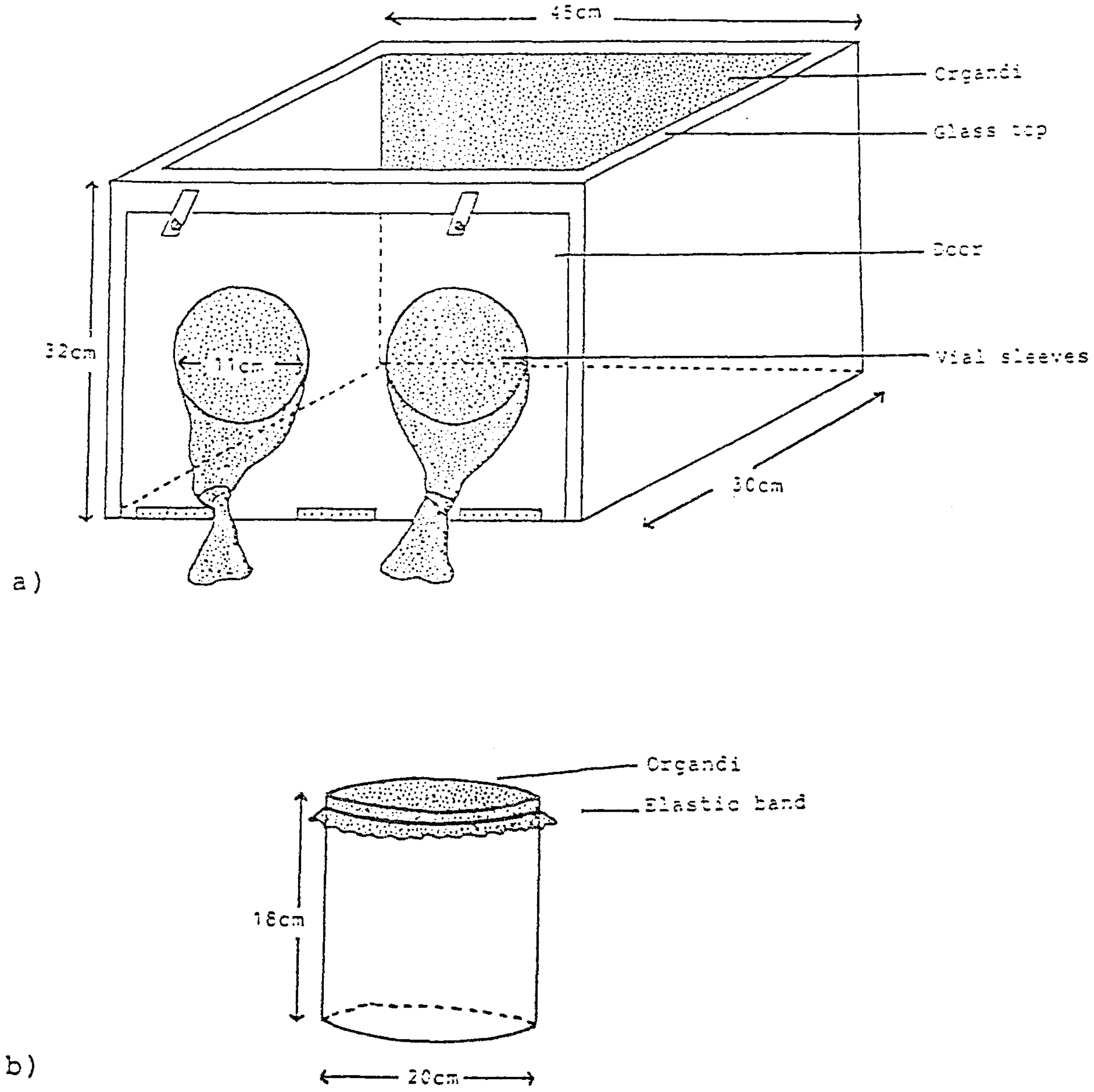

Fig. 1. Insect cages, a) used for rearing and b) cylindrical Perspex containers.

CHAPTER 3

HOST INSTAR PREFERENCE, ALTERNATIVE HOSTS, SEASONALITY AND PERCENTAGE PARASITISM

HOST INSTAR PREFERENCE OF *Palexorista laxa*

The aim of the study was to determine the host instar preference of ovipositing *P. laxa* females. This is a prerequisite for effective rearing of the flies in the laboratory.

Methods

The tests were done in two ways. 1) The flies were provided with a choice between the various *H. armigera* instars or 2) the flies had no choice and were provided with hosts all of the same instar. In the choice experiments five 3rd, five 4th and five 5th instar *H. armigera* were exposed in each of six cages in a first series and in each of seven cages in a second series. In the no-choice experiment 20 2nd instar larvae and 15 3rd, 4th or 5th instar larvae were exposed in each cage. Five cages of 2nd instar and three cages of each of the other instars were set up. The larvae were exposed to 25 male and 25 female flies for 60 minutes and then placed singly in glass vials. Third and 4th instars were provided with artificial diet whereas 5th instars were kept without food. All larvae were inspected daily and all parasitoid development recorded.

Dead or lost larvae were taken in account in the calculations but were not reflected in the tables in order to simplify the tables.

Larvae were recorded as parasitised when _P_. _laxa_ puparia formed. The number of puparia produced was also used by Bryan _et_ _al_. (1969) since the counting of eggs was impossible due to the variation in hatching time and the dissection of each host larva to determine the number of maggots it contained, impractical.

Chi-square analysis of data was done using 3x2 tables. The rows represented the different instars and the columns the events (parasitised and surviving unparasitised larvae).

Results and Discussion

_P_. _laxa_ showed a preference for the 4th and 5th instars of _H_. _armigera_. When the females were provided with a choice between the different instars 77% 5th instars were parasitised compared to 64% 4th and 35% 3rd instars (Table 1). When no choice was provided (Table 2) 80% 5th, 70% 4th and 44% 3rd instars were parasitised. All the second instars died but the cause of death was not investigated. There was no significant difference in the percentage of parasitism of the 4th and 5th instars although values were numerically slightly higher in the 5th instars.

The highest mortality of parasitised _H_. _armigera_ larvae occurred in 3rd instar (48% & 44%), followed by the 4th instar (19% & 20%) and the 5th instar (8% & 0%). This method of assessment probably underestimated the percentage of parasitism and the number of parasitoids as some larvae might have died in or with the host and never pupated.

More or less equal proportions of hosts escaped parasitism in the various instars. When the female had a choice between the instars 17% 3rd, 18% 4th and 15% 5th instars survived to maturity. When no choice was provided 12% 3rd, 10 % 4th and 20% 5th instars were not parasitised.

The global Chi-square value for the 3x2 table was 21,91 (df = 2) where a choice was provided and 12,93 (df = 2) without a choice, both highly significant at the 5% level. This shows the difference between ratios of frequencies of the three groups. The table Chi-square value was 5,99. This shows the existence of significant heterogeneity. Individual Chi-square tests were done on the different 2x2 tables by using combinations of the rows of the 3x2 table, these results are shown in Table 3.

On the basis of these findings it was decided to use only 5th instars for rearing P. laxa because 1) a high percentage parasitism occurred, 2) more puparia per host formed, 3) a high percentage of fly emergence occurred and 4) the 5th instars did not have to feed to complete development.

Previous workers reported that P. laxa preferred to parasitise 4th to 6th instars Heliothis spp. (Gerling & Rotary 1973; Jackson et al. 1976; Reed 1965). Parsons

TABLE 1. Parasitism by *Palexorista laxa* of third, fourth and fifth instar *Heliothis armigera*, with choice.

Instar	Larvae exposed	Larvae parasitised		Puparia formed	Puparia/ parasitised host	Emerged flies	
		N	%		$\bar{x}$ ± SE	N	%
3rd	54	19	35,19	63	3,32 ± 0,24	56	88,89
4th	63	40	63,49	139	3,48 ± 0,37	118	84,89
5th	65	50	76,92	347	6,94 ± 0,67	231	66,57

TABLE 2. Parasitsm by *Palexorista laxa* of third, fourth and fifth instar *Heliothis armigera*, without choice.

Instar	Larvae exposed	Larvae parasitised		Puparia formed	Puparia/ parasitised host	Emerged flies	
		N	%		$\bar{x}$ ± SE	N	%
3rd	41	18	43,90	33	1,83 ± 0,25	26	78,79
4th	40	28	70,00	70	2,50 ± 0,26	56	80,00
5th	45	36	80,00	231	6,42 ± 0,72	169	73,16

TABLE 3. Chi-square tests based on the difference in numbers of third, fourth and fifth instar *H. armigera* parasitised by *P. laxa* with and without a choice between various instars.

Comparison between instars	Choice x^2-value	No choice x^2-value
3rd & 4th	8,22*	4,61 NS
3rd & 5th	19,41**	10,47**
4th & 5th	2,16 NS	0,66 NS

* - $P<0,05$

** - $P<0,01$

NS - Not significantly different at the 5% level

df = 1

(1940) reported parasitism by *S. inconspicua* on *H. armigera* from the 2nd to the 6th instars, although parasitism of the 5th and 6th instars predominated. These latter studies were not done with *P. laxa* on *H. armigera* specifically and only the range of instars parasitised was reported, not the preferred instar.

ALTERNATIVE HOSTS OF *Palexorista laxa*

Methods

The aim of this study was to determine the host range of *P. laxa* assuming that *H. armigera* is the main host. Due to the confusion of identity of *P. laxa* discussed under Taxonomic Review in Chapter 1 the literature recording alternative hosts is suspect and earlier work requires confirmation.

Large larvae of *Busseola fusca* (Fuller), *Chilo partellus* (Swinhoe), *Eldana saccharina* Walker, *H. armigera*, *Spodoptera littoralis* Boisduval and *Trichoplusia* (*Plusia*) *orichalcea* (F.) were tested for acceptability as hosts for *P. laxa*. One species at a time was exposed in 45cm x 30cm x 32cm cages to 10 day old *P. laxa* females for 60 minutes. *B. fusca* larvae were exposed in two cages, which contained five and eight larvae respectively; 20 *C. partellus* larvae were exposed per cage in three cages; two cages with 20 and one cage with 11 *E. saccharina* larvae were exposed; 240 *S. littoralis* larvae were exposed in 12 cages, with 20 larvae per cage, and 13 *T. orichalcea* larvae in a single cage.

Ten male and 10 female flies had been placed in the cages a day prior to each experiment. After exposure the larvae were removed and placed singly in glass vials which were examined daily for parasitoid development.

The larvae of *C. partellus*, *E. saccharina*, *H. armigera* and *S. littoralis* used in the tests were reared in the laboratory while larvae of *B. fusca* and *T. orichalcea* were collected in the field. Diapausing larvae of *B. fusca* were collected in winter on maize and grain sorghum at Delmas, where they overwintered in the stalks of the plants. *T. oricalcea* larvae were collected on maize and sunflowers at Warmbaths.

Results and Discussion

In these laboratory tests *B. fusca*, *C. partellus*, *E. saccharina* and *H. armigera* were parasitised by *P. laxa* (Table 4). *P. laxa* failed to develop in *S. littoralis* and *T. orichalcea*, even though the females showed interest in the larvae and oviposited on them, no parasitoids developed. All exposed *S. littoralis* (N = 240) and *T. orichalcea* (N = 13) larvae escaped parasitism, and emerged as moths. The highest percentage parasitism (90%) was recorded on *H. armigera*.

Although no records exist in the literature of *C. partellus* being parasitised in the field by *P. laxa*, *P. laxa* was recently recovered from both borers (*B. fusca* and *C. partellus*) in the field though in very low numbers (R.

TABLE 4. Parasitism by Palexorista laxa on Busseola fusca, Chilo partellus, Eldana saccharina and Heliothis armigera in the laboratory.

Host	Larvae exposed	Larvae parasitised N	Larvae parasitised %	Puparia/host $\bar{x} \pm SE$
B. fusca	13	10	77	4,30 ± 0,88
C. partellus	60	24	40	1,95 ± 0,22
E. saccharina	51	9	18	1,33 ± 0,17
H. armigera	20	18	90	3,00 ± 0,63

Kfir, personal communication). This happened during a heavy borer infestation when some larvae were forced to feed in exposed situations. B. fusca and C. partellus occur simultaneously with H. armigera on maize and grain sorghum, although on different parts of the plant. H. armigera mostly feeds in an exposed position on the maize cobs whereas B. fusca and C. partellus bore inside the stalks. E. saccharina also feeds inside sugar cane and there are no records of it being parasitised by P. laxa under natural conditions.

Gerling & Rotary (1973) also reported that P. laxa females oviposit readily upon S. littoralis but no parasitoid development occurs. Possibly P. laxa (recorded as Sturmia (Prosturmia) imberbis) did not to any extent parasitise Diparopsis watersi (Roths) on cotton in the Sudan (Tunstall 1958).

Crosskey (1967) was of the opinion that P. laxa is host specific on H. armigera, but this is not supported by the present laboratory study; P. laxa is not a specific parasitoid of H. armigera but rather polyphagous.

SEASONALITY AND PERCENTAGE PARASITISM

It is important to record the parasitoid complex of a pest on a specific crop and the mortality caused by the different parasitoids in order to establish the importance of any single parasitoid. In this study special attention was given to P. laxa on sunflowers.

Methods

Five sunflower plots at Towoomba Experimental Farm, with different planting dates were used during each of the seasons 1988/89, 1989/90 and 1990/91. Different cultivars and plots of different sizes were used. Fifty plants, randomly selected weekly per site were scouted. All eggs and larvae of H. armigera were counted and collected. Larvae were placed singly in glass vials with artificial diet and the eggs placed singly in gelatine capsules. All collected material was kept in the insectary at 25°C and 60% RH. Parasitoids that emerged were sent to the National Collection of Insects (PPRI) for identification.

Results

In the present study 709 H. armigera larvae were collected during the three seasons. The complex of

TABLE 5. The parasitoid complex recorded for *Heliothis armigera*, on sunflower in South Africa.

Parasitoids	
EGG PARASITOIDS: Hymenoptera	
TRICHOGRAMMATIDAE	-*Trichogrammatoidea lutea* Girault
SCELIONIDAE	-*Telemonus ullyetti* Nixon
LARVAL PARASITOIDS:	
Hymenoptera: BRACONIDAE	
	Unidentified sp. 1
	Unidentified sp. 2
	Apanteles diparopsidis Lyle
	Cotesia sp. Cameron
	Dolichogenidea sp. Vier.
	Glyptapanteles sp. Ashm.
	Meteorus sp. Wesm.
	Microgaster sp. Latreille
ICHNEUMONIDAE	
	Unidentified sp.
	prob. *Chriodes* sp. Cameron
	Pristomerus sp.
	Temelucha sp.
Diptera: TACHINIDAE	
	Ethilla prob. sp. nov. Rob.-Des.
	Goniophthalmus halli Mesnil
	Palexorista laxa (Curran)
	Paradrino prob. *halli* Curr.
	Tachina sp.

parasitoids recorded on sunflowers during the past seasons is shown in Table 5. Total parasitism varied from 24,7% (1988/89), to 32,2% (1989/90) and 40,3% (1990/91). During the 1988/89 season, 47,7% parasitism was caused by *P. laxa*, 10,5% in 1989/90, and 45,7% in 1990/91 (E.F. von Maltitz, personal communication). Parasitism by the other parasitoids occurred at very low levels.

Discussion

The annual variation in percentage parasitism may be due to variation in the occurrence of the host *H. armigera*, other hosts, or to environmental conditions such as rainfall and relative humidity, which were not studied. *H. armigera* occurred in very low numbers during the study.

P. laxa can be regarded as one of the most important parasitoids of *H. armigera*; this parasitoid caused the highest larval mortality during the study period. Within the African continent, striking differences exist between parasitoid complexes reported from different areas (van den Berg *et al*. 1988). Van den Berg *et al*.(1988) compared *H. armigera* parasitoids from the two best-studied areas, southern Africa (Botswana, South Africa and Zimbabwe) and East Africa (Kenya, Tanzania and Uganda). Only three species are important in both areas and *P. laxa* is one of these.

Table 6 shows the percentage parasitism, countries, years and crops on which *P. laxa* has been recorded. The Botswana study was done in different localities, during two seasons on all the crops grown in Botswana. The parasitoid was most effective during the 1967-1968 season, being the main cause of larval mortality at the end of the season (Roome 1971). *P. laxa* is absent during the dry season in

TABLE 6. The year, crop, percentage parasitism and country in which P. laxa has been recorded.

Year	Crop	% Parasitism	Country, Reference
1934-39	maize, cotton	4,5	Barberton, Parsons (1940) (SA)
1962	cotton	25,0	Tanzania, Reed (1965)
1962	cotton and other plants	72,5	Tanzania, Robertson (1973)
1963		13,0	
1964		17,3	
1967-68	cotton, cowpeas, sunflower, tomatoes	14,5	Botswana, Roome (1971)
1967-68	grain sorghum	64,0	Botswana, Roome (1971)
1988	tobacco	25,0	Zimbabwe, Zimbabwe Tobacco Research Board (1988)
	cotton	3,9	
	maize	0,6	
	grain sorghum	24,2	
	cleome	0,4	

Tanzania (van den Berg et al. 1988).

King & Coleman (1989) regarded P. laxa as one of the three most important parasitoids of H. armigera in India.

Possibly P. laxa (recorded as D. imberbis) was the most common parasitoid of H. armigera on cotton in Tanzania (Reed 1965). Robertson (1973) recorded variation in the percentage parasitism possibly caused by P. laxa (recorded as P. imberbis) in the early sixties (Table 6). During 1934-1939, higher parasitism possibly caused by P. laxa (recorded as _S_. _inconspicua_) was observed on maize than on cotton, in the Eastern Transvaal, Natal and Swaziland (Parsons 1940). Parasitism levels by the tachinid varied considerately during the years as recorded by the various authors, in various countries.

CHAPTER 4

DEVELOPMENTAL STAGES OF *Palexorista laxa*

THE EGG OF *Palexorista laxa*

According to Clausen (1940) four general types of eggs are produced by the Tachinidae:

1. **Macrotype:** This type is broadly oval to ellipsoidal in outline, with a thick chorion on the dorsum and sides, and a flat and membranous ventral surface. The egg is attached externally to the integument of the host by its flat ventral surface. Strong adhesion is ensured by a mucilaginous material which accompanies the egg at deposition.
2. **Microtype:** This type of egg is of minute size in relation to the body of the parent female. The embryo is enveloped by a tough vitelline membrane.
3. **Membranous:** This type of egg is distinguished in general by its elongated form and thin transparent chorion, the few species that deposit unincubated eggs of this type inject them directly into the body of the host.
4. **Pedicellate:** Only in the genus *Carcelia*, the eggs which have a membranous chorion bears a slender cylindrical pedicel.

Jackson *et al*. (1976) made some observations on the developmental stages of *P*. *laxa* developing on *H*. *zea* and *H*. *virescens*. The current study supplements some of their descriptions on *H*. *armigera*.

Methods

After oviposition by P. laxa on 5th instars H. armigera, the host larvae were removed from the cages and the time from oviposition to larval penetration of the host body was measured. Ten day old P. laxa females were dissected, the fully developed eggs removed from the uterus, and measured with a measuring eye piece attached to a stereo microscope. Only ten days old females were used in the experiments due to a long pre-oviposition period (7,37 ± 0,28 days) (discussed later in text).

Results and discussion

The oval eggs, length 0,72 ± 0,17 mm (x ± SE)(N = 50), were enclosed in a thin whitish membrane. The black mouth hook of the maggot is visible towards the narrow end of the egg through the fragile transparent ventral chorion and membranous covering (Fig. 2a & b). The time from egg deposition to larval penetration into the host was 1,31 ± 0,09 minutes (x ± SE)(N = 50), ranging from 1 second to 2,29 minutes.

DESCRIPTION OF THE EGG OF P. laxa - A LITERATURE REVIEW

The eggs of P. laxa have a very heavy dorsal chorion and a flat thin transparent ventral chorion with a membranous covering (Fig. 3). They differ from other types (microtype, membranous, pedicellate) in size, colour, stage of development of the embryo at the time of deposition and

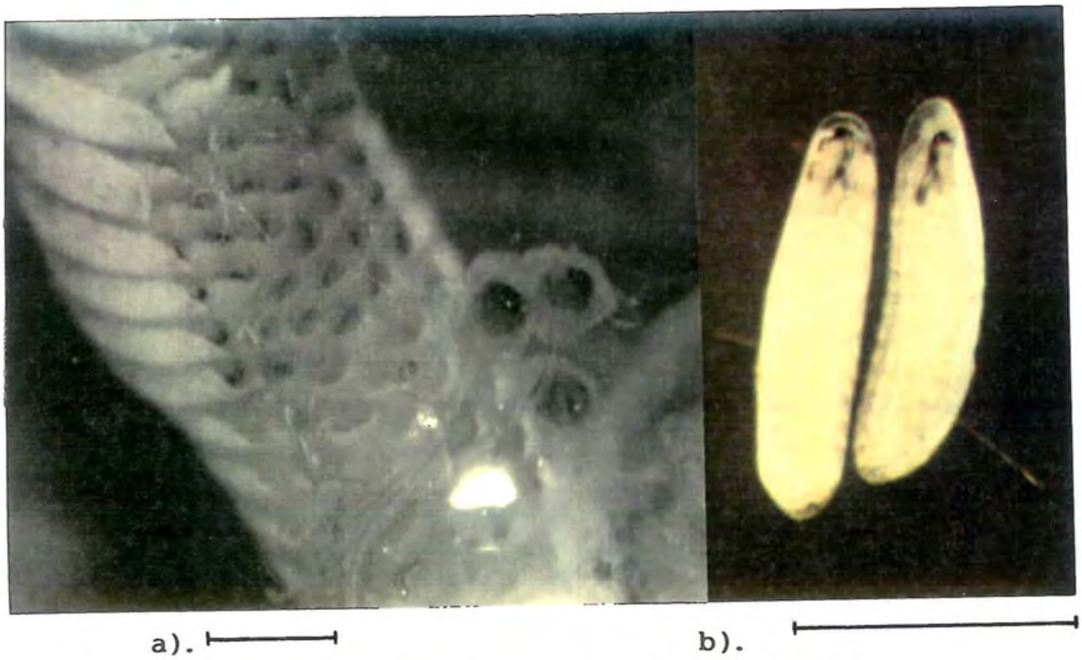

Fig. 2a). Mature eggs in *Palexorista laxa* female uterus showing the black mouth hooks of young larvae towards the narrow end of the egg.

b). Eggs of *Palexorista laxa* dissected from the females uterus (Bar = 0,5mm).

Fig. 3. A dissected egg of *Palexorista laxa* to show the heavy dorsal chorion and thin transparent chorion of the flat ventral surface (Bar = 0,5mm)

the manner in which hatching is accomplished. The general form is oblong, the colour is usually creamy or glossy-white. P. laxa attached its incubated eggs externally to the larval cuticle of its host (Clausen 1940).

According to Clausen (1940) the manner of hatching is "indehiscent" with no special provision for hatching, which is accomplished by cutting through the thin ventral shell and host cuticle directly into the host body. The macrotype eggs carry a quantity of mucilaginous material at the time of deposition, which fastens them securely to the body of the host (Clausen 1940).

It was observed that the incubated macrotype eggs hatched immediately after oviposition and penetrated the host integument. A major part of the embryonic development is completed inside the parent body. Similar observations were recorded by Gerling & Rotary (1973) and Jackson et al. (1976). Chauthani & Hamm (1967) recorded an incubation period of D. munda (possibly P. laxa) to be between 0 and 15 seconds.

DESCRIPTION OF LARVAL STAGES - A LITERATURE REVIEW

FIRST INSTAR P. laxa

The first instars of P. laxa may be considered as normal for the Tachinidae (Clausen 1940), where there are no marked modifications in form or structure to adapt them to a specialized mode of life. The body is robust with the cuticle colourless and transparent with bands of minute spines on each segment.

Clausen (1940) provides the following description of the first instar larvae respiratory system: The tracheal system consists of two main longitudinal trunks, with relatively few branches, and connected by a posterior commissure. The posterior spiracles consist of two papillae, each spiracle being kidney-shaped in outline. Anterior spiracles are absent. Early first instars respire by cutaneous diffusion, later the maggots attach to the hosts tracheal system after tearing an opening with the stigmatic hooks.

Clausen (1940) described three general forms of first instars in the Tachinidae: tachiniform, microtype and planidium.

P. laxa produces a tachiniform first instar type larvae (Fig. 4). The other two types of larvae are described below (Clausen 1940):

1. **Microtype:** These larvae hatch within the digestive tract of the host and are very small. The frequent absence of an open tracheal system is correlated with their mode of life where they are usually embedded in some host organ.
2. **Planidium:** The adaptive characters are essentially for the purpose of protection from injury and desiccation during a more or less protracted period of free life before the host is reached. They consist of a cuticular armature of closely set polygonal sclerotized plates or imbricated scales covering the dorsum and pleural areas.

All first instars mentioned above have eight abdominal segments. The buccopharyngeal apparatus consists, with very few exceptions (Clausen 1940), of a simple unjointed structure of which the three principal parts are the median tooth and the intermediate and basal regions. The basal region is lightly sclerotized. There are small lateral plates at the sides of the median tooth, and the small salivary-gland plates, often delicate and inconspicuous, lie beneath the intermediate region. These instars are haemophagous (Ziser & Nettles 1978).

SECOND INSTAR P. laxa

The second instars in Tachinidae are more uniform in structure than the first instar. Clausen (1940) suggests that this is because they all occur in the same environment - within the body of the host while some of the first instars are unprotected on plants while others are in host bodies. Second instars feed on haemolymph and fat tissue, and require an adequate supply of oxygen before growth is initiated (Ziser & Nettles 1978).

Clausen (1940) provides the following description of the second instar larvae: In all types of larvae the integument is thin and transparent. The cuticular armature of this instar consists of bands of setae. The spines of the last two segments of the great majority of species are usually directed cephalad, and they serve to hold the larvae more firmly in position in the respiratory funnel of the host (Clausen 1940). Maggots may make new respiratory connections at any time during larval development (Ziser & Nettles 1978).

The buccopharyngeal apparatus is more robust and highly developed in the second instar. Paired mandibular hooks are present in contrast to the single median tooth of the first instar (Clausen 1940).

The respiratory system of the second instar is also more highly developed in response to the greater need for oxygen. The two longitudinal trunks are heavier, with a considerable number of branches and both posterior and anterior commissures are present. Anterior spiracles are very minute in size and situated intersegmentally in the pleural area between the first and second thoracic segments. The spiracular chamber in most species is very short, often being broader than long (Clausen 1940).

THIRD INSTAR _P. laxa_

Clausen (1940) described the third instar of Tachinidae as follows: (this corresponded with _P. laxa_) the integumentary armature consists of spines (Fig. 5). The buccopharyngeal apparatus is more robust and highly developed. Distinct articulations separate the three principal regions. The anterior region is generally in the form of paired mandibles which are hooked. The respiratory system reaches its greatest size and cutaneous respiration is now less important as the respiratory system consists of a pair of heavy longitudinal trunks, anterior

Fig. 4. First instar *Palexorista laxa* with two posterior spiracles and two main longitudinal trunks of the tracheal system and buccopharyngeal apparatus (Bar = 0,5mm).

Fig. 5. The third instar *Palexorista laxa* just before pupation. The robust body is entirely covered with minute spines (Bar = 0,5mm).

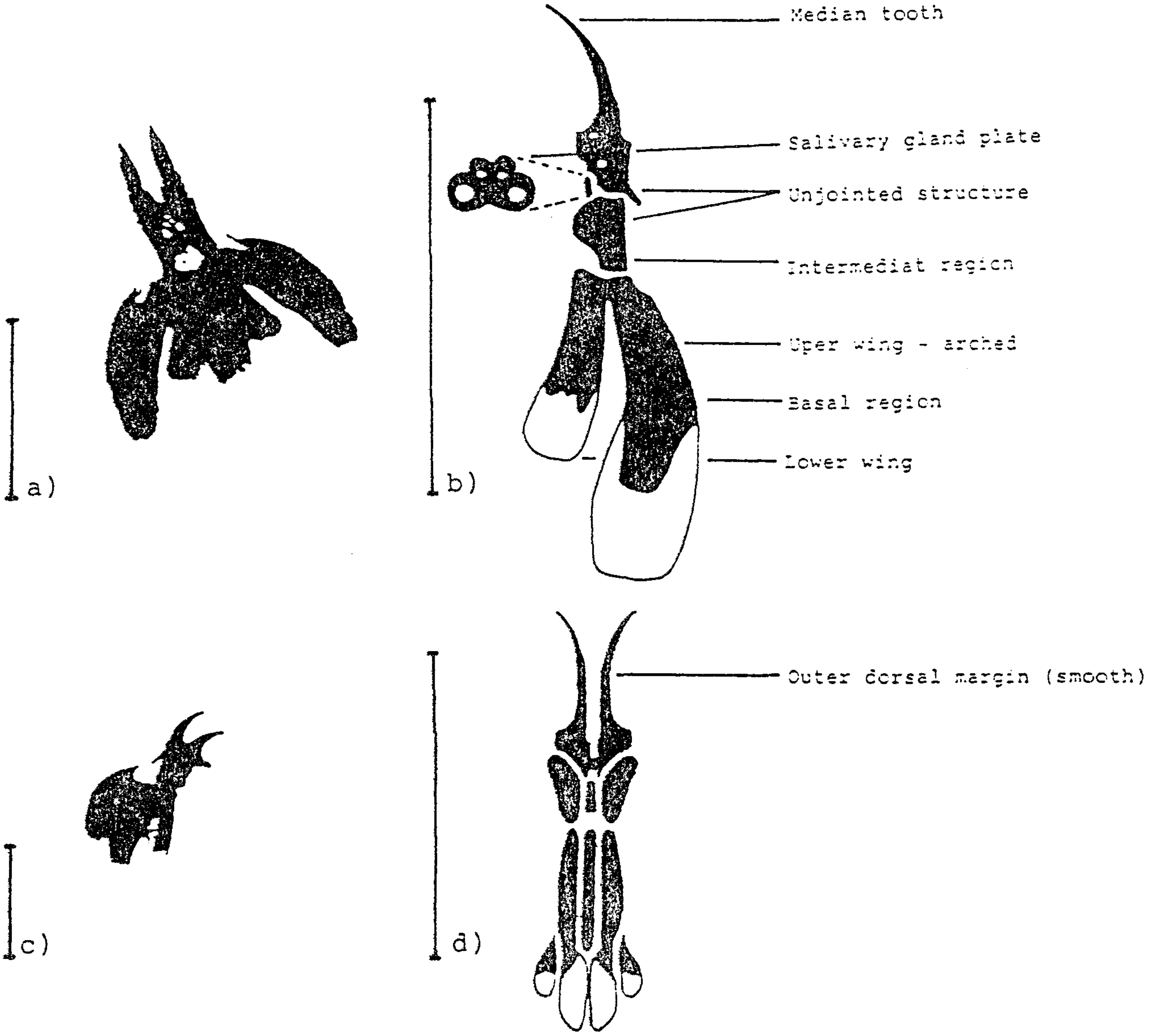

Fig. 6. The buccopharyngeal apparatus of the third instar _Palexorista_ _laxa_. a) & c) dorsal and lateral view - photos and b) & d) lateral and dorsal view - diagrams (Bar =0,1mm).

and posterior commissures and anterior and posterior spiracles.

The larval stages of _P_. laxa feed inside the host throughout development. The most striking differences between subsequent larval stages occurred in the structure of the mandibles in the buccopharyngeal apparatus (Fig. 6).

_P_. laxa larvae, in general, are muscoidiform (maggot like) upon attaining the final instar (Chauthani & Hamm 1967). The maggots consume all but the host larval cuticle before emerging to pupate. The pupa is coarctate with the third instar's skin hardening and forming the outer shell or puparium which encloses the pupa (Chauthani & Hamm 1967).

DURATION OF DEVELOPMENT OF THE LARVAL STAGES OF Palexorista laxa

Methods

After 5th instar _H_. armigera were exposed to _P_. laxa females, as described in General Materials and Methods, the larvae were placed singly in glass vials, in an insectary at 25°C and 60% RH. Daily records were kept of parasitoid development.

Results

The duration of development of the combined incubated egg and larval stages of _P_. laxa was 6,68 ± 0,031 days ($\bar{X}$ ± SE) with a range of 5 - 12 days (N = 874) (Table 7). The two stages could not be separated due to the short period in time from egg deposition to hatching and larval penetration (1,31 ± 0,09 minutes).

TABLE 7. Duration of development of *Palexorista laxa* egg and larva in *Heliothis armigera* at 25°C and 60% RH.

N days	5	6	7	8	9	10	11	12	TOTAL
N larvae	26	409	303	109	17	6	1	3	874

Discussion

The duration of development of the incubated egg and the larval stages of *P. laxa* in *H. armigera* corresponds with the duration of development of six days by *P. laxa* developing in *H. zea* recorded by Jackson *et al*. (1976). Parsons (1940), recorded a longer period for *S. inconspicua* (10 - 14 days) developing in *H. armigera* and Chauthani & Hamm (1967) recorded only 4,1 and 6 days development of *D. munda* in *H. zea* and *H. virescens* respectively. The differences in the development time might be due to species variation or different species. Parsons (1940) worked in South Africa on *S. inconspicua* which is probably *P. laxa*. *D. munda* (=*D. imberbis*) a parasitoid of *H. armigera*, was imported from India, to be tested in the USA against *H. virescens* and *H. zea*. According to Crosskey (1967) and van den Berg *et al*. (1988) this parasitoid might also be *P. laxa*.

Also, Parsons (1940) gave no information on temperatures, host larval size, number of hosts or number of parasitoids per host which might have an influence on the duration of development of the egg and the larval stages. The experimental conditions of temperature, host larval size and exposure time of hosts to parasitoids in this study were the same conditions as used by Chauthani & Hamm (1967), but the hosts that were used were different. This could have influenced the developmental time.

THE PUPARIUM OF *Palexorista laxa*

Methods

The methods used were the same as those described in Chapter 2. One day old puparia were measured and then returned to glass vials where they were examined daily until the adults emerged.

Results

Newly formed puparia of *P. laxa* were soft and light brown in colour, gradually becoming hard and dark brown within a few hours. The length of the puparium was 6,22 ± 0,12 mm ($\bar{x}$ ± SE) with a range of 4,0 - 9,0 mm (N = 100). The width was 2,81 ± 0,07 mm ($\bar{x}$ ± SE) with a range of 1,5 - 4 mm (N = 100). The duration of development of the pupal stage was 10,4 ± 0,04 days ($\bar{x}$ ± SE) with a range of 7 - 15 days, in females (N = 300) and 9,43 ± 0,05 days ($\bar{x}$ ± SE) with a range of 7 - 13 days, in males (N = 300) (Table 8). Student's t-test for independent samples and the

Mann-Whitney nonparametric U-test both indicated a significant difference at the P<0,01 level between the duration of development in males and females.

TABLE 8. Duration of pupal period in Palexorista laxa.

Days	7	8	9	10	11	12	13	14	15	Total
No. females	1	16	165	94	22	0	2	0	0	300
No. males	1	0	15	157	120	6	0	0	1	300

Discussion

Similar results were recorded by previous workers. They recorded the pupal period for P. laxa to be 9,4 days at 25°C in H. zea (Jackson et al. 1976), 12 days for D. imberbis (Reed 1965)(this work was done on H. armigera in Tanzania), between 9 and 12 days for D. munda (Chauthani & Hamm 1967) and between 8 and 12 days for S. inconspicua. Emergence from overwintering puparia may take between 60 and 120 days (Parsons 1940). As discussed on p. 32 these species could be P. laxa or closely related species.

DESCRIPTION OF PUPARIUM - A LITERATURE REVIEW

According to Clausen (1940) the general form of the puparium of P. laxa is subelliptical and slightly wider in the abdominal area, with both ends smoothly rounded. The longitudinal axis is straight. The segmentation is usually indistinct and is indicated by faint lines or by a variation in the pubescence. The anal opening is represented by a distinct groove at varying distances below the spiracles, frequently occurring almost at the anterior ventral margin of the last segment. The colour of the puparium usually deepens appreciably with age. The outer surface of the puparium bears the armature as well as the anterior and posterior spiracles of the third-instar larva. The stigmata are those of the mature larva being trifid bosses with simple slids (Crosskey 1984). Any external prothoracic cornicles are lacking in the majority of tachinids (Clausen 1940). The internal prothoracic spiracles of the pupa at the base of the prothoracic cornicle axis beneath the puparial wall, are present in all species. There are two lines of cleavage which separate the two halves of the puparial cup from each other longitudially and from the remainder of the puparial wall and both these halves split away at the time of emergence of the adult fly.

THE EFFECT OF PUPARIAL MASS ON GREGARIOUSNESS BY *Palexorista laxa*, IN THE LABORATORY

Methods

The newly-formed puparia were classified according to the different densities of puparia in the hosts from which they emerge. The puparia were then weighed and placed singly in glass vials. The sex ratio of the emerged flies was noted.

Results and discussion

The puparial mass of *P. laxa* decreased significantly as the number of puparia per host increased, ranging from 5,6 ± 0,36 mg ($\bar{x}$ ± SE) when only one parasitoid per host developed, to 1,1 ± 0,11 mg ($\bar{x}$ ± SE) when 10 puparia per host developed (Table 9).

TABLE 9. *Palexorista laxa* puparial mass in relation to gregariousness.

N puparia/host	1	2	3	4	5	6	7	8	9	10
$\bar{x}$ mass (mg)	5,64	5,21	4,08	2,56	2,39	1,96	1,72	1,65	1,61	1,12
SE	0,36	0,16	0,33	0,38	0,15	0,23	0,18	0,10	0,18	0,11
N	10	12	18	8	10	12	13	16	18	20

When more than one *P. laxa* puparium developed in a single *H. armigera* larva, all the puparia were more or less the same size and there was no obvious variation in the developmental time. The resulting flies were smaller and their life-span was shorter than flies developing singly. It was observed that these small flies usually died before the pre-oviposition period was completed.

It was found by Chauthani & Hamm (1967), that if a single *H. zea* larva was superparasitised by *D. munda* (possibly *P. laxa*), only two or three puparia reached the normal size. The others developed slowly, forming smaller sized puparia, or died in the first or second instar. This variation in developmental time of *D. munda* puparia in *H. zea* as host could be the result of different exposure times to the female/females, resulting in maggots of different ages. It is not clear under what circumstances these results were obtained by Chauthani & Hamm (1967) but present results make it seem unlikely that some maggots develop faster than others of the same age in an environment with a limited food source.

The size of the puparium depends upon the food material available to the larvae during its development (King et al. 1976). Variation in size due to food supply was also recorded by Patel & Singh (1972) in the tachinid Goniophthalmus halli Mesnil and Adam & Watson (1971) in Exorista mella (Walker), both of which are larval parasitoids of H. species in the USA. Mani & Nagarkatti (1981) noted that older larvae provided more food for parasitoid development, resulting in larger puparia. The duration of development of the maggots decreased significantly with increasing parasitoid density. When more than three maggots developed in a single host, all available host tissue was utilized, and the maggots received proportionally less food. The host was consumed faster by the developing maggots, resulting in earlier pupation (Mani & Nagarkatti 1981).

The puparial mass of Eucelatoria sp. (Ziser et al. 1977) and Lixophaga diatraeae (Townsend) (King et al. 1976) also decreased as the density of maggots per host increased. The decrease in puparial mass of Eucelatoria sp. (Ziser et al. 1977) corresponded with the shortened larval development time of the maggot as crowding increased.

NUMBER OF PUPARIA PER HOST, PERCENTAGE EMERGENCE, MORTALITY AND SEX RATIO

Number of puparia per host: During the 1986-1989 seasons 1713 H. armigera larvae were collected on sunflowers and 248 (15%) of these had been parasitised by P. laxa (total no. of puparia formed was 319).

The percentage parasitism was also calculated using the method described by Broadley (1984). He calculated the level of larval parasitism by dividing the number of parasitoids emerged by the sum of the number of parasitoids and moths emerged. According to that method percentage parasitism was 17,88.

Up to six puparia per host were recorded (Table 10). The mean number of puparia formed was 1,29 ± 0,08 ($\bar{x}$ ± SE) (N = 248) per host under field conditions (Table 10) and 2,17 ± 0,05 ($\bar{x}$ ± SE) (N = 501) under laboratory conditions (Table 11). P. sp. nr. laxa produced up to 5 flies per host (Roome 1971), D. imberbis (possibly P. laxa) up to 8 (average 1,4 - 1,7) (Reed 1965; Robertson 1973), and S. inconspicua (possibly P. laxa) between 1 and 8 (Parsons 1940). The number of puparia obtained per host range from 1 to 12 in P. laxa (Jackson et al. 1976) and appears to be related to the age of the ovipositing flies and the degree of exposure in time and numbers. The number of progeny produced also depends on the mass of the fly (Mani & Nagarkatti 1981).

TABLE 10. *Palexorista laxa* field collected from *Heliothis armigera* larvae. (N = 248)

No. puparia/host	1	2	3	4	5	6
No. hosts collected	212	16	9	8	2	1
Sex ratio*	0,80	0,77	0,85	1,46	1,0	0,33

* Ratio of female:male, with the males = 1

TABLE 11. Number of *Palexorista laxa* puparia developing in a single *Heliothis armigera* larvae, percentage females emerging and percentage mortality under laboratory conditions.

No. puparia/host	1	2	3	4	5	6	7	8	9	10	13
No. hosts	501	231	126	80	49	26	11	3	6	2	1
No. males	260	261	176	145	106	63	31	10	10	7	1
No. females	231	217	166	134	101	58	28	5	18	3	4
Sex ratio*	0,89	0,83	0,94	0,92	0,95	0,92	0,90	0,5	1,80	0,42	4,00
% Mortality	2,0	4,8	9,5	12,8	15,5	22,4	23,4	37,5	48,1	50,0	61,5

* Ratio of female:male, with the males = 1

Mortality and emergence: A progressive increase in mortality and a decrease in emergence occurred with an increase in the number of puparia per host under laboratory conditions (Table 11). Only 2% mortality occurred when one puparium per host formed but this increased to 61,5% when 13 puparia per host formed. A maximum of 23 puparia per host was observed (this was probably the progeny of more than one female) as a result of superparasitism in the laboratory, but only 13% of these puparia emerged. Reed (1965) also reported that pupal numbers had an effect on the duration of the pupal stage and mortalities of _D. munda_ (possibly _P. laxa_). According to Clausen (1940), the surplus larvae are usually killed in the second or third stage when superparasitism occurs. Their death is caused by overcrowding, starvation or direct combat.

Sex ratio: The sex ratio of _P. laxa_ was 1:1. No significant difference occurred in the different groups of puparia per host (statistically proven by using the binomial test 50/50 P = Q = 0,5), in both field collected material (Table 10) and laboratory reared flies (Table 11). Chauthani and Hamm (1967) also recorded a 1:1 sex ratio in _D. munda_.

Discussion

During this study the following questions were raised: why does superparasitism occur and why are some hosts ignored while others are attacked and parasitised frequently during the exposure time?

In the field collected material not more than 6 puparia per host formed, and this happened very rarely (Table 10). In the laboratory it occurred more frequently (Table 11). The reason for this could be the fact that females were provided with hosts in an enclosed cage and did not have to use a lot of energy searching for hosts, more energy could then be used for oviposition - increasing the number of eggs laid. In the laboratory superparasitism only occurred when hosts were exposed to more than one female.

According to Charnov & Skinner (1985), oviposition behaviour could be affected by: the time required to find hosts, the size of the host patches, the ratio of parasitised and unparasitised hosts, the females ability to determine the sex ratio of the offspring and the clutch size.

There is no indication that the flies try to avoid superparasitism as some of the larvae were ignored while others were heavily parasitised (Fig. 7). The flies were not forced to superparasitise because hosts were not limited. These results were obtained from host instar preference of P. laxa in Chapter 3. According to Clausen (1940), females that deposit macrotype eggs, like P. laxa, appear to lack discrimination in their choice of hosts for parasitization. This frequently resulted in individual hosts receiving an excessive number of eggs. Adam & Watson (1971) also found no discrimination in choosing between previously parasitised and non-parasitised host larvae by E. mella. Host movement was found to be more important than the size of hosts in stimulating the interest of females.

The presence of several females ovipositing on the same host may lead to a larger clutch size. When the clutch size increase less food become available for each offspring influencing the survivorship to adulthood. The second female's offspring usually suffer greater competition from the first female's offspring because they hatch later, after some food has been consumed.

Immatures growing up in a crowded host may emerge as small adults. Crowding could cause immature survival to decline or adult size to decrease or both. Body size in turn may have an effect on adult fitness, altering both life-span and egg production.

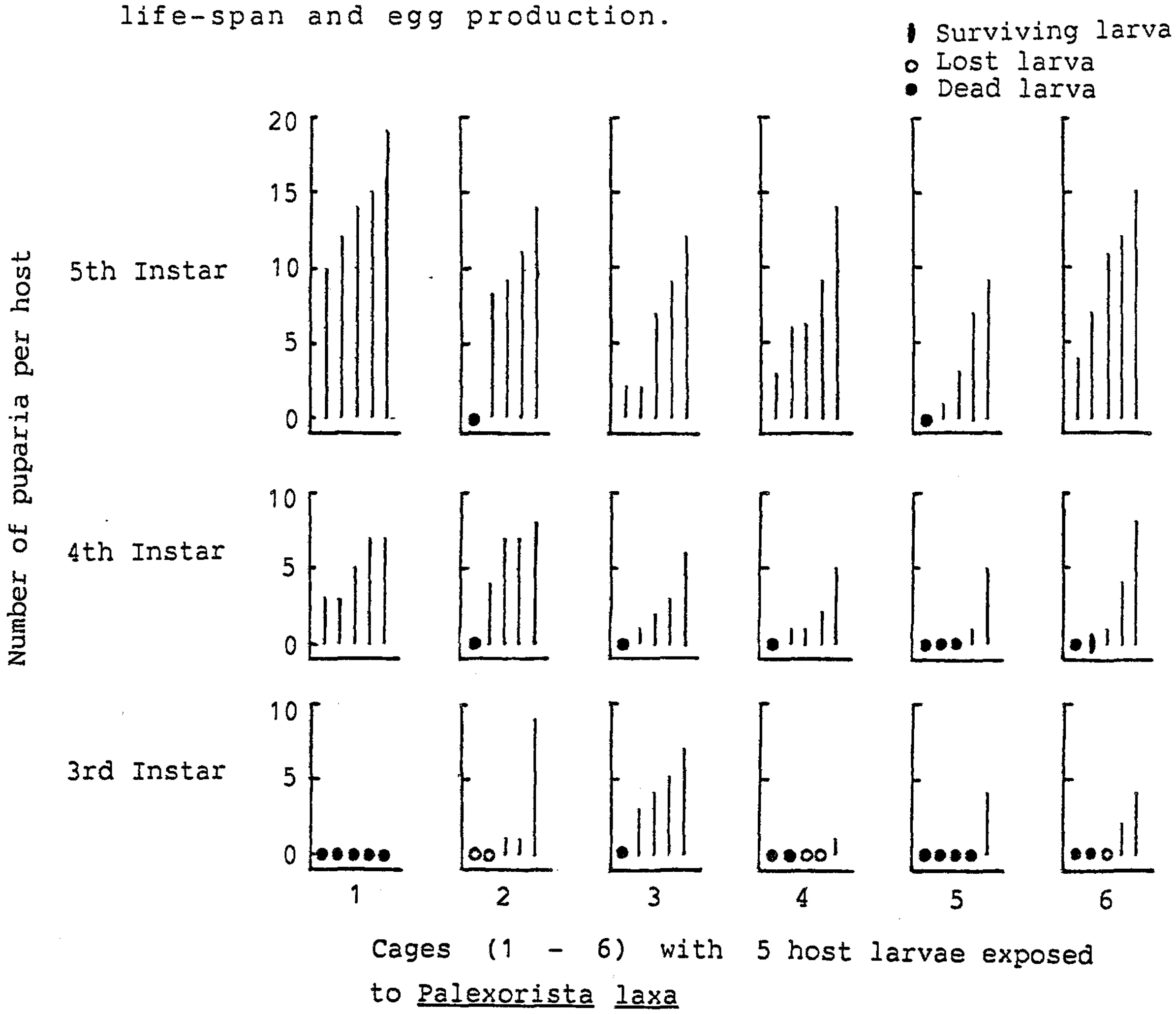

Fig. 7. The lack in discrimination of Palexorista laxa females in a choice of hosts for parasitisation. Vertical lines or symbols in their place represent the five Heliothis armigera larvae exposed to the females in individual experiments.

CHAPTER 5

BIOLOGY OF *Palexorista laxa* ADULTS

GENERAL OBSERVATIONS

Adults feed on nectar and plant secretions and honeydew secreted by aphids, scale insects and leaf hoppers in the field. Females were observed to imbibed the body fluids of their hosts.

RESULTS AND DISCUSSION

FLY EMERGENCE

P. laxa males on average emerged about one day before the females. The males are dark in colour with fasicles of long dense hairs on the fourth tergite. The females are light brown with the ovipositor visible (Fig. 8 & 9). Males emerged 9,43 ± 0,05 days ($\bar{x}$ ± SE), range 7 - 13 days (N = 300) after the puparia was formed. Females emerged after 10,4 ± 0,04 days ($\bar{x}$ ± SE), range 7 - 15 days (N = 300)(Table 8). Student's t-test for independent samples and the Mann-Whitney nonparametric U-test both indicated significant differences at $P < 0,01$. Emergence usually took place early in the mornings.

According to Chauthani & Hamm (1967) *D. munda* males emerge two to three days before the females, compared to only one day as found in the present study.

Fig. 8. The ventral view of a Palexorista laxa male - dark in colour with fasicles of long dense hair on the fourth tergite (Bar = 0,5mm).

Fig. 9. The ventral view of a Palexorista laxa female - light brown in colour with ovipositor visible (Bar = 0,5mm).

SEX RATIO

The sex ratio in relation to the number of P. laxa larvae developing per host was studied in the laboratory (Table 11) and compared to that from field collected material (Table 10). Regardless to the number of puparia per host that were formed (up to 13 puparia per host in the laboratory and 6 puparia in field collected material) the sex ratio for P. laxa was 1:1 (binomial test 50/50p = Q = 0,5). Chauthani & Hamm (1967) also reported a sex ratio of 1:1 for D. munda.

LONGEVITY

Methods

Longevity measurements of adult male and female P. laxa were made under three different sets of conditions at 25°C and 60% RH. In all cases the flies were held in Perspex containers and supplied with food and water. 1) 10 males only or 10 females only, 2) five males together with five females and 3) males and females isolated as couples and provided daily with five 5th instar H. armigera for 60 minutes. Mortality was recorded daily.

Results and discussion

Longevity was tested under three different conditions to acertain whether the presence of males influenced the longevity of females. The presence of hosts might also shorten the life-span of females as more energy is needed to produce offspring and the aggressiveness of the hosts could lead to an early death.

In all experiments females lived slightly longer than males (Table 12). The longevity of male and female flies was compared using Student's t-test. There was a significant difference between the longevity of males and females under all conditions. However, tests with probit analysis demonstrated no significant difference in longevity under the three different experimental conditions.

TABLE 12. Longevity in days of *Palexorista laxa* adults at 25°C.

	males only	females only	without hosts		with hosts	
			males	females	males	females
$\bar{x} \pm SE$	14,92±1,25	22,5±1,76	23,58±1,44	26,74±1,69	20,27±2,86	24,73±3,55
N	50	50	50	50	15	15
range	1-37	4-50	1-39	5-50	7-40	6-48

MATING

Methods

Five newly emerged females and a single male of *P. laxa* were caged together in a Perspex container for 24h, food and water were provided. This was repeated 15 times. The males were provided with new females daily for their total life-span. The already exposed females were kept for later examination. Ten days after exposure the females were dissected to determine if they had been fertilized. The criterion used for fertilization was the descent of the eggs into the uterus, where incubation takes place (Fig. 10), in unfertilized females the eggs remained in the ovaries (Fig. 11). This criterion for fertilization was previously used by a number of authors in various groups of tachinids and was found effective for P. laxa (Godfray 1985, Jackson et al. 1976, Patel & Singh 1972).

Observations on mating behaviour were also made.

Results and discussion

Mating took place soon after emergence, 21,12 ± 2,03 minutes ($\bar{x}$ ± SE) and ranged from 6 - 76 minutes (N = 50 pairs). Males mated with more than one female. Females however were observed to mate only once during their lifetime.

Multiple mating was recorded by Jackson et al. (1976) in P. laxa where one male mated with and fertilized up to four females. They did not determine if males could mate with more than four females or at what age mating ceased. The males of D. munda could also mate with more than one female, but it is not known whether the females mated more than once (Chauthani & Hamm 1967).

Males were active in days 2 - 15 with peak activity in days 2 - 8 (Fig. 12). Males needed a day after emergence to reach sexual maturity. After eight days mating activity decreased and after 16 days no fertilization occurred. However, males were occasionally observed to mount females. A male fertilized 17,87 ± 1,93 females ($\bar{x}$ ± SE)

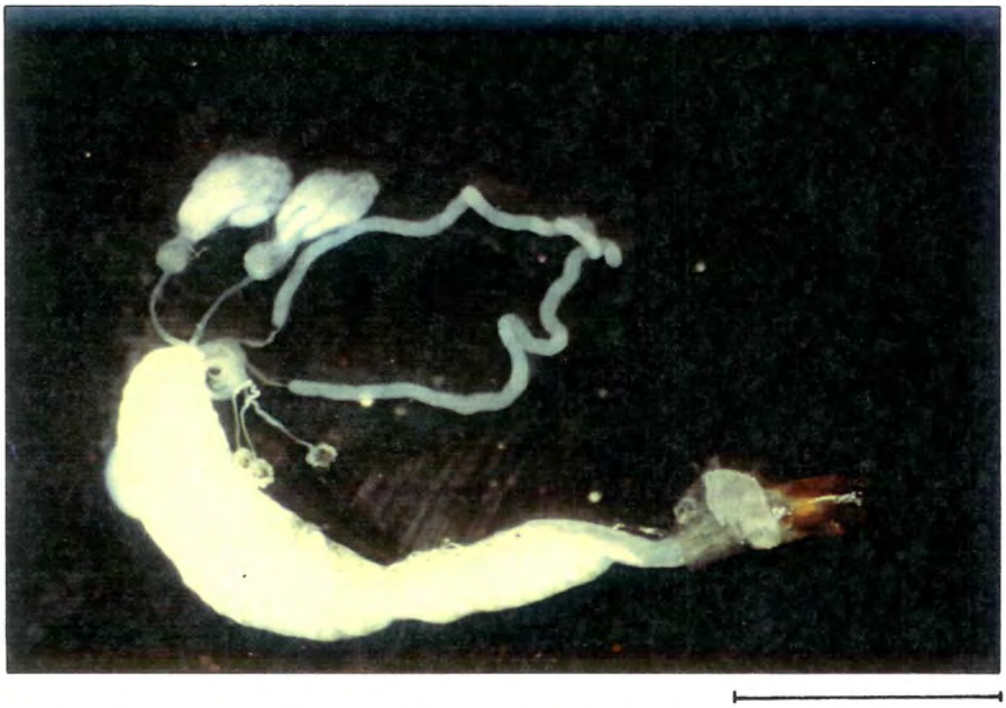

Fig. 10. The reproduction system of a fertilized *Palexorista laxa* female (Bar = 0,5mm).

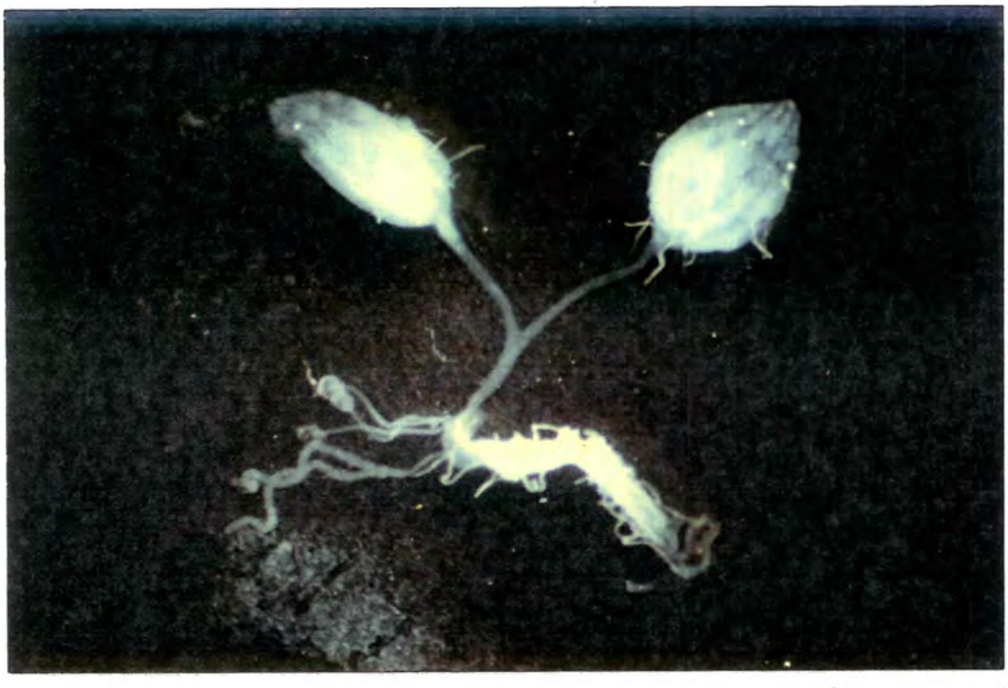

Fig. 11. The reproduction system of an unfertilized *Palexorista laxa* female (Bar = 0,5mm).

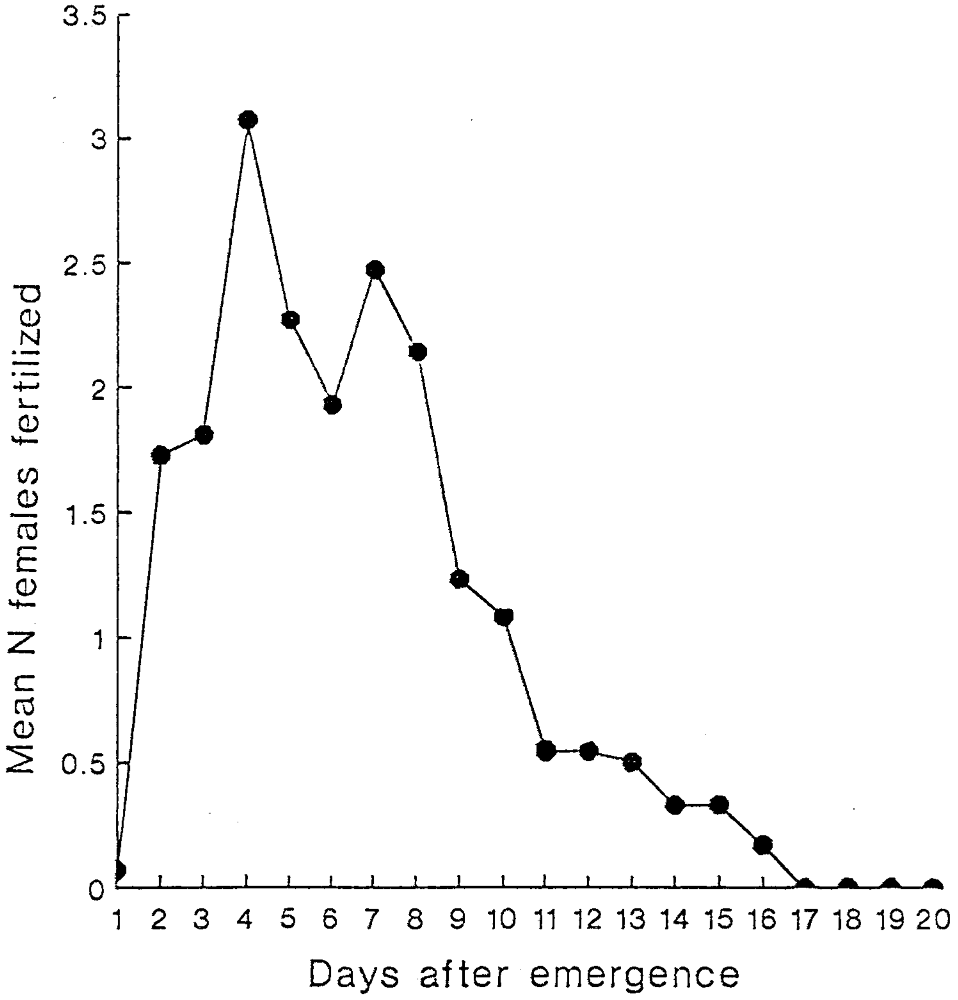

Fig. 12. The mean number of Palexorista laxa females fertilized by a single male.

range 8 - 30 females during his lifetime. Daily fertilization varied from zero to five, in 11 cases all five females were fertilized. It was not determined if males can fertilized more than five females per day.

FERTILITY

Methods

Pairs of *P. laxa* adults (N = 33) were placed in Perspex containers and provided with food and water. Daily, five 5th instar *H. armigera* were exposed to each pair for 60 minutes under 25°C. After exposure the larvae were removed and placed singly in glass vials. Daily inspections were carried out and the formation of parasitoid puparia were recorded. The female flies were dissected after death to confirm that they had been fertilized.

Results and discussion

The pre-oviposition period at 25°C for *P. laxa* with *H. armigera* as host was 7,37 ± 0,28 days ($\bar{x}$ ± SE), range 6 - 9 days (N = 33). The oviposition period for *P. laxa* females was 26,9 ± 0,70 days ($\bar{x}$ ± SE), range 16 - 36 days. The progeny production by *P. laxa* females was highly variable. The mean daily production of progeny per female was 7,91 ± 0,32 ($\bar{x}$ ± SE), range 1 - 24 puparia. Total progeny per female was 126,26 ± 23,73 ($\bar{x}$ ± SE), range 3 - 318 puparia (N = 2399) (Fig. 16).

After the pre-oviposition period daily oviposition

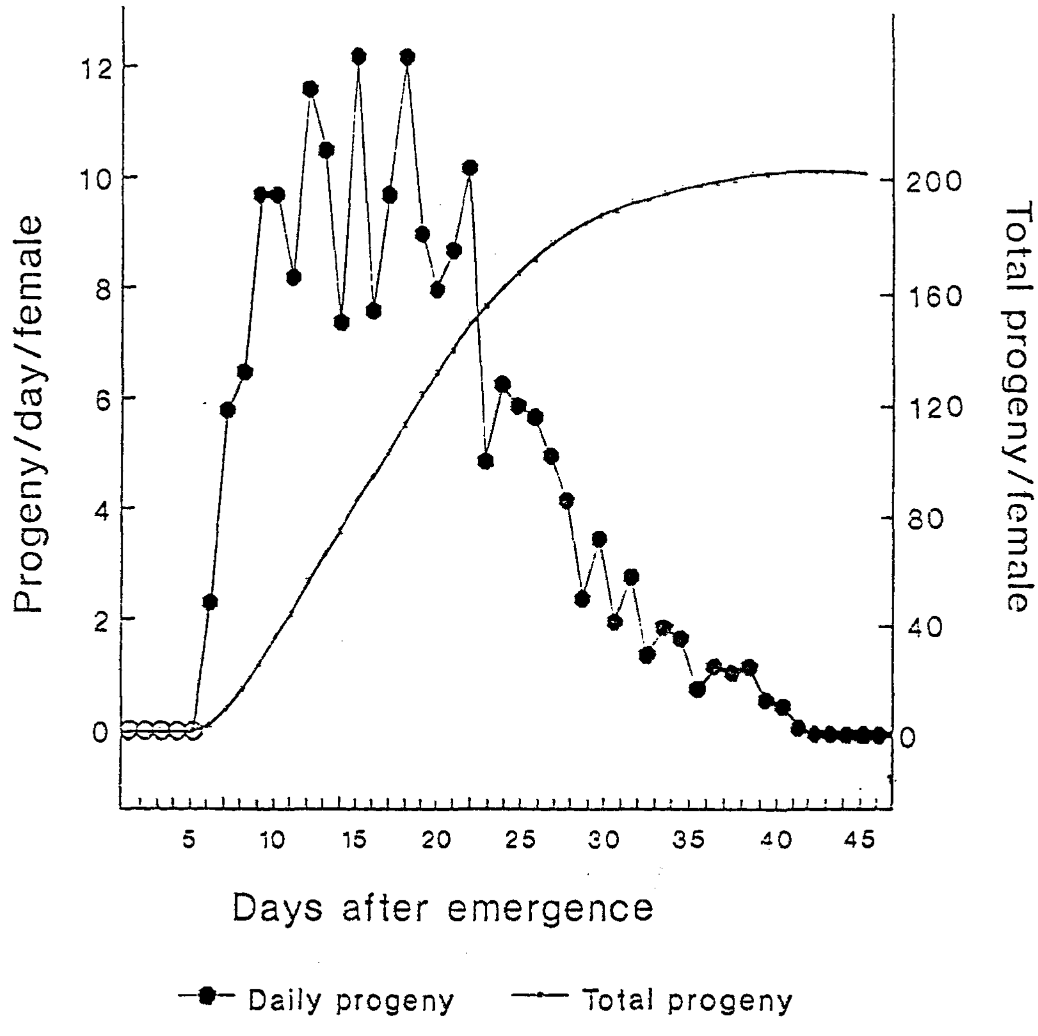

Fig. 16. The mean daily and total progeny production of *Palexorista laxa* females.

increased sharply and peaked between days 9 and 22. After day 22 a steady decline occurred until the females died. Progeny production occurred up to 42 days after emergence. It was not possible to measure fecundity because some host larvae died after being parasitised, some eggs were destroyed or removed by the hosts, and some progeny died before the formation of puparia.

Chauthani & Hamm (1967) and Jackson *et al*. (1976) reported a pre-oviposition period for *D*. *munda* of 8 - 9 days, and 6,9 days for *P*. *laxa* at 25°C, on *H*. *zea* and *H*. *virescens* respectively.

The oviposition period of about 27 days in the present study for *P*. *laxa* is slightly longer than the 24,5 days at 25°C and 17,5 days at 30°C recorded by Jackson *et al*. (1976). They also noted that the oviposition period declined with an increase in temperature. Chauthani & Hamm (1967), recorded a much shorter oviposition period of 5,1 days for *D*. *munda* at 25,6 - 27,8°C.

The maximum progeny produced recorded by Jackson *et al*. (1976) was 72,2 puparia per female at 35°C, and according to them this compared well with an average of 77,2 eggs in each of the oviducts of fertilized females. They also found that the total production of puparia by individual females was variable and ranged from 0 - 203. They came to the conclusion that the optimum temperature for reproduction was 25°C.

FEMALE REPRODUCTIVE SYSTEM

Methods

Pairs of flies were kept in the laboratory in Perspex containers and provided with food and water. Five 5th instar H. armigera were exposed daily for 60 minutes to each pair. After parasitization, larvae were placed singly in glass vials. When puparia formed their mass was determined and they were placed in petri-dishes until the adults emerged. The newly emerged flies were weighed, killed and dissected and the number of ovarioles in each ovary and the number of eggs in two ovarioles on each side were recorded (Table 13).

Results and discussion

A significant linear correlation was found between the pupal mass and adult mass (Fig. 13), between the adult mass and number of ovarioles (Fig. 14), and between the adult mass and average number of eggs per female (Fig. 15).

These results could be of significance in progeny production. When an increase in the number of puparia per host occurred a lower percentage emerged and a higher percentage mortality of puparia occurred (Table 11). Pupal and adult mass as well as the number of ovaries per female and the number of eggs per female declined (Table 13). Smaller, light females thus produced smaller progeny, were short lived and less fecund.

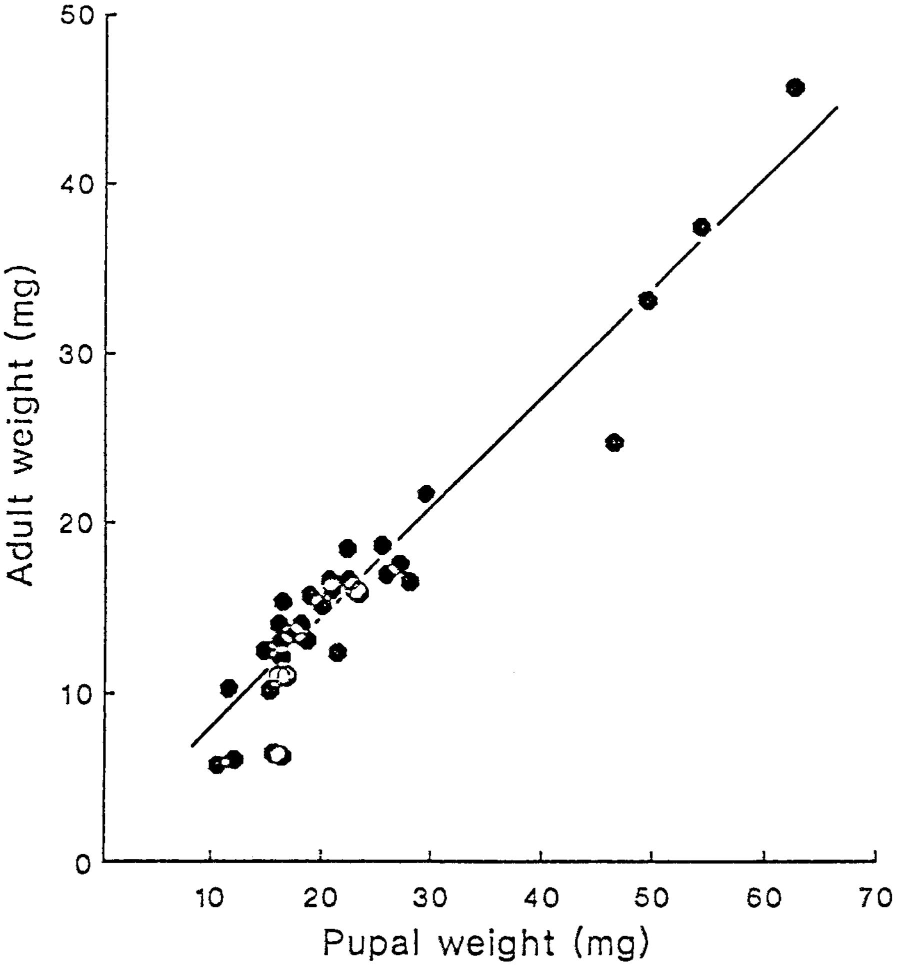

Fig. 13. The relationship between pupal mass and adult mass of <u>Palexorista</u> <u>laxa</u> ($y = 0{,}008 + 1{,}32X$, $r = 0{,}93$, $P < 0{,}05$).

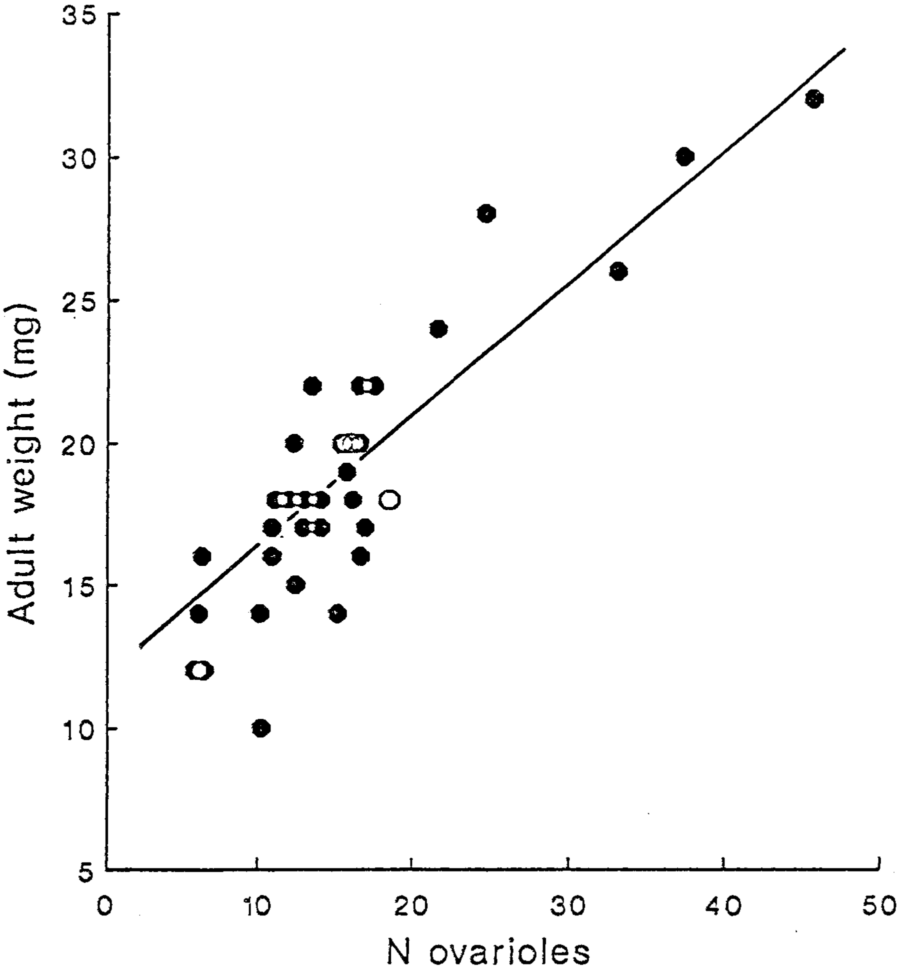

Fig. 14. The relationship between adult mass and number of ovarioles in females of <u>Palexorista laxa</u> (y = 11,23 + 486,84X, r = 0,78, P < 0,05).

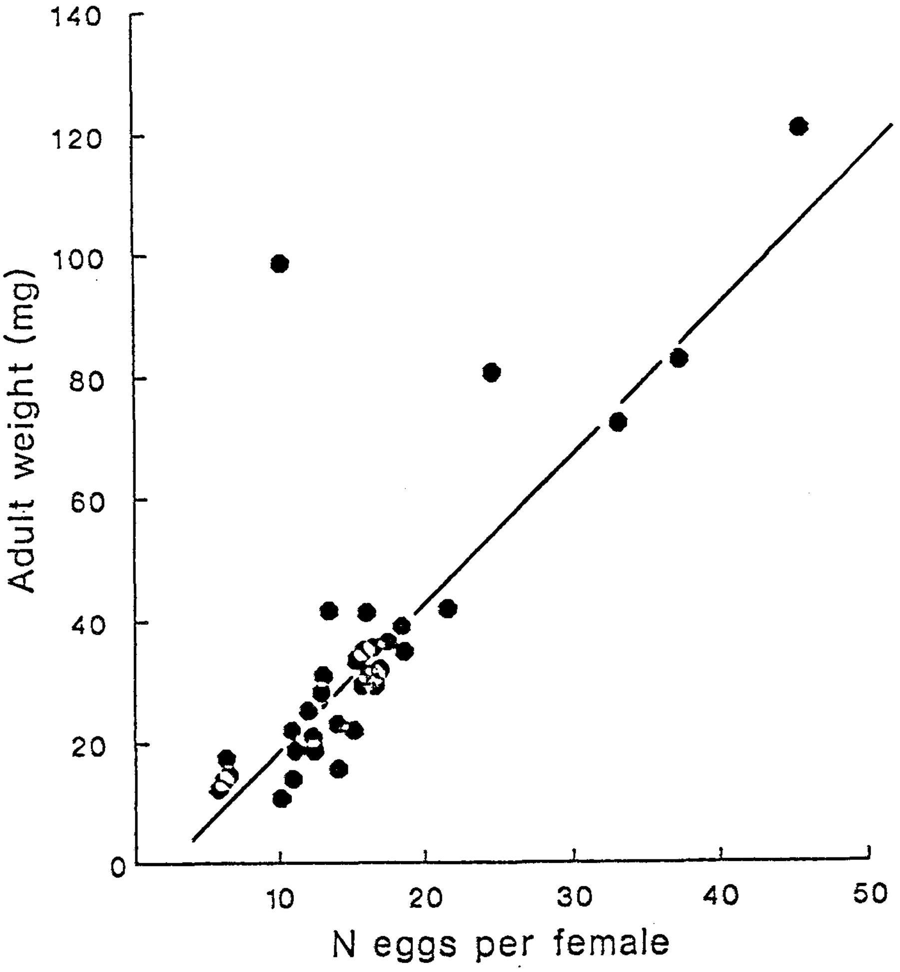

Fig. 15. Relationship between adult mass and the number of eggs in females of <u>Palexorista</u> <u>laxa</u> ($y = 15,67 + 3250,64X$, $r = 0,87$, $P < 0,05$).

TABLE 13. Palexorista laxa pupal mass, adult mass, N ovaries and N eggs/female.

N pupae/ host	N females	Pupal mass (mg)	Adult mass (mg)	N ovarioles /female	N eggs/ female*
1	1	62,5	45,6	32	1204
2	2(1)	54,3	37,4	30	825
	(2)	49,5	33,1	26	722
3	1	46,5	24,7	28	805
4	2(1)	26,0	16,9	17	319
	(2)	17,4	13,4	22	418
4	1	29,5	21,6	24	420
5	2(1)	22,3	18,4	18	392
	(2)	20,9	16,0	20	414
5	1	16,4	15,3	20	334
6	4(1)	22,5	16,6	16	293
	(2)	20,0	15,1	14	220
	(3)	25,5	18,6	18	348
	(4)	23,0	16,1	18	310
7	1	16,1	14,0	17	230
7	2(1)	20,7	16,6	20	310
	(2)	18,9	15,7	19	293
8	6(1)	23,4	15,8	20	349
	(2)	16,3	12,0	18	252
	(3)	16,1	10,9	17	220
	(4)	27,1	17,5	22	365
	(5)	16,2	12,9	17	282
	(6)	28,0	16,5	22	355
8	1	18,6	13,0	18	309
9	3(1)	16,5	11,1	18	187
	(2)	15,6	6,5	12	147
	(3)	16,8	10,9	16	140
9	4(1)	21,4	12,3	20	210
	(2)	10,6	5,8	12	123
	(3)	12,1	6,1	14	138
	(4)	16,4	6,3	16	175
10	4(1)	14,8	12,4	15	187
	(2)	11,6	10,2	10	98
	(3)	18,1	14,0	18	157
	(4)	15,3	10,1	14	108

* Calculated

DESCRIPTION OF REPRODUCTIVE SYSTEM

P. laxa females produced incubated macrotype eggs which hatched immediately after oviposition. The two ovaries each comprised of 5 to 16 ovarioles, containing various numbers of eggs in different stages of development (Table 13). The paired oviducts were long and slender and united to form a common oviduct which opened into the wider uterus. The long uterus was thick-walled for the greater portion of its length and covered with abundant tracheae which indicated that the eggs were incubated before oviposition. Behind the opening of the oviduct into the uterus opened a pair of accessory glands and three spermathecae. After fertilization the eggs descended into the uterus which expanded considerably in length and width. The eggs were arranged in transverse rows in the anterior portion and longitudinally in the posterior section. The ovaries at this stage were small and athrophied (Fig. 10).

DISTRIBUTION OF EGGS

Methods

This test was done in two ways: 1) five 5th instar *H. armigera* were exposed to individual "inexperienced" (females without any oviposition experience) *P. laxa* females. For 60 minutes the site on which the eggs were deposited was recorded. For recording purposes the host body was divided into a dorsal, lateral and ventral parts and eggs on all 11 segments were recorded (excluding the head). 2) Five 5th instar *H. armigera* larvae were exposed, as in 1) to "experienced" females 15 days old. These females had gained "experience" during previous exposure to hosts.

Results and discussion

The eggs deposited by "experienced" females were placed mainly on the head and thorax (Table 14). The thoracic position was advantageous because eggs placed further back were accessible to the mandibles of the host and were removed or destroyed. The presence of hatching eggs and maggots busy burrowing into the host, apparently caused irritation as the host attempted to brush the eggs off or to destroy them. When the females were "inexperienced" (Table 15) the eggs were deposited on all the hosts segments. The distribution of eggs could be a behaviour pattern not yet fully functional in "inexperienced" flies, experience was gained through exposure to larvae as flies started to show experience from their second encounter with larvae irrespective of age.

H. armigera larvae were very active and responded to larval penetration by raising the anterior part of their bodies and jerking their heads backwards and sideways. This is a common physical reaction to parasitoid attack by various lepidopterous larvae (Allen 1925; Herrebout 1969; Martin *et al.* 1989; Neser 1973). According to Martin *et* al. (1989), a number of tactics have evolved in parasitoids which allow them to avoid or overcome both physical and hemocytic defensive tactics of their host as is demonstrated by P. laxa flies selective placement of eggs on the host. P. laxa females, in response to this physical defence were extremely quick, during oviposition.

TABLE 14. Distribution of Palexorista laxa eggs on Heliothis armicera larvae by "experienced" females.

Segment	1	2	3	4	5	6
Dorsal	10	10	11	4	2	1
Lateral	6	7	4	1	0	0
Ventral	4	3	3	4	0	0
Total	20	20	18	9	2	1

TABLE 15. Distribution of Palexorista laxa eggs on Heliothis armicera larvae by "inexperienced" females.

Segment	1	2	3	4	5	6	7	8	9	10	11
Dorsal	3	10	2	8	4	1	7	9	11	11	9
Lateral	2	6	6	2	3	0	1	7	4	3	6
Ventral	1	3	5	3	3	5	2	4	11	6	12
Total	6	19	13	13	10	6	10	20	26	20	27

CHAPTER 6

EFFECT OF TEMPERATURE ON DEVELOPMENT

The effect of temperature on development of P. laxa was investigated by Jackson et al. (1976) using H. zea as host. The question arose whether development time in a different host, H. armigera would differ. In H. zea differences did not occur in the number of puparia produced per host at different temperatures and the percentage emergence in adults was the same at 25° and 32,2°C (68,6%). Low percentage parasitism of 11,0% and 30,8% were recorded by Jackson et al. (1976), under 20° and 32°C respectively. Such low parasitism could have influenced the results. It is possible that H. armigera is a more suitable host for P. laxa than H. zea.

Methods

The effect of temperature on larval and pupal development time and on survival was studied at 20°, 22°, 25°, 28°and 30°C.

Host larvae were exposed to flies at 25°C and then placed singly in glass vials in controlled temperature cabinets. Daily records were kept on any parasitoid development.

Results and discussion

The mean number of puparia produced per host at the various temperatures did not differ significantly (Table 16), according to Chi-squared tests.

As expected, duration of development decreased with an increase in temperature (Fig. 17). Exponensial regression analysis showed a highly significant difference in duration of developmental time from the larval stage to the adult stage at different temperatures. The larval developmental period of *P. laxa* in *H. armigera* varied from 7,48 ± 0,08 days (x ± SE) at 20°C to 3,48 ± 0,05 days ($\bar{x}$ ± SE) at 30°C. Total development time from larval penetration to adult emergence varied between 24,94 ± 0,06 days ($\bar{x}$ ± SE) at 20°C and 11,30 ± 0,07 days ($\bar{x}$ ± SE) at 30°C. Jackson *et al*. (1976), using *H. zea* as host, recorded developmental times that were slightly longer, the larval stage required 8,5 days at 20°C and 4,6 days at 30°C. The highest percentage emergence recorded occurred at 30°C (71,1%).

In the present study percentage adult emerging varied from 59,68% at 20°C to 77,86% at 30°C (Table 16). Although the percentage emergence showed an increase with an

TABLE 16. Effect of temperature on rearing *Palexorista laxa* on *Heliothis armigera*.

Temp. (°C)	No. hosts exposed	No. hosts parasitised	No. puparia obtained	Mean No. puparia/host	% adults emergence
20	36	28 (77,80%)	64	2,29 ± 0,28	59,68
22	57	41 (71,93%)	128	3,12 ± 0,24	64.84
25	25	19 (76,00%)	70	3,68 ± 0,36	72.86
28	49	36 (73,47%)	131	3,64 ± 0,26	73,44
30	64	48 (75,00%)	124	2,58 ± 0,23	77,86

increase in temperature this was not significantly different at the 5% level when Chi-square tests were done.

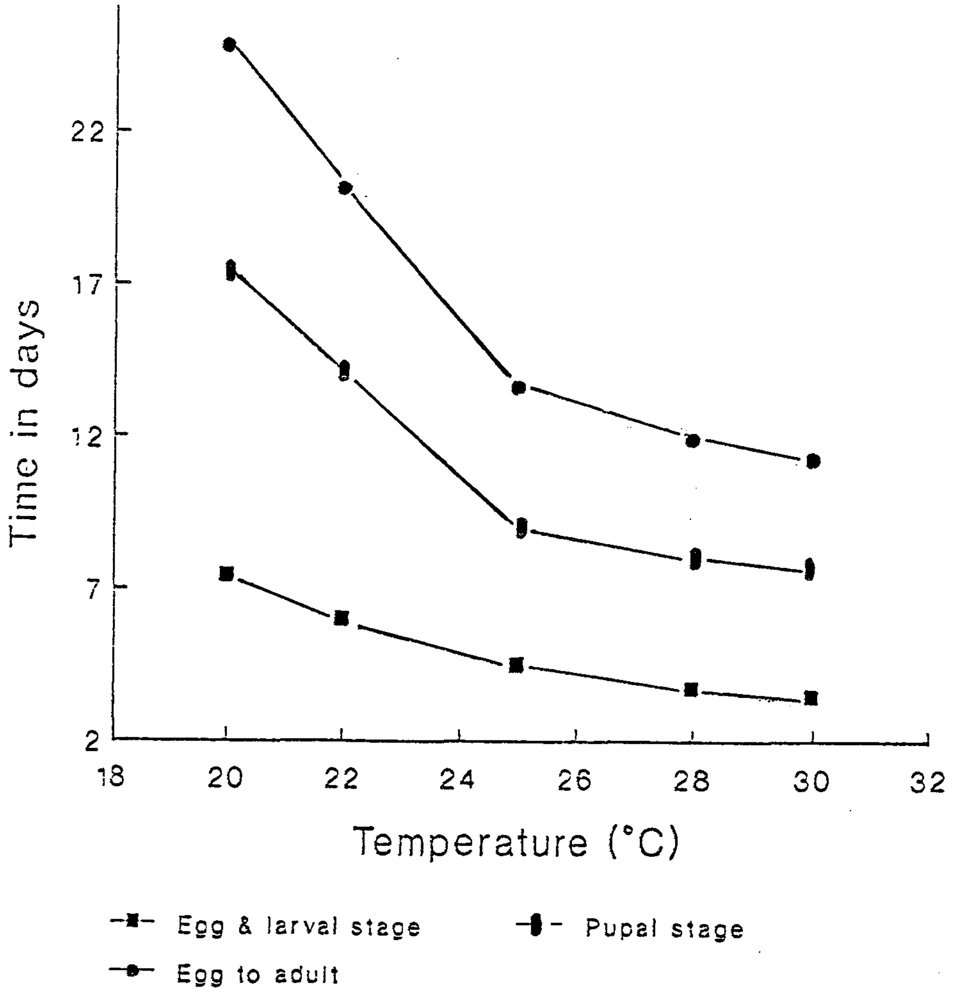

Fig. 17. The influence of temperature on the duration of developmental stages of Palexorista laxa.

GENERAL DISCUSSION

The aim of this study was to contribute to the understanding of tachinid biology in general. P. laxa is the most important parasitoid of H. armigera, which has been identified as the most polyphagous and injurious pest of agricultural crops in South Africa (Annecke & Moran 1982). Biological control is a major component of integrated pest management which seeks to maximize the contribution of parasitoids in pest control. Only limited data exist on the role tachinids play in controlling pests, and on their biology, behaviour and ecology. This study was mainly concerned with the biology of P. laxa, emphasis also fell on seasonality and percentage parasitism; distribution and host plant association; host range; host instar preference; hyperparasitoids and superparasitism.

It is easy mass rear P. laxa in a laboratory as no special conditions are needed for mating and oviposition. Most tachinids are difficult to mass rear in the laboratory because environmental factors such as sunlight and air movement may play an important role in mating. The fact that it is easy to rear P. laxa in the laboratory could influence a decision of whether to use the insect for biological control programmes.

P. laxa was found to be an efficient parasitoid of H. armigera on sunflower. High mortalities of bollworm larvae due to parasitism by P. laxa occurred on sunflower during seasons when both H. armigera and P. laxa populations were high (Chapter 3 p. 18). When densities of larvae were high, parasitism exceeded 45% compared to 10% when larval densities were low. The fact that when infestation levels by H. armigera were high, a higher proportion of larvae was parasitised by P. laxa than at low infestation levels indicate a density dependant reaction by the parasitoid. The parasitoid reacted to high densities of hosts by increasing its own activities and showing a positive functional response. However, the low parasitism levels in low host densities might indicate a poor searching ability for P. laxa.

In sunflower, due to the fact that insecticides are rarely used, P. laxa can maintain its populations unharmed. P. laxa was introduced into Arizona, USA, as a biological control agent against H. zea and H. virescens. This parasitoid could also be used as a biological control agent in other countries where various species of Heliothis occur as pests.

Although P. laxa is mentioned in the literature as an important natural enemy of H. armigera in cotton in Botswana (Roome 1971), Chad and Senegal (van den Berg et al. 1988), South Africa (Cuthbertson & Munro 1941; Parsons 1940; Taylor 1932), Sudan (Tunstall 1958), Tanzania (Reed 1965; Robertson 1973), Uganda (Greathead 1966) and Zimbabwe (Jones 1939; van den Berg et al. 1988), it was not recorded on cotton in South Africa since 1985. P. laxa was also recorded on maize and grain sorghum. However, *P. laxa* was abundant on sunflower. This is an indication that the parasitoid have habitat preferences, or that it was eliminated from cotton fields in South Africa due to severe pesticide sprayings against bollworms.

P. laxa can be regarded as an oligophagous parasitoid. *P. laxa* preferred to parasitise *H. armigera* since the percentage parasitism in the laboratory was higher on *H. armigera* than on *B. fusca* and *C. partellus*. *P. laxa* was recorded from *B. fusca* and *C. partellus* during heavy borer infestations on maize. Both borers, together with *E. saccharina*, served as hosts for *P. laxa* in the laboratory. No recoveries of *P. laxa* were made from other lepidopterous larvae occurring in sunflower during the 1988/89, 1989/90 and 1990/91 seasons. During this time *T. orichalcea*, *Taraché* sp. and various loopers and semi-loopers were fairly abundant on sunflower. In the laboratory *S. littoralis* and *T. orichalcea* were also tested for acceptability as hosts for *P. laxa*. Although the females showed interest in the larvae and oviposited on them, no parasitoids developed. There are other possible hosts as mentioned in Chapter 1 & 3 (p. 5 & 14 respectively), although here *P. laxa* might not be so effective. Tests are still to be done to establish the full extent of the host range of *P. laxa*.

P. laxa showed a preference for the 4th and 5th instars of *H. armigera* (Chapter 3 p. 10), although low numbers of

3rd instars were also parasitised. High mortality occurred in the 3rd instar. It could be due to the fact that young larvae do not contain enough food to support parasitoid development.

Two hyperparasitoids, Perilampus maurus Walker (Hymenoptera: Perilampidae) and Brachymeria sp. nr. cowani Kirby (Hymenoptera: Chalcididae), were recorded on Palexorista sp. by Robertson (1973) in Tanzania. Another facultative hyperparasitoid, Tetrastichus howardi Olliff (Hymenoptera: Eulophidae) which was introduced from the Philippines to South Africa against the stalk borer C. partellus also developed on both P. laxa and H. armigera in the laboratory (R. Kfir, personal communication). In the present study no hyperparasitoids were recovered from P. laxa. The rarity of hyperparasitism on P. laxa makes this parasitoid an attractive biological control agent to be used in biological control programmes against the cosmopolitan pest H. armigera.

No superparasitised host larvae were collected in the field and the number of progeny per host never exceeded six. The maggots were always of the same age indicating that they might have been progeny of the same female. However, under laboratory conditions superparasitism occurred often raising the following question: why would a female risk her offspring's chance of survival?

No reference could be found in the literature of the marking of parasitised hosts by dipteran parasitoids. Thus it is possible that females of P. laxa are unable to distinguish between parasitised and unparasitised host larvae. Since females were provided with hosts in an enclosed area and did not have to use energy searching for hosts, more energy was available for oviposition, increasing the number of eggs laid. The clutch size influenced the survivorship to adulthood of offspring. In addition, with an increase in clutch size, less food was available for each offspring which often emerged as small adults. The duration of development of larvae and puparia decreased significantly with an increase in parasitoid density per host. Puparial mass also declined progressively from 5,64 mg when one pupa per host formed to 1,12 mg when 10 puparia per host formed. The emerging small flies usually died before the pre-oviposition period was completed (Chapter 4 p. 36). Mortality also increased from 2% when only one puparium per host formed up to 50% when 10 formed and 62% when 13 puparia per host formed. Mortality as high as 87% occurred when 23 puparia per host formed. Thus, crowding may cause immature survival to decline or adult size to decrease, or both. This would have an effect on adult fitness, altering both life-span and egg production.

Although in the laboratory females showed no discrimination between previously parasitised and non-parasitised host larvae, it seems that some discrimination does occur. This might also happen in the field as host larvae of the same size can occur together on the same sunflower head, only one being parasitised. It is possible that the artificial conditions in the laboratory and the high parasitoid per host ratio obscured the discriminatory ability of the parasitoids.

The position on the host where eggs were deposited by "experienced" and "inexperienced" females was different. The learning process forced "experienced" females to place eggs only on the head and thorax in order to avoid being injured or killed by the mandibles of the aggressive hosts. Also, eggs placed further back are accessible to the mandibles of the host and are easily destroyed or removed. It is very unlikely that females could "observe" that hosts removed eggs placed on other parts of the body and the distribution of the eggs should be seen as a "learning" behaviour pattern. This behaviour developed probably for the adults own safety.

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