OBSERVATIONS ON NATURAL MORTALITY, PARASITES AND PREDATORS OF WHEAT BULB FLY, *LEPTOHYLEMYIA COARCTATA* (FALL.).

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Knowledge of natural mortality of wheat bulb fly, *Leptohylemyia coarctata* (Fall.), is fragmentary, and losses during the complete life-cycle have not been studied. Dobson, Stephenson & Lofty (1958) found from cage experiment that at least 4·7 per cent. of the eggs present in mid-March survived to produce flies, and in field experiments Raw (1960) observed survival varying from 2·7 to 17 per cent. between the end of oviposition and pupation.

Losses to eggs varying from 90 per cent. (Bremer, 1929; Gough, 1947) to 18–27 per cent. (Raw, 1960) have been recorded and attributed partly to " non-viability " and partly to predation. Many larvae perish because they fail to find food-plants, either when they are newly hatched or when they are moving to fresh shoots (Gough, 1947), and both F. Raw & J. R. Lofty and D. B. Long (*in* Mellanby, 1958) and Raw (1960) showed that the proportion of survivors is affected by plant density.

Losses of pupae were estimated as 78 per cent. by Dobson, Stephenson & Lofty (1958) and, although this figure was thought to be an overestimate, a loss of at least 66 per cent. was apparent. Parasites kill some pupae (Van Miegroet, 1950; Bardner & Kenten, 1957) and Van Miegroet recorded between 18 and 27·35 per cent. parasitisation of populations in Belgium.

Life-span of the adult fly has been studied (Dobson & Morris, 1961) but little is known of causes of mortality. Predators (Bardner & Kenten, 1957) and entomophagous fungi (Gough, 1947; Bardner & Kenten, 1957; Long, *in* Mellanby, 1958) cause some deaths.

The present paper discusses mortality during the pupal stage with special reference to parasitism and describes simple experiments with predators. In 1957 and 1958, the observations were incidental to the main line of work, but from the summer of 1959 were its main purpose. [This, however, was curtailed after a few months because the writer left Rothamsted in November 1959.]

TABLE I.

Losses amongst pupae kept in pots of soil at Rothamsted in 1957 and 1958.

Year	Total no. of pupae collected	No. of flies emerging	No. of pupae parasitised	No. of pupae found dead	No. seen to be removed by ants	No. of pupae missing
1957	900	296	90	46	3	465
1958	4,010	2,240	206	53	0	1,511

* Work completed at present address: Zoology Department, University, Glasgow W.2.

TABLE II.

Losses amongst pupae obtained from Whittlesey and Peterborough during 1959.

Site	Date of collecting	No. of pupae collected	No. of flies emerging	Parasites					Died due to unknown causes
				Aleochara inconspicua	*Aleochara bipustulata*	*Aleochara*?	*Phygadeuon trichops*	Unknown parasites	
Whittlesey ..	May 5	461	357	3*	0	10	0	0	91
	12	467	374	11	7	3	0	0	72
	19	501	361	10	15	20	1	0	94
	26	468	347	5	17	7	1	0	91
	June 2	463	310	0	16	3	0	0	134
	Total	2,360	1,749	29	55	43	2	0	482
Peterborough ..	May 8	479	331	49*	0	20	0	1	78
	15	476	330	11	39	20	0	0	76
	22	464	302	11	59	9	0	0	83
	29	513	387	4	34	3	0	0	85
	June 4	509	332	1	69	3	0	0	104
	Total	2,442	1,682	76	202	55	0	1	426

* Underestimate

Mortality amongst pupae.

Observations during 1957 and 1958.

In 1957 and 1958, in the course of a study on the life-span and behaviour of adult flies in eastern England, many pupae from a wheat crop at Rothamsted were placed in soil in gauze-covered plant pots and kept in the field until flies ceased to emerge. The pots were then searched and any pupae remaining were examined directly for parasites (1957) or were counted and replaced so that parasites could emerge naturally (1958).

The results (Table I) show that, as in the field-cage observations reported earlier (Dobson, Stephenson & Lofty, 1958), losses were high, and that although parasites and predators accounted for some, most were unexplained. Clearly, more detailed observations were needed.

Two species of parasitic Hymenoptera were obtained during these observations. One, a Braconid, occurred as a single imperfect specimen in 1957 and could not be identified, the other, a Cynipid, affected about 10 and 5 per cent. of the populations in 1957 and 1958, respectively, and has been named *Trybliographa spaniandra* by Kerrich & Quinlan (1960).

Observations in 1959.

In 1959, a full-time study of mortality was started. As the Rothamsted population was sparse, pupae were obtained at weekly intervals for five weeks from two fenland sites, Whittlesey and Peterborough. Most of the pupae were placed singly in moist peat in glass tubes and kept in an outside insectary at Rothamsted, and the rest, including many damaged, were examined directly or were kept in small batches in the laboratory. These methods enabled the fate of individuals to be watched closely (Table II). Total numbers of flies and parasites were recorded from the whole of the material, but emergence dates (discussed later) were recorded only from that kept in the insectary.

Parasites accounted for between 5·5 (Whittlesey) and 13·7 per cent. (Peterborough) of the deaths observed, and three species, *Aleochara bipustulata* (L.), *A. inconspicua* Aubé (Col., STAPHYLINIDAE) and *Phygadeuon trichops* Thoms. (Hym., ICHNEUMONIDAE) were identified. Parasitisation by *Aleochara* spp. was often evident, but for various reasons, *e.g.*, where only the empty puparium was found or where the parasite died during development, the parasitising species could not be identified.

Taking both Whittlesey and Peterborough material together, about 20 per cent. of the pupae died from various causes other than parasitism. Fifty-one young flies failed to emerge from the puparium or died soon after emerging, and 49 individuals, included as " emerged flies " in Table II, failed to expand and died within a few days. A hundred and sixty-one pupae developed a black pigmentation which affected first the setae, then the appendages and finally the whole body, and 110 became hard and solid without shrivelling or, except for three which also became black, without change of colour. In all, out of 4,802 pupae observed, 3,382, *i.e.*, 70·4 per cent., produced viable flies. It must be remembered that these pupae, unlike the previous ones, were not exposed to predation.

Notes on biology of the parasites.

Aleochara bipustulata.

This species parasitises various Anthomyiid flies (listed by Fuldner, 1960), but there is no published account of its attacking wheat bulb fly. Dr. H. C. Gough, of the National Agricultural Advisory Service informs me (*in litt.*), however, that he has observed it attacking wheat bulb fly on several occasions. Its life-cycle, outlined by de Wilde (1947) and Fuldner (1960) is similar to that of *A. bilineata* Gylh. (Wadsworth, 1915). Eggs are laid in the soil and the active, campodeiform

first-instar larva bores into the host puparium and lives ectoparasitically on the pupa within. There are three larval instars and, at each moult, hypermetamorphosis occurs involving changes in the mandibles, reduction and simplification of the appendages and the assumption of an eruciform condition. The full-grown larva pupates within the empty host puparium and the adult escapes by cutting a slit all round the puparium near one end so that a circular, cap-like portion around its tip is detached. This detached portion is then inverted and transferred to the opposite end before the beetle escapes. Out of 15 empty puparia examined, nine had the emergence hole at the anterior end and six had it at the posterior end.

Adult beetles laid eggs in damp sand in the laboratory and first-instar larvae were seen 12 to 14 days after putting the sexes together. They fed on freshly killed adults of wheat bulb fly, removing the soft tissues and leaving the disarticulated exoskeleton, and attacked eggs, biting them across the middle and extracting the contents. When starved they soon turned cannibal. Adult beetles will also feed on the eggs (Hughes, 1959), on the larvae and on the contents of the broken puparia of *Erioischia brassicae* (Bch.) (de Wilde, 1947).

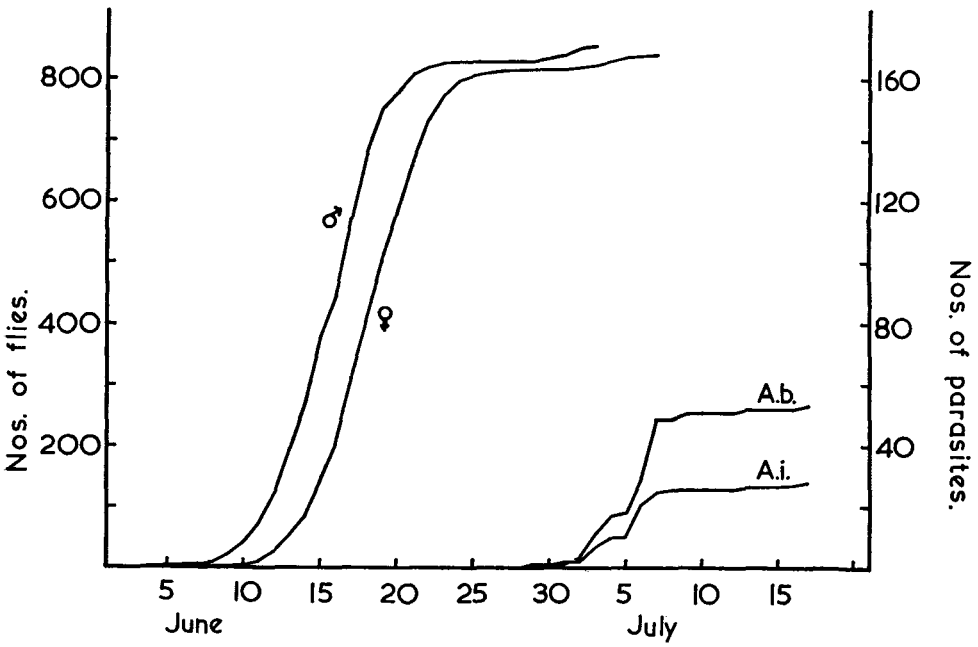

Fig. 1.—Emergence of flies and parasites from pupae collected at Whittlesey in 1959. (♂ & ♀, male and female flies; A.b., *Aleochara bipustulata*; A.i., *Aleochara inconspicua*.)

A. bipustulata was the most abundant parasite found at Whittlesey and Peterborough and, although not in the first batch of pupae from both sites, occurred in all later ones. The emergence data for flies and parasites observed in the Rothamsted insectary (figs. 1, 2) are thought reasonably representative, because the mean emergence dates of flies bred from pupae collected on different dates

were similar (Table III). Had the insectary been warmer or colder than the field, then a trend in the emergence dates of successive batches would have been expected.

TABLE III.

Mean emergence dates of flies obtained from pupae collected at Whittlesey and Peterborough in 1959.

Site	Date of collecting	Mean emergence dates of flies	
		Male	Female
Whittlesey	May 5	June 16	June 19
	12	17	20
	19	16	19
	26	16	19
	June 2	15	19
Peterborough	May 8	June 14	June 18
	15	14	17
	22	13	16
	29	14	16
	June 4	16	18

The adult beetles emerged 2½ to 3 weeks after the flies and, allowing seven to eight weeks from the onset of parasitisation to the appearance of the first beetles (*i.e.*, early May to late June), the entire life-cycle, from pairing of the sexes to appearance of young beetles appears to take 9 to 10 weeks.

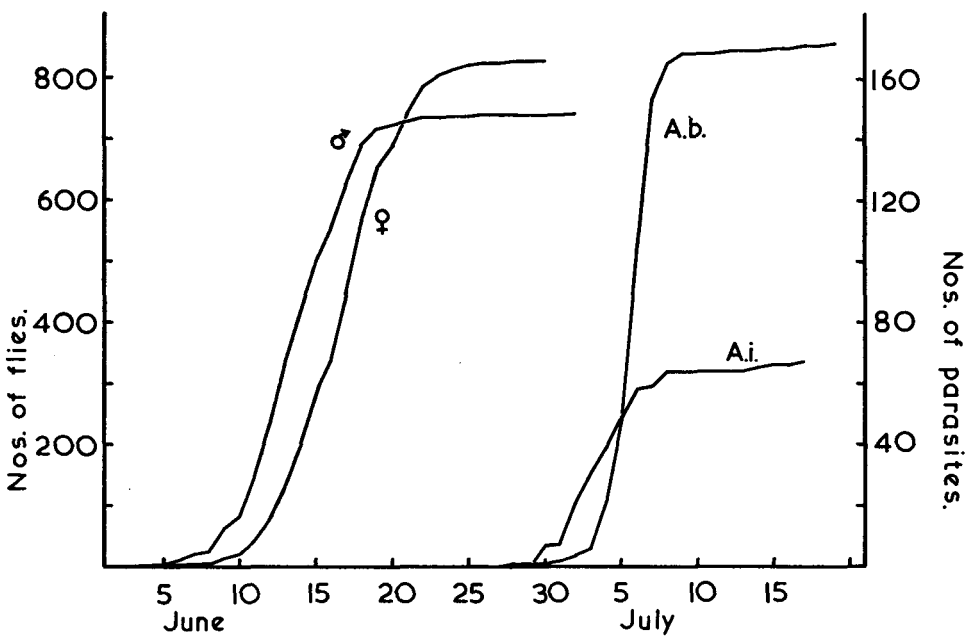

Fig. 2.—Emergence of flies and parasites from pupae collected at Peterborough in 1959.

Aleochara inconspicua.

This species is usually regarded as rare in Britain and was included in Fowler's monograph (1888) as very doubtfully British. Its presence was, however, confirmed by Blair (1933), who found a single specimen near Southwold (Suffolk). Clearly, the species is common at Whittlesey and Peterborough.

There is no published account of its parasitic habit, but it has been obtained from wheat bulb fly previously (C. E. Tottenham, private communication). Its life-history somewhat resembles that of *A. laevigata* Gylh., which also parasitises wheat bulb fly (Speyer, 1954) and of *A. curtula* Goeze (Kemner, 1926) in that the third-instar larva is campodeiform and active, and leaves the host puparium when fully grown. It escapes through a jagged hole in the side of the puparium, usually near the anterior end, and pupates in a small silk-lined chamber in the soil. *A. inconspicua* is a small beetle and its larva consumes only one-half to two-thirds of the contents of the host puparium. Pupation outside its host may therefore be advantageous, for inside there might be risk of being stifled by the decaying remains of the pupa.

As with *A. bipustulata*, the adult beetles fed on the soft parts of eggs and recently killed adults of wheat bulb fly, and they soon turned cannibal when starved. They did not lay eggs in damp sand provided in insectary cultures.

A. inconspicua occurred in all except the last batch of pupae from Whittlesey and was more numerous in the earlier than in the later batches (Table II). (It is believed that its numbers were grossly under-estimated in the first batch from Whittlesey and to a lesser extent in the first from Peterborough because for a time it was not realised that it vacates the host puparium before pupating.) The falling incidence of infestation from batch to batch suggests that many mature larvae had already left the puparia when these were collected and that increasingly higher proportions of stragglers were being obtained. This is supported by a tendency for beetles from the earlier batches to emerge before those from the later ones, *e.g.*, the mean emergence date for those collected at Peterborough on 8th May was 3rd June, whereas that for the remainder of the Peterborough material combined was 7th June. Like *A. curtula* (Kemner, 1926), *A. inconspicua* may attack only young puparia.

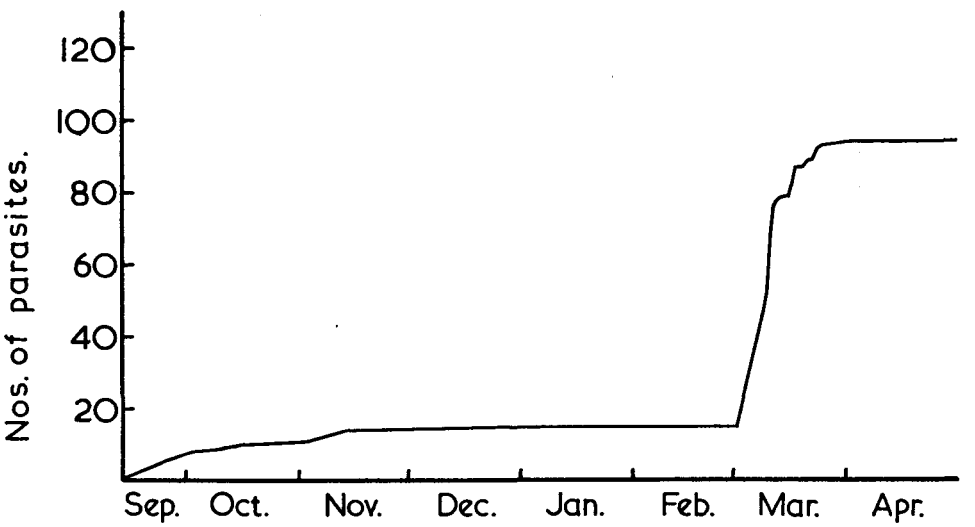

Fig. 3. Emergence of *Trybliographa spaniandra* during 1958–59.

The emergence data (figs. 1, 2) suggest that the beetles emerge 2½ to 3 weeks after the flies, but it must be stressed that these figures may be based on only part of the true population.

Trybliographa spaniandra.

This species was the most abundant parasite obtained from wheat bulb fly at Rothamsted in 1957 and 1958. Females greatly outnumbered males; in 1957, all 81 specimens examined were female and, in 1958, only 2 out of 110 were male. "*Cothonaspis* sp." recorded from wheat bulb fly by Van Miegroet (1950) may have been this species as this name was formerly, but incorrectly, attributed to *Trybliographa* (G. J. Kerrich, *in litt.*).

In 1958, most parasites (18 out of 20 examined) had pupated by August and the first adults appeared in September. The main emergence, however, was not until the next spring (fig. 3). Because of this, it seems likely that, in common with other species of EUCOILINAE (Clausen, 1940), *T. spaniandra* attacks the larva of its host.

Adult parasites survived for some time without food or water (*e.g.*, over 25 per cent. of them survived for four weeks), and although they were quiescent at insectary temperatures, they rapidly became active when warmed.

Phygadeuon trichops.

This species is a well-known parasite of Anthomyiid flies but has not been recorded from wheat bulb fly before. Its biology was studied by Monteith (1956) who showed that the eggs are deposited on the host pupa within the puparium.

Observations on predation of wheat bulb fly.

Reference has already been made to predation by the species of *Aleochara* which parasitise wheat bulb fly. *Scopeuma stercoraria* (L.) (Dipt., CORDYLURIDAE) (the species commonly cited as *Scatophaga stercoraria* (L.)) and *Tetragnatha extensa* (L.) (Araneida) preyed on adult flies in the laboratory, and workers of *Myrmica rubra* (L.) (Hym., FORMICIDAE) removed buried pupae and newly emerged flies from pots of soil in the field.

Simple laboratory tests were devised in which adults of possible predator species, a complete list of which is shown in Table IV, were offered eggs or pupae of wheat bulb fly as food. It is evident from the results in Table IV that *Notiophilus biguttatus*, a species adapted for preying on small moving arthropods (Davies, 1953*a*), attacked neither eggs nor pupae, but *Clivina fossor* and both the *Bembidion* spp. tested ate eggs readily. *Bembidion* species also eat eggs of *Erioischia brassicae* (Wishart, Doane & Maybee, 1957; Hughes, 1959) and *B. lampros* which is an important predator on the eggs of this species was studied by Mitchell (1958).

The two *Harpalus* spp. and *Bradycellus verbasci* ate eggs, and *H. rufipes*, the only species tested, also ate pupae. Other *Harpalus* spp. tested by Wishart, Doane & Maybee (1956) refused eggs of *E. brassicae*. Davies (1953*a*) regarded the Harpalini as predominantly herbivorous but as taking animal food in small amounts.

The *Amara* spp., except for *A. aulica*, showed predation, and this is interesting because reports of predation by *Amara* spp. have been few (Allen, 1953; Davies, 1953*b*) whereas their herbivorous habits are well-known (*e.g.*, Westwood, 1839; Hart, 1884; Webster, 1903; Aubrook, 1949; Davies, 1953*a*). The attack of *A. familiaris* on the pupa was striking: within minutes of being introduced, the beetle tore open the abdomen of the pupa and consumed much of its contents. A single beetle could destroy several pupae in quick succession.

Feronia melanaria, a pest of strawberries, takes animal food both as a larva (Briggs, 1957) and as an adult (Williams, 1959). It refused eggs of wheat bulb fly

as it refused those of *E. brassicae* (Wishart, Doane & Maybee, 1957). *F. madida*, another pest of strawberries, was not tested with eggs but ate pupae. This species takes both animal and plant food and was regarded as an unspecialised feeder by Davies (1953*a*).

Agonum dorsale sometimes accepted and sometimes refused eggs, but neither of the individuals tested attacked pupae. *Demetrias atricapillus* attacked eggs but not pupae.

None of the STAPHYLINIDAE tested attacked pupae, but all the *Tachyporus* spp. tested with eggs ate them. Neither *Stenus* spp. nor *Astilbus canaliculatus* ate eggs. The former are specialised for the pursuit and capture of small motile prey (Schmitz, 1943) but will attack maimed adults of Diptera (Voris, 1934) and the latter is associated with, and predatory on, ants (Donisthorpe, 1927).

TABLE IV.

Results of laboratory observations on predation of eggs and pupae.

Species tested	Number tested with:		Results	
	Eggs	Pupae	Eggs	Pupae
Coleoptera (CARABIDAE)				
Notiophilus biguttatus (F.)	4	1	—	—
Clivina fossor (L.)	1	0	+	
Bembidion lampros (Hbst.)	11	0	+	
B. quadrimaculatum (L.)	1	0	+	
Harpalus aeneus (F.)	1	0	+	
H. rufipes (Deg.)	1	3	+	+
Bradycellus verbasci (Duft.)	1	0	+	
Amara similata (Gylh.)	0	1		+
A. familiaris (Duft.)	2	9	+	+
A. aulica (Panz.)	1	0	—	
Feronia melanaria (Ill.)	1	0	—	
F. madida (F.)	0	1		+
Agonum dorsale (Pontoppidan)	4	2	±	—
Demetrias atricapillus (L.)	1	7	+	—
Coleoptera (STAPHYLINIDAE)				
Stenus clavicornis (Scop.)	2	1	—	—
S. atratulus Erichs.	1	0	—	
Philonthus fuscipennis (Mannh.)	0	1		—
P. varius (Gylh.)	0	1		—
Tachyporus chrysomelinus (L.)	1	0	+	
T. solutus Erichs.	2	0	+	
T. obtusus (L.)	0	1		—
T. hypnorum (F.)	4	1	±	—
Astilbus canaliculatus (F.)	1	0	—	
Aleochara bipustulata (L.)	Many	0	+	
A. inconspicua Aubé	Many	0	+	
Dermaptera				
Forficula auricularia L.	1	0	+	
Chilopoda				
Lamycetes fulvicornis Meinert	5	0	+	
Lithobius variegatus Leach	1	0	+	
Necrophloeophagus longicornis (Leach)	0	2		±

\+ Predation observed
— No predation
± Variable result

Summary.

Observations in eastern England during 1957, 1958 and 1959 showed natural mortality of pupae of wheat bulb fly, *Leptohylemyia coarctata* (Fall.), to be high. The part of this due to parasitisation is considered in some detail.

At Rothamsted, the main parasite was *Trybliographa spaniandra* Kerrich & Quinlan, and this affected about 10 per cent. of the population in 1957 and about 5 per cent. in 1958. At Whittlesey and Peterborough, in 1959, parasitisation affected 5·5 and 13·7 per cent. of the populations, respectively. The two main parasites found were *Aleochara bipustulata* (L.) and *A. inconspicua* Aubé (Coleoptera, STAPHYLINIDAE). *Phygadeuon trichops* Thoms. (Hymenoptera, ICHNEUMONIDAE) also occurred but was much less frequent. Notes and original observations on the biology of these parasites are given.

Several insects and other small arthropods were observed to prey on various stages of wheat bulb fly. Details of these and notes on the biology of some of them are given.

Acknowledgements.

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