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SOME FACTORS AFFECTING ECLOSION OF *GLOSSINA MORSITANS* WESTW. FROM PUPAE

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According to Bursell (1959), eclosion of tsetse flies (*Glossina morsitans* Westw.) from pupae occurs predominantly between 1500 and 1800 hr. under variable field conditions, while emergence occurs at all hours with pupae bred from females maintained in the laboratory at constant temperature (Bursell, 1960). The reason for this difference was not investigated. Buxton (1955) indicated that further information on eclosion would be necessary for studies on the population dynamics of tsetse flies, and Dean & Wortham (in press) indicated its importance in current programmes on sterilisation. This paper presents results obtained from studies on the biological variability of pupae and the effects of gamma-radiation and temperature on emergence.

Methods

The term pupa in this paper refers to the fourth-instar larva within the puparium, which lasts for the first four days, and the true pupa up to the eclosion of the adult fly. Pupae of unknown ages, between recent larviposition and just prior to eclosion of the adult fly, were used in most of these tests. They were collected by field teams in the Zambezi Valley, Rhodesia, and flown to Salisbury where they were floated, immediately after arrival, in methylated spirits to remove the dead and parasitised pupae (Phelps,[1] pers. comm.). Pupae of known age used in some tests were bred from a colony maintained in the laboratory. All the pupae were stored in 8 × 8 × 11 in. wire mesh cages maintained at 25±2°C., 70 per cent. relative humidity and on a 12-hr. light cycle. The total emergence of male and female flies during the previous 24 hr. was recorded between 0800 and 0900 hr., while observations on diurnal emergence were made at half-hour intervals between 0600 and 1800 hr. on successive days. Records were kept of the number of runts, flies dying within a day or obviously deformed, associated with each batch of field-collected pupae. In the field trials, the pupae were held in similar cages and screened from direct solar radiation by a thatched grass roof. Temperature within the mass of pupae and adjacent air and relative humidity were noted in addition to the number of flies emerging at half-hour intervals between 0500 and 2300 hr. Samples of pupae from these field tests were held as controls in the laboratory.

The pupae were given dosages of gamma-rays from an Eldorado Cobalt 60 Teletherapy Unit at Salisbury's Central Hospital. They were held in fine cotton mesh bags and received a dose rate of about 105 rad/min. on a 15 cm.^{2} surface at 55 cm. below the source. The Cobalt room was maintained at 26°C. during irradiation and the pupae were transported to and from the laboratory in an insulated polystyrene box.

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Results and conclusions

Effects of environment

Biological variability of pupae collected in the field.—The homogeneity of the data for runts and live male and female emergence for batches of pupae regularly collected from the field during 1964–66 was tested by Chi-square analysis (Snedecor, 1961, pp. 197–199). There is a single rainy season in Rhodesia between November and April and the remaining months become increasingly arid. The coolest months occur between May and August and the hottest are October and November when the humidity is low. The analyses were made on the raw data but in this paper the proportions of live emergence, runts and males are expressed as percentages of the total number of pupae used in each sample. In Table I are shown the variations in total emergence obtained from untreated batches collected during the cool months May to August and the hotter months September to December. There were highly significant differences ($P=0{\cdot}001$) in the homogeneity of the batches, with a tendency in 1964 for there to be a lower emergence during the hotter months. To examine the association of low emergence with a large proportion of runts, the figures in Table I were used. The contributions to Chi-square were ranked, and the Spearman rank correlation coefficient (Snedecor, 1961, pp. 190–192) was calculated. The value found (0·0586) does not confirm any association of low emergence with large numbers of runts. A separate analysis indicated that proportionately there were no more male than female runts (Ayers,[2] unpublished).

The results in Table II cover the period September 1965 to April 1966, which contains no winter months. There was generally a higher emergence rate than in the preceding months (Table I) but again the samples of pupae were not homogeneous. However, there was a definite connection between low total emergence and the presence of runts in this analysis, with a Spearman rank correlation coefficient of 0·6285, which is significant at the 99 per cent. level.

Ellis[3] (pers. comm.) found that parasitism of tsetse pupae by *Mutillia* (Hymenoptera) and *Thyridanthrax* (Diptera) species increases during the hot summer months, and suggested that a high proportion of dead or parasitised pupae collected from flotation in methylated spirits indicates a subsequent low emergence from the remaining pupae. Phelps (pers. comm.) also has demonstrated that the size of the field pupae and subsequent adult tsetse decreases from June until the start of the rains in November. This decrease in fly size does not necessarily mean less viable pupae because at this time temperatures are increasing and pupal periods are short so that small size and small fat reserves may not be a disadvantage. However, results indicate that the quality of successive batches of pupae vary, and that generally they are not so viable at the end of the dry season.

Eclosion from laboratory-bred pupae during 1964–66 varied between 54·2 and 100 per cent. (mean—75·5 per cent.) in 37 samples ranging from 10 to 52 pupae. Thus, the variations in viability between samples of wild pupae may not have been entirely due to field conditions. Dean & Wortham (in press) obtained a mean eclosion rate of 88 per cent. compared with the 87 and 89 per cent. for *G. morsitans* obtained by Potts (1933, 1958) and the 83 per cent. for *G. palpalis* (R.-D.) (Geigy, 1948).

Diurnal emergence.—The diurnal emergence of flies from field-collected pupae exposed to different conditions was analysed by means of Chi-square tests. Under standard laboratory conditions, few flies emerged during the dark hours between 1800 and 0600 hr. or from 0600 to 1030 hr. (fig. 1, A). Eclosion significantly increased to a peak between 1400 and 1730 hr. ($P=0{\cdot}001$) when

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TABLE I. *Analysis with Chi-square for variations in total emergence of* G. morsitans, *and percentage of males and runts from untreated pupae collected between May 1964 and September 1965*

	Emergence (%)	Contribution to χ^2	Males (%)	Contribution to χ^2	Runts (♂, ♀) among emerging flies (%)	Contribution to χ^2	Total no. of pupae
1964							
May	75·71	18·28	48·65	0·00	7·82	1·13	980
June	69·03	4·42	48·69	0·00	1·84	40·19	935
July	61·33	24·26	49·08	0·09	6·22	11·74	2,123
Aug.	46·78	293·69	53·51	7·47	7·52	1·95	1,064
Sept.	54·53	102·57	49·21	0·10	5·84	10·43	1,632
Nov.	44·16	704·34	44·38	10·37	17·57	129·07	3,184
Dec.	55·53	83·51	46·19	2·17	14·11	28·99	2,375
1965							
May	67·83	2·22	48·37	0·06	6·02	16·66	2,353
June	85·49	165·79	50·12	0·72	5·89	9·84	1,013
July I	66·70	0·13	50·03	1·28	8·90	0·00	2,610
July II	77·74	105·13	49·58	0·46	9·05	0·03	1,819
July III	69·05	6·85	46·58	2·59	15·10	69·15	2,139
Aug.	90·84	184·52	50·08	0·49	4·64	14·13	688
Sept. I	79·54	142·75	47·61	0·67	7·05	6·36	1,838
Sept. II	87·70	460·36	50·05	1·50	8·73	0·09	890
	Mean 66·38	Sum 2318·82***	Mean 48·62	Sum 27·97**	Mean 8·93	Sum 339·75***	25,643

Significance: ** at 0·5 per cent. level, *** at 0·1 per cent. level.

TABLE II. *Analysis with Chi-square for variations in total emergence of* G. morsitans *and percentage of males and runts from untreated pupae collected between late September 1965 and April 1966*

	Emergence (%)	Contribution to χ^2	Males (%)	Contribution to χ^2	Runts (♂, ♀) among emerging flies (%)	Contribution to χ^2	Total no. of pupae
1965							
Sept. I	79·38	60·72	47·70	0·82	7·06	4·00	1,459
Sept. II	75·30	22·18	53·48	16·71	8·73	0·11	1,982
Sept. III	54·57	242·99	45·11	5·68	11·60	12·09	991
Oct. I	74·36	18·65	41·54	12·34	8·41	0·04	2,747
Oct. II	77·73	71·79	48·37	0·28	5·29	0·18	2,642
Oct. III	64·32	92·53	51·28	5·97	11·84	37·09	2,627
Nov.	50·05	213·48	46·65	0·99	13·18	13·75	493
Dec.	72·49	0·37	47·85	0·13	6·93	0·92	303
1966							
Jan.	73·09	1·16	49·46	0·06	6·54	2·32	459
Feb. I	71·19	0·00	48·41	0·01	4·76	2·28	126
Feb. II	72·22	0·11	51·05	0·27	10·49	0·71	143
Feb. III	77·53	1·77	49·28	0·00	4·35	1·54	69
Feb. IV	67·80	0·64	52·50	0·42	11·25	0·76	80
Mar. I	77·06	8·69	50·89	0·63	2·29	19·57	393
Mar. II	77·73	39·47	48·23	0·15	4·10	21·94	377
Mar. III	75·29	9·33	48·57	0·04	6·44	4·64	838
Apr. I	72·72	0·92	49·91	0·23	5·57	6·24	557
Apr. II	60·98	10·33	55·20	1·99	0·80	0·04	125
	Mean 71·14	Sum 795·13***	Mean 48·89	Sum 46·73***	Mean 8·52	Sum 128·31***	16,911

*** Significant at 0·1 per cent. level.

50 per cent. of the flies emerged, and then rapidly dropped to zero. The presence or absence of light in these tests did not appear to influence emergence as there was a similar pattern when pupae were held continuously in the dark except for brief periods of subdued light every half-hour when the flies were collected (fig. 1, B). It is possible that these very short periods of illumination might have been enough to change any response to a dark environment into the normal response to a light environment. However, it seems unlikely that light could penetrate the puparial wall and elicit any response. Phelps and Jackson (pers. comm.) found that continuous periods of dark replacing the normal light cycle do not affect the diurnal pattern of eclosion.

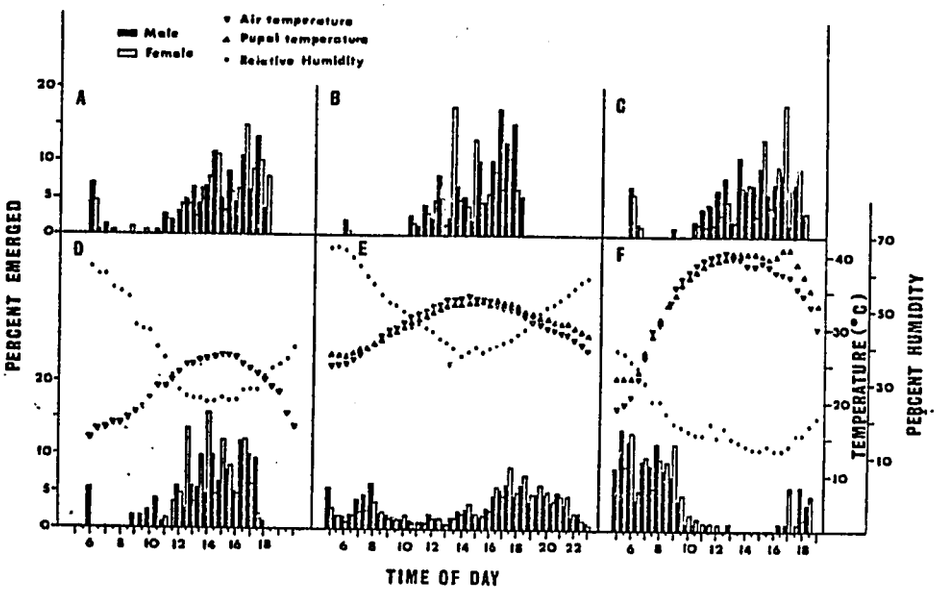

Fig. 1.—Diurnal emergence of males and females of *G. morsitans* from pupae collected in the field and exposed to (A) constant laboratory conditions, (B) the absence of light, (C) 15,000 rads, (D–F) increasing ranges of ambient temperature in the field.

There were significant differences between the field trials and the laboratory controls. Pupae held under field conditions where air temperatures were lower and more variable than in the laboratory, varying from 14·5°C. to 26°C., showed a peak of adult emergence between midday and 1730 hr. (fig. 1, D). Flies did not start to appear until temperatures exceeded 15°C., and the highest numbers were directly correlated with the hottest period during the day. The humidity ranged from 59 per cent. at dawn to 23 per cent. at 1400 hr. This pattern of eclosion was comparable to that obtained from the laboratory controls (fig. 1, A).

Flies emerged throughout most of the 24 hr. when air temperatures ranged between 24·5° and 34°C. during the daylight hours (fig. 1, E). There was a significant increase in the numbers of both sexes appearing between 1800 and 0600 hr. ($P=0{\cdot}001$), and a decrease in the morning and afternoon emergences. A small peak occurred in the early morning (0700–0830 hr.), and there was a larger peak in the late afternoon and evening (1600–2200 hr.). Emergence generally declined when temperatures rose above about 27°C., and increased again as the temperature began to fall. The lower temperatures ($<$ 20°C.) after midnight apparently inhibited eclosion and few flies appeared between 2300 and

0500 hr. This pattern was inversely correlated with temperature, and contrasted sharply with the laboratory control (A) and with the field trial (D) where temperatures rarely exceeded 25°C. The humidity was higher than in series D and ranged from a mean of 69 per cent. at 0530 hr. to a minimum of 37 per cent. at 1400 hr.

In fig. 1, F an extreme change is shown in the emergence pattern with higher ambient temperatures than in series E. There was a significantly dominant peak of fly eclosion between 0500 and 0930 hr. ($P = 0{\cdot}001$), but the small peak in the late afternoon was associated with significantly fewer emergences than were recorded at lower temperatures ($P = 0{\cdot}001$). Large numbers of flies again appeared during the night. Emergence was inversely correlated with temperatures exceeding 25°C. Humidities were lower than in the other trials, ranging from 39 per cent. at 0500 to 12 per cent. at 1500 hr. However, it appears unlikely that eclosion and humidity recorded in the three field trials are related to each other. Bursell (1959) reported that flies emerged predominantly between 1500 and 1800 hr. in the field, an observation that agrees with the results obtained in series D where the temperatures did not exceed 26°C.

Temperatures recorded within the mass of individual pupae in the field tests were initially slightly higher than the surrounding air temperatures until about 0830 hr. The air temperatures became higher and exceeded the pupal temperature by up to 7·5°C. at 1630 hr. (fig. 1, E & F). The pupae lost heat, and at a slower rate than the air, only after air temperatures had been falling for one to two hours.

The reason for eclosion from field collected pupae held under constant laboratory conditions occurring predominantly in the afternoon has not yet been investigated. Bursell (1960) reported that eclosion from laboratory-reared pupae occurred at all hours. However, in similar tests Phelps and Jackson (pers. comm.) found a peak during the afternoon and were unable to demonstrate a correlation between times of larviposition and eclosion. Diurnal emergence in the field trials appeared to be correlated with the length of the period during the day when temperatures rose above 17·5°C. and were below 27–33°C., and eclosion was supressed above 37·7°C. (100°F.). In series F, temperatures exceeded 37·7°C. for over six hours on the last two days of the trial and emergence declined to zero by the third day, and all the pupae were found to be dead. Glasgow (1963) concluded that the most favourable temperature for the adult tsetse is about 24°C., and that departures from this cause various ill effects which increase with the extent of the departure. Adults of *G. morsitans orientalis* Vanderplank are killed by a five-minute exposure to 46°C. and a three-hour exposure to 40°C. (Jack, 1939). Other species of *Glossina* show slightly different reactions to high temperature but are killed at various exposures above 40°C. Humidity could not be correlated with emergence and its effect was probably negligible in these trials, but Bursell (1957*a*, 1957*b*, 1959) has demonstrated that it is critical for the survival of both pupae and adults.

According to Phelps (unpublished) larviposition at the end of the dry season occurs predominantly in ant-bear holes where temperatures and humidities are less severe than those of the outside air. Thus, pupae and emerged adults are unlikely to experience the extreme temperatures associated with series F (fig. 1), though those in series D and E may be fairly common. Vanderplank (1948) and Jack & Williams (1937) showed that adult *G. pallidipes* Aust. and *G. morsitans orientalis* became negatively phototrophic when temperatures exceeded 32° and 30°C., respectively, while Jack (1939) working with *G. morsitans* reported a reversal of the light response at 40°C. in diffuse light and at 35°C. in very strong light. Thus, flies emerging in ant-bear holes are unlikely to leave them for the less favourable environment outside until there is a decrease in temperature.

Effect of gamma-radiation

Dean & Wortham (in press) demonstrated that the effective pupal mortality of field pupae of unknown age due to gamma-radiation increased with an increase in dosage, and was greater during the hotter months (September–December) than in cool months (May–August). This indicated that cytoplasmic damage due to radiation may be more extensive, or less easily repaired, when the pupae are less viable during the hot months at the end of the dry season. There were no indications that the proportions of young and old pupae varied between batches.

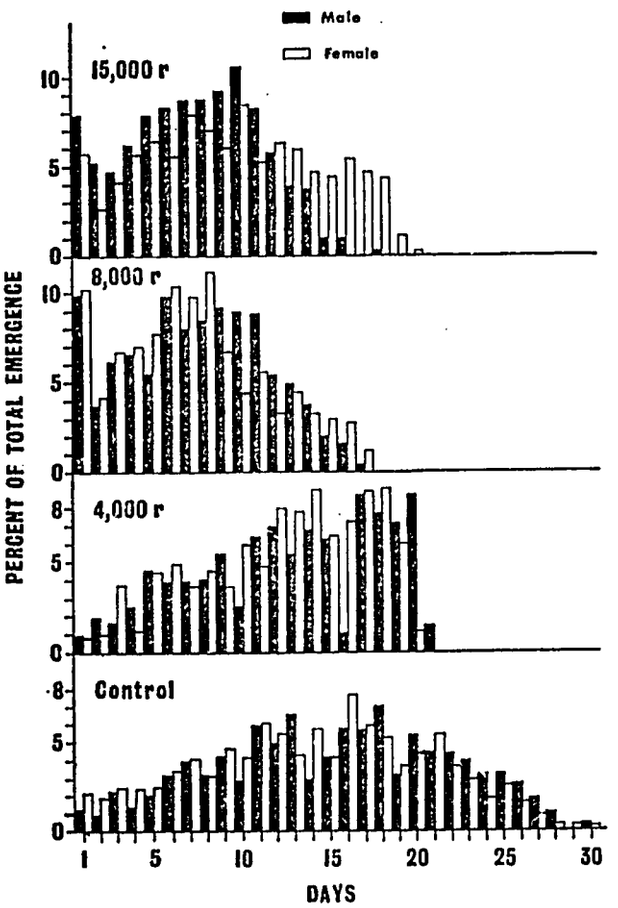

Fig. 2.—Daily emergence of males and females of *G. morsitans* from batches of field pupae held under constant laboratory conditions after dosages of 0, 4,000, 8,000 and 15,000 rads.

The pattern of male and female emergence from treated and untreated pupae over a 30-day period is shown in fig. 2. More female flies than males emerged from the untreated pupae during the first half of the period, while males predominated during the last week. Dosages of 4,000 rads given immediately after receiving the pupae terminated eclosion 21 days after treatment compared with

17 days after treatment with 8,000 rads. Higher dosages up to 18,000 rads did not shorten the period any further. However, the number of male flies emerging two days and eight days before the end of the total emergence period was reduced with dosages of 8,000 and 15,000 rads, respectively. Tests where the pupae were held for 11 days before irradiation with 8,000 rads produced an apparently normal emergence compared to the untreated controls (Dean, unpublished). Dosages above 4,000 rads increased the rate of eclosion during, and immediately after, irradiation while it was generally reduced during the next day. Thus, gamma-rays appeared to kill all of the youngest pupae, while the males remained sensitive longer than the females and were killed.

Pupae of known age, from recent larviposition to just prior to adult eclosion, were divided into two groups, one for treatment with 8,000 rads and the other to act as an untreated control. The emergence of male and female flies was checked daily, and pupal mortality was measured as the percentage of pupae held for 40 days that failed to produce flies. Abbott's correction (Finney, 1952) was applied in order to compensate for the natural mortality exhibited by parallel batches of untreated pupae. The percentage effective mortality due to irradiation was calculated from $\frac{P_{obs} - C_{obs}}{100 - C_{obs}} \times 100$, where P = per cent. mortality of irradiated pupae and C = per cent. mortality of untreated pupae. The same formula was used to adjust the percentages of males emerging from the treated pupae.

The effective mortality per cent. due to gamma-radiation from the batches irradiated between the 29th and 16th days after larviposition showed considerable variation (fig. 3), probably because the batches were not homogeneous even though the pupae were divided randomly. However, the individual mortalities during

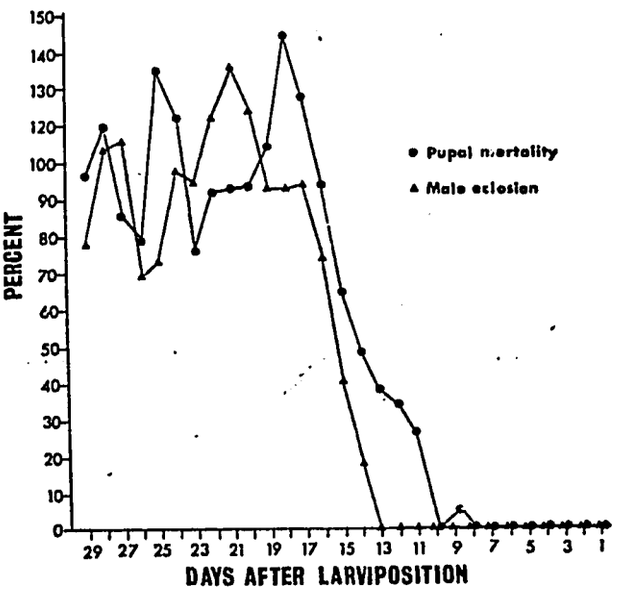

Fig. 3.—Per cent. effective pupal survival and per cent. effective emergence of male *G. morsitans* from pupae of known age given 8,000 rads during their first to 29th day after larviposition.

this period tended to cancel out and the mean did not differ significantly from the controls ($P=0{\cdot}8$). Pupal mortality sharply increased in batches irradiated within 15 days of larviposition and, except for one female fly, there was no emergence from pupae irradiated during the first ten days following larviposition.

The per cent. effective emergence of male flies from pupae irradiated between the 29th and 16th day after larviposition showed similar fluctuations, but an average of 98·2 per cent. of the males emerged during this period compared to the untreated controls. The proportion of emergent male flies from pupae irradiated between the 15th and 13th days declined rapidly to zero, and only a few females survived when 13- to 9-day-old pupae were irradiated. MacLeod (1957) concluded that blowfly pupae were more susceptible to gamma-radiation during the first third of their life. Dean & Wortham (in press) also found that survival of the adult tsetse flies was reduced with a decrease in the pupal age at the time of treatment.

Substantial amounts of water are produced by the oxidation of fat which constitutes the main food reserve of the tsetse pupa (Buxton & Lewis, 1934). Bursell (1958) showed that the third and fourth larval instars within the puparium last for the first four days after larviposition, and are characterised by a high rate of water loss through the supernumerary stigmata of the polypneustic lobes and through the puparial shell. During the true pupal stage, from the fifth day after larviposition, the rate of transpiration rapidly falls to a minimum on about the ninth day as the supernumerary stigmata are blocked by remnants of the third-instar tracheal apparatus. The rate of metabolism is greatest at the start and end of the pupal stage.

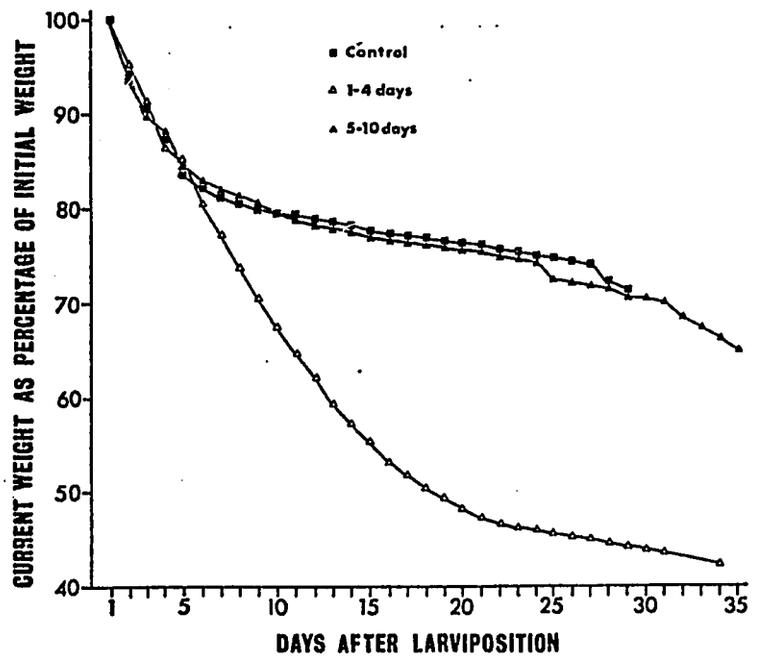

Fig. 4.—Mean rate of water loss from known-aged pupae of *G. morsitans* (a) untreated, and (b and c) given 8,000 rads during (b) the 1st to 4th days and (c) 5th to 10th days after larviposition.

The known-aged pupae were weighed within a day of larviposition and every day following until the first adult emerged. The daily weight loss exhibited by the untreated pupae was rapid during their first five days and was then reduced until the 29th day (fig. 4). Pupae irradiated between five and ten days after larviposition failed, with one exception, to produce any adult flies and their mean daily weight loss paralleled that obtained from the untreated controls. This indicated that these pupae were not killed immediately after irradiation and probably did not die until after the 30th day. Pupae irradiated during the first four days after deposition, and containing the third and fourth instars, showed a similar weight loss for the first five days but the loss continued at the same rate for about 15 days. Bursell (1958) estimated that pupae of *G. morsitans* can tolerate a loss of up to 29 per cent. of their original weight, which is equal to 40 per cent. of the amount of water originally present in the pupae, without loss of viability. The very young pupae (1–4 days old) suffered this loss within a mean of nine days after larviposition, or within five and eight days after treatment. The unblocked supernumerary stigmata are responsible for about 40 per cent. of all water loss in both dead and live pupae (Bursell, 1958) and it appears likely that irradiation of the very young pupae prevented larval moulting and blocking of these stigmata. Thus, death could have occurred either soon after treatment or well before the 30th day.

Diurnal emergence from mixed-aged field pupae given 15,000 rads was also investigated (fig. 1, C). The pattern obtained, compared to that observed with the untreated pupae, appeared to be unaffected by the treatment. However, significantly more females appeared in the afternoon ($P=0{\cdot}01$) and this may be associated with the male's greater sensitivity to, and mortality from, gamma-radiation.

Summary

Observations on biological variability of pupae of *G. morsitans* Westw. collected in the field, and effects on eclosion of the adult fly due to temperature, light and gamma-radiation are reported.

The homogeneity of eclosion from wild pupae varied during the year owing to variations in pupal viability. Emergence was lower in the warmer months September to December than in the cooler ones, May to August, and in one season low eclosion rates were connected with a high proportion of runts, although another analysis revealed no correlation.

Gamma-radiation reduced eclosion by killing all pupae treated during their first ten days after larviposition. Mortality of male pupae was increased by irradiation between the 15th and 13th day of pupal life, while eclosion was apparently normal with treatments given between the 16th and 29th day. Weight losses indicated that five- to ten-day-old pupae possibly did not die before the 30th day after larviposition while younger pupae containing fourth-instar larvae at the time of treatment were killed either immediately or by the 15th day.

Diurnal emergence from wild pupae in the laboratory showed a peak during the afternoon (1400–1730 hr.) which was not affected by light or gamma-radiation. In the field, eclosion occurred primarily between 15° and 27°C. and was apparently inhibited by higher and lower temperatures. Relative humidity did not appear to be involved in the timing of emergence.

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