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The Influence of Maternal Physiology on the Incidence of Diapause

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THE INFLUENCE OF MATERNAL PHYSIOLOGY ON THE INCIDENCE OF DIAPAUSE

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1. Introduction

During the study of the biology of two hymenopterous parasites which were being bred with a view to their utilization as biological control agents, certain interesting facts were observed with regard to the occurrence of diapause. It was found that the age of the parent female when an egg was laid had some influence on the tendencies of the larval progeny to enter diapause. This effect has already been briefly described (Simmonds 1946). Further, it was found that variations in the diet and temperature of development of the parent female had marked effects on her progeny in the same respect.

Observations on the occurrence of diapause in many different species are legion, and it is not intended to enumerate these or to discuss in detail the manner in which each example may possibly be correlated with the experimental data obtained here. Various aspects of diapause and numerous examples occurring in the literature have been discussed by Cousin (1932) and Wigglesworth (1939), and examples occurring in the parasitic Hymenoptera by Flanders (1944).

The term 'diapause' has been used with different meanings by various authors, and it is necessary at the outset to be clear as to the meaning ascribed to it in this paper.

The term diapause was originally applied by Wheeler (1893) to the phase in the embryological development of various insects which intervenes between anatrepsis and katatrepsis. These latter are respectively the movements of the rudimentary embryo from the ventral to the dorsal side of the egg and vice versa. At diapause the embryo is motionless between the two oscillatory phases of blastokinesis. Henneguy (1904) employs the term in this sense, but also uses it to designate an arrest in growth occurring at any stage during development, and he distinguishes between embryonic, larval and pupal diapause. Henneguy has thus taken a very precisely defined term of Wheeler's and given it an entirely different and rather vague meaning. Since then the term diapause has been used loosely to indicate a condition in insect development where growth processes or maturation of tissue have stopped, or have been reduced to a very low level. Often in applying the term little consideration has been given to the exact nature of this reduction in developmental activity or to the causes which have induced it. However, some authors (e.g. Shelford 1929) use the term in a somewhat more restricted sense, and limit it to a fairly definite type of arrest in development. This may occur at any stage in the life history, but with an individual species the arrest occurs usually at one definite invariable stage. It is usually of such a nature as to be distinguishable from the cessation or reduction of growth that occurs when some stage of the insect is removed from the range of conditions over which development will take place. In the latter case the arrest is only temporary, is caused by the immediate surrounding environment, and on return to suitable conditions normal development proceeds almost immediately. Diapause, as the term will be used in this paper, signifies a different state, that in which a reduction of growth processes or maturation occurs which is not necessarily caused by immediate environmental influences, does not depend for its continuance on unsuitable conditions, and is not easily or quickly altered by change to a more favourable environment. However, once the state of diapause comes to an end normal growth and development are resumed.

This definition is still not perfect, and it is possible that, from the very nature of the physiological processes involved in diapause, no exact division can be made between true diapause and, on the one hand, temporary and readily reversible arrests in development brought about by changes in the environment, and, on the other hand, the permanent cessation of growth and possible alteration of the course of development which result in the production of weakly individuals, teratological specimens [e.g. prothetely and metathetely (Singh Pruthi 1924)], or of definite castes within the same species. Each case must be carefully studied (as has been done by Kevan (1944) with *Diatraea lineolata* Wlk.) before a decision can be made as to whether an arrest in development should be considered a state of true diapause.

It is thus difficult to set exact limits to the state to which the term diapause should be applied. There is, too, a wide variety of factors which tend to induce this condition—cold, heat, desiccation, excess humidity, deficient nutrition, excess nutrition (Baumberger 1914), asphyxiation, etc. In fact, any wide departure from the optimum conditions for a particular stage of a given species may induce diapause at that time, or, more usually, at a later period in development.

The possibility has been pointed out by Cousin (1932) that abnormal conditions acting on the parent may be an underlying cause of diapause in the progeny, weakly parents producing weakly offspring more sensitive to an unfavourable environment, with higher than average mortality, and with a greater proportion of individuals going into diapause. This she has shown for *Lucilia*, and it has also been seen to occur with the single generation a year and two generations a year strains of *Pyrausta nubilalis* Hbn. (Babcock 1927). According to many authors (e.g. Pictet 1913; Heller 1926; Babcock 1927; Uvarov 1928, 1929) there is a definite genetical control of diapause and an inborn cyclical or seasonal rhythm in its occurrence which is not altogether obscured when the species concerned is bred for several generations under constant environmental conditions. However, more critical experimental work in many cases has indicated that this rhythm is not so fixed as was formerly supposed.

The results given below certainly indicate no obvious or simple genetical basis for diapause in the two species investigated, but rather that this state is caused by physiological disturbances often occurring at a very early stage in development, and which later entail a complete breakdown in the regular sequence of growth processes.

2. Experimental

Spalangia drosophilae Ashm.

Whilst studying the parasites of the frit-fly in North America *Spalangia drosophilae* Ashm. was reared as an ectoparasite of the pupa of *Oscinella frit* (L.). Apart from investigations on diapause, extensive experimental studies were made with this species to determine its biological constants, the power of avoidance of superparasitism by ovipositing females, etc., and these results will be published in the near future, together with a detailed account of the life history of the parasite.

The species was successfully bred in large numbers using puparia of *Drosophila melanogaster* Mg. as hosts (Simmonds 1944*b*), and it is with this host that the present results have been obtained. *Spalangia* females on emergence begin to oviposit immediately if host puparia are available. This occurs whether mating has taken place or not, unfertilized eggs producing male progeny. The eggs are laid on the outside of the host pupa between its surface and the enclosing puparial wall, after the host has been paralyzed by means of stings inflicted by the ovipositor of the female. The female feeds on the host body fluids exuding from the punctures made at stinging. On hatching the parasite larva feeds ectoparasitically on the host pupa, passing through three larval stages, at the end of which the host is entirely consumed.

When diapause occurs it takes place in this full-grown larval stage; the parasite larva either continues development to pupa and adult, or else enters a state of true diapause and remains as a full-grown larva for several months before development proceeds. This state of diapause was found to occur both in the field and in the laboratory. In the field 26·4 % of the total material collected in 1942 was in diapause, and it was found that approximately the same percentage of larvae entered diapause in both the early and the later parts of the seasonal period of parasitism by *Spalangia*. It was not an effect that could be correlated with the onset of colder weather in the autumn. In the laboratory the percentage of larvae entering diapause in the general rearing at 75° F was approximately the same. However, during investigations on the oviposition rate, etc., of individual females it was found that individual 'families' (here meaning the total progeny of an individual female) bred and reared at the same temperature differed considerably with regard to the proportion of the progeny entering diapause. In some, all the eggs laid produced larvae which went into diapause; in others all, or nearly all, the progeny emerged with no arrest in development. These differences occurred with females that had been bred, had emerged, and were laying under identical constant conditions.

This suggested that there might be a genetical basis for the occurrence of diapause in *Spalangia*, and an effort was made to demonstrate this. Individuals from a family in which all the progeny had entered diapause were allowed to emerge at 75° F, and from these single females, both mated and unmated, were selected. These were placed individually in $4\frac{1}{2} \times 1$ in. glass vials, stoppered with a cork bearing a pad of damp cotton-wool and a raisin, which were changed at frequent intervals before they became mouldy. Into each vial 25 day-old *Drosophila* puparia were placed daily, the previous day's puparia being removed, and all the vials were kept at a constant temperature of 75° F.

The relative humidity of the exterior was also kept constant, but the humidity inside the vials must have been consistently high, since in each closed vial was a damp cotton-wool pad. Each day's puparia from each vial were kept separately at 75° F, and the sex and date of emergence of all progeny and the numbers of larvae in diapause from each day's oviposition were recorded. Similar experiments were then started using individuals (out of diapause) from a family in which only 25·5 % of the progeny had entered diapause. In both the above experiments brother-sister matings were used, and in a third set cross-mated individual females of both families were used.

From these results it was apparent that there was no definite simple genetical basis for the occurrence of diapause, the number of families with high and low percentage of diapause being similar in all three sets.

However, an interesting fact did emerge, namely, that the age of the parent female when an egg is laid has some bearing on the tendency of the larva hatching from it to go into diapause. To illustrate this the results of ten of the above experiments are shown in table 1 and figure 1. Only the averages from the ten experiments are given, but each individual family shows the same trend, namely, that the percentage of progeny entering diapause increases with the age of the parent female at the time of oviposition. Contemporaneous with this increase are variations in oviposition rate, developmental time of emergent progeny, and sex ratio of emergents. These various factors will be discussed fully below, but it became immediately obvious that the eggs laid by a female throughout her life were by no means uniform in their potentialities with regard to their subsequent development.

It has been observed with many species that temperature is an important factor in determining diapause, and that, in general, low temperatures during the whole or certain critical phases of development favour diapause, while moderately high temperatures favour continuous development and emergence of progeny. Many results have been obtained in most orders of insects along these lines. However, it was found, as mentioned above, that there seems to be a certain amount of 'predetermination' in the egg with respect to diapause, and it is therefore possible that the temperature at which the eggs themselves develop within the female is an important factor in determining diapause in the fully grown larvae. Hence not only the temperature of larval development was varied, but also the

TABLE 1. VARIATION WITH AGE OF PARENT FEMALE *SPALANGIA* IN OVIPOSITION RATE, NUMBERS OF PROGENY GOING INTO DIAPAUSE, ETC., AT 75° F

age of female in days	1	2	3	4	5	6	7	8	9
eggs per female per day	10·0	6·9	7·0	7·3	8·7	7·4	8·9	6·8	6·2
percentage larvae in diapause	20·0	22·2	18·6	30·1	32·2	39·2	62·9	75·0	62·9
percentage females in emergents	40·0	44·4	52·6	51·0	45·8	33·3	18·2	35·3	17·4
average developmental time ♂	22·89	23·52	24·11	24·20	24·28	24·80	24·81	24·82	25·21
♀	23·92	25·25	25·50	25·81	25·89	26·33	26·50	27·00	27·00

age of female in days	10	11	12	13	14	15	16	17
eggs per female per day	6·1	6·5	5·2	4·9	4·5	4·7	5·0	4·2
percentage larvae in diapause	82·0	83·1	88·5	85·7	91·1	87·3	86·0	78·6
percentage females in emergents	—	9·1	—	—	—	—	14·3	33·3
average developmental time ♂	24·82	23·60	22·33	22·40	23·00	24·32	24·33	22·37
♀	—	25·00	—	—	—	—	27·00	26·33

age of female in days	18	19	20	21	22	23	24	25
eggs per female per day	4·9	4·3	3·8	4·3	3·9	4·1	3·7	3·4
percentage larvae in diapause	89·8	79·1	89·5	90·7	97·4	82·9	97·3	97·1
percentage females in emergents	—	11·1	25·0	—	—	—	—	—
average developmental time ♂	23·00	23·00	23·00	24·33	24·00	25·00	—	—
♀	—	26·00	27·00	—	—	—	—	—

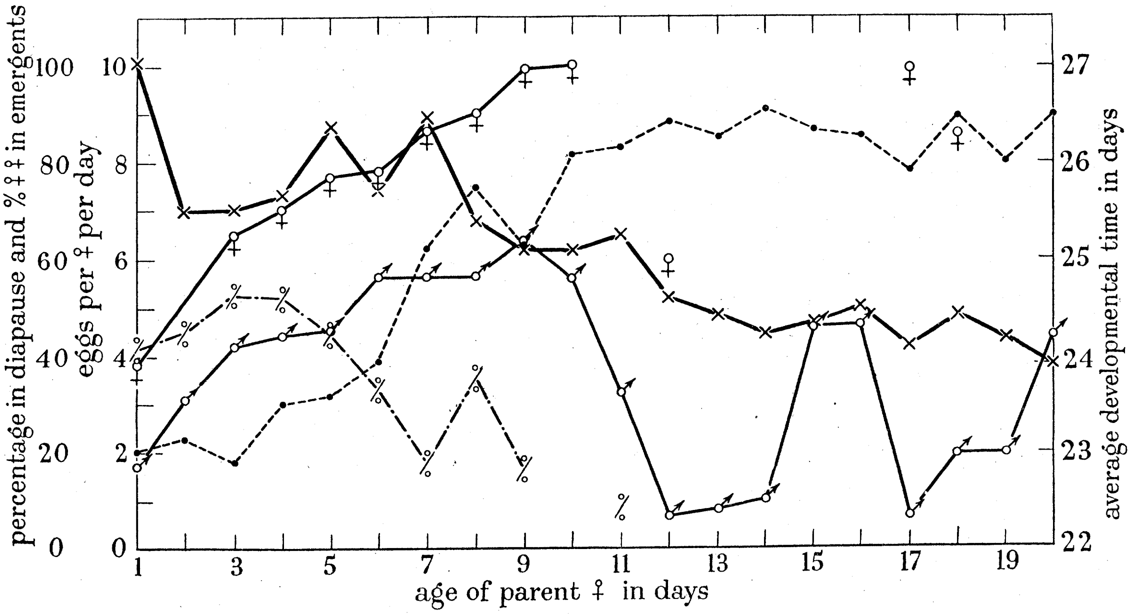

FIGURE 1. Variation with age of parent female *Spalangia* in oviposition rate, numbers of progeny going into diapause, developmental time and sex ratio of emergents (75° F).

×——× Oviposition rate: eggs per female per day. ---- Percentage of larvae going into diapause. ♂——♂, ♀——♀ Average developmental times of emergent progeny. %-·-·-·-% Percentage of females in emergent progeny.

temperature at which the females had been reared and kept prior to oviposition. A whole series of results was obtained using the experimental technique described above with individual females ovipositing in $4\frac{1}{2} \times 1$ in. glass vials. Females reared and emerging at 85°, 75° and 70° F were allowed to oviposit at the same or different temperatures from that at which they had themselves been reared. These experiments and their results are described below.

(*a*) *General*

As a preliminary to the detailed day by day analysis of the oviposition of individual females, it is perhaps as well to obtain a general impression of the effect of temperature on the progeny of *Spalangia* as a whole, results such as are usually obtained in investigations of the effect of temperature on diapause. In this section three cases will be investigated: first, that where the female oviposits at the same temperature at which she herself was reared; secondly, that in which she oviposits at a different temperature; and thirdly, that in which, at a point during oviposition, the temperature is changed. The sum total of these results are given in table 2.

(i) *Oviposition with no change of temperature on emergence*

In this case the effect is seen of a steady temperature throughout the life of the moth and her progeny. Table 2 shows that 83°, 75° and 70° F during rearing, produce 31·1, 88·3 and 100·0 % respectively of progeny entering diapause. Thus the effect of temperature in this case is quite simple—a high temperature causes a greater proportion of the larvae to develop without an arrest in development. The results are consistent with those found for many other species.

TABLE 2. GENERAL EFFECT OF TEMPERATURE AND TEMPERATURE CHANGES ON THE BIOLOGICAL CHARACTERISTICS AND PROGENY OF *SPALANGIA*. ALL EGGS LAID THROUGHOUT LIFE OF FEMALE CONSIDERED TOGETHER

temperature group (°F)	length of life of ♀	pre-oviposition period	post-oviposition period	laying period	total eggs	progeny			diapause	% diapause	average developmental time	
						♂	♀	%♀			♂	♀
83–83	20·9	—	4·4	16·5	111·1	36·3	39·3	52·0	35·6	31·1	15·82	17·2
83–75	31·2	0·1	5·2	25·9	117·1	15·8	12·2	43·6	89·1	76·1	24·53	24·3
83–70	42·6	—	6·8	35·8	111·5	1·5	0·9	38·5	109·1	97·8	26·44	30·5
75–83	20·9	—	2·9	18·0	130·6	46·3	76·4	62·3	7·4	5·7	16·06	17·0
75–75	41·5	—	5·9	35·6	142·8	6·6	10·1	60·4	126·2	88·3	24·01	25·7
75–70	46·3	—	4·7	41·7	136·7	16·3	1·3	5·8	119·0	87·0	27·83	35·7
70–83	18·0	0·67	4·3	13·3	116·7	112·7	—	—	4·0	3·4	15·64	—
70–75	28·0	—	1·0	27·0	137·5	86·5	38·0	30·5	13·0	9·5	23·71	23·84
70–70	100 % in diapause in this temperature group											

(ii) *Changing temperatures*

A further analysis of the effect of temperature on diapause may be made by making the temperature at which a female lays her eggs differ from that at which she herself was reared and at which she emerged. In this way it was hoped to determine whether the temperature at which the gonads developed and the general physiology of the female prior to oviposition had any influence on the potentialities of her progeny with regard to diapause. For this purpose females bred at 83°, 75° and 70° F were removed immediately on emergence, placed at a different temperature, and supplied daily with hosts in the usual way. From table 2 the results of this can be seen, and it is obvious that here is an effect of temperature different from that when it is constant over the life of both mother and progeny. When the temperature is constant at 83° F for the rearing of the mother and her progeny, 31·1 % of the latter enter a state of diapause. However, if the mothers are bred at 75° F and then allowed to oviposit at the higher temperature of 83° F only 5·7 % of their progeny enter diapause.

If the mothers are transferred from 70° to 83° F the figure is only 3·4 %. Thus, even though the temperature at which the progeny develop is the same in the three cases, the proportion of progeny entering diapause is decreased when the temperature at which the females oviposit is higher than that at which they themselves were bred. This is seen, too, in comparing the experiments in which females are reared and oviposit at 75° F (diapause 88·3 %) with those at which females reared at 70° F oviposit at 75° F (diapause 9·5 %).

In these general results there is no striking effect on the tendencies towards diapause caused by *decreasing* the temperature on emergence of the females. The tendencies of their progeny to enter diapause are not strikingly different from those of larvae from females emerging at the same constant temperature as the subsequent rearings.

Thus it is seen that raising the temperature at the time of emergence of a female decreases the proportion of her progeny entering diapause below that usual for progeny from mothers bred at and emerging at this higher temperature. The change of temperature seems to give an added stimulus to the eggs, decreasing the possibility of subsequent arrest in development.

(iii) *Changing the temperature during oviposition*

In connexion with the results obtained in the next section experiments were set up where females which were reared and emerged at 83° F were then put at 70° F for oviposition, and after 15 days placed again at 83° F. Considering these results in a general way in line with those discussed above, of the progeny reared at 70° F from eggs laid in the first 15 days of the females' lives, 100 % went into diapause, and the subsequent raise of temperature to 83° F reduced this figure to 62·7 %. Thus, raising the temperature in the middle of the oviposition period does not have as marked an effect as the same change on emergence, where females raised from 70 to 83° F produce only 3·4 % diapause in their progeny.

(*b*) *Variations with the age of the ovipositing female*

Since each day's oviposition of each individual female was kept separate throughout these experiments, and the dates of emergence and numbers going into diapause recorded separately, it was possible to investigate any variation in the tendencies of progeny to enter diapause that occurred with ageing of the female. As stated above it became immediately apparent when rearing individual females and their progeny at a constant temperature of 75° F that eggs laid in the early part of the life of the female showed less tendency to produce larvae going into diapause than those laid at the end of the oviposition period. This is seen clearly in tables 1 and 3 and figures 1 and 2.

Similar results for the other temperature combinations were obtained. All the eggs laid by all the females on the first day after emergence were added together, and also the numbers of adults emerging from these eggs and the numbers of larvae entering diapause. The total of the second day's ovipositions were treated similarly, and so on. Thus table 3 and figure 2 give generalized figures for the variation with age of the parent in numbers entering diapause, developmental time, etc., of progeny from eggs laid by a number of females in each group.

From these figures it is obvious that effects of temperature on the tendency of an individual to enter diapause are not confined to a direct effect during larval development, but that the

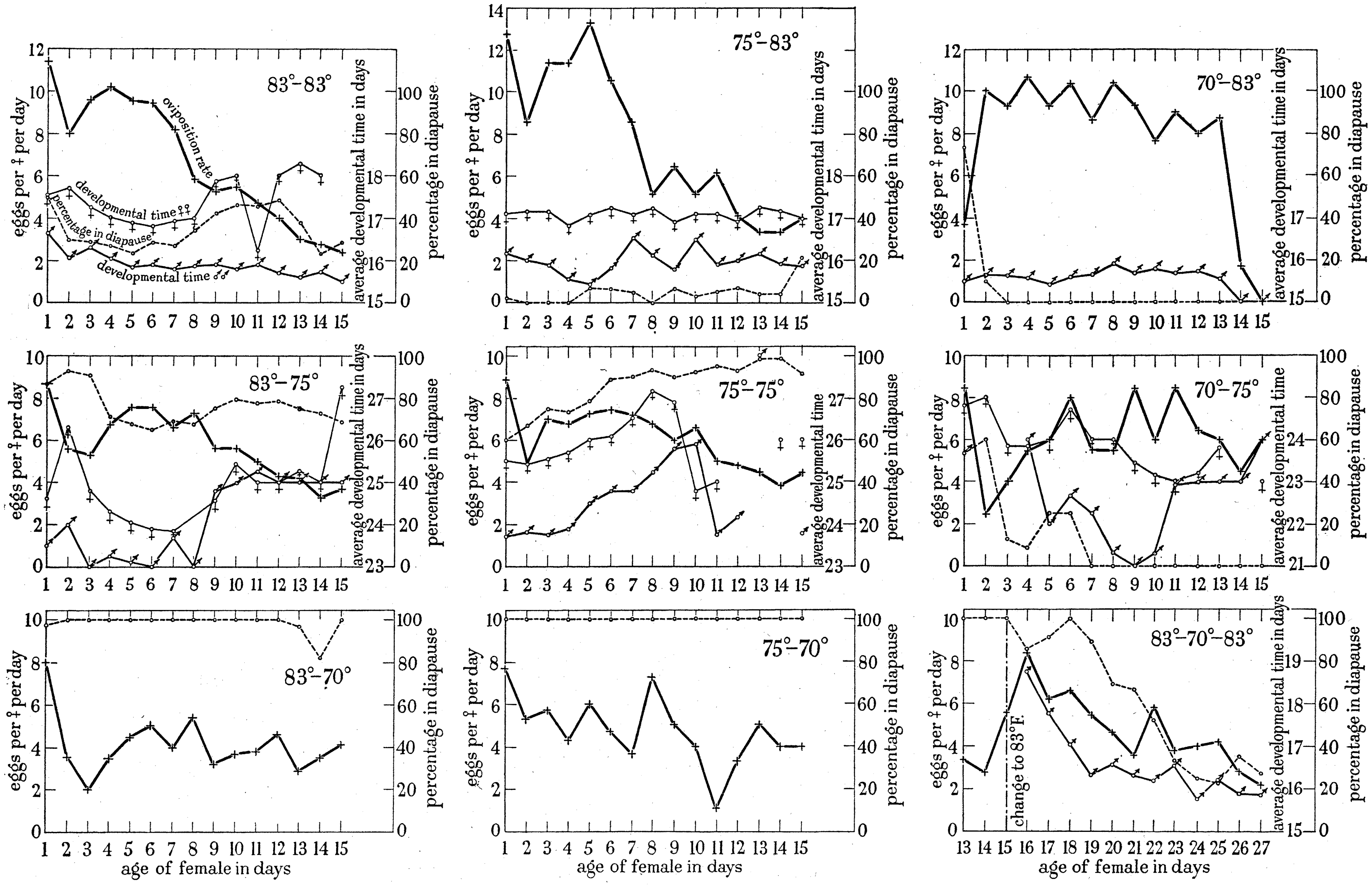

FIGURE 2. Variation with age of parent female *Spalangia* in the oviposition rate, percentage of progeny going into diapause and the developmental time of the emergent progeny at different temperatures. Parent females developing at 70°, 75° and 83° F ovipositing at all three temperatures. First temperature given is that at which parent female developed, the second that at which eggs were laid and progeny developed. Temperature change occurred at time of emergence of parent female.

×——× Oviposition rate: eggs per female per day. ---- Percentage of larvae going into diapause.
♂——♂, ♀——♀ Average developmental time of emergent progeny.

TABLE 3. VARIATION OF OVIPOSITION RATE, PROPORTION OF LARVAL PROGENY ENTER

83°–83° F group (23)

of t ♀ ys n aid	total eggs	eggs per ♀ per day	emerging progeny			progeny in diapause		average developmental time	
			♂	♀	%♀		%	♂	♀
	262	11·4	26	102	79·7	134	51·1	16·62	17·53
	184	8·0	24	105	81·4	55	29·9	16·17	17·70
	221	9·6	22	134	85·9	65	29·4	16·32	17·28
	235	10·2	35	135	79·4	65	27·7	16·06	17·04
	218	9·5	46	120	72·3	52	23·8	15·85	16·91
	217	9·4	42	113	72·9	62	28·6	15·93	16·86
	188	8·2	45	93	67·4	50	26·6	15·80	16·94
	135	5·9	51	38	42·7	46	34·1	15·88	17·03
	123	5·3	50	21	29·6	52	42·3	15·91	17·86
	127	5·5	53	16	23·2	58	45·7	15·79	18·00
	108	4·7	51	8	13·5	49	45·4	15·96	16·25
	92	4·0	44	3	6·4	45	48·9	15·73	18·00
	68	3·0	39	3	7·2	26	38·2	15·59	18·33
	65	2·8	45	5	10·0	15	23·1	15·73	18·00
	56	2·4	40	—	—	16	28·6	15·50	—

75°–83° F group (7)

of t ♀ ys n aid	total eggs	eggs per ♀ per day	emerging progeny			progeny in diapause		average developmental time	
			♂	♀	%♀		%	♂	♀
	89	12·7	16	71	81·6	2	2·2	16·19	17·10
	60	8·6	11	49	81·7	—	—	16·00	17·16
	79	11·3	16	63	79·7	—	—	15·88	17·14
	79	11·3	18	61	77·2	—	—	15·56	16·84
	93	13·3	15	71	82·6	7	7·5	15·47	17·07
	74	10·6	17	52	75·4	5	6·8	15·82	17·27
	60	8·6	23	34	59·6	3	5·0	16·52	17·09
	36	5·1	10	26	72·2	—	—	16·10	17·23
	45	6·4	15	27	64·3	3	6·7	15·80	16·93
	36	5·1	12	23	65·7	1	2·7	16·50	17·09
	43	6·1	18	22	55·0	3	5·5	15·89	17·09
	29	4·1	13	14	51·8	2	6·9	16·00	16·93
	23	3·3	18	4	18·2	1	4·3	16·17	17·25
	23	3·3	16	6	27·3	1	4·3	15·94	17·17
	28	4·0	16	6	27·3	6	21·4	15·87	17·00

70°–83° F group (3)

of t ♀ ys n aid	total eggs	eggs per ♀ per day	emerging progeny			progeny in diapause		average developmental time	
			♂	♀	%♀		%	♂	♀
	11	3·7	2	—	—	9	81·8	15·50	—
	30	10·0	27	—	—	3	10·0	15·63	—
	28	9·3	28	—	—	—	—	15·61	—
	32	10·7	32	—	—	—	—	15·59	—
	28	9·3	28	—	—	—	—	15·43	—
	31	10·3	31	—	—	—	—	15·58	—
	26	8·7	26	—	—	—	—	15·62	—
	31	10·3	31	—	—	—	—	15·90	—
	28	9·3	28	—	—	—	—	15·68	—
	23	7·7	23	—	—	—	—	15·78	—
	27	9·0	27	—	—	—	—	15·67	—
	24	8·0	24	—	—	—	—	15·69	—
	26	8·7	26	—	—	—	—	15·54	—
	5	1·7	5	—	—	—	—	15·00	—
	—	—	—	—	—	—	—	—	—

83

total eggs	eggs per ♀ per day	emerging p	
		♂	♀
157	8·7	4	16
100	5·6	1	6
96	5·3	3	6
123	6·8	16	20
137	7·6	12	32
138	7·6	10	38
121	6·7	6	31
131	7·3	19	23
102	5·7	14	12
103	5·7	14	7
90	5·0	15	5
78	4·3	10	6
75	4·2	12	7
60	3·3	13	3
67	3·7	17	4

75°

total eggs	eggs per ♀ per day	emerging pr	
		♂	♀
232	8·9	43	50
128	4·9	11	31
182	7·0	8	37
177	6·8	14	33
189	7·3	8	31
194	7·5	6	15
188	7·2	10	8
178	6·8	5	7
157	6·0	6	9
172	6·6	9	5
129	5·0	5	1
125	4·8	6	2
118	4·5	1	—
100	3·8	—	1
115	4·4	8	2

70

total eggs	eggs per ♀ per day	emerging pr	
		♂	♀
17	8·5	3	5
5	2·5	—	2
8	4·0	—	7
11	5·5	4	6
12	6·0	1	8
16	8·0	4	8
11	5·5	8	3
11	5·5	8	3
17	8·5	8	9
12	6·0	6	6
17	8·5	12	5
13	6·5	8	5
12	6·0	7	5
9	4·5	9	—
12	6·0	9	3

RING DIAPAUSE, AND AVERAGE DEVELOPMENTAL TIME OF EMERGENTS WITH THE AGE OF THE PARE

3°–75° F group (18)

rogeny	progeny in diapause		average developmental time	
%♀		%	♂	♀
80·0	137	87·3	23·50	24·50
85·7	93	93·0	24·00	26·33
66·7	87	90·6	23·00	24·83
55·6	87	70·7	23·25	24·30
72·7	93	67·9	23·08	24·03
79·2	90	65·2	23·00	23·87
83·8	84	69·4	23·66	23·84
54·8	89	67·9	23·00	24·22
46·2	76	74·5	24·71	24·58
33·3	82	79·6	25·00	25·43
25·0	70	77·8	25·27	25·00
37·5	62	79·5	25·00	25·00
36·8	56	74·7	25·00	25·29
18·8	44	73·3	25·00	25·00
19·0	46	68·7	25·00	27·25

83°–70° F group (11)

total eggs	eggs per ♀ per day	emerging progeny			progeny in diapause		a deve
		♂	♀	%♀		%	♂
88	8·0	1	1	50·0	86	97·7	—
40	3·6	—	—	—	40	100·0	—
22	2·0	—	—	—	22	100·0	—
39	3·5	—	—	—	39	100·0	—
50	4·5	—	—	—	50	100·0	—
55	5·0	—	—	—	55	100·0	—
44	4·0	—	—	—	44	100·0	—
59	5·4	—	—	—	59	100·0	—
35	3·2	—	—	—	35	100·0	—
41	3·7	—	—	—	41	100·0	—
42	3·8	—	—	—	42	100·0	—
51	4·6	—	—	—	51	100·0	—
32	2·9	—	1	100·0	31	96·9	—
38	3·5	6	1	14·3	31	81·6	—
45	4·1	—	—	—	45	100·0	—

°–75° F group (26)

rogeny	progeny in diapause		average developmental time	
%♀		%	♂	♀
53·8	139	59·9	23·70	25·50
73·8	86	67·2	23·82	25·45
82·2	137	75·3	23·75	25·56
70·2	130	73·4	23·91	25·70
79·5	150	79·4	24·50	26·00
71·4	173	89·2	24·80	26·07
44·4	170	90·4	24·80	26·57
58·3	166	93·3	25·20	27·17
60·0	142	90·4	25·80	26·89
35·7	158	91·9	25·89	24·80
16·7	123	95·3	23·75	25·00
25·0	117	93·6	24·17	31·00
—	117	99·2	28·00	—
100·0	99	99·0	—	26·00
20·0	105	91·3	23·75	26·00

75°–70° F group (3)

total eggs	eggs per ♀ per day	emerging progeny			progeny in diapause		av devel
		♂	♀	%♀		%	♂
23	7·7	—	—	—	23	100·0	—
16	5·3	—	—	—	16	100·0	—
17	5·7	—	—	—	17	100·0	—
13	4·3	—	—	—	13	100·0	—
18	6·0	—	—	—	18	100·0	—
14	4·7	—	—	—	14	100·0	—
11	3·7	—	—	—	11	100·0	—
22	7·3	—	—	—	22	100·0	—
15	5·0	—	—	—	15	100·0	—
12	4·0	—	—	—	12	100·0	—
3	1·0	—	—	—	3	100·0	—
10	3·3	—	—	—	10	100·0	—
15	5·0	—	—	—	15	100·0	—
12	4·0	—	—	—	12	100·0	—
12	4·0	—	—	—	12	100·0	—

°–75° F group (2)

rogeny	progeny in diapause		average developmental time	
%♀		%	♂	♀
62·5	9	52·9	23·67	24·80
100·0	3	60·0	—	25·00
100·0	1	12·5	—	23·84
60·0	1	9·1	24·00	23·83
88·9	3	25·0	22·00	24·00
66·7	4	25·0	22·67	24·75
27·3	—	—	22·25	24·00
27·3	—	—	21·37	24·00
53·0	—	—	21·00	23·44
50·0	—	—	21·33	23·16
29·4	—	—	22·92	23·00
38·5	—	—	23·00	23·20
41·7	—	—	23·00	23·80
—	—	—	23·00	—
25·0	—	—	24·00	23·00

83°–70°–83° F group (5)

total eggs	eggs per ♀ per day	emerging progeny			progeny in diapause		av devel
		♂	♀	%♀		%	♂
17	3·4	—	—	—	17	100·0	—
14	2·8	—	—	—	14	100·0	—
28	5·6	—	—	—	28	100·0	—
changed to 83° F							
42	8·4	4	2	33·3	36	85·7	18·75
31	6·2	3	—	—	28	90·3	17·75
33	6·6	—	—	—	33	100·0	—
27	5·4	3	—	—	24	88·9	16·33
23	4·6	7	—	—	16	69·6	16·57
18	3·6	6	—	—	12	66·7	16·33
29	5·8	14	—	—	15	51·7	16·21
19	3·8	12	1	7·7	6	31·6	16·58
20	4·0	15	—	—	5	25·0	15·80
21	4·2	16	—	—	5	23·8	16·19
14	2·8	9	—	—	5	35·7	15·89

E PARENT FEMALE

average developmental time ♂	average developmental time ♀
—	—
—	—
—	—
—	—
—	—
—	—
—	—
—	—
—	—
—	—
—	—
—	—
—	35·0
—	33·0
—	—

average developmental time ♂	average developmental time ♀
—	—
—	—
—	—
—	—
—	—
—	—
—	—
—	—
—	—
—	—
—	—
—	—
—	—
—	—
—	—

average developmental time ♂	average developmental time ♀	age of parent ♀ in days when eggs laid
—	—	13
—	—	14
—	—	15
18·75	21·00	16
17·75	—	17
—	—	18
16·33	—	19
16·57	—	20
16·33	—	21
16·21	—	22
16·58	21·00	23
15·80	—	24
16·19	—	25
15·89	—	26

26	8·7	26	—	—	—	—	15·54	—	12	6·0	7	5
5	1·7	5	—	—	—	—	15·00	—	9	4·5	9	—
—	—	—	—	—	—	—	—	—	12	6·0	9	3

In each group the figures are obtained by the addition of each day's oviposition of a number of fema since in this period the pertinent changes in the various characters are visible. In the 83°–70°–83° F group t to 83° F occurring on the fifteenth day.

The figures in brackets after each group heading indicate the numbers of individual experiments used

41·7	—	—	23·00	23·80	19	3·8	12	1	7·7	6	31·6	16·58
—	—	—	23·00	—	20	4·0	15	—	—	5	25·0	15·80
25·0	—	—	24·00	23·00	21	4·2	16	—	—	5	23·8	16·19
					14	2·8	9	—	—	5	35·7	15·89
					11	2·2	8	—	—	3	27·3	15·87

ales, and the progeny resulting therefrom. Since with age the oviposition rate tends to decrease only 15 d
he results from the 13th to the 27th days are given since the first 15 days are the same as to the 83°–70° F gr

l to obtain the totals.

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[illegible]	[illegible]	[illegible]
15·80	—	24
16·19	—	25
15·89	—	26
15·87	—	27

ly 15 days of life are given,
70° F group, the change back

condition of the egg at and prior to oviposition affects the potentialities of the resulting larva with respect to diapause.

This condition of the egg is determined by the state of physiology of the parent female prior to oviposition, and this in turn is affected by the temperature at which the female has herself been reared and at which she is ovipositing.

This is, in general, the deduction that can be made from the series of results obtained here, and now each group of females will be considered separately. In the designation of each group the temperature at which the parent female was reared prior to emergence is given first, that at which she oviposited is given second, the change (where a change occurs) being made on emergence except where otherwise stated. Thus the 83°–75° F group is that at which females reared at 83° F were placed on emergence at 75° F and allowed to oviposit at this temperature.

Owing to individual variations there are certain anomalies in the results. For example, in the 75°–70° F group there is a decrease in percentage of larvae entering diapause towards the end of the laying period. This is due to one individual female, and must be put down to some oddity in her physiology. These abnormalities also occur elsewhere, usually towards the latter part of the oviposition time where the numbers involved are small, and are due to individual peculiarities of single females or their eggs. However, the general trends are clear.

83°–83° F *group*

There is a peculiar change in the proportion of larvae entering diapause. From the first day's oviposition 51·1 % of the progeny enter diapause. This figure declines to 20 to 25 %, and then, after a week, a further rise occurs followed by a second decline. It is obvious that the factors influencing diapause are more complex than in the 75°–75° F group, and that in the female the physiological changes that are reflected in the behaviour of her progeny are possibly influenced by adverse effects occasioned by the high temperature.

75°–83° F *group*

Compared with the 83°–83° F group the change on emergence from 75° to 83° F causes a sharp reduction in diapause in the larval progeny. Towards the end of the oviposition period the percentage going into diapause increases with age as in the 75°–75° F group, although the actual percentage is lower owing to the direct effect on development of the higher temperature of rearing.

70°–83° F *group*

From the first few days' oviposition a large percentage of progeny enter diapause, reflecting the development of the eggs within the female at 70° F. Following this there is a rapid decline in the percentage of progeny going into diapause, until all eggs laid produce emergent progeny. Thus the stimulus of the rise in temperature on emergence of the females is sufficient to ensure all-emergent progeny from eggs laid after the first few days, and it apparently overrides the effect of senility tending to increase the proportion of larvae entering diapause.

83°–75° F *group*

The variation with age of the female of the tendency of the progeny to enter diapause is similar to that shown by the 83°–83° F group, although at a generally higher level and slower time basis, reflecting the direct influence of the lower temperature in slowing down developmental physiology and on the tendency to enter diapause as compared with 83° F. However, the prehistory of the females reared at 83° F apparently causes an effect, similar to that seen in the 83°–83° F group, of lowering the percentage of larvae entering diapause at the very beginning of oviposition. This is followed by a steady increase as in the 75°–75° F group due to the effect of senility.

75°–75° F *group*

As stated above, with ageing of the female there is an increasing tendency for the progeny to enter diapause.

70°–75° F *group*

The trend here is similar to that in the 70°–83° F group, but the effect of the change of temperature is less pronounced and of longer duration, reflecting the smaller change and lower subsequent rearing temperature.

83°–70° F *and* 75°–70° F *groups*

In both these groups practically 100 % of the progeny enter diapause. The temperature of rearing is the factor dominating the others in these groups.

83°–70°–83° F *group*

Females reared at 83° F were placed at 70° F for 15 days and then transferred to 83° F again. For the first 15 days, as with the 83°–70° F group, 100 % of the progeny enter diapause. On the second change, however, the proportion of individuals going into diapause drops to 85·7 %, rises again to 100 % and then drops fairly rapidly. Thus, even though this change from 70° to 83° F occurs in the middle of the oviposition period when 100 % of the larvae produced enter diapause, the stimulus of the change to the higher temperature is sufficient to cause a fairly rapid decline in the tendency towards diapause.

There are obviously here at least two factors influencing the tendency of a larva to enter a state of diapause. In the first place there is the direct effect of the temperature at which development takes place after oviposition. Comparing the results of the various groups, especially those where no change of temperature occurs on emergence of the female, it is obvious that at the lowest temperature nearly 100 % go into diapause, at 75° F there are some emergents, and at 83° F this tendency is greater. This effect of temperature is sufficient partially to mark the second effect, namely, the influence that the age of the female at the time of oviposition has subsequently on larval diapause. Moreover, alteration of temperature on emergence of the female or during oviposition markedly affects diapause in her progeny. In previous work on diapause these effects have not been taken into account, but it is obvious here that they play an important part in the determination of diapause in the particular species studied.

(*c*) *Further analysis*

A further analysis of this problem of the effect of maternal physiology on the potentialities for development of the eggs she lays may be attempted along two lines. In the first place some indication of the physiological level of activity of the female, particularly with respect to reproductive physiology, at the various temperature combinations tried may be obtained by consideration of the daily oviposition rate. Secondly, if some physiological predetermination of diapause occurs in the eggs before they are laid, this might possibly be reflected in variations in the speed of development of those individuals that do emerge, correlating the entry into a state of diapause with the speed of development of the preceding stages. This in turn would fit in with the general difference in tendency towards diapause and in speed of development at higher and lower temperatures. Further, there is the question as to whether one sex is more prone to enter diapause than the other. This, of course, if it did occur, would only be a secondarily complicating factor, since the main effects noted above occur with the entirely male progeny from virgin females. This possibility was investigated, and it was found that no such difference in sex ratio occured between those individuals emerging directly and those going into diapause.

(i) *Daily oviposition rate*

The variation with age of parent female of the daily oviposition rate in the various temperature groups has been worked out fully, and certain general conclusions can be drawn (see table 3). Consider first the 75°–75° F group, which represents the medium temperature, without abrupt temperature change. The first day's oviposition is large; there is a sharp drop on the second day, followed by a rise for 4 days, and a subsequent gradual decline. At 75° F females emerge with the development of eggs well advanced and a number of eggs ready for immediate oviposition. There is, as is seen from the tables, no preoviposition period during which eggs reach full maturity. Moreover, prior to the commencement of the experiments females remain up to 24 hr. in the emergence vials during which time further eggs reach maturity. It has been shown by depriving females of hosts for several days at a time that mature eggs can accumulate to a certain extent, that when abundant hosts are available these are laid as rapidly as possible, and that on the following day, with abundance of hosts, the numbers of eggs laid drops very considerably, to build up again on the third and fourth days to a comparatively steady figure. A similar effect occurs in the first few days' oviposition following emergence. All the eggs stored in the oviducts are laid on the first day; on the second day the 'egg pressure' within the female is low, and only few eggs are laid; subsequently 'egg pressure' builds up as more eggs reach maturity, and a rise in numbers laid occurs. After the sixth day (at 75° F) the number laid drops steadily, reflecting a slowing up with age of the rate of egg production in the ovarioles. Thus there are two factors here affecting the quantity (as opposed to quality) of the eggs laid. First, there is the effect of pressure of mature eggs in the oviducts when the rate of maturation is high, which causes the irregularities in the oviposition rate in the first 2 or 3 days of the laying period. Secondly, there is with age a slowing up of the rate of maturation and subsequent oviposition rate, connected with a decreased level of physiological activity in the reproductive cells. It is this latter effect that might be expected to be correlated with the variation in the potentialities of the eggs laid for producing larvae going into diapause, since a slowing of the rate of maturation might possibly have a qualitative as well as a quantitative effect on the eggs produced. It is found that, ignoring the irregularities of the first few days' oviposition explicable as above, decrease in oviposition rate in the 75°–75° F group is contemporaneous with an increase in proportion of the larvae entering diapause.

Let us now consider each of the other groups in turn.

83°–83° F *group*

The general shape of the oviposition curve is similar to that of the 75°–75° F group, except that the oviposition rate is higher and the effect of ageing in reducing the rate causes a sharper decrease, as might be expected from the general effect of a higher temperature.

75°–83° F *group*

Oviposition rate changes are similar in trend to those of the 83°–83° F group, except that the peak is higher (as is the total egg production per female) and the rate of reduction with ageing is greater, as though a female reared at 75° F responds more readily to the effects of a high temperature than does one reared at 83° F. This is seen, too, in the proportion of larvae going into diapause, and it is only at the end of the life, when, with old age, there appears a tendency for the larvae produced to enter diapause.

70°–83° F *group*

Following emergence there is a sharp increase in oviposition rate to a high level followed by a very gradual decline. The proportion of eggs producing larvae entering diapause is high on the first day but drops rapidly to zero, 'all-emergent' progeny being correlated with a high oviposition rate.

83°–75° F *group*

The shape of the oviposition rate curve is similar to that of the 83°–83° F group except that the decreases and increases are slower and the general rate is not so high, as might be expected from the effect of the lower temperature both on actual egg production and on the reactions to 'egg pressure'. The ageing effect is similar to that of the 75°–75° F group. The changes of proportions of larvae going into diapause follows the oviposition rate closely, increasing when the later decreases and vice versa.

70°–75° F *group*

There is an initial drop and a subsequent rise in daily oviposition rate which is correlated with a decrease in numbers of larvae entering diapause. The number of larvae that do enter diapause are from eggs laid early in the life of the female, and these are eggs which have developed and reach maturity within the female, not at 75° F, but at 70° F, and have hence greater potentialities for entering diapause owing to their slower earlier development.

83°–70°, 75°–70°, 70°–70° F *groups*

All these groups show similar oviposition curves. An initial high daily rate for the first day decreases, this time over a period of 2 days due to the general slowing of activity at the lower temperature, and the subsequent rise is more gradual, reaching a lower maximum level, and is followed by a more gradual decline. With this lower level of reproductive activity is found a condition in which nearly all the larvae produced enter diapause.

83°–70°–83° F *group*

The oviposition rate and condition in which 100 % of the larvae enter diapause are identical, naturally, to the 83°–70° F group for the first 15 days. On raising the temperature to 83° F egg production immediately increases, at first owing to the 'egg-pressure' effect, subsequently to actual increased production. Following this it gradually diminishes with age. The effect on diapause is similar to that in the 70°–83° and 70°–75° F groups. For

3 days the percentage going into diapause remains high while eggs which were developed at 70° F are laid. Then, as in the other two groups, there is a gradual decrease in percentage going into diapause reflecting the change of temperature. This effect is, as before, sufficient to mask any ageing effect that would increase the percentage going into diapause towards the end of the life.

Thus there seems to be a correlation between rate of egg production and incidence of diapause in the resulting larvae, not only conditioned by a general high or low temperature, but also by ageing of the female, and by subjecting the female to sudden changes of temperature.

Egg production expresses quantitatively the physiological level of activity of the ovarioles, while the percentage of larvae going into diapause, although modified or completely altered by the effects of various factors on the subsequent larval development, reflects qualitatively the physiological state of the ovaries at the time of egg formation.

(ii) *Rate of development*

Since all the emergents from every day's oviposition were noted together with dates of emergence, data had only to be collected together suitably to demonstrate whether or not there was, throughout the life of the parent female, any change of rate of development of those eggs and larvae which produced emergents that could be correlated with the proportion of the eggs producing larvae going into diapause. If this effect did in fact occur, it might be obvious in two ways. (1) If we consider the total progeny of individual females in any one temperature group we may find that some produce progeny of which a high percentage enter diapause, while others produce progeny of which a low percentage enter diapause; and in this case there might be a difference in the average developmental times of the progeny not entering diapause in the two categories. (2) If there appeared any variation in the developmental time of those individuals that did emerge from eggs laid at different times during the life of the parent female, this might be correlated with variation in the proportions of her progeny going into diapause.

It should be pointed out here that the results given below could not be attributed to slight variations in the controlled temperatures, since these results are the sum of individual experiments carried out at different times.

(A) *Total progeny of individual females.* Disregarding for the present any possible alteration of the developmental time of her offspring with the ageing of a female it is of interest to compare the average developmental times of all the progeny of individual females, and to consider this in relation to the proportion of their progeny entering diapause.

In table 4 are shown all those females of the 75°–75° F group which produced any emergent progeny. They are arranged according to the percentage of their progeny going into diapause, and the average developmental time for the emergent offspring of each female is also given. In table 5 these results are grouped according to the percentages of the offspring entering diapause. From both tables it is seen that there is a marked, though not absolute, correlation, between the percentage of the progeny of an individual female that goes into diapause and the length of the average developmental time of those individuals that do emerge. The smaller the percentage that goes into diapause, the shorter is the average developmental time.

TABLE 4. FEMALE *SPALANGIA* OF THE 75°–75° F GROUP ARRANGED ACCORDING TO THE PERCENTAGE OF THEIR PROGENY ENTERING DIAPAUSE AND GIVING THE AVERAGE DEVELOPMENTAL TIME OF THE EMERGENT PROGENY IN EACH FAMILY

		number of emergents			average developmental time	
family	percentage in diapause	males	females	percentage females	males	females
1	99·5	—	1	100·0	—	—
2	99·3	1	—	—	27·00	—
3	99·1	1	—	—	26·00	—
4	98·7	2	—	—	28·00	—
5	98·6	1	1	50·0	24·00	25·00
6	98·3	—	3	100·0	—	24·67
7	98·1	1	1	50·0	32·00	—
8	98·1	1	2	66·7	—	27·00
9	97·6	2	1	33·3	25·00	24·00
10	97·1	1	3	75·0	22·00	26·33
11	96·7	1	4	80·0	26·00	25·33
12	96·2	—	5	100·0	—	25·60
13	96·3	4	—	—	26·25	—
14	96·1	4	1	20·00	26·00	26·00
15	95·7	6	—	—	25·17	—
16	95·7	9	—	—	24·00	—
17	90·1	3	9	75·0	23·33	25·63
18	89·8	12	—	—	24·22	—
19	89·4	17	—	—	23·94	—
20	88·2	3	14	82·4	23·67	25·36
21	85·9	18	2	10·0	23·56	26·00
22	83·7	16	—	—	24·81	—
23	81·8	1	5	83·3	27·00	29·75
24	80·5	20	12	37·5	23·56	26·18
25	80·4	27	—	—	24·37	—
26	75·7	18	37	67·3	22·76	26·62
27	80·1	39	—	—	24·08	—
28	73·0	54	—	—	24·02	—
29	72·6	13	46	78·0	23·64	25·37
30	66·7	12	38	76·0	24·09	25·82
31	66·2	10	13	56·5	23·44	25·18
32	65·6	54	—	—	23·81	—
33	63·1	32	37	53·6	24·41	25·30
34	62·1	29	21	42·0	24·56	25·58
35	36·3	142	—	—	23·76	—
36	18·6	162	—	—	23·81	—
37	0·7	138	—	—	23·16	—

TABLE 5. RESULTS GIVEN IN TABLE 4 GROUPED ACCORDING TO PERCENTAGE OF PROGENY GOING INTO DIAPAUSE, AND GIVING THE AVERAGE DEVELOPMENTAL TIME FOR ALL EMERGENTS IN EACH GROUP

		number of		average developmental time	
percentage in diapause	number of experiments	males	females	males	females
0– 10	1	138	—	23·16	—
10– 20	1	162	—	23·81	—
20– 30	—	—	—	—	—
30– 40	1	142	—	23·76	—
40– 50	—	—	—	—	—
50– 60	—	—	—	—	—
60– 70	5	137	109	24·11	25·52
70– 80	3	85	83	23·69	25·93
80– 90	9	153	33	24·08	26·36
90–100	20	38	33	25·21	25·61

Table 6. Female *Spalangia* of the 83°–83° F group arranged according to the percentage of their progeny entering diapause, and giving the average developmental time of the emergent progeny of each family

percentage in diapause	number of emergents		percentage females	average developmental time	
	males	females		males	females
98·1	1	1	50·0	19·00	19·00
92·2	2	7	77·8	19·50	19·19
91·8	—	10	100·0	—	18·60
85·3	3	16	84·2	18·67	18·82
83·3	2	13	86·7	18·00	19·33
65·8	3	50	94·3	17·00	17·84
34·4	15	44	74·6	17·00	18·00
28·6	5	40	88·9	16·00	17·00
27·0	17	48	73·8	16·31	17·37
22·5	71	46	39·3	15·93	17·30
16·5	7	59	83·9	17·00	17·34
14·7	34	30	46·9	15·79	17·23
13·1	121	25	17·1	15·55	17·20
12·0	131	30	18·6	15·76	17·43
11·9	16	58	78·4	16·00	16·95
8·1	54	70	56·5	15·81	16·91
8·0	6	52	86·6	15·83	16·62
4·0	13	59	81·9	15·85	16·85
3·6	76	31	29·0	15·78	16·88
3·2	55	64	53·8	15·73	16·88
2·5	58	59	50·4	15·60	16·76
2·0	86	59	40·7	15·67	17·05
0·0	58	32	36·7	16·05	17·16

Table 7. Results given in table 6 grouped according to percentage of progeny going into diapause, and giving the average developmental time for all emergents in each group

percentage in diapause	number of experiment	number of		average developmental time	
		males	females	males	females
0– 10	8	406	426	15·74	16·90
10– 20	5	309	202	16·04	17·21
20– 30	3	93	134	16·01	17·23
30– 40	1	15	44	17·00	18·00
40– 50	—	—	—	—	—
50– 60	—	—	—	—	—
60– 70	1	3	50	17·00	17·44
70– 80	—	—	—	—	—
80– 90	2	5	29	18·48	19·05
90–100	3	3	18	19·33	18·85

Similarly in tables 6 and 7 the same results are shown for the 83°–83° F group.

The other groups, where temperature changes occur, show irregularities, particularly at the low percentage of diapause end of the scale. Towards the high percentage of diapause end there are few individuals emerging giving irregularities due to individual variation, but the general trend is similar.

Thus, taking individual females at any one temperature, those that produce most offspring entering diapause also have emerging progeny that develop somewhat more slowly than those of females with few larvae entering diapause amongst their progeny. This indicates some definite relationship between speed of development and tendency towards diapause.

(B) *Variation in average developmental time of progeny with age of the female*. For each of the various temperature groups, the emergents and individuals entering diapause from each day's oviposition have been recorded, together with the developmental time and sex of each emergent. Thus from the addition of each day's results for each individual parent an 'average' idea is obtained of the variation of developmental time of progeny with the age of the female when the eggs are laid. In table 3 these results are shown, and expressed graphically in figure 2. As before, only the first 15 days are shown, for convenience, and because even with some of the results here the small numbers of individuals involved gives erratic results—a factor becoming more important as the females grow older and lay fewer eggs.

Considering first the 'central' 75°–75° F group, it is obvious that the average developmental time of both male and female progeny increases as the parent female grows older. The first day's eggs give progeny having as their average developmental time: males 23·70 days, females 25·50 days. This value rises steadily until on the eighth day the figures are: males 25·20, females 27·57. Following this the results are irregular, since the emergents consist of a few individuals only.

In the 83°–83° F group the curve showing the relation between the average developmental time of the female progeny and the age of the female when the eggs were laid is similar in general form to the curve showing the proportion of larvae going into diapause; the curve for the males, after a slow initial fall, remains fairly constant. There is some correlation observable in the other groups, but the changing of temperatures on emergence of the female tends to complicate this point.

The general trend of the change in average developmental time tends to follow that for the percentage of larvae going into diapause. It cannot be said that the effect is well marked, but it is hardly to be expected that an effect of this nature would remain up till now unnoticed if it were very striking.

It was also thought possible that with the variation occurring in the developmental time of the females, the progeny from a fast-developing mother might show propensities with regard to diapause different from those of progeny of a slowly developing female. This is logical, since a rapid development would indicate a physiological reaction to a given temperature on a higher level than the average, which might in turn affect the developing eggs within the female, producing effects on the developmental time and potentialities for diapause in the next generation.

For this purpose single females, mated and unmated, were selected from emergents of the 83°–83° F group progeny that had completed their development in 20, 19 and 16 days respectively. These were treated as before, and the offspring noted—with regard to diapause, developmental time, etc. No difference was seen between the three groups, and apparently the causes which determine the rate of development of an individual female are not transmitted in a simple way to her progeny.

The foregoing experiments thus show that individual differences between females in the proportions of their progeny entering diapause are not transmitted to their offspring in a simple genetical way.

(*d*) *Discussion*

These results on oviposition rates, tendency to enter diapause, and variation in developmental time of *Spalangia* at different temperatures and temperature combinations may now be discussed with a view to obtaining a general idea of the causes underlying the various effects that are seen.

It is obvious that a high temperature increases oviposition rate, decreases developmental time, and decreases the percentage of larvae entering diapause. This is a direct effect of a high temperature increasing the rate of physiological processes.

It is seen, however, that the effect of temperature on diapause is not limited to its immediate effect on the developing larvae, but that the temperature to which a female has been subject during development and temperature changes prior to the commencement of oviposition affect the potentialities with regard to diapause of eggs laid subsequently. The temperature of development of eggs within the ovarioles prior to the initiation of cleavage has some effect on the quality of the eggs and their potentialities for future development. This variation in the quality of eggs is shown in different developmental times and different proportions of the progeny entering diapause, even though the subsequent temperature of development is the same in all cases. Also, at a constant temperature of 75° F (75°–75° F group), ageing of the female during oviposition has a similar effect to a lowering of the temperature; the oviposition rate decreases, the average developmental time of the eggs and the resulting larvae increases, and the percentage of the progeny entering diapause increases as she grows older.

This would point to the underlying cause determining these various effects as being physiological, influenced both by changes of temperature and by a general slowing down of metabolic processes with old age (shown quantitatively by the decrease in daily egg production). It may be that lower temperatures or old age cause the production of eggs within the ovarioles with slightly different protoplasmic structure or chemical compostion, which tends to slow down speed of development and produces individuals with a longer developmental period and with a greater proportion of them entering diapause. In some way, prior to the onset of cleavage, the eggs are predetermined with regard to their potentialities for reacting to the environment. The actual mechanism by which this is brought about is beyond the scope of this work, but the effect is well marked, and it is evident that the observed variations in speed of development and incidence of diapause are both influenced by this 'pre-natal' factor or factors. These potentialities may be masked by the direct effects of temperature during subsequent development, but are realized under certain temperature conditions.

Cryptus inornatus Pratt

In view of the results obtained with *Spalangia* it was felt desirable to see if the effect of ageing of the parent female on the incidence of diapause in her progeny was of general occurrence. Work was being carried out on the biology of *Cryptus inornatus* Pratt, an ectoparasite of the full-grown larvae of *Loxostege sticticalis* L. Details of the biology have been given elsewhere (Simmonds 1948).* Briefly, the female *Cryptus* attacks host larvae within their spin-ups in or on the soil. The larvae are stung and killed (a little feeding on host body fluids by the female apparently sometimes occurring). Eggs of the parasite are then laid within the host cocoon so that they lie close to the dead host. On hatching the parasite larva feeds ectoparasitically on the host, and when full-grown has entirely devoured

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* In course of publication.

the latter. The parasite larva then spins a cocoon within that of the host, and it is at this point that a state of diapause occurs in a number of individuals. The full-grown parasite larva remains as such within its cocoon for several months, even though conditions are favourable for further development. Then, as with those individuals developing without the intervention of diapause, a prepupa and pupa are formed followed by the emergence of the adult parasite.

In these experiments freshly emerged females were mated with males several days old (mating was not always successful as is shown by the fact that a few of the females produced only male progeny). These females were then kept individually in small cages, $4\frac{1}{2} \times 4\frac{1}{2} \times 2\frac{1}{2}$ in., which were of wood with cheese cloth back and sides and a sliding celluloid front. No variations in temperature were made, all being kept at 75° F, but, since apparently very little feeding on the host occurs, the diet of the adult females was varied. Some females were supplied with a lump of cane-sugar, others with cane-sugar and raisin, and others with raisin alone. All were given, in addition, a dish containing cotton-wool soaked in water and a pad of dental cotton dipped in honey-water (50 % honey, 50 % water). In view of the effect seen with *Spalangia* of varying the temperature during the development of the eggs within the parent female it was thought possible that varying the diet of the parent female *Cryptus* might alter the proportions of eggs producing larvae that go into diapause.

The effect of the two factors, ageing of the parent female and variations in her diet, on diapause in the resultant progeny will be discussed below.

(*a*) *General*

The figures given in table 8 are the totals for the combined oviposition of ten females on each diet (nine in the case of the cane-sugar). The results are grouped into 5-day periods for convenience of presentation, and because the daily variation in numbers of eggs laid was more irregular than in the case of *Spalangia*. Also there did not occur in the few days immediately after emergence the regular variations in oviposition rate seen in the latter species. Apparently at 75° F female *Cryptus* do not emerge with a number of eggs in the oviducts ready for oviposition, but maturation of eggs takes place gradually after emergence. However, there does appear to be a similar 'egg-pressure' effect which is indicated in the oviposition of individual females by wide variation in the number of eggs laid from day to day under constant conditions. The conclusions to be drawn from the figures given are obvious, and the two factors under investigation may conveniently be considered separately. In estimating percentage of females in progeny only those families with bisexual progeny have been considered, i.e. only progeny from parent females where mating has been successful.

(*b*) *Effect of the diet of the parent female on the tendency of the progeny to enter diapause*

Considering only the totals and averages in Table 8 it is obvious that on a diet of cane-sugar and honey-water alone the average length of life of the females is much less than when raisin is present in the diet. Also the preoviposition period appears to be longer, though this may not be a significant difference. The average total number of eggs laid per female is 27·0 as opposed to 90·7 with raisin and cane-sugar and 113·1 with raisin alone. The mortality during development is 34·2 %, considerably lower than in either of the other

TABLE 8. EFFECT OF VARIATION OF THE DIET AND AGE OF THE PARENT FEMALE *CRYPTUS* ON OVIPOSITION RATE, MORTALITY AND SEX RATIO OF HER PROGENY AND THE PROPORTION OF THEM GOING INTO DIAPAUSE

food in addition to water and honey-water		days after emergence												
		1–5	6–10	11–15	16–20	21–25	26–30	31–35	36–40	41–45	46–50	51–55	56–60	totals
cane-sugar	total eggs	72	111	32	12	16	—	—	—	—	—	—	—	243
	dead	19	34	12	9	9	—	—	—	—	—	—	—	83
	emergent progeny: males	42	58	14	3	6	—	—	—	—	—	—	—	123
	females	10	18	5	—	—	—	—	—	—	—	—	—	33
	larvae in diapause	1	1	1	—	1	—	—	—	—	—	—	—	4
	% diapause in living individuals	0·2	0·1	0·5	—	14·3	—	—	—	—	—	—	—	2·5
	% dead	26·4	30·6	37·5	75·0	56·2	—	—	—	—	—	—	—	34·2
	% females from mated females	20·8	35·3	35·7	0·0	0·0	—	—	—	—	—	—	—	38·4
cane-sugar and raisin	total eggs	157	249	207	141	75	35	11	8	10	14	—	—	907
	dead	59	123	108	68	35	23	6	2	3	9	—	—	436
	emergent progeny: males	68	52	30	26	7	1	—	—	—	—	—	—	184
	females	25	56	24	5	2	—	—	—	—	—	—	—	112+3*
	larvae in diapause	5	17	43	42	31	11	5	6	7	5	—	—	172
	% diapause in living individuals	5·1	13·6	44·3	57·5	77·5	91·7	100·0	100·0	100·0	100·0	—	—	36·5
	% dead	37·6	49·4	52·2	48·2	46·7	65·7	54·5	25·0	30·0	64·3	—	—	48·1
	% females from mated females	36·2	67·5	80·0	100·0	100·0	—	—	—	—	—	—	—	59·9
raisin	total eggs	152	315	259	197	67	60	29	25	11	5	9	2	1131
	dead	55	152	125	80	32	27	13	9	6	2	3	2	506
	emergent progeny: males	78	108	55	27	8	13	2	4	3	2	3	—	303+2*
	females	19	41	47	24	3	2	—	—	—	—	—	—	136+1*
	larvae in diapause	—	13	31	65	24	18	14	12	2	1	3	—	183
	% diapause in living individuals	0·0	8·0	23·3	56·0	68·6	54·5	87·5	75·0	40·0	100·0	50·0	0·0	29·3
	% dead	36·2	48·3	48·3	40·6	47·7	45·0	44·8	36·0	54·5	40·0	33·3	100·0	44·3
	% females from mated females	26·0	34·7	57·3	58·5	75·0	28·6	0·0	0·0	—	—	—	—	41·2

* Date of oviposition doubtful.

two series. Of the total living material only 2·5 % goes into diapause when the parent females have a cane-sugar diet compared with 36·5 % when on a cane-sugar and raisin diet and 29·0 % when on raisin alone. The percentage of females in the individuals emerging without passing through a state of diapause is 38·4 %, compared with 59·9 % on cane-sugar and raisin and 46·4 % on raisin alone.

With those individuals that emerge without arrested development there is a definite difference of average developmental time betwen individuals whose mothers were fed on cane-sugar only and the rest. The average developmental time for progeny of cane-sugar-fed mothers was: males 17·35 days, females 18·93 days; when cane-sugar and raisin was their diet: males 18·23 days, females 20·44 days; when raisin alone was fed: males 18·27 days, females 19·79 days. Thus with a cane-sugar diet alone both males and females showed a definitely shorter developmental time.

These facts obviously indicate that, with all other conditions identical, the diet of the parent female has a marked effect not only on herself but also on her progeny. Addition of raisin to the female diet increases the length of life and total eggs laid by the female, and also causes a greater number of her progeny to enter diapause, with a correlated increase in the developmental time of those individuals that develop without arrest. The effect of a different diet on the sex ratio is more complex and varies during the life of the individual parent females, but in general addition of raisin to the diet favours the production of more females.

(c) *Variation in larval diapause with age of female at the time of oviposition*

It is seen from table 8 that there is a definite variation with the age of the parent female, not only in the oviposition rate, but also with regard to the subsequent development of her progeny. A maximum oviposition rate is reached in the sixth to tenth day period after emergence whatever the diet of the female, though this maximum is considerably lower when cane-sugar alone is supplied.

When the females are fed on cane-sugar only there is an initial period of egg-laying of about 15 days; after this, most of the females lay no eggs for a further period of about a week, and then lay a few eggs over a period of perhaps 5 days. (This effect is masked by the 5-day grouping in table 8.) This second period of egg-laying is undoubtedly correlated with the deficiency of protein in the diet, and it is probable that after the initial period of oviposition which depletes all stores of readily available protein in the body of the female, there occurs, during the period when no eggs are laid, a readjustment of physiology which makes available for developing ova a further quantity of protein. It may be that resorption (Flanders 1942) plays some part in this process.

The egg and larval mortality, comparatively low when cane-sugar is the sole diet, nevertheless increases from 26·4 % in the first 5-day period to around 60 % at the end of the females' short life. When the diet is cane-sugar and raisin or raisin alone, mortality is consistently high whatever the age of the female at the time of oviposition, and, except for a slight increase in the second 5-day period, without apparent increase as she grows older. The percentage of progeny going into diapause is very low throughout the life of the female when cane-sugar alone is the diet, age apparently having little effect in this case. However, when raisin is added to the diet there is a steady increase in percentage of progeny in diapause with increasing age of the parent female, as is very clearly seen in table 8. This is parallel to what was found to occur with *Spalangia* in certain temperature groups. In general, the percentage in diapause is somewhat lower throughout the life of the parent female when raisin alone is her diet than when she is fed cane-sugar and raisin, but this difference may not be significant.

From a comparison of the sex ratio of those individuals emerging without arrest in development and those emerging from individuals in diapause it is obvious that there is no selective entry into diapause of larvae of one sex. There is, however, an indication that the state of diapause of male individuals is more easily broken than that of female-producing larvae, and also that there is a slightly greater mortality of females than males when the adults are almost mature, some short time before emergence would have occurred.

The sex ratio of the progeny varies with the age of the parent female. After mating, sperm transferred to the female are stored in the spermatheca where they are kept alive by secretions from the mother, and some of the eggs are fertilized by these sperm as they pass down the oviduct. The factors involved in the fertilization or otherwise of an individual egg, or the extent if any to which this process is controlled by sensory impressions received by the ovipositing female are uncertain. However, it is clear that such factors as temperature affect the activity and longevity of the sperm within the female, and it is reasonable to assume that alterations in the physiology of the female have similar effects. From table 8 it is seen that with a diet of cane-sugar alone the proportion of females in the progeny is low, and that after the sixteenth day no female progeny are produced, indicating that sperm in the spermatheca are dead. With a parental diet of cane-sugar and raisin there is a greater proportion of females in the progeny than with cane-sugar alone, and, moreover, this ratio steadily increases with age of the parent female. At the same time the percentage of the progeny entering diapause is also steadily increasing, and although it would appear that there may be no connexion between these two characters, both are reflexions of changes in the physiology of the parent female.

With the first eggs laid in all three groups the proportions of females is abnormally low, indicating possibly that sperm are at first inactive on transference to the female and that a period of maturation is necessary before they reach maximum activity. After the peak of oviposition is reached the activity of the sperm may remain the same when raisin is present in the diet. However, a decreasing number of eggs passing down the oviducts results in an increased proportion of them being fertilized. Following this (30 days after emergence) when raisin alone is the diet the sperm are finally exhausted and only unfertilized eggs are laid.

In connexion with all the above results on variation of diapause, sex ratio, etc., with the diet and age of the parent female, it is to be expected that at the beginning of her life the effects of a difference in diet would be less marked than after she had been feeding for some time. This follows since during development and in the period prior to emergence the females of all groups were subject to the same environmental conditions, and a number of the eggs laid at the beginning of the life had a longer or shorter period of their development under conditions uninfluenced by variations in parental diet.

As had been done with *Spalangia* an attempt was made to correlate the increase with age of the parent female in the proportion of progeny entering diapause with an increase in developmental time. However, no definite correlation was found in this regard. There was, however, with a raisin and cane-sugar diet some indication that mortality in the immature stages and diapause might be correlated.

(*d*) *Discussion*

The above experiments with *Cryptus* were carried out under constant conditions of temperature and humidity both during the later stages of development of the parent females and throughout the immature stages of all the progeny. The females admittedly came from field-collected material, but were taken at random from emergents in the laboratory, so that no selection of different groups of parents could account for these results. Thus it may be safely concluded that the differences noted between the three groups and variations during the lifetime of the females are due to differences in the diet of the adults and to the effects of senility on the females, the former probably having considerable effect on the latter.

The shortness of the life of the female and the comparatively few total eggs laid when cane-sugar alone is the diet indicate that something, presumably a form of protein, is missing from the diet, and that when raisin is provided to remedy this deficiency length of life is increased by 100 % and reproductive capacity by nearly 400 %. (Composition of raisin, for dried unsulphured material on the basis of 100 g. of edible portion: protein 2·3 g., fat 0·5 g., carbohydrate 71·2 g., vitamin A value 50 i.u., together with small amounts of minerals and other vitamins: from *Misc. Publ. U.S. Dep. Agric.* no. 572, 1945).

With cane-sugar alone as a diet females produce very few progeny going into diapause (2·5 %), and there is in these experiments no increase in this regard with age of the female at the time of oviposition. However, when cane-sugar and raisin or raisin alone is the females' diet a considerable proportion of the eggs produce progeny going into diapause (36·5 and 29·3 % respectively), and, moreover, this percentage increases steadily from a very low figure for the eggs laid on the first 5 days after emergence to 100 % after the 30th day when the female is fed on cane-sugar and raisin, and 87·5 % when fed on raisin alone. There is a definite correlation between parental diet and developmental time of emergent progeny. Individuals from females fed on cane-sugar alone develop faster than when raisin has been added to their diet. Some correlation is seen then between developmental time and percentage going into diapause.

There is, as noted above, a marked effect on sex ratio of both parental diet and age of parent female at the time of oviposition, but this is something apart from the effects on diapause, although investigation of one may shed some light on the cause of the other. In *Cryptus* the percentage of females in the progeny is correlated with the activity and longevity of sperm in the spermatheca and is therefore susceptible to influences from the body fluids of the female, and hence to the general physiological condition of the female.

3. CONCLUSIONS

It would appear that there is with both *Cryptus* and *Spalangia* an underlying physiological process or complex of processes which influences rate of development, potentialities for diapause, and possibly general vitality. With *Spalangia* temperature changes and senility of the parent female at the time of oviposition affect both diapause and developmental time of the progeny, and in the case of *Cryptus* senility and the diet of the parent female have been seen to have an effect. Thus in both species these characters are affected by maternal influences during ovarian development, as well as directly by subsequent environmental conditions. It seems unlikely that the basic causes of these correlated results will be different in the two species considered, and it is possible that the observations made here may throw some fresh light on the fundamental problem of the actual processes involved in the phenomenon of diapause.

Of the theories put forward to account for diapause and which have been discussed in detail by Cousin (1932) none is able to explain satisfactorily all of the numerous observations that have been made, but all of them, not unnaturally, have a bearing on the problem, and appear to be partially true. Fundamentally, however, they are based on the principle that diapause is caused by influences, internal or environmental, that affect the physiology of growth of the insect during development. From a general consideration of the observations made on diapause it does not appear that diapause is caused exclusively by the auto-intoxication suggested by Roubaud (1922, etc.) or that diapause is a periodic phenomenon necessary for the rejuvenation of the species; evidence is also meagre in support of the theory that enzymatic activity (Townsend 1926; Shelford 1927) or hormone deficiency (Wigglesworth 1934) is in general the cause of diapause. It seems more probable that a number of these processes that have been described as the causal agents of diapause are, as with the gonad development of male *Pyrausta* larvae (Parker & Thompson 1927), merely contemporaneous results of the fundamental causes underlying the onset of diapause. The experiments and conclusions of Cousin support this. She made extensive investigations with several species on the effect of environmental factors in producing a state of diapause, on the possible influence of genetical factors, and on a possible correlation between metabolic rate and entry into diapause. She discusses the relationship between a state of diapause and differences in a number of physico-chemical properties: hydration, 'bound water', respiratory rate, physical state of the protoplasm, etc., and concludes that any unfavourable variation in any of a number of factors will increase the tendency towards diapause. Fundamentally her general conclusions are similar to those to be put forward here. There are, however, two of her conclusions that do not seem to be justifiable. She uses the term diapause to include temporary arrests in development due to immediate environmental influences, where growth processes are resumed directly conditions are again suitable. It is claimed here that these instances are not true diapause. Undoubtedly some of the processess occurring during such an arrest may be similar to those found during true diapause, but one or more of the fundamentals involved in true diapause is lacking; namely, the factors which prevent return to normal growth when environmental conditions are again favourable. Moreover, Cousin concludes that there is not a single state of diapause but that there are a variety of such conditions dependent on the environmental influences which produced the state. Thus she claims diapause brought on by malnutrition differs from that caused by desiccation, and both from that due to low temperature. Also she claims that in breaking diapause shocks have to be applied to the dormant individuals such that they counteract the conditions which caused diapause. For example, an individual that goes into a state of diapause owing to adverse conditions of humidity will not be brought out of diapause by thermal or chemical shocks, but only by those involving water relations. In those cases which she terms diapause but which are not 'true diapause' as it is defined here this is undoubtedly true, and temporary arrests in development are terminated when environmental conditions are altered back to normal in that sense in which they were unfavourable (e.g. with *Diatraea*, Kevan 1944). With true diapause this does not seem to be the case, as is shown, for example, by the work of Duclaux (1869, 1876) in breaking the diapause of silkworm eggs by a variety of different stimuli: thermal, chemical, electrical, etc. Again, in the case of the codling moth it has been observed (Simmonds 1944*a*) that the quality of larval feeding alters the proportions of larvae entering diapause. This diapause can then be broken by various means, but no feeding is occurring. This apparent nutritional cause may, of course, be due to differences in water content of the foods rather than to chemical differences between them, a factor seen to have considerable bearing on the general phenomenon of diapause. It appears that diapause is not a term encompassing a number of different separate states but that it is a single fundamental phenomenon, which may be caused by physiological disturbances due to a variety of factors.

Cousin also suggests that the conditions of the parent female may affect the subsequent development of her progeny: 'On peut évidemment concevoir que, dans certaines conditions une génération, voire plusieurs, nettement défavorisées dans leur developpement par de mauvaises conditions de milieu, ne puissent engendrer que œufs débiles, donnant par la suite des larves chétives, prédisposées à vivre en diapause.'

She concludes that any unfavourable conditions tend to increase the chances of diapause either at the time of their action or subsequently. This appears in general to be true, but the experimental results obtained here indicate that it does not cover fully all the factors influencing diapause. However, it does seem that the factor of metabolic rate is fundamental, not only during diapause itself, when metabolic rate is greatly reduced, but also in the genesis of diapause. Any conditions tending to cause abnormalities in physiological processes and hence in the metabolic rate increase the chances of the occurrence of diapause either at that time or subsequently. This seems to be the fundamental principle underlying diapause, and the present work has indicated several ways in which this influence may be exerted. By this means the phenomenon of diapause, in its many aspects, may be explained without resort to conceptions of excretory intoxication, hormone deficiencies, growth inhibitors, etc. This is, admittedly, a very simple explanation of diapause, but it will be elaborated further here in an attempt to explain the results obtained in these experiments.

High temperatures during the development of the parent female or a sudden rise in temperature on emergence tend to decrease the percentage of *Spalangia* progeny entering diapause. With *Cryptus* a diet that is deficient in protein and has excess energy-producing sugar induces the formation of eggs very few of which give rise to larvae which enter diapause. Either of these effects would raise the level of physiological activity and metabolic rate of the parent female. Senility, on the other hand, would be expected to slow down physiological activity and decrease the metabolic rate of the female, and, in fact, oviposition rate decreases with age. Correlated with this there is an increase in the proportion of the eggs laid which produce progeny going into diapause. Certain apparently similar effects have been shown by Schmieder (1933, 1939) but are seen on analysis to be due to different causes. He found (Schmieder 1933) that *Melittobia chalybii* Ashm., a gregarious parasite of *Trypoxylon*, *Sceliphron*, etc., occurred in two separate types, one a form in which dispersal of the species occurred, the other, progeny of the first type within individual host cells, acting as a means of increasing reproductive rate. A first type female stings a host within its cell, feeds at the punctures and oviposits. The first few eggs she lays produce rapidly-developing larvae which give adults without arrested development. These adults are, however, of the second morphological type, do not move from the already parasitized host, and quickly lay a large number of eggs. These, together with the eggs laid subsequently by the original female, produce larvae which enter diapause and eventually produce adults of the first type. It would appear at first glance that there was here an effect of ageing of the parent female on the quality of her eggs: the eggs produced when the female was young producing larvae without diapause, later eggs giving larvae with a definite diapause. Schmieder's experiments showed, however, that this was not the case, nor was there any genetical difference between the types. By transference of eggs to fresh hosts or to partially devoured hosts he showed that the differences were due entirely to variation in larval nutrition. Larvae feeding on fresh hosts develop without diapause and produce second type adults. However, after a certain number of larvae have developed thus (several hundred parasites can develop on a single host) the nutritional value of the host is apparently altered, and larvae developing from eggs laid subsequently all go through a period of diapause and produce adults of the first type.

Later, working on *Sphecophaga burra* (Cress.), a parasite of *Vespa* sp., Schmieder (1939) found that 'eggs laid upon the same host presumably by the same mother and under the same conditions of physical environment may develop into either one of two types of larvae. One of these spins only a delicate white cocoon within which it develops forthwith into an imago; the other spins a tough, brown cocoon, and, before transforming, undergoes an extended diapause, normally lasting through the fall and winter, before it, too, pupates and finally emerges'. *Sphecophaga*, like *Melittobia*, is a gregarious parasite, and Schmieder produces evidence that, as with *Melittobia*, larval nutrition determines incidence of diapause. However, he also says 'differentiation into one or more possible types of individual may take place as early as the ovarian egg. That differentiation may occur so early in ontogeny is shown in *Melittobia*, in which of the many eggs obtainable from unmated females ordinarily only 3 % are capable of development (Schmieder 1933). In *Sphecophaga*, the observation that white cocoons appear more commonly in host cells containing a larger number of parasites would suggest that rapid egg-production yields a larger number of white individuals, while a slower egg-production or longer retention of eggs in the ovary has the opposite effect'. Although the evidence for this is very meagre the idea is similar to the state that has been shown definitely to occur with *Spalangia* and *Cryptus*. Flanders (1944) in quoting this example confuses rate of egg-production and rate of egg-deposition, which latter varies considerably with availability of hosts, as has been clearly demonstrated in experiments with *Spalangia*. Egg-production is only one factor influencing rate of deposition; egg-pressure, avoidance of superparasitism, etc., exerting strong influences in this regard.

These two examples do indicate the effects of larval nutrition in inducing diapause; the first example shows a false correlation between the age of the parent female at the time of oviposition and incidence of diapause in her progeny, and the second shows a possibility that some correlation between rate of egg production and incidence of diapause in the progeny may occur in *Sphecophaga*.

It is reasonable to assume that with a female *Cryptus* feeding on a diet of cane-sugar alone the eggs developing within the ovarioles will contain a relatively higher proportion of energy-producing sugars and therefore may possibly start development with a comparatively high metabolic rate. When further nutritional elements in the form of raisin are added to the diet of the female she lives longer and produces more eggs, obviously impossible on a purely sugar diet owing to the amount of protein, etc., necessary for the formation of these large anhydropic eggs. With this difference in the diet it is probable that the eggs have a decreased proportion of sugar, and that development commences at a comparatively lower rate, both of physiological activity and metabolism. This same difference is brought about in the early stages of development of *Spalangia* eggs by the formation of the ova within the ovarioles at different temperatures. Subsequent to laying all these eggs are subject to the same environmental conditions. However, those eggs which have thus started development with an increased metabolic rate proceed with growth at a somewhat higher rate, a fact shown by the shorter developmental time of those individuals belonging to this category that emerge without passing through a stage of diapause. Correlated with this, fewer of this latter type of egg produce individuals going into diapause.

To envisage this effect clearly we must consider the development of the insect from the formation of the egg to the full-grown larval stage (where diapause may occur in these two species) and even beyond. From the initiation of cleavage, growth consists in general of the assimilation of nutritive material, the incorporation of this into the body, and the organization of the whole organism along certain well-defined lines of morphological and physiological development. This is accomplished by means of a complex series of numerous interconnected physico-chemical reactions all dependent, from the nature of things, on the results of preceding reactions and upon the concentrations of the various individual reactants in each system. Now before any individual physiological process can occur smoothly to completion certain concentrations of reactants must be present initially, and before these concentrations are present the reaction will not proceed normally. Also excessive accumulation of products of a given physiological process will tend to slow down this developing process. The concentration of reactants, hence the rate of reaction, is usually sufficient to ensure that the chain of growth processes is continuous from the egg to adult, the actual rate being dependent on environmental conditions of temperature, humidity, etc. There must, however, be certain stages in the chain of physiological reactions that are more difficult to conclude than others. It is at these critical points in development that slight variations in physiological activity, conditioned by immediate or by previous environmental factors, will have the maximum effect on the course of development. If, for some reason, at one of these critical physiological stages one or more of the reactants necessary for the conclusion of some given developmental process is present in inadequate concentrations owing to an abnormality in a former reaction (i.e. a slight reduction in a particular aspect of physiological activity or metabolic rate), then normal development will cease. The same effect would be obtained if the immediate environmental conditions were such that the rate of physiological reaction was reduced below a certain level. In the latter case the arrest in development might be only temporary, and resumption of activity would occur immediately there was a return to the original environmental conditions. In the former case there can be no continuance of normal development until, by readjustment of physiological processes and concentration of individual reactants, the whole physiological system involved in normal growth can again be set in motion.

Thus, by altering conditions during early development, or by arranging, as in the present work, for physico-chemical differences to be present before actual development starts, diapause can be induced or prevented at a later critical period of development. It follows that any factor which disturbs the normal physiological activity of a developing insect may be capable in itself, or in conjunction with other factors, of causing diapause later during development. These factors need not necessarily be such as are generally termed 'unfavourable', although in the majority of cases an alteration of environmental conditions of sufficient magnitude to cause physiological disturbances inducing diapause is definitely unfavourable to the developing insect. In the present work it is seen that changing the diet of the parent female *Cryptus* from cane-sugar to a more 'balanced' diet of cane-sugar and raisin is a favourable change in so far as the female is concerned; it increases total egg-production some 400 % and the length of life of the female some 100 %, but at the same time it raises the incidence of diapause in her progeny from 2·5 to 36·5 %. Baumberger (1914) also states that codling moth larvae may enter diapause owing to overfeeding, a condition certainly not brought about by unfavourable environmental conditions.

This brings up the question as to the exact definition of 'favourable conditions'. In general the term has a vague significance but lacks scientific precision. Each stage of each insect has a set of conditions that is more favourable for rapid and successful growth than others, but these conditions vary with the stage of the insect and the particular aspect of its life that is being considered. For example, given a generally 'favourable' environment it is of advantage, for the long-term increase of the species, that all individuals should emerge without the incidence of diapause. It is clear that increase of the numbers of the species would be favoured by this. Thus one could postulate that a diet of cane-sugar alone was favourable to *Cryptus* even though egg-production of individual females was lowered and their adult life was considerably less, facts which would indicate that conditions were definitely unfavourable. Although, in general, it is obvious what is meant by favourable or unfavourable conditions these terms must be accepted with caution, and both their immediate and 'long-term' effects considered.

The possible genetical background that has been postulated in a number of examples of diapause may now be considered in the light of the above. Obviously, in a general way, the rate of physiological activity in a developing organism depends on its reactions to environmental influences, and this reaction is governed broadly to the same extent as morphological characters by the genetic constitution of the individual. In the same way as with morphological characters there will be minor genotypic and phenotypic variations between individuals in their general developmental physiology, in speed of development, and in their reaction to the environment. This in turn will resolve itself into a variable susceptibility to enter a state of diapause. Thus there may be a generalized inheritable genetical background for diapause, but no example has yet been found where diapause is definitely controlled by any single factor or group of factors.

In this connexion one may consider the numerous species with a single generation a year where a state of diapause intervenes regularly at a definite stage of the insect. Often this arrest in development is not apparently explicable by peculiarities in immediate or preceding environmental conditions (though further investigation may prove this to be so), and such arrests may be due to physiological disturbances which are definitely part of the inheritable complex of the species. It is possible that with further investigation these cases of diapause will prove to be due to environmental influences, but until such time as this is shown, one cannot dismiss the possibility that the phenomenon has a genetical background, or that examples will be found where a clear-cut inheritance of diapause can be demonstrated.

This aspect of the problem is obviously complicated by the influence of the maternal physiology on the developing eggs, so clearly shown in the experiments recorded here. This influence has also been shown to occur in the silkworm, where transplants of immature ovaries from larvae of bivoltine and polyvoltine races to individuals of another race resulted in the production of eggs showing the voltinism of the new mother (Umeya 1926). There is no necessity to postulate the existence of an inhibitory substance to explain alteration of voltinism (Watanabe 1918*a*, *b*). A similar effect of maternal somatic influence has been demonstrated by Kuhn for the wing coloration of *Ephestia kuhniella* Zell., and it affords a good example of the two types of gene action that might affect diapause, and the principles involved in maternal somatic influence on her progeny. In the one type of gene action its influence is confined locally to the cells in which the genes occur, as is shown by mosaics in wing coloration of *Ephestia* caused by somatic mutation. The second type of gene action is that of the production of diffusible substances, which, diffusing through the tissues or discharged into the body fluid from the cells in which they originated, affect the whole body remote from the point of production. In *Ephestia* such genes occur affecting the pigmentation of the larval epidermis, eyes and testes, the pigmentation of the imaginal eyes and brain, and the *velocity of development and general vitality*. Their action has been demonstrated experimentally by Kuhn & Plagge (1937), Caspari (1933), etc., and it is important to note here that this type of gene may affect the general physiology and rate of development, and 'general vitality', which have been shown to have an important bearing on the occurrence of diapause. These genes, acting through the medium of diffusible substances, may, unlike genes with a purely localized effect, influence the characters of the offspring, since ova developing within the female are exposed to their influence. *Ephestia* larvae which are homozygous for the recessive 'red-eyed' factor, but which are from eggs laid by a heterozygous mother show 'black-eyed' pigment characters in the early larval stages (Kuhn & Plagge 1937), an effect that may also be obtained by implanting into homozygous red-eyed mothers testes or brain tissue from black-eyed *Ephestia* or even from other Lepidoptera. Here the eggs within the female are subject to the influence of diffusible substances, the production of which is genetically controlled in the soma of the parent female. The eggs are so affected that this influence finds expression in morphological characters of the early larvae, and as the larvae grow their own genetic constitution exerts itself and the effect of maternal influence is gradually lost.

It is clear that diapause never occurs 'more or less spontaneously' (Flanders 1944), but is always caused by disturbances in developmental physiology at some time during development, that these physiological variations may be caused by a large number of factors, environmental or possibly genetical, and that they induce diapause immediately or at some subsequent period of development. It has been seen that, correlated with the immense variety of type and severity of physiological disturbances, diapause is not a strictly definable state but merges, on the one hand, into easily reversible temporary arrests in development caused by immediate environmental influences, and on the other hand to cases where severe physiological disturbances bring about high mortality, and deformity of the emerging adults. Also, it is clear that some cases of diapause may possibly be caused by abnormalities of physiology resulting from the accumulation of excretory products, some possibly by deficiencies of hormone-like substances, and some by more or less definite genetical influences. Thus the various theories put forward to account for diapause have some evidence supporting them, but they appear each to deal only with certain aspects of the phenomenon, and the actual fundamental cause underlying all cases of diapause is found to be an abnormal physiological disturbance of developmental processes. It would appear, too, that the beneficial results which the occurrence of diapause confers on a number of species in producing an ideal condition in which the species may carry on over periods of adverse environmental conditions (aestivation and hibernation), is fortuitous, except in so far that adverse conditions at the beginning of a period of possibly injurious heat or cold may cause a condition of diapause in which the remainder of the unfavourable period may successfully be passed. The seasonal life history of many species includes a state of diapause which fits in very well with unsuitable environmental conditions, but it has been seen in many cases that these are not definite genetically fixed states and are themselves dependent on previous environmental influences. Also a number of species (e.g. *Spalangia*) enter a state of diapause in the field when conditions are very suitable for further increase of the species, and here this dormant condition is a definite disadvantage to the species as a whole. Thus the adaptive character of diapause is questionable; even though many examples can be cited to indicate the advantage conferred on the species by this dormant state, further investigation will perhaps show that diapause is of a pathological rather than adaptive nature, and that its usefulness in a number of cases is only fortuitous, even though a superficial consideration indicates otherwise.

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TABLE 3. VARIATION OF OVIPOSITION RATE, PROPORTION OF LARVAL PROGENY ENTERING DIAPAUSE, AND AVERAGE DEVELOPMENTAL TIME OF EMERGENTS WITH THE AGE OF THE PARENT FEMALE

83°–83° F group (23)

total eggs	eggs per ♀ per day	emerging progeny			progeny in diapause		average developmental time	
		♂	♀	%♀		%	♂	♀
262	11·4	26	102	79·7	134	51·1	16·62	17·53
184	8·0	24	105	81·4	55	29·9	16·17	17·70
221	9·6	22	134	85·9	65	29·4	16·32	17·28
235	10·2	35	135	79·4	65	27·7	16·06	17·04
218	9·5	46	120	72·3	52	23·8	15·85	16·91
217	9·4	42	113	72·9	62	28·6	15·93	16·86
188	8·2	45	93	67·4	50	26·6	15·80	16·94
135	5·9	51	38	42·7	46	34·1	15·88	17·03
123	5·3	50	21	29·6	52	42·3	15·91	17·86
127	5·5	53	16	23·2	58	45·7	15·79	18·00
108	4·7	51	8	13·5	49	45·4	15·96	16·25
92	4·0	44	3	6·4	45	48·9	15·73	18·00
68	3·0	39	3	7·2	26	38·2	15·59	18·33
65	2·8	45	5	10·0	15	23·1	15·73	18·00
56	2·4	40	—	—	16	28·6	15·50	—

83°–75° F group (18)

total eggs	eggs per ♀ per day	emerging progeny			progeny in diapause		average developmental time	
		♂	♀	%♀		%	♂	♀
157	8·7	4	16	80·0	137	87·3	23·50	24·50
100	5·6	1	6	85·7	93	93·0	24·00	26·33
96	5·3	3	6	66·7	87	90·6	23·00	24·83
123	6·8	16	20	55·6	87	70·7	23·25	24·30
137	7·6	12	32	72·7	93	67·9	23·08	24·03
138	7·6	10	38	79·2	90	65·2	23·00	23·87
121	6·7	6	31	83·8	84	69·4	23·66	23·84
131	7·3	19	23	54·8	89	67·9	23·00	24·22
102	5·7	14	12	46·2	76	74·5	24·71	24·58
103	5·7	14	7	33·3	82	79·6	25·00	25·43
90	5·0	15	5	25·0	70	77·8	25·27	25·00
78	4·3	10	6	37·5	62	79·5	25·00	25·00
75	4·2	12	7	36·8	56	74·7	25·00	25·29
60	3·3	13	3	18·8	44	73·3	25·00	25·00
67	3·7	17	4	19·0	46	68·7	25·00	27·25

83°–70° F group (11)

total eggs	eggs per ♀ per day	emerging progeny			progeny in diapause		average developmental time	
		♂	♀	%♀		%	♂	♀
88	8·0	1	1	50·0	86	97·7	—	—
40	3·6	—	—	—	40	100·0	—	—
22	2·0	—	—	—	22	100·0	—	—
39	3·5	—	—	—	39	100·0	—	—
50	4·5	—	—	—	50	100·0	—	—
55	5·0	—	—	—	55	100·0	—	—
44	4·0	—	—	—	44	100·0	—	—
59	5·4	—	—	—	59	100·0	—	—
35	3·2	—	—	—	35	100·0	—	—
41	3·7	—	—	—	41	100·0	—	—
42	3·8	—	—	—	42	100·0	—	—
51	4·6	—	—	—	51	100·0	—	—
32	2·9	—	1	100·0	31	96·9	—	35·0
38	3·5	6	1	14·3	31	81·6	—	33·0
45	4·1	—	—	—	45	100·0	—	—

75°–83° F group (7)

total eggs	eggs per ♀ per day	emerging progeny			progeny in diapause		average developmental time	
		♂	♀	%♀		%	♂	♀
89	12·7	16	71	81·6	2	2·2	16·19	17·10
60	8·6	11	49	81·7	—	—	16·00	17·16
79	11·3	16	63	79·7	—	—	15·88	17·14
79	11·3	18	61	77·2	—	—	15·56	16·84
93	13·3	15	71	82·6	7	7·5	15·47	17·07
74	10·6	17	52	75·4	5	6·8	15·82	17·27
60	8·6	23	34	59·6	3	5·0	16·52	17·09
36	5·1	10	26	72·2	—	—	16·10	17·23
45	6·4	15	27	64·3	3	6·7	15·80	16·93
36	5·1	12	23	65·7	1	2·7	16·50	17·09
43	6·1	18	22	55·0	3	5·5	15·89	17·09
29	4·1	13	14	51·8	2	6·9	16·00	16·93
23	3·3	18	4	18·2	1	4·3	16·17	17·25
23	3·3	16	6	27·3	1	4·3	15·94	17·17
28	4·0	16	6	27·3	6	21·4	15·87	17·00

75°–75° F group (26)

total eggs	eggs per ♀ per day	emerging progeny			progeny in diapause		average developmental time	
		♂	♀	%♀		%	♂	♀
232	8·9	43	50	53·8	139	59·9	23·70	25·50
128	4·9	11	31	73·8	86	67·2	23·82	25·45
182	7·0	8	37	82·2	137	75·3	23·75	25·56
177	6·8	14	33	70·2	130	73·4	23·91	25·70
189	7·3	8	31	79·5	150	79·4	24·50	26·00
194	7·5	6	15	71·4	173	89·2	24·80	26·07
188	7·2	10	8	44·4	170	90·4	24·80	26·57
178	6·8	5	7	58·3	166	93·3	25·20	27·17
157	6·0	6	9	60·0	142	90·4	25·80	26·89
172	6·6	9	5	35·7	158	91·9	25·89	24·80
129	5·0	5	1	16·7	123	95·3	23·75	25·00
125	4·8	6	2	25·0	117	93·6	24·17	31·00
118	4·5	1	—	—	117	99·2	28·00	—
100	3·8	—	1	100·0	99	99·0	—	26·00
115	4·4	8	2	20·0	105	91·3	23·75	26·00

75°–70° F group (3)

total eggs	eggs per ♀ per day	emerging progeny			progeny in diapause		average developmental time	
		♂	♀	%♀		%	♂	♀
23	7·7	—	—	—	23	100·0	—	—
16	5·3	—	—	—	16	100·0	—	—
17	5·7	—	—	—	17	100·0	—	—
13	4·3	—	—	—	13	100·0	—	—
18	6·0	—	—	—	18	100·0	—	—
14	4·7	—	—	—	14	100·0	—	—
11	3·7	—	—	—	11	100·0	—	—
22	7·3	—	—	—	22	100·0	—	—
15	5·0	—	—	—	15	100·0	—	—
12	4·0	—	—	—	12	100·0	—	—
3	1·0	—	—	—	3	100·0	—	—
10	3·3	—	—	—	10	100·0	—	—
15	5·0	—	—	—	15	100·0	—	—
12	4·0	—	—	—	12	100·0	—	—
12	4·0	—	—	—	12	100·0	—	—

70°–83° F group (3)

total eggs	eggs per ♀ per day	emerging progeny			progeny in diapause		average developmental time	
		♂	♀	%♀		%	♂	♀
11	3·7	2	—	—	9	81·8	15·50	—
30	10·0	27	—	—	3	10·0	15·63	—
28	9·3	28	—	—	—	—	15·61	—
32	10·7	32	—	—	—	—	15·59	—
28	9·3	28	—	—	—	—	15·43	—
31	10·3	31	—	—	—	—	15·58	—
26	8·7	26	—	—	—	—	15·62	—
31	10·3	31	—	—	—	—	15·90	—
28	9·3	28	—	—	—	—	15·68	—
23	7·7	23	—	—	—	—	15·78	—
27	9·0	27	—	—	—	—	15·67	—
24	8·0	24	—	—	—	—	15·69	—
26	8·7	26	—	—	—	—	15·54	—
5	1·7	5	—	—	—	—	15·00	—
—	—	—	—	—	—	—	—	—

70°–75° F group (2)

total eggs	eggs per ♀ per day	emerging progeny			progeny in diapause		average developmental time	
		♂	♀	%♀		%	♂	♀
17	8·5	3	5	62·5	9	52·9	23·67	24·80
5	2·5	—	2	100·0	3	60·0	—	25·00
8	4·0	—	7	100·0	1	12·5	—	23·84
11	5·5	4	6	60·0	1	9·1	24·00	23·83
12	6·0	1	8	88·9	3	25·0	22·00	24·00
16	8·0	4	8	66·7	4	25·0	22·67	24·75
11	5·5	8	3	27·3	—	—	22·25	24·00
11	5·5	8	3	27·3	—	—	21·37	24·00
17	8·5	8	9	53·0	—	—	21·00	23·44
12	6·0	6	6	50·0	—	—	21·33	23·16
17	8·5	12	5	29·4	—	—	22·92	23·00
13	6·5	8	5	38·5	—	—	23·00	23·20
12	6·0	7	5	41·7	—	—	23·00	23·80
9	4·5	9	—	—	—	—	23·00	—
12	6·0	9	3	25·0	—	—	24·00	23·00

83°–70°–83° F group (5)

total eggs	eggs per ♀ per day	emerging progeny			progeny in diapause		average developmental time		age of parent ♀ in days when eggs laid
		♂	♀	%♀		%	♂	♀	
17	3·4	—	—	—	17	100·0	—	—	13
14	2·8	—	—	—	14	100·0	—	—	14
28	5·6	—	—	—	28	100·0	—	—	15
changed to 83° F									
42	8·4	4	2	33·3	36	85·7	18·75	21·00	16
31	6·2	3	—	—	28	90·3	17·75	—	17
33	6·6	—	—	—	33	100·0	—	—	18
27	5·4	3	—	—	24	88·9	16·33	—	19
23	4·6	7	—	—	16	69·6	16·57	—	20
18	3·6	6	—	—	12	66·7	16·33	—	21
29	5·8	14	—	—	15	51·7	16·21	—	22
19	3·8	12	1	7·7	6	31·6	16·58	21·00	23
20	4·0	15	—	—	5	25·0	15·80	—	24
21	4·2	16	—	—	5	23·8	16·19	—	25
14	2·8	9	—	—	5	35·7	15·89	—	26
11	2·2	8	—	—	3	27·3	15·87	—	27

In each group the figures are obtained by the addition of each day's oviposition of a number of females, and the progeny resulting therefrom. Since with age the oviposition rate tends to decrease only 15 days of life are given, since in this period the pertinent changes in the various characters are visible. In the 83°–70°–83° F group the results from the 13th to the 27th days are given since the first 15 days are the same as to the 83°–70° F group, the change back to 83° F occurring on the fifteenth day.

The figures in brackets after each group heading indicate the numbers of individual experiments used to obtain the totals.