3

Waite Agricultural Research Institute,

Adelaide, South Australia.

ECOLOGICAL STUDIES ON THE DIAMOND-BACK MOTH (*PLUTELLA MACULIPENNIS* CURTIS) AND ITS PARASITES.

A thesis submitted

by

A. S. ATWAL

to the University of Adelaide in partial fulfilment of the requirements for the degree of Doctor of Philosophy.

November, 1953.

INDEX I.

CHAPTER.	CONTENTS.	PAGE.

INDEX (Contd.) II.

Chapter 1.

I N T R O D U C T I O N

Painter (1936) criticized the classification of phytophagous insects as polyphagous, oligophagous and monophagous which was based on lists of plants which an insect ate rather than those which furnished equal nourishment. He pointed out that different varieties of a single species of plant differed from each other in nutrients. An insect may feed on a plant but fail to grow as for example, the larva of the potato beetle on Solanum hendersonii (Trouvelot et al, 1933). Those insects which may feed on more than one host species may show unhealthy growth, may be more susceptible to disease or have a higher death rate on some than on others; and this may be due to a deficiency of some nutrients in the poorer quality food. When Melanoplus differentialis was fed on a mixed diet of lettuce, wheat leaves and apple fruit 83 percent reached the adult stage, on wheat alone 72 percent, on barley 44 percent, on rye 42 percent, on lettuce 21 percent and on oats 4 percent (Hodge, 1933). The quality of food eaten may also affect the reproductive capacity. The flea beetle Epitrix tuberis lived for a shorter time and laid fewer eggs when its food was bean, ground cherry, marsh elder or kochia than when it fed on potato; it responded to potato foliage within 2-3 days when this was substituted for less favourable food (Hill, 1946).

In the so called monophagous insects the differences in plant nutrients affecting growth would vary from variety to variety or with change in physiological condition of the plants or with difference in type of soil and also as affected by other environmental factors through the host plants. Since proper nutrition is necessary for the survival and growth of individuals and for their normal reproduction, these factors must play an important role in determining the economic importance of the species. Most of the work done on nutrition of insects refers to the rate of growth and metamorphosis of species which are scavengers or live on stored food-stuffs like grain or clothing. Little work has been done on phytophagous and parasitic insects.

In certain insects the nutritional requirements of the sexes have been found to be different. There are some species of aphelinid parasites in which the females before mating are attracted only to the parasitized hosts and the eggs that are deposited develop as hyperparasites and transform into males but after mating the females are attracted to unparasitized hosts and the progeny develop into females. Thus the females are primary parasites but the males are hyperparasites. In some other hymenopterous parasites larger hosts are selected for fertilized eggs which develop into females while smaller hosts are used only for unfertilized eggs which develop into males (Chewyreuv, 1913: Clausen, 1939).

The activities of many insects are known to be influenced not only by temperature and humidity but also by light intensity and wave length or even by polarization (Vowels, 1950). In certain insects the seasonal occurrence of diapause is evidence that photoperiodism has a profound influence on their life cycle. In addition to the direct effect of light on insects its effect through the food plants (if any) should also be considered. When the behaviour of an insect in a given environment is being studied the direct effect of the physical factors is important; so are their indirect effects through the biological factors of the environment.

The presence of diapause may enable an insect to survive during periods when the environment is not favourable for development. Both incipient and intense forms of diapause should be physiologically very much the same. Diapause shows a marked seasonal incidence in many different sorts of insects. The univoltine bug Reduvius enters diapause towards the middle of winter irrespective of any of its five instars (Readio, 1931). In a two generation area the proportion of Cydia larvae that entered diapause varied from 27 percent to 50 percent in a period of 5 years' study but the date on which they entered diapause varied ± 3 days from 24th August (Garlick, 1948). Similarly diapause occurs seasonally in other insects like the larvae of Laspeyresia (Dickson, 1949), Loxostege (Pepper, 1938) and Phlebotomus (Theodor, 1934); pupae of Antheraea (Zolotarev, 1938), Deilephila (Heller, 1926) and Telea (Dawson, 1931); adults of Halicta (Picard, 1926) and Leptinotarsa (Breitenbrecher, 1918), etc. Leaving aside a few exceptions like Lucilia (Cousin, 1932), Popillia (Ludwig, 1922) or

Spalangia (Simmonds, 1918) etc, the incidence of diapause in multivoltine life cycles seems to be closely related to the season of the year. Components of the environments that change with the season are temperature, humidity, maturity of food and duration of day-light (Andrewartha, 1952).

In this thesis I describe certain experiments with *Plutella maculipennis* Curtis. (Tineidae) and its parasites. The larvae of *P. maculipennis* were reared on food of different qualities, at different temperatures and they were exposed during their development to different photoperiods. The plants on which the larvae were reared were also exposed to different photoperiods during their development to see whether this influenced their quality as food for the insect. The respective influenses of the treatments were assessed by recording the speed of development of the larvae, the duration of life of the adults and their fecundity.

Chapter 2.

MATERIAL and METHOD

This research work was done on diamond-back moth of cabbage *Plutella maculipennis* Curtis. (Tineidae : Lep), its larval parasite *Horogenes* (*Angitia*) *cerophaga* Grav. (Ichneu : Hymen) and pupal parasite *Diadromus collaris* Grav. (Ichneu : Hymen).

Most of the eggs for the experiments were laid by female moths which had been reared in the laboratory - perhaps during previous experiments. When this source was inadequate, especially in the spring pupae or adult moths were collected from cabbage fields in the Waite Institute grounds or suburbs of Adelaide mostly from Findon and Montacute.

Moths collected from the fields were kept in batches of 20-25, males and females together, in cylindrical specimen tubes 5" x 1" containing a piece of green cabbage leaf and corked or covered with a piece of muslin cloth at the mouth. They laid eggs quite readily on the piece of leaf inside or even on the cylindrical walls of the tubes. The eggs could be removed easily with a camel hair brush soaked in a dilute solution of sodium hypo-chlorite. Sometimes the water transpired by the leaf would condense on the sides of the tube and drown the moths or stick them to the glass by their wings so that they died. Except when this happened the moths laid plenty of eggs and it was possible to get enough for each experiment of nearly the same age - varying within 24 to 72 hours. When the eggs were got from material left over from the previous experiment they were usually from single females which had been kept with two or three males in specimen tubes 2" x 13/16".

Moths were offered dilute honey solution by soaking a plug of cotton wool in it and sticking that to the inside of a cork at the mouth of a tube. Since the moths are negatively geotropic and the specimen tubes in which they were encaged stood upright they reached the food quite quickly. Moths did not hesitate to lay eggs even in the absence of honey solution or water though in high temperatures and dry atmosphere they died very quickly if some watery food were not provided.

Petri dishes containing eggs on damp filter papers were placed in Fowler's air-tight glass jars. At the bottom of a jar another damp filter paper was placed to provide sufficient humidity inside without letting loose any free water. The jars were then placed in incubators which maintained the temperature constant within $\pm$ 0.2°C. Ordinarily eggs were incubated at the same constant temperatures that were used subsequently for feeding experiments. But sometimes eggs laid late were brought from lower to a higher temperature to quicken the development so that they could be hatched at the same day or very near to the ones laid earlier. In these cases caterpillars were distributed equally in all the treatments.

Such extremes of temperatures as 11°C and 25°C appeared to have some harmful effects on the normal growth of caterpillars. Temperatures ranging from 17°C - 24°C were found to be quite optimum and most of the experiments were done at temperatures within this range.

The eggs of Plutella are fairly resistant to excessive water around them and in dry atmosphere too they can remain alive for a limited time. Eggs which are nearly ready to hatch may be stimulated to hatch by dryness. On the other hand eggs which are not quite ready to hatch may be hampered in their development or may be killed by exposure to dryness. Special care, therefore, needs to be taken to keep the filter paper just damp particularly as the time of hatching approaches. Eggs were placed on the filter papers either singly or in batches; they developed and hatched equally well in either case. Since the newly-hatched caterpillars are very small they can drown themselves in a slight excess of water that might be ignored on a filter paper, or even in the microscopic droplets of water sticking to the inside of jars, it is very important to keep the right humidity conditions after hatching.

In different experiments as mentioned in their respective places, caterpillars hatched from within 6-8 or 12 hours were distributed at random in all the treatments, unless stated otherwise, as one or more than one lots. During these intervals of time no food was given to the larvae and no visible harm was seen done to them but if they were allowed to roam about for more than 12 hours they appeared to have exhausted themselves by constant locomotion. If larvae which had so exhausted themselves were later transferred to food, either they could not appreciate its presence or they failed to mine in despite repeated attempts to bite; and consequently they died. In the presence of excessive dampness inside the hatching jars, however, they became exhausted, if not half drowned, far more quickly.

Caterpillars were reared in specimen glass tubes 2" x 13/16", corked on top. At their bottom circles of filter paper were spread which were irrigated with a drop of water every morning for the first few days of the caterpillars' life so as to keep the pieces of cabbage leaf inside turgid. A piece of cabbage leaf ¾" x ¾" for a larva was considered of a reasonable size for a start. As the larvae grew and chances of losing them were reduced the size of the leaf was increased. In all the food experiments, within any treatment, after cutting the pieces of cabbage leaves they were thoroughly mixed before distribution to various caterpillars under observation. Any unhealthy or abnormal looking (virus attached) leaves were rejected. Mid ribs were not given.

Within a few hours of the transference of caterpillars on leaves they mine in usually from the lower surface (probably because it is easier to cut through the spongy mesophyll than through the palisade layer). But they can bore through the upper surface also. During the first two instars they feed inside mines changing to a new one after the first moulting. Quite commonly the first exuvium was observed outside a mine.

The first change of food was regulated in such a way that at any one temperature it was done after the first moulting to avoid injury to the small first instar caterpillars. For example at 24-22°C, 20°C or 18-17°C food was changed on the 3rd, 4th or 5th day respectively. However, it was changed earlier if perchance it became yellowish before that time. Subsequently, food was changed every other day and at the same time tubes were also cleaned. In certain conditions when the food given was undesirable, a high mortality was noticed which was found to be associated with some species of bacteria and mould.

For observations the start of the prepupal stage was taken as from the time caterpillars started spinning and pupal stage as after the time the last larval skin was pushed back towards the anal end of the silken cocoon. As mentioned in respective places, in the tables for analysis of variance, the prepupal life was either added to the larval or pupal life. When the duration of the life of larvae or pupae was being measured observations were taken after every 8 or 12 hours depending upon an experiment and those which had completed a certain stage of development were considered to have done so at the mid-point of the duration of that period.

The pupae were left in cleaned tubes along with a little piece of leaf to provide humidity and were not separated out of their cocoons unless they were needed for weighings.

Sexes could be differentiated as easily in adults as in pupal stages (Sexes in pupae : Robertson, 1939). The female moths were recognized by a small tuft of hair at the end of the abdomen whereas males by the two distinct valves. In those experiments where the fecundity of a female was being measured two or three males were placed in the tube with each female because some males were sterile. The males were usually, one bred in the laboratory and the others from the field. This increased the chance that there would be at least one fertile male in the tube with the female. If any of the females failed to lay eggs her males were replaced by fresh ones to ensure that at any one time a fertile male was available.

The larval parasite Horogenes (Angitia) cerophaga and the pupal parasite Diadromus collaris were also reared at different temperatures to test their oviposition behaviour and to discover how many eggs they laid. They were kept with the host material in 5" x 1" specimen tubes with pieces of muslin cloth ringed around their mouths and a split raisin attached to the inside. The parasitized hosts were dissected under a binocular microscope after every 24 hours so that a daily record of the number of eggs laid by the parasites could be kept.

Chapter 3.

R E S U L T S

---

x = Significant at 5%
xx = Significant at 1%
xxx = Significant at .1%
x = Interaction
d.f.= degree of freedom
S.S = Total sum of squares
M.S = Mean square
G.M = General mean

EXPERIMENT 1.

Effect of cabbage leaves of different ages on some of the characteristics of Plutella.

A factorial experiment was designed in which larvae were reared at two temperatures and on four different foods. Levels of the factors were:

Temperature : 18°C and 25°C.

Food : 1. White leaves from the heart of a cabbage plant, say P_1

2. Green leaves, vigorously growing, from another cabbage plant P_2 (2 feet away from P_1 in the field)

3. Mature leaves from plant P_1

4. Old senescent leaves from plant P_1

Observations on the following characteristics were taken both on males and females separately:-

Characteristics studied.	No. of observations in each treatment.
i. Speed of development in larval life (hatching to pupation)	12
ii. Live weight of pupa	12
iii. Weight of silk produced (cocoon)	12
iv. Weight of dry matter of pupa	5
v. Ratio of dry matter to live weight of pupa	5

Eggs were taken from moths reared in the laboratory. Each of the treatments shown above was started with 35 caterpillers hatched within 8 hours on 8th April, 1952, and it was expected that some of them would die while being reared. All the young larvae on mature and old senescent leaves failed to mine in and died within 48 hours. On 10th April, therefore, a fresh lot of larvae was started for these sets of treatments, feeding them on tender green leaves during their first instar, and then changing to the experimental foods. Even then they did not survive on the old senescent leaves.

To measure the duration of larval life observations were taken twice a day at 9 a.m. and 5 p.m. Weighings of the wet weight of pupae were done 24 hours after pupation at 25°C and 48 hours after at 18°C to let the chrysalis become reasonably hard in order to avoid injury at the time the cocoon was removed.

To get the weight of dry matter pupae were dried in the oven at 102°C ; the first reading was taken after 24 hours and the second after 48 hours. During the period of transition of pupae from the oven to the balance, they were kept in a desiccator.

The silk (cocoons without the last larval skin) was weighed on a 5 m.gm. torsion balance.

Tables showing summaries of results and analyses of variance for different characteristics studied are given in respective order.

Table 1.

(a) **Mean length of larval life (hatching to pupation) in days at different levels of temperature and quality of food.**

Temperature	18°C		25°C		18°C	25°C	Mean of 18° x 25°		Mean
Sex	Male	Female	Male	Female	Male x Female	Male x Female	Male	Female	
S.D. ±	(0.30)[a]				(0.21)[b]		(0.21)[b]		(0.15)[c]
Food:									
White leaves	16.6	17.3	8.4	8.6	16.9	8.5	12.5	12.9	12.7
Green leaves	16.5	16.8	8.4	8.8	16.7	8.6	12.4	12.8	12.6
Mature leaves	21.3	23.0	9.2	9.6	22.2	9.4	15.2	16.3	15.8
S.D. ±	(0.17)[d]				(0.12)[e]		(0.12)[e]		G. Mean
Mean	18.1	19.0	8.7	9.0	18.6	8.8	13.4	14.0	13.7

Least significant differences:

	5%	1%	.1%
a	0.8	1.1	1.4
b	0.6	0.8	1.0
c	0.4	0.5	0.7
d	0.5	0.6	0.8
e	0.3	0.4	0.6

(b) **Analysis of variance** : (Larval life in days)

Variance due to	d.f.	S.S.	M.S.
Total	143	4045.4	
Treatments	11	3907.0	
Temperature	1	3409.6	3409.6 ***
Food	2	306.6	153.3 ***
Food x Temp.	2	165.8	82.9 ***
Sex	1	14.9	14.9 ***
Sex x Temp.	1	3.3	3.3
Sex x Food	2	3.4	1.7
Sex x Food x Temp.	2	3.4	1.7
Error	132	138.5	1.05

The effects of temperature, food and sex and interaction of food and temperature were significant at .1 percent level. Caterpillars developed significantly more slowly on mature leaves as compared with young green and white leaves and this speed was still slower at 18°C than at 25°C. Females developed more slowly than males.

Table 2

(a) Mean live weight of pupa in m.gms at different levels of temperature and quality of food.

Temperature	18°C		25°C		18°C	25°C			Mean
Sex	Male	Female	Male	Female			Male	Female	
S.D. ±	(0.183)[a]				(0.129)[b]		(0.129)[b]		(0.091)[c]
Food:									
White leaves	6.67	8.13	4.86	5.54	7.40	5.20	5.76	6.83	6.30
Green leaves	6.62	8.41	4.46	5.55	7.51	5.01	5.54	6.98	6.26
Mature leaves	6.17	6.15	4.15	4.51	6.16	4.33	5.16	5.33	5.24
S.D. ±	(0.106)[d]				(0.075)[e]		(0.075)[e]		G.Mean
Mean	6.49	7.56	4.49	5.20	7.02	4.84	5.49	6.38	5.93

Least significant differences:

	5%	1%	.1%
a	0.51	0.67	0.85
b	0.36	0.47	0.60
c	0.25	0.33	0.43
d	0.29	0.39	0.49
e	0.21	0.27	0.35

(b) Analysis of variance : (Live weight of pupa)

Variance due to	d.f.	S.S.	M.S.
Total	143	303.661	
Treatments	11	250.732	
Temperature	1	171.065	171.065 xxx
Food	2	34.220	17.110 xxx
Food x Temp.	2	2.765	1.383 x
Sex	1	28.792	28.792 xxx
Sex x Temp.	1	1.179	1.179
Sex x Food	2	10.197	5.098 xxx
Sex x Food x Temp.	2	2.514	1.257 x
Error	132	52.929	0.401

The effects of temperature, food, sexes and interaction of food x sexes were significant at P <.1 percent and that of interaction food x temperature significant at 5 percent level. At 18°C the live weight of pupa was higher than at 25°C. Pupae did not become so heavy on mature leaves as on white and young green leaves. Females were heavier than males on the whole, but on mature leaves their weight was reduced relatively more than that of the males. Both sexes on mature leaves as compared with the other two types of food had a greater drop in weight at 18°C than at 25°C.

Table 3.

(a) Mean weight of silk (cocoon) in m.gms. at different levels of temperature and quality of food.

Temperature	18°C		25°C		18°C	25°C			Mean
Sex	Male	Female	Male	Female			Male	Female	
S.D. ±	$(0.0106)^{a}$				$(0.0075)^{b}$		$(0.0075)^{b}$		$(0.0053)^{c}$
Food:									
White leaves	0.222	0.257	0.167	0.174	0.239	0.170	0.194	0.215	0.205
Green leaves	0.225	0.258	0.164	0.196	0.242	0.180	0.195	0.227	0.211
Mature leaves	0.220	0.212	0.137	0.148	0.216	0.142	0.178	0.180	0.179
S.D. ±	$(0.0061)^{d}$				$(0.0043)^{e}$		$(0.0043)^{e}$		G.Mean
Mean	0.222	0.242	0.156	0.173	0.232	0.164	0.189	0.207	0.198

Least significant differences:		5%	1%	.1%
	a	0.029	0.039	0.049
	b	0.021	0.027	0.035
	c	0.015	0.019	0.025
	d	0.017	0.022	0.029
	e	0.012	0.016	0.020

(b) Analysis of variance: (Weight of silk)

Variance due to	d.f.	S.S.	M.S.
Total	143	0.3949	
Treatments	11	0.2166	
Temperature	1	0.1667	0.1667 ***
Food	2	0.0275	0.0138 ***
Food x Temp.	2	0.0009	0.0005
Sex	1	0.0121	0.0121 **
Sex x Temp.	1	0.0001	0.0001
Sex x Food	2	0.0060	0.0030
Sex x Food x Temp.	2	0.0033	0.0017
Error	132	0.1783	0.00135

The effects of temperature and food were significant at .1 percent level and that of sex at 1 percent. At 18°C more silk was produced than at 25°C. On mature leaves less silk was produced but there was no difference between young green and white leaves. Females made heavier cocoons than males.

Table 4.

(a) Mean weight of dry matter of pupa in m.gms. at different levels of temperature and quality of food.

Temperature	18°C		25°C		18°C	25°C			Mean
Sex	Male	Fe-male	Male	Fe-male			Male	Fe-male	
S.D. ±	(0.0102)[a]				(0.0072)[b]		(0.0072)[b]		(0.0051)[c]
Food:									
White leaves	0.165	0.226	0.120	0.160	0.195	0.140	0.142	0.193	0.168
Green leaves	0.167	0.249	0.113	0.169	0.208	0.141	0.140	0.209	0.174
Mature leaves	0.160	0.169	0.104	0.109	0.164	0.106	0.132	0.139	0.135
S.D. ±	(0.0059)[d]				(0.0042)[e]		(0.0042)[e]		G.Mean
Mean	0.164	0.215	0.112	0.146	0.189	0.129	0.138	0.180	0.159

Least significant differences:

	5%	1%	.1%
a	0.029	0.039	0.051
b	0.021	0.027	0.036
c	0.015	0.019	0.025
d	0.017	0.022	0.029
e	0.012	0.016	0.021

(b) Analysis of variance: (Weight of dry matter of pupa)

Variance due to	d.f.	S.S.	M.S.
Total	59	0.13525	
Treatments	11	0.11048	
Temperature	1	0.05412	0.05412 xxx
Food	2	0.01743	0.00871 xxx
Food x Temp.	2	0.00035	0.00018
Sex	1	0.02697	0.02697 xxx
Sex x Temp	1	0.00111	0.00111
Sex x Food	2	0.01013	0.00507 xxx
Sex x Food x Temp.	2	0.00037	0.00018
Error	48	0.02477	0.00052

The same effects were significant as in live weight of pupa except that interaction of food x temperature was not significant which suggests that the relatively greater influence of food on live weight at 25°C than at 18°C may have been due largely to differences in the water content of the body, unless it was due to chance; the interaction was significant only at $P < 0.05$.

Table 5.

(a) Mean ratio of live weight to dry matter in the pupa at different levels of temperature and quality of food.

Temperature	18°C		25°C		18°C	25°C			Mean
Sex	Male	Female	Male	Female			Male	Female	
S.D. ±	(0.107)[a]				(0.075)[b]		(0.075)[b]		(0.053)[c]
Food:									
White leaves	4.06	3.52	3.92	3.47	3.79	3.70	3.99	3.50	3.75
Green leaves	3.85	3.70	3.82	3.53	3.78	3.67	3.83	3.62	3.72
Mature leaves	4.11	3.84	4.10	3.92	3.97	4.01	4.10	3.88	3.99
S.D. ±	(0.062)[d]				(0.044)[e]		(0.044)[e]		G.Mean
Mean	4.00	3.69	3.95	3.64	3.85	3.79	3.98	3.66	3.82

Least significant differences:	5%	1%	.1%
a	0.30	0.41	0.53
b	0.22	0.29	0.38
c	0.15	0.19	0.25
d	0.18	0.23	0.31
e	0.12	0.17	0.22

(b) Analysis of variance: (Ratio of live weight to dry matter of pupa)

Variance due to	d.f.	S.S.	M.S.
Total	59	5.488	
Treatments	11	2.758	
Temperature	1	0.043	0.043
Food	2	0.889	0.444 **
Food x Temp.	2	0.062	0.031
Sex	1	1.463	1.463 ***
Sex x Temp.	1	0.001	0.001
Sex x Food	2	0.253	0.127
Sex x Food x Temp.	2	0.047	0.023
Error	48	2.730	0.057

The effect of food was significant at 1 percent and that of sex at .1 per cent. On mature leaves the ratio was higher due to a greater percentage of water in their bodies. Males had a higher ratio than females which means the latter were more solidly built.

Plate 1. Wooden boxes used to control hours of daylight on cabbage plants grown in the field (Expt. 2).

EXPERIMENT 2.

Influence of quality of food and photoperiod at different temperatures on fecundity and speed of development of Plutella.

Caterpillars were reared at two temperatures viz. 18°C and 21°C on pieces of leaf from cabbage plants grown in the field in 9 hours and 15 hours of daylight. Further, in the incubators growing larvae were exposed to electric light during the daytime, for either 9 hours or 15 hours. Thus levels of different factors were:-

Temperature:	18°C, 21°C.
Food:	A - Cabbages grown in long-day of 15 hours of daylight B - Cabbages grown in short-day of 9 hours of daylight
Light-exposure:	9 hours, 15 hours (in incubators).

The experiment was started with caterpillars hatched within 6 hours. An extra set of caterpillars was reared on food A in 15 hours of exposure to light at each temperature. In the adult stage those reared at 18°C were brought to 21°C and vice versa. The fecundity of those moths was compared with that of those reared and kept at the same temperatures throughout the life cycle because it was thought that an abrupt change of temperature at the beginning of the adult stage might influence the fecundity of the moths.

The two types of plants were grown in six little plots of five plants each in the field; to overcome soil fertility differences the plots were distributed at random. Since the plants were grown during the summer months of November and December, those required to be grown in a short-day were covered by light-proof wooden boxes during the night and for part of each day. The boxes 18" x 18" x 16" were lined with Sisalkraft and were painted white on the outside to reflect sun-rays and black on the inside to help provide complete darkness (Plate 1). Three predetermined plots were covered by such boxes at 5 o'clock every evening and uncovered at 9 o'clock next morning. To ensure total darkness, every evening after inverting the boxes their edges were sealed with soil all around. Plants in the other three plots growing in 15 hours of daylight were also covered with similar boxes except that one of their walls was made of glass. These boxes were also placed over plants and removed at the same time as the others so as to provide equal conditions of temperature to the plants growing under them; the glass walls were kept facing the south to avoid direct rays of the sun from penetrating inside a box and thus possibly raising the temperature.

The light-conditions were first controlled about two weeks after the seedlings had been transplanted; and six weeks later the caterpillars were first fed on them. During the course of the experiment plants remained growing in the same conditions. For feeding leaves were picked at random and were cut into square pieces which were thoroughly mixed before distributing within the various treatments.

The caterpillars used were hatched from eggs collected in Experiment 3; as hatching started, after every 6 hours they were distributed among all the treatments in equal numbers so that within 24 hours each treatment was started with 60 larvae. Two caterpillars were reared in each specimen tube.

The duration of larval and pupal life of 20 individuals from each treatment selected at random, was measured after every 8 hours. Eggs of all the females that reached the adult stage were counted every day; there were, therefore, a variable number of observations in the different treatments. Each female moth was provided with two males, though not necessarily the same two, throughout her life.

Remarks : Plants grown in controlled photoperiod in the field showed appreciable response to this treatment within six weeks; towards the end of this period those grown in 9 hours of day-light were 3"-4" high whereas the ones grown in 15 hours were 7"-9", which showed that long photoperiod favoured plant growth.

Table 6.

(a) Duration of larval and pupal life and fecundity of moths at different levels of temperature, photoperiod, and quality of food.
(Means per insect).

Treatments			Fecundity		Speed of Development	
Food grown in	Caterpillars reared in		No. of Females	Av. No. of eggs	Length of larval life (days)	Length of prepupal + pupal life (days)
	Hours of light each day	Temp. °C.				
Long-day	9	18	15	175	15.3	10.4
Short-day	9	18	19	193	14.6	10.3
Long-day	15	18	15	229	14.0	10.1
Short-day	15	18	18	208	14.2	10.2
Long-day	9	21	12	157	10.3	7.4
Short-day	9	21	15	125	10.4	7.1
Long-day	15	21	14	191	10.6	7.3
Short-day	15	21	20	150	10.6	7.2

(b) Summary of effects. (Mean per insect)

Effect of:	No. of eggs per moth	Length of larval life (days)	Length of prepupal + pupal life (days)
Mean S.D. ±	179 (13.89)	12.5 (0.16)	8.7 (0.10)
Food (Short-day - Long-day	-19.0	-0.1	-0.1
Light exposure (15 hrs. - 9 hrs.)	32.0 x	-0.3 x	-0.1
Light x Food	-12.0	0.3 x	0.1
Temperature (21°C - 18°C)	-45.5 xx	-4.0 xxx	-3.0 xxx
Temp x Food	-17.5	0.2	-0.1
Temp x Light	- 2.5	0.5 xxx	0.1
Temp. x Food x Light	7.5	-0.3 x	-0.01

Least significant effects:

5%	27.2	0.3	0.20
1%	35.8	0.4	0.26
.1%	45.7	0.5	0.33

Table 6. (Cont'd)

(c) Interactions: (length of larval life); (Mean per insect)

Light x Food				Temperature x Light			
Light	9 Hrs.	15 Hrs.	Mean	Light	9 Hrs.	15 Hrs.	Mean
Food:				Temp.:			
Short-day	12.9	12.3	12.6	18°C	14.9	14.1	14.5
Long-day	12.5	12.5	12.5	21°C	10.4	10.6	10.5
Mean	12.7	12.4			12.7	12.4	

(d) Analyses of Variance.

Variance due to	d.f.	S.S.	M.S.
(i) Number of Eggs laid:-			
Total	150	983961.0	
Treatments	9	135844.0	15093.8 **
Error	141	848117.0	6015.0
(ii) Length of larval life (days):-			
Total	199	1025.9	
Treatments	9	840.8	93.4 ***
Error	190	185.1	0.97
(iii) Length of prepupal + pupal life (days):-			
Total	199	548.9	
Treatments	9	471.1	52.34 ***
Error	190	77.8	0.41

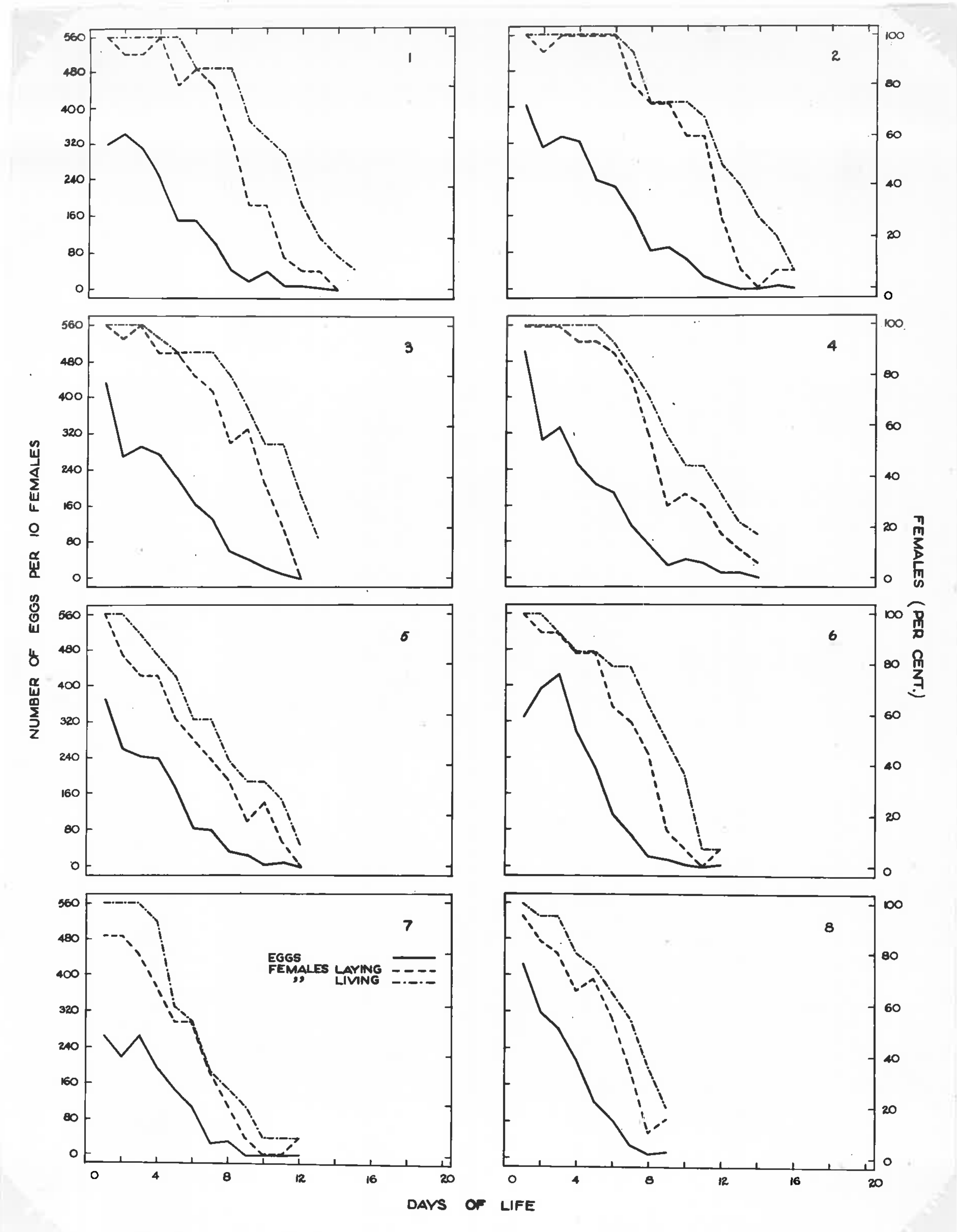

Fig. 1. Graphs showing the fecundity and oviposition behaviour of Plutella moths at different levels of temperature, photoperiod and quality of cabbage leaves (Expt. 2).

Graph No.	Treatment		
	Food grown in	Caterpillars reared in	
		Hrs. of light each day	Temperature °C
1	Long day	9	18
2	Short day	9	18
3	Long day	15	18
4	Short day	15	18
5	Long day	9	21
6	Short day	9	21
7	Long day	15	21
8	Short day	15	21

Table 7.

Effect of change of temperature on fecundity.

Treatments				Fecundity of Female Moths		
Food grown in	Insects reared in					
	Larvae		Adults			
Daily exposure to light (Hours)	Daily exposure to light (Hours)	Temperature °C	Temperature °C	No. laying eggs	Av.No. of eggs	S. D. ±
15	15	18	18	15	229	20.02
15	15	18	21	14	152	20.72
15	15	21	18	9	184	25.85
15	15	21	21	14	191	20.73

Significant differences:

The only significant effect in Table 7 is that of raising the temperature from 18°C to 21°C ($P < .01$).

At 18°C more eggs were produced (46 eggs per female) than at 21°C ($P < .01$). Caterpillars reared in 15 hours' photoperiod produced significantly more eggs ($P < .05$) than in 9 hours' photoperiod with a difference of 32 eggs per female, but the length of larval life was longer at the shorter photoperiod, being one-third of a day more. Larvae feeding on plants grown in 9 hours of daily light developed more slowly when exposed to 9 hours of light than when exposed to 15 hours of light each day ($P < .05$), but those feeding on plants grown in 15 hours of light each day developed equally quickly whether they were exposed to 9 hours or 15 hours of light each day in the incubator. At 21°C the shortening of life was not as much in the 15 hours' photoperiod as in the 9 hours, or conversely, at 18°C the lengthening of life was not as great in the 9 hours' photoperiod as in the 15 hours ($P < .001$). Apart from temperature no other factor influenced the length of pupal life. Those caterpillars which were reared at 18°C and then transferred to 21°C in the adult stage laid fewer eggs than those which were reared and kept at 18°C throughout their life cycle. Figure 1 shows the graphs of oviposition behaviour and longevity of female moths in different treatments.

EXPERIMENT 3.

Influence of temperature and photoperiod on speed of development and fecundity of Plutella.

Caterpillars were reared at 20°C and 24°C in 15 hours and 9 hours exposure to electric light (40 watts) in incubators.

For starting this experiment moths were caught in the fields under early-spring cabbages and swede crops. They laid eggs at 20°C which were incubated at 24°C. The hatching of the larvae was spread over 4 days. Each larva was placed on the appropriate food within 6 hours of hatching. They were reared individually in separate tubes.

Marked differences were observed in the speed of development between larvae hatched on different days. These differences were therefore removed from the estimate of error. Due to unequal survival, there was a varying number of replications in different treatments with respect to the measurement of both the length of life and the fecundity.

Each female on emergence was provided with three males, one from the experiment and two from the fields collected in pupal stage.

Remarks:

1. The number of caterpillars started in each treatment on different days were: 18 on 24th October; 26 on 25th October; 6 on 26th October; and 19-20 (varying in different treatments) on 28th October. The caterpillars that hatched on the 24th were given tender green leaves from a plant say No. 1, of the same stock as had been used in experiment 8; (there was very high mortality then, which I suspected might be due to undesirable food). In their second instar white leaves from the heart of another plant say No. 2 from a different stock (probably different variety) were given to them. On the other three dates this food from plant No. 2 was given to larvae from the start. After this plant was eaten up another one of the same variety was used for the rest of the larval period in all treatments. These three plants of cabbage were growing in the field within a distance of two feet from each other. As may be seen from the Table 8a there was no difference in the length of life of the caterpillars hatched on 24th and 25th.

The greatest difference in the food occurred between these two dates whereas there was no difference in the food given to those hatching on the 25th, 26th and 28th. It therefore seems likely that the difference in the speed of development of the larvae which hatched on the first two days and those which hatched on the last two days must be due to some other cause.

2. On the 24th when the experiment was started, electric lights were put on in the incubators and from then on the developing eggs lying inside remained in continuous light. Thus the eggs that hatched on the 25th remained in light for 24 hours; those on the 26th for 48 hours; and those on the 28th had their entire embryonic development in continuous light.

Table 8.

(a) Average length of larval + pupal life (days) at different levels of temperature and photoperiod.

Temperature	24°C				20°C				Weighted Mean
Photoperiod	15 Hrs.		9 Hrs.		15 Hrs.		9 Hrs.		
Date	No. of insects	Av. life	No. of insects	Av. life	No. of insects	Av. life	No. of insects	Av. life	
24th Oct.	3	14.6	2	17.9	3	21.1	3	20.6	18.6
25th "	4	15.8	2	16.2	4	19.8	4	20.1	18.2
26th "	5	12.6	6	12.3	4	16.3	4	15.9	13.9
28th "	9	13.3	11	12.7	7	16.6	12	16.0	14.6
Weighted Mean		13.8		13.4		17.9		17.3	15.7

Table 8 (Cont'd)

(b) Summary of results (length of larval + pupal life per insect in days).

Treatments: Temperature	Treatments: Photoperiod	Date: 24th Oct.	Date: 25th Oct.	Date: 26th Oct.	Date: 28th Oct.	Mean
24°C	15 hrs.	14.6	15.8	12.6	13.3	14.1
24°C	9 hrs.	17.8	16.2	12.3	13.0	14.8
20°C	15 hrs.	21.1	19.8	16.3	16.3	18.4
20°C	9 hrs.	20.6	20.1	15.9	16.0	18.2
Mean		18.5	18.0	14.3	14.6	16.4
Effect of:- Temp. (24°C-20°C)		- 4.6	- 4.0	- 3.6	- 3.0	- 3.8
Photoperiod (15-9 hrs.)		- 1.4	- 0.4	0.4	0.3	- 0.2
Interaction (24°C-20°C) (15 - 9 hrs)		- 1.8	0	0	0	- 0.4
S.D. of effects		± 0.94	± 0.86	± 0.72	± 0.50	± 0.39
Significant effects:- (d.f.65)						
	5%	1.9	1.7	1.4	1.0	0.8
	1%	2.5	2.3	1.9	1.3	1.0
	.1%	3.2	3.0	2.5	1.7	1.3

Date of Hatching Oct. 1952	Av. length of life (days)	S.D. ±	Least significant differences: 5%	1%	.1%
24th + 25th	18.2	0.90	1.8	2.4	3.1
26th + 28th	14.4	0.62	1.2	1.6	2.1
Difference:	3.8	1.10	2.2	2.9	3.8

(c) Analysis of Variance: (length of life in days).

Variance due to	d.f.	S.S.	M.S.
Total	80	635.76	
Treatments	15	485.28	
Photoperiod	1	0.75	
Temperature	1	227.53	227.53 ***
Temp. x Photoperiod	1	3.77	
Dates	3	229.18	76.39 ***
Dates x Photoperiod	3	7.46	
Dates x Temp.	3	5.61	
Dates x Photoperiod x Temp.	3	10.78	
Error	65	150.48	2.315

Table 9.

(a) Average number of eggs per female at different levels of temperature and photoperiod.

Photoperiod	15 Hrs.	9 Hrs.	Mean.
Temperature:			
24°C	115.4	109.2	111.8
20°C	72.2	92.9	82.6
Mean	93.8	102.3	97.4

(b) Analysis of variance (Number of eggs at different treatments)

Variance due to	d.f.	S.S.	M.S.
Total	34	307847.0	
Treatments	3	9299.1	
Temperature	1	7420.0	Not significant
Photoperiod	1	628.5	
Interaction	1	1250.6	
Error	31	298547.9	9630.6

Variability is too high in the experiment. Coefficient of variability = $\frac{98.1}{97.4} \times 100 > 100\%$.

(c) Summary of Results (Eggs per female).

Effect of	Eggs per female
S.D.	(± 33.49)
Temperature (24°C-20°C)	60
Photoperiod (15 hrs-9 hrs.)	-15
Interaction (24°C-20°C)(15 hrs-9hrs.)	27
General Mean	97

Least significant differences: (d.f.31)
5% 68.3

Caterpillars that hatched on the 26th and 28th October developed significantly more quickly than those hatched on the 24th and 25th October. As variability in the experiment was too high the effect of temperature and photoperiod on fecundity could not be detected.

EXPERIMENT 4.

Effect of cabbage leaves of different ages on fecundity of Plutella.

Caterpillars were reared at a constant temperature of 17°C on the following three types of food:-

A: White leaves from the heart of a cabbage plant say P_1 growing in field
B: Vigorously growing green leaves from another plant P_2 two feet away
C: Mature leaves from plant P_1

These foods were given either in the entire larval life or were changed in different instars; the treatment combinations tried were:

Sr. No. of Treatment	Foods given in Larval Instars 1st.	2nd.	3rd.	4th.
(1)	A	A	A	A
(2)	A	A	A	B
(3)	A	A	B	B
(4)	B	B	B	B
(5)	B	B	B	C
(6)	B	B	C	C
(7)	A	A	A	C
(8)	A	A	C	C

The caterpillars were not reared in separate tubes; instead 40-50 of one treatment were together in a Fowler's glass jar.

The caterpillars used were hatched from eggs laid by moths of Experiment 1. Hatching was spread over a period of six days from 16th May, 1952 to 21st May, 1952 and the young larvae were distributed in different treatments according to the plan given below.

Sr. No. of Treatment	Incubation of eggs Laid on May-1952	Hatched on	Date of Transfer to the second food May-June	Pupation Period Started June	Ended	Emergence Started June
1	9th	16th	-	4th	7th	15th
2	12th	19th	2nd June	7th	10th	17th
3	12th	19th	29th May	7th	11th	18th
4	7th	14th	-	3rd	5th	14th
4	14th	21st	-	10th	13th	21st
5	7th	14th	28th May	3rd	6th	14th
6	14th	21st	1st June	11th	14th	23rd
7	9th	16th	29th May	4th	8th	15th
8	12th	19th	29th May	8th	11th	20th

From every treatment (except treatment No. 5 with seven replications) 10 female moths on emergence were provided with two males each, one from the experiment and one from the field, and their eggs were counted every day.

Remarks:

In treatment No. 5, 16 of the 23 female and 14 of the 20 male

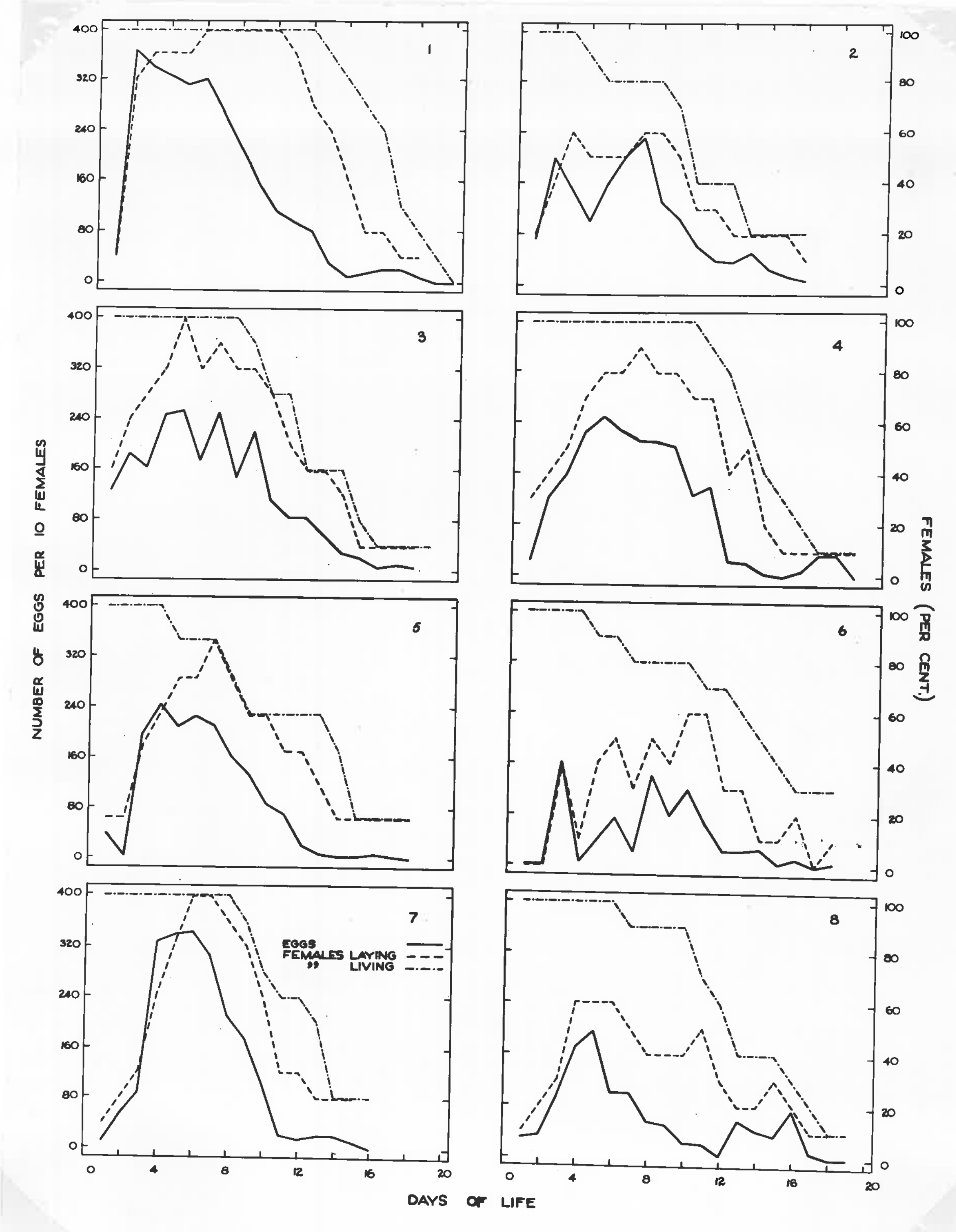

Fig. 2. Graphs showing the fecundity and oviposition behaviour of Plutella moths reared on cabbage leaves of different ages (Expt. 4).

Graph No.	Treatment			
	Food grown in larval instars			
	1st	2nd	3rd	4th
1	A	A	A	A
2	A	A	A	B
3	A	A	B	B
4	B	B	B	B
5	B	B	B	C
6	B	B	C	C
7	A	A	A	C
8	A	A	C	C

A- White leaves from heart
B- Young green leaves
C- Mature green leaves

pupae died with characteristic symptoms not noticed in any other case. They became hard, looked as if calcified, were dark brown in colour with dirty white spots on their bodies. No pathological organisms were found in them.

Table 10.

(a) Average number of eggs per female fed on different qualities of food.

	Treatments. Type of food given in different instars. 1st	2nd	3rd	4th	Eggs per moth.
				S. E. ±	26.8
(1)	A	A	A	A	274
(2)	A	A	A	B	160
(3)	A	A	B	B	221
(4)	B	B	B	B	201
(5)	B	B	B	C vv	163
(6)	B	B	C	C	80
(7)	A	A	A	C	199
(8)	A	A	C	C	110
	General Mean				176
	Least significant differences:				(69 d.f.)
				5%	76
				1%	100
				.1%	130

vv This value is based on 7 observations only; all the remaining pupae failed to emerge. The S.E. of this mean is $\frac{s}{\sqrt{7}}$ or 32.0. The least significant differences for the comparison of this mean with other means in the table are:

5%	83
1%	110
.1%	143

(b) Analysis of variance (average number of eggs:-)

Variance due to	d.f.	S.S.	M.S.
Total	76	761006.0	
Treatments	7	267015.5	38145.1 xxx
Error	69	493990.5	7159.3

Caterpillars fed on white leaves laid more eggs than those fed on young green leaves but the difference is not quite significant at 5 percent. When the former food was given in the first two instars and the latter in the second two the number of eggs laid was in between the above two values. Whenever mature leaves were given to the larvae in the second two instars of their life after feeding them on tender foods in the first two, their egg laying capacity was depressed ($P < 1$ percent), but if this food was given only in the fourth instar the fecundity was not depressed so much

Figure 2 shows the graphs of oviposition behaviour and longevity of female moths in different treatments.

EXPERIMENT 5.

Effect of photoperiod and quality of food on fecundity of Plutella.

Caterpillars were reared at two temperatures 19°C and 24°C in 15 hours' and 9 hours' exposure to electric light in incubators on two types of food.

Food: A: Cabbages grown in long-day of 15 hours photoperiod.
B: Cabbages grown in short-day of 9 hours photoperiod.

One type of cabbage was grown in earthen pots of 9" diameter, containing similar soils. Some of these were allowed to grow in ordinary day-light, being about 9 hours in June-July (1952) and the rest were exposed to extra hours of electric light (40 watts), 3 hours in the morning before sunrise and 3 in the evening after sunset, thus making a photo-day of 15 hours. Plants were used for the experiment after six weeks' growth in these conditions.

Eggs were procured from moths reared in Experiment 4, and were incubated at 19°C or 24°C alternately. The caterpillars (hatched within 6 hours) of a particular treatment were reared en masse in Fowler's glass jars. To provide a required photoperiod in an incubator the jars were enclosed in light-proof metal tins; the same photo-conditions were maintained during the pupal stage. Almost all the caterpillars being reared at 24°C died so that half of the experiment had to be dropped.

Of the remaining treatments, all the females that reached adult stage, were provided with three males each and the eggs laid by them at 19°C were recorded every day. In each case two of the males were collected as pupae from the field.

Remarks:

At 24°C most of the insects died in the larval or the pupal stage. Since the leaves became yellowish and looked unhealthy within a few hours it appeared as if after growing them in low temperatures outside and then bringing them to high temperatures of the incubator, certain undesirable chemical changes were produced in them: it is interesting that those getting the same photoperiod in which they were grown, remained in apparently desirable condition for a longer period than the ones subjected to a different photoperiod of the incubator.

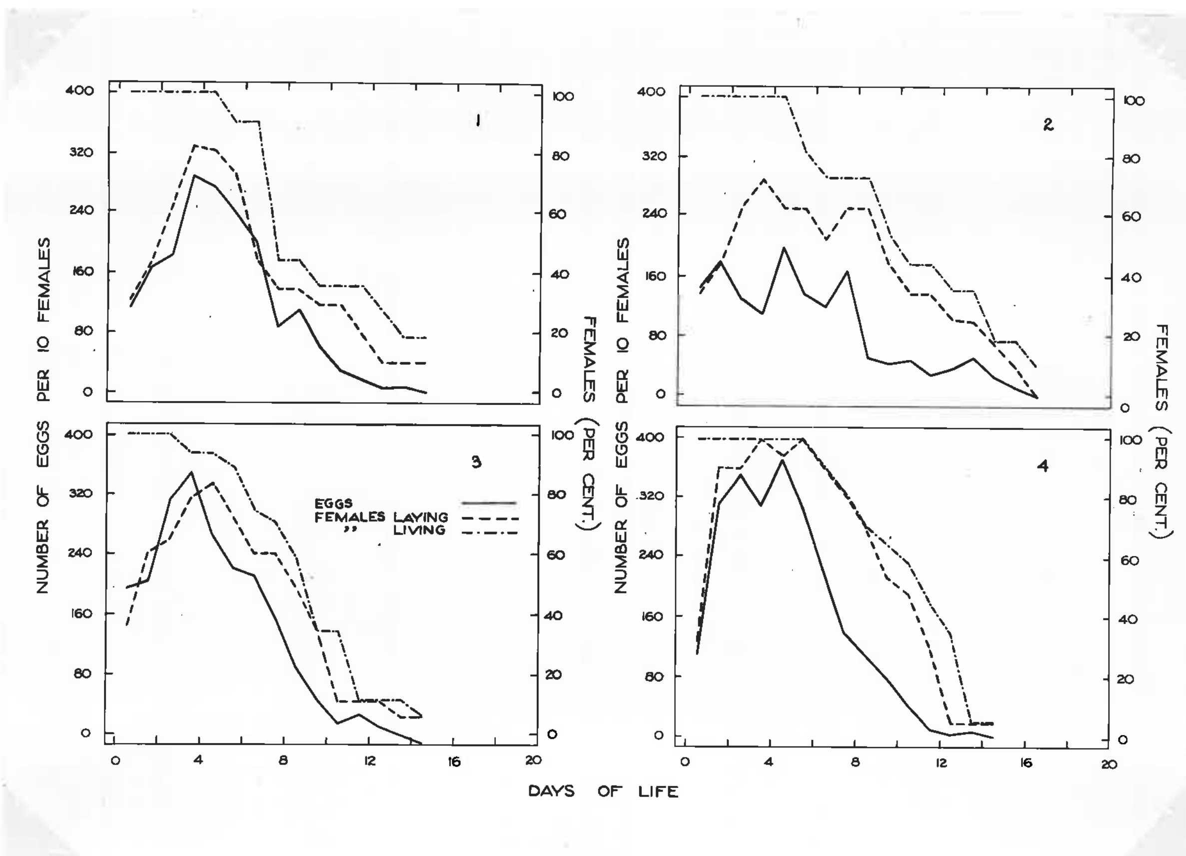

Fig. 3. Graphs showing the fecundity and oviposition behaviour of Plutella moths at 19°C on different qualities of cabbage leaves in different photoperiods (Expt. 5).

Graph No.	Treatments	
	Food grown in	Caterpillars reared in Hrs. of light each day
1	Short day	9
2	Short day	15
3	Long day	9
4	Long day	15

Table 11.

(a) Average number of eggs per moth at 19°C, at different levels of photoperiod and quality of food.

F o o d.	Photoperiod				Weighted Mean.
	15 hours		9 hours		
	No. of Females	Eggs per Female	No. of Females	Eggs per Female	
Grown in long-day	17	212.2	10	216.2	214.1
Grown in short-day	15	149.7	10	178.3	164.0
Weighted Mean.		189.0		201.0	189.1

(b) Summary of Effects (per Female Moth).

Effect of	Eggs per Female
S. D.	(± 27.1)
Food: (Long-day - Short-day)	50.0
Photoperiod: (9 Hrs. - 15 Hrs.)	16
Interaction: (Long-day - Short-day) (9 Hrs. - 15 Hrs.)	-12
General Mean	189

Least significant differences: (d.f. 48)
5% : 55

(c) Analysis of variance: (number of eggs at different treatments)

Variance due to	d.f.	S.S.	M.S.	
Total	51	468316.0		
Treatments	3	35063.2		
Food	1	30849.5	30849.5	Not quite significant at 5%
Photoperiod	1	1869.9	1869.9	
Interaction	1	2343.8	2343.8	
Error	48	433252.8	9026.1	

Caterpillars fed on cabbages grown in a long photoperiod of 15 hours of light each day laid more eggs than those fed on food grown in 9 hours' photoperiod each day but the difference was not quite significant at 5 percent level.

Figure 3 shows the graphs of oviposition behaviour and length of life of female moths in different treatments.

EXPERIMENT 6.

Speed of development and survival rate of Plutella as affected by varieties of cabbage given different fertilizers.

Caterpillars (hatched within 12 hours) were reared at 20°C on two varieties of cabbage grown in a temperature-control-room (75-80°F) which were given different fertilizers. An attempt was also made to measure pot to pot and plant to plant differences. The factors tried were:

Varieties: Sugarloaf, Succession.

Fertilizers: 1. Control (1)

2. Ammonium sulphate : 2 cwt/acre.
3. Superphosphate : 4 cwt/acre.
4. Potassium sulphate : 2 cwt/acre.
5. Ammonium sulphate + Superphosphate : 2 cwt. + 4 cwt/acre. Respectively
6. Ammonium sulphate + Potassium sulphate: 2 cwt. + 2 cwt/acre "
7. Superphosphate + Potassium sulphate: 4 cwt. + 2 cwt/acre "
8. Ammonium sulphate + Superphosphate + Potassium sulphate: 2 cwt. + 4 cwt. + 2 cwt/acre "

2 Pots : (a) , (b) in each treatment
2 Plants : (1) , (2) in each pot.

The plants were grown in February-March (1953) and the rearing was done in April-May.

'Yates seeds' of the above two varieties were used. Plants were grown in earthen pots of 9" diameter filled with homogeneous mixture of 'Waite-Institute-soil' and washed beach sand in equal quantities. Five seeds were sown in each pot, nearly all of which germinated; as the plants became a bit bigger two of them of the same height and health were kept ultimately. In all there were 32 pots (arranged in 8 rows of 4 each) which were placed on a wooden bench along the south double-glass wall of the temperature control room. To give equal chance of exposure to light to the plants, the pots were shifted in position within a row and from row to row twice a week. I tried to give equal quantities of water to all the plants.

When the plants were 4 weeks old, they were given the appropriate

Plate 2. Healthy cabbage plants grown in the temperature control room (centre). The bigger plants in the central rows were the 'Sugarloaf' variety (Expt. 6).

fertilizers dissolved in distilled water in two doses separated by an interval of a fortnight. The quantities for each pot were calculated from the rates per acre given above. The experiment was started 4 weeks after the second application of fertilizer. These three particular manures were selected because sulphate radical was common to them all.

Eggs were procured from moths reared in the laboratory for this purpose. The eggs were incubated at different temperatures varying from 20°C-24°C with the hope that they might hatch more or less at the same time. Hatching was spread over two days. At the end of each 12-hour period the larvae that had hatched since the last inspection were distributed at random but in equal numbers among all the treatments. Eventually 20 caterpillars were started on food from each of the 64 experimental plants. The total of 1280 larvae was reared in 640 tubes, being two in each tube; their position in the incubator was fixed at random in batches of 10 tubes containing food from the same plant. Food was changed every other day after the first change which was on the third day.

To measure the duration of larval and pupal life, observations were taken after every 8 hours.

Remarks:

All the plants appeared in excellent condition after the application of fertilizers (Plate 2). Nevertheless there was unusually high mortality among the caterpillars in this experiment. Cut pieces of leaves on which the caterpillars were feeding in the incubator became yellowish earlier than normally expected but this characteristic was not related to mortality or any of the fertilizers applied, so I could not think of any adequate explanation for the high mortality-rate among the caterpillars in this experiment.

Table 12.

(a) Percentage survival (transformed to degrees) on two varieties of cabbage given different fertilizers.

Fertilizers	Variety: Sugarloaf					Succession				
	Pots: (a)		(b)		Mean	(a)		(b)		Mean
	Plants: (1)	(2)	(1)	(2)		(1)	(2)	(1)	(2)	
Control (1)	33.2	42.1	33.2	42.1	37.7	22.8	33.2	26.6	30.0	28.2
Ammonium sulphate	33.2	33.2	30.0	33.2	32.4	22.8	22.8	30.0	39.2	28.7
Superphosphate	26.6	39.2	26.6	26.6	29.8	26.6	12.9	30.0	18.4	22.0
Ammonium sulphate x Superphosphate	30.0	18.4	26.6	33.2	27.1	22.8	26.6	26.6	33.2	27.3
Potassium sulphate	39.2	39.2	22.8	36.3	34.4	22.8	36.3	12.9	39.2	27.8
Ammonium sulphate x Potassium sulphate	39.2	39.2	22.8	30.0	32.8	45.0	30.0	33.2	36.3	36.1
Superphosphate x Potassium sulphate	30.0	12.9	30.0	30.0	25.8	30.0	30.0	18.4	26.6	26.3
Ammonium sulphate x Superphosphate x Potassium sulphate	30.0	30.0	26.6	30.0	29.2	22.8	26.6	26.6	42.1	29.5
Mean	32.7	31.8	27.3	32.7	31.1	27.0	27.3	25.5	33.1	28.2

Table 12 (Cont'd)

(b) Summary of effects (percentage survival converted to degrees)

	Variety		Mean
	Sugarloaf	Succession	
S.D.	(± 1.22)		
Mean	31.1	28.2	29.7
Effects and interactions	(± 2.4)		(± 1.7)
Ammonium sulphate	- 1.5	4.4	1.4
Superphosphate	- 6.4	- 3.9	- 5.2 **
Potassium sulphate	- 1.2	3.4	1.1
Ammonium sulphate x Superphosphate	1.9	- 0.1	0.9
Ammonium sulphate x Potassium sulphate	2.5	1.4	1.9
Superphosphate x Potassium sulphate	0.2	- 0.1	0.1

	(d.f. 48)	5%	1%	.1%
Least significant difference between varietal means:		3.5	4.6	6.1
Least significant effects:				
Body of the table:		4.9	6.6	8.6
Margin :		3.5	4.6	6.1

(c) Analyses of variance (percentage survival converted to degrees)

Variance due to		d.f.	S.S.	M.S.
Total		63	3295.33	
Between pots		31	1765.99	
Varieties (V)		1	133.11	
Fertilizers	N	1	32.35	
	P	1	425.90 **	
	NP	1	13.23	
	K	1	19.25	
	NK	1	60.26	
	PK	1	0.04	
	NPK	1	13.60	
Interaction of varieties and fertilizers:				
	VN	1	138.95	
	VP	1	24.13	
	VNP	1	15.31	
	VK	1	84.41	
	VNK	1	4.15	
	VPK	1	0.43	
	VNPK	1	37.67	
	Remainder:	16	763.20	47.70
Within pots		32	1529.34	47.79
Error		48	2292.54	47.76

Table 13.

(a) Average length of larval life (days) on two varieties of cabbage given different fertilizers.

Fertilizers	Variety: Sugarloaf					Succession					Overall Weighted Mean
	Pots: (a)		(b)		Weighted Mean	(a)		(b)		Weighted Mean	
	Plants: (1)	(2)	(1)	(2)		(1)	(2)	(1)	(2)		
Control (1)	14.1	13.6	17.0	15.7	15.1	14.3	16.1	14.7	14.7	15.0	15.1
Ammonium sulphate	13.7	15.5	14.3	15.6	14.9	14.1	15.6	14.9	16.8	15.4	15.2
Superphosphate	18.4	16.3	14.6	16.0	16.4	14.5	16.0	17.1	17.2	16.0	16.2
Ammonium sulphate x Superphosphate	13.9	13.4	16.7	16.5	15.0	15.1	16.2	17.5	15.7	16.2	15.6
Potassium sulphate	14.0	15.7	14.4	15.2	14.9	14.5	16.9	15.0	13.4	15.0	15.0
Ammonium sulphate x potassium sulphate	16.3	13.9	15.3	14.4	15.0	16.0	15.0	15.8	14.9	15.5	15.2
Superphosphate x potassium sulphate	15.0	16.3	15.4	15.4	15.4	13.3	16.0	15.7	16.9	15.6	15.5
Ammonium sulphate x Superphosphate x Potassium sulphate	14.4	14.7	14.7	13.6	14.3	15.5	16.8	14.0	13.8	14.8	14.6

Table 13 (Cont'd)

(b) Analysis of variance (length of larval life in days)

Variance due to	d.f.	S.S.	M.S.
Total	63	2205.96	
Between pots	31	472.01	
Treatments	15	121.11	8.07
Remainder	16	350.90	21.93
Within pots	32	1733.95	54.19

A higher mortality was observed among caterpillars fed on cabbages given phosphate fertilizer (Sig 1 percent), but mortality among those fed on the plants given nitrogen and potash was not any different from the control. Similarly speed of development on the phosphate-plants was also slower as compared with the others but the difference was not significant.

EXPERIMENT 7.

Effect of temperature and photoperiod on fecundity of Plutella.

Caterpillars were reared at two temperatures 15°C and 20°C in 9 hours and 15 hours' exposure to electric light (40 watts) in incubators on two types of food.

Food: A. cabbages grown in long-day of 15 hours of light.
B. cabbages grown in short-day of 9 hours of light.

The nursery plants were procured from a local shop and were grown in earthen pots at two photoperiods in the same manner as described in Experiment 5 during July-August (1952).

Eggs from moths reared in the laboratory were used which were incubated at 25°C. For rearing, caterpillars were started in individual tubes. Food was changed and tubes were cleaned every other day. Almost all the caterpillars died sooner or later. Comparatively few caterpillars mined into leaves when food was provided within 8 hours of hatching. The larvae which survived during their earlier instars were overpowered by disease after some days. The following pathogenic organisms were identified from the dead larvae:-

1. Fungus. A strain of Aspegillus flavus Link.
Fam. Aspegilleceae.

2. Bacteria.

i. Red: Small grain, negative rod, coagulates milk; does not produce gas from glucose; rapidly liquefies nutrient gelatin with formation of sediment; agar slope cultures bright red at 25°C; white and slightly less growth at 35°C: Serratia sp. probably closest to Serratia marcescens, atypical because of growth at 35°C.

ii. White: Small grain, negative rod; non-motile at 35°C, motile at 25°C - growth greater at 25°C; slowly ferments lactose with production of acid; gives acid and gas from glucose; grows on McConkey's agar; is methyl red positive, and Voges-Proskauer negative; utilizes citrate as sole source of carbon; coagulates litmus milk.

Aerobactor aerogenes atypical in that it is much slower to ferment lactose than are type species.

The above micro-organisms were most probably the indirect cause of death in caterpillars, overpowering them because of their weak health. Presumably food was of an undesirable quality. In incubators the pieces of leaves remained quite turgid, green in colour and appeared quite normal. The seedling plants which were bought as such might have been of some resistant strain or of a variety out of season.

EXPERIMENT 8.

Effect of quality of food on sterility in Plutella males.

In Experiment 4 it was seen that quality of food eaten had a profound influence on the fecundity of female moths. To investigate some similar effect in males, two sets of caterpillars were reared in January (1953) on white leaves from the heart and maturer green leaves of cabbage. On emergence the male and female moths from these were mated in the following manner:

1. Ten males from white food were given one female each from white food and as they started laying eggs (which meant they were fertilized) new unmated females were replaced to see the number of females they could fertilize. All the 10 males fertilized one female each; 3 of them 2 females each; and one male fertilized even 3 females duringa its lifetime.

2. None of the 50 females kept without males laid any eggs.

3. In another test 20 females from white leaves were selected at random. Half of them were kept with 10 males (one each) from white food and the others with 10 males from green leaves. In the former set all the 10 females were fertilized whereas in the latter only 6 females laid eggs which indicated that poor quality of food might cause sterility in males. X^2 test of significance could not be applied as the number of observations was not enough.

EXPERIMENT 9.

Effect of temperature and host material on longevity and fecundity of parasite, Diadromus collaris.

Adult parasites were kept at 18°C and 25°C with two levels of host material, viz. 4 and 8 pupae every day. The experiment was done in February-March-April, 1952.

Pupae of Plutella supposed to be recently parasitized (within 48 hours) were collected from the field and were reared in incubators at the above two temperatures. Those pupae which contained well-developed parasite embryos could be recognized by the presence of semi-transparent areas which became bigger with age.

After emergence males and females were kept together for 24 hours to give them a chance of mating; most of them mated soon after emergence. One female with a male was then transferred to a glass specimen tube 5" x 1" in which they lived for the rest of their lives. A fresh male was provided if the first one died before the female. Six of such females at each temperature were offered 4 host pupae and four of them 8 host pupae in which they could lay eggs. The used host material was changed by a new one after every 24 hours. The pupae were dissected individually, under a binocular microscope, to count the number of eggs laid in them. In this way a daily record of the degree of parasitization of individual female parasites was kept. It was not possible to arrange to have enough parasites emerging on the one day, so parasites which emerged during a period of 7 days were distributed through the various treatments. Once put in they were not removed from their home tubes as they were liable to be damaged by an aspirator.

For providing host pupae, 4th instar caterpillars were collected from the field two days before they would be needed and they were kept in rearing jars at 24°C. As they pupated on the cabbage leaves provided, they were removed by cutting a small square area around them without touching the pupae. While offering these pupae to the parasites, they were arranged in a row along the length of the glass tube which was lying horizontally.

The average length of life of females in different treatments and the number of eggs laid by them are given in the tables below.

Table 14.

(a) Average length of life per female at different levels of temperature and host material.

Temperature	Host material				Weighted Mean
	8 Pupae		4 Pupae		
	No. of Females	Av. life of a Female	No. of Females	Av. life of a Female	
25°C	4	17.0	6	16.0	16.4
18°C	4	24.0	6	28.0	26.4
Weighted Mean		20.5		22.0	21.4

(b) Summary of effects (life in days per female)

Effect of	Av. life/days per Female
	S.D. (± 2.62)
Temperature (18°C-25°C)	10.0 **
Number host pupae (4-8)	1.5
Interaction (18°C-25°C)(4 - 8)	2.5
General Mean	21.4
Least significant effects:	
5%	5.6
1%	7.6
.1%	10.5

(c) Analysis of variance (Life of females in days)

Variance due to	d.f.	S.S.	M.S.
Total	19	1066.8	
Temperature	1	500.0	500.0 **
Host pupae	1	10.8	10.8
Interaction	1	30.0	30.0
Error	16	526.0	32.88

Table 15.

(a) Average number of eggs per female at different levels of temperature and host material.

Temperature	Host Material				Weighted Mean
	8 Pupae		4 Pupae		
	No. of Females	Av. eggs per Female	No. of Females	Av. eggs per Female	
25°C	4	64.5	6	85.2	76.9
18°C	4	96.8	6	96.3	96.5
Weighted Mean		80.6		90.8	86.2

(b) Summary of effects (average number of eggs per female)

Effect of	Av. number of eggs per female.
S.D.	(± 19.5)
Temperature (18°C-25°C)	19.6
Host pupae (4 - 8)	10.2
Interaction (18°C-25°C)(4-8)	-10.6
General Mean	86.2

Least significant effect (d.f.16): 5% 41.3

(c) Analysis of variance (average number of eggs)

Variance due to	d.f.	S.S.	M.S.
Total	19	32140.2	
Temperature	1	1920.8	1920.8
Host pupae	1	530.4	530.4 Not significant
Interaction	1	512.5	512.5
Error	16	29176.8	1823.55

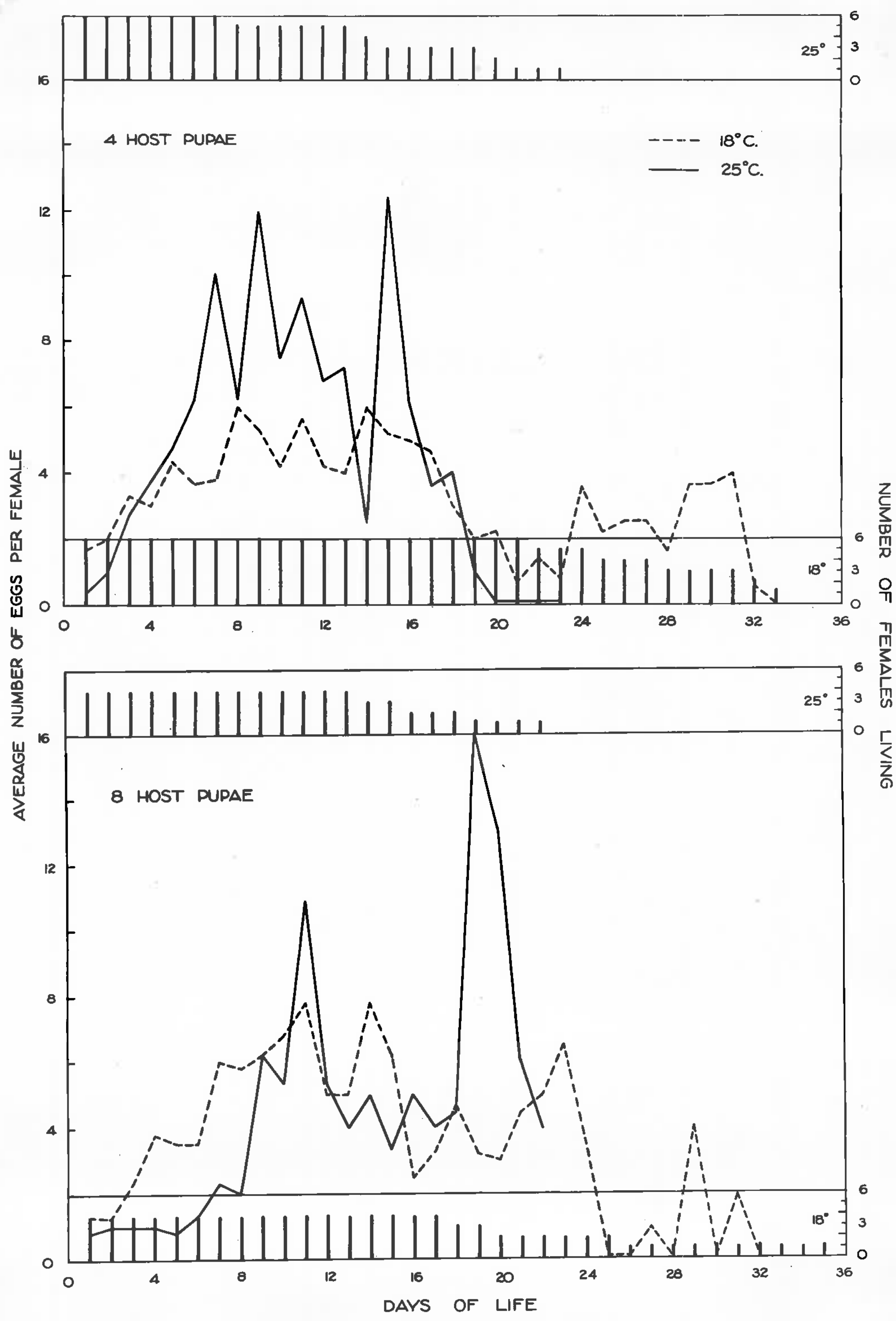

Fig. 4. Graphs showing the fecundity and oviposition behaviour of Diadromus at different levels of temperature and host pupae (Expt. 9).

Table 16.

(a) Average number of eggs per female per day of life at different levels of temperature and host material.

Temperature	Host Material				Weighted Mean
	8 Pupae		4 Pupae		
	No. of Females	Eggs per Female per day.	No. of Females	Eggs per Female per day	
25°C	4	3.53	6	5.08	4.45
18°C	4	4.26	6	3.42	3.76
Weighted Mean		3.89		4.25	41.08

(b) Summary of effects (number of eggs per female per day of life)

Effect of		Av. number of eggs per female per day of life.
	S.D.	(± 0.874)
Temperature (18°C-25°C)		- 0.70
Host pupae (4 - 8)		0.36
Interaction (18°C-25°C)(4-8)		- 1.20
General Mean		41.08
Least significant effect (d.f.16)	5%	1.85

(c) Analysis of variance (number of eggs per female per day of life)

Variance due to	d.f.	S.S.	M.S.	
Total	19	68.651		
Temperature	1	2.478	2.478	Not significant
Host pupae	1	0.532	0.532	
Interaction	1	7.046	7.046	
Error	16	58.595	3.662	

The females of Diadromus lived longer at 18°C than at 25°C (Sig. 1 percent). But neither temperature nor the number of host pupae provided every day had any influence on the total number of eggs laid by a female. The average number of eggs per female per day of life in different treatments was also not significantly different from each other.

Figure 4 shows the graphs of oviposition behaviour and longevity of female parasites in different treatments.

EXPERIMENT 10.

Fecundity of Horogenes (Angitia) cerophaga.

Parasite pupae were collected in the field in January (1952) and allowed to develop at 25°C. As the adults emerged, spread over two days, males and females were kept together for 24 hours to let them mate. After that period a female with two males was transferred to a glass specimen tube 4" x 1" covered at the mouth with a piece of muslin cloth with a raisin attached to it. A long piece of cabbage leaf cut to just fit in the tube was inserted after perforating a few holes in it so that the parasites could move about quite freely.

Five 3rd instar Plutella caterpillars were offered for parasitization which were changed by new ones every morning; the older ones were then dissected under a binocular microscope to count the number of eggs laid by individual females. A daily record of egg laying was thus made for the 12 females kept at 25°C.

Before changing the host material parasites were sucked in an aspirator and afterwards were returned to their tubes. It appeared from their short life that they might have been injured by this treatment.

Table 17.

Eggs laid by Horogenes females on different days of life.

Sr. No. of Female	Date of Emergence	Eggs laid on day of life												Total
		1st	2nd	3rd	4th	5th	6th	7th	8th	9th	10th	11th	12th	
1	8.1.52	8	1											9
2	"	3	4											7
3	"	2	2											4
4	"	7	17	11	17	14	8	12	13	6	11			116
5	"	1												1
6	"	5	6	7	18	11	13	14	16	21	16	21		148
7	"	12	15	19	37	63	20	13	15					194
8	"	5	5											10
9	11.1.52	4	7	7	12	5								35
10	"	2	1	3	2	9	11	2						30
11	"	-	1	2										3
12	12.1.52	9	22	21										52

EXPERIMENT 11.

Dispersal-behaviour of Horogenes (Angitia) adults in the field.

Two hundred (100 males + 100 females) parasite adults were released in the field at a point X and the number of parasites flying were observed at predetermined posts in four directions at right angles to it and their activity recorded after certain intervals of time.

The parasites were reared in the laboratory in small cages 12"x9"x18" made of wire gauze; Plutella caterpillars were released on cabbage leaves standing in small beakers containing free water and covered on top with cotton wool. After putting a cage over them some parasites were let loose which parasitized the caterpillars. As parasite pupae of the progeny appeared, they were transferred to an incubator at 24°C for further development. To complete the required number of adults more pupae were collected from the field.

The adults emerged spread over a period of one week. During this time males and females were kept together in a cage at room temperature (23°C-25°C) and were offered dilute honey solution and split raisins. When 200 adults were available for release, they were aspirated in a conical glass flask and were shaken out in the field at the fixed spot.

The point X was situated in the centre of a circular grass lawn of 30 feet radius, where an earthen pot containing 9" high cabbage plant was placed. More pots were placed in four rows at right angles to this point making three plants in each row. Within the rows the distance from plant to plant was 5 feet as shown in the plan (Figure 5). The total surface area of the leaves of each plant is given below.

Half an hour before the release of the parasites, 10 3rd instar Plutella caterpillars reared in the laboratory free from any previous contact with parasites, were placed in the heart of each plant. They were collected after 24 hours and dissected to see if they were parasitized and the number of eggs in them were recorded.

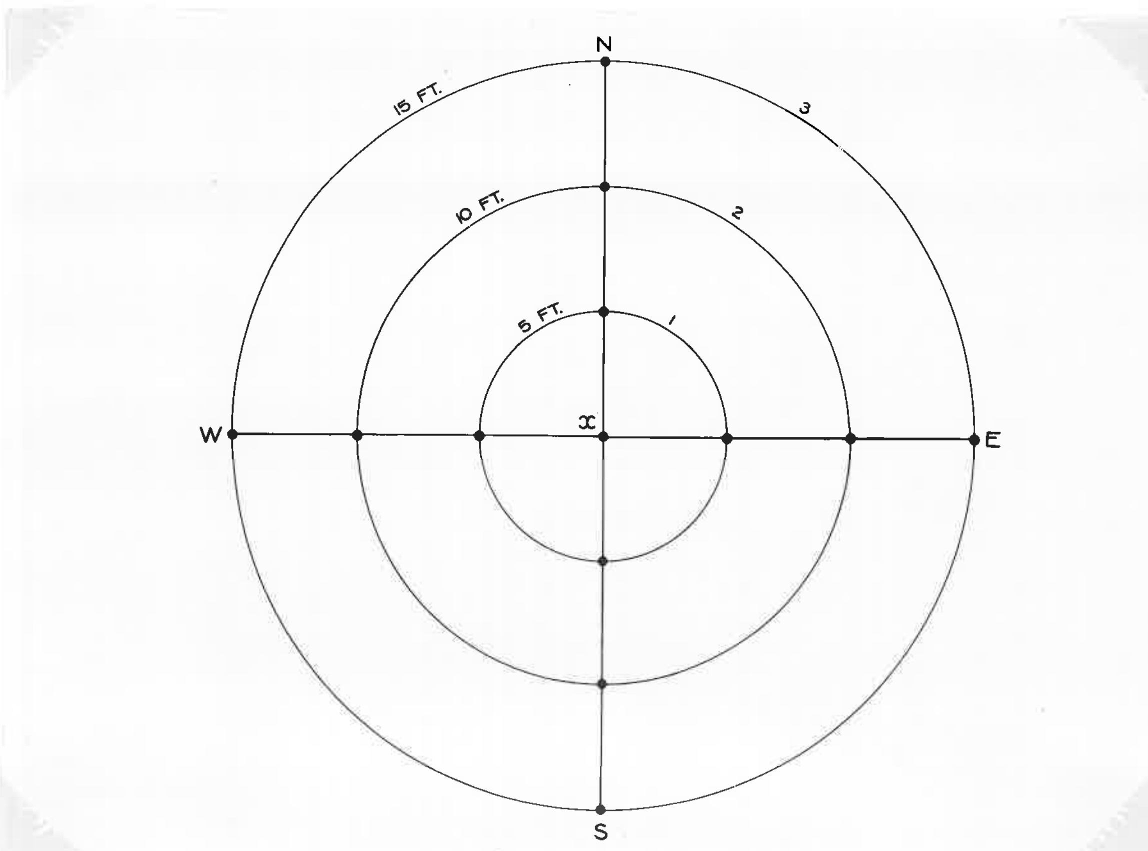

Fig. 5. Plan showing the position of cabbage plants on which the Horogenes (Angitia) adults were counted after they were released at the point X (Expt. 11).

The first observation of the flight of adults was taken five minutes after the release of the parasites by four persons, one for each row. Each plant in a row (starting from the end nearer the centre) was watched for one minute and during that time the number of parasites sitting or moving on the plant and the pot was recorded. As time passed the interval between observations was progressively increased as shown in the table, and after the fourth observation I inspected all the plants, spending half a minute on each one.

There was no shrub or tree within 40 feet of the experimental area and the nearest cabbage patch was about 200 yards away from it with a barrier of a big building in between. There was very little chance of any stray parasites appearing there. The weather was windy (W to E), broken up clouds were in the sky and the sun appeared occasionally.

The activity and movements of the parasites were doubtless influenced by the wind. Certainly more parasites moved with the wind as shown by the record on plants in row D (Table 18). The parasites were observed to shelter from the wind behind pots, soil or leaves of plants. Most of the caterpillars could not be traced and they were thought to have been shaken off the plants by the wind and were thus lost.

The above experiment was repeated after two weeks when the weather was fine. It was a clear sunny day without any wind. Table 19 shows the observations taken.

Remarks: In both attempts relatively few of the caterpillars released on the plants were found again and therefore a complete record of the oviposition activity of parasites could not be kept. In the first attempt (relating to Table 18) larvae were dissected on the third day of exposure to parasites out in the field. Out of the 10 larvae from each plant not more than five were found on any plant and on some of the plants none was found. The number of eggs deposited by parasites in each row varied from 2 - 8.

In the other experiment (relating to Table 19) larvae were gathered from plants after 24 hours' exposure to parasites, hoping that few would be lost in that time, but the complete number could not be recovered and 2 - 10 larvae were collected from different plants and 5 - 14 parasite eggs per row were found in them on dissection. Unparasitized caterpillars were released on plants after removing the old ones and they were dissected next day. Only one egg was found deposited in the caterpillars which could be collected.

Table 18.

B Number of parasites observed on plants at given distances after certain intervals of time.

Number of Plant	Area of leaf surface in sq. inches	Date and time of observation after release												
		14th December, 1951										15.12.51 morning	16.12.51 morning	17.12.51 morning
		11.45 a.m.	11.53 (5)	12.1 p.m. (5)	12.14 (10)	12.27 (10)	1.3 (30)	1.30 (30)	2.36 (60)	4.42 (120)	6.48 (120)			
X	128	200	x	xx										
N/1	149													
N/2	109													
N/3	108													
W/1	125		x	x	x									
W/2	112													
W/3	140													xx
S/1	137		x	x										
S/2	139			x										
S/3	190													x
E/1	108		xx	ẋẋẋ	x	xx							x	
E/2	129		xx	xẋẋx	xxx	xxxx				x	x			
E/3	126					x	ẋ	x		xx	xx	x	x	

( ) : Interval in minutes.

x : On leaves, one parasite observed; moving or stationary.

ẋ : On a pot, one parasite observed; sitting.

N,W,S,E : Four rows of plants starting from point X facing north, west, south and east respectively.

Table 19.

Number of parasites observed on plants at given distances after certain intervals of time.

Number of Plant	Area of leaf surface in sq. inches.	Date and time of observation after release of parasites											
		24th December, 1951										25.12.51 morning	26.12.51 morning
		2.0 p.m	2.8 (5)	2.16 (5)	2.24 (5)	2.37 (10)	2.50 (10)	3.26 (30)	4.2 (30)	4.53 (45)	5.44 (45)		
X	Same as in Table 18 + a little growth	200											
N/1			xxẋẋẋẋ	xxxẋẋẋ	xẋẋẋ	xxẋ	xxẋ	xxxẋ	xxẋ	x	xx		
N/2			xxẋẋ	ẋẋẋ	ẋẋẋẋ	ẋẋẋẋ	xxẋẋẋẋ	xxx			x		
N/3			x	xxx	xẋ	xx	x		ẋ	x		x	
W/1			xẋẋ	xxxxẋẋ	ẋẋẋẋẋ	xẋẋẋẋ		x	x	x			
W/2			ẋ		ẋẋ	ẋ	xẋẋ	xx	xẋẋẋẋẋ	xxx			
W/3			x	xẋ	x	xxẋ	xxẋẋẋẋ	ẋẋ	x	x			
S/1			x	x	xẋ	xx	x	xẋ		x			
S/2			ẋ		ẋ	x	xxxẋẋ		ẋ				
S/3				x	ẋ	ẋ	ẋ	xxẋ	xẋ				
E/1			ẋẋẋ	xx		xxx	xxx			x			
E/2				ẋẋ	xẋẋ			xẋ	ẋ	x			
E/3			ẋ	ẋ	xẋẋ	ẋ	xxẋ	ẋ	xx				

( ) : Interval in minutes.
x : On leaves, one parasite observed; moving or stationary.
ẋ : On a pot, one parasite; sitting.

N, W, S, E : Four rows of plants starting from point X facing north, west, south and east respectively.

Remarks. In both attempts most of the larvae were lost on plants.
Most of those which were collected were found to be parasitized.

Chapter 4

DISCUSSION

Section I.

SPEED OF DEVELOPMENT IN *PLUTELLA*.

(a) Effect of temperature.

It is well-known that speed of development in insects increases with increasing temperature and that the relationship is best expressed by a sigmoid curve. Davidson (1942) gave a mathematical formula for such a curve.

Experiments done on *Plutella* showed that the speed of development from egg to adult was greater at 25°C than at 18°C (Expt. 1, Table 1). Pupae which developed from larvae reared at 18°C weighed more than those from larvae which had been reared at 25°C but the ratio of dry matter to water was the same for both lots of pupae. Perhaps the increased rate of metabolism at the higher temperature did not favour the storage of nutrients.

(b) Effect of photoperiod.

Caterpillars kept at a constant temperature and exposed to 9 hours of light per day took longer to complete their larval and pupal life than those which were kept at the same temperature and exposed to 15 hours of light each day (Expt. 2, Table 6 a, b; Expt. 3, Table 8 a, b, c) ; the difference was significant only in Experiment 2 at 5 percent level, being one-third of a day. In Experiment 3 (Table 8 a, b, c) caterpillars which hatched from eggs exposed to continuous light during incubation developed more quickly than those hatched from eggs exposed to short days of 10 hours light each; the difference was significant at $P < 0.001$.

Certain photoperiods are known to induce diapause in many insects. Such photoperiods usually correspond to the time of the year when these insects normally enter diapause and when unfavourable environmental conditions appear in nature. When tested by experiments the eggs or early-instar larvae of *Bombyx* which were exposed to long photoperiods developed into moths which laid diapausing eggs (Kogure, 1933). In *Laspeyresia* a certain ratio of light to darkness was found to be necessary to imprint diapause on the developing larvae (Dickson, 1949). Similarly photoperiod is influential in the inception of diapause of *Diatarsia*, (Way, Hopkins and Smith, 1949), *Deilephila*, (Heller, 1926), *Halicta*, (Picard, 1926) and others. It has been observed in *Laspeyresia* and also in other insects in which diapause appears during the late larval or pupal stage that those larvae which entered diapause usually developed more slowly.

Plutella does not enter into an intense diapause and under suitable conditions of temperature it can be bred throughout the year. But during cold temperatures in winter it was observed to hibernate as an adult in Colorado (Marsh, 1917) and in Hong Kong (Chan, 1940) and probably also as a pupa in England (Hardy, 1938) and in Russia (Romanova, 1931). It is believed that because of its ability to tolerate a wide range of temperature *Plutella* has established itself so successfully throughout the world (Hardy, 1938 ; Robertson, 1939). In the experiments done on *Plutella* it was observed (above) that photoperiod influenced its speed of development. Continuous light in the spring (Expt. 3) caused the developing embryo to grow more quickly during the subsequent larval stage. However, in the Experiment 2 done in summer, the shorter photoperiod caused the caterpillars to develop more slowly. It appears from the behaviour of caterpillars in both of these cases that *Plutella* may be undergoing an incipient diapause during the winter. As pointed out by Andrewartha (1952), since the same factors influence incipient as well as intense forms of diapause, physiologically these two phenomena may be similar to each other.

(c) Interaction of temperature and photoperiod.

The increase in the speed of development with an increase in temperature was greater for larvae exposed to 9 hours of light each day than for those exposed to 15 hours of light daily. This interaction was significant at 0.1 percent level (Expt. 2, Table 6 b, c). Thus it seems that light and temperature counteracted each other in their effects. In a part of

Experiment 3, however, this interaction showed the opposite effect with a difference of nearly two days (Table 8 a, b, - 24th Oct.) in the length of life at 20° and 24°C, although it was not significant. The larvae in Experiment 3 took an unusually long time to complete their development; this may have been associated with an incipient diapause. If this were so it might be that the same photoperiod exerted a different influence on the speed of development of the larvae. On the other hand the same photoperiod may have a different influence at different levels of temperature, so much so that it may even have been reversed, as in these two experiments. At moderate temperatures (18° - 20°C) a check on the lengthening of life due to a short day of 9 hours' light may be beneficial to the insect whereas at a higher temperature (24°C or so) the check on the shortening of life due to a long day of 15 hours may be more helpful. The shortening of pre-imaginal life at a higher temperature may also be associated with reduced body weight (and thus lower fecundity) and at a comparatively lower temperature excessive length of larval life is not a healthy sign as it usually ends in some physical deformity or death.

In relation to the inception of diapause, observations on silkworms (Kogure, 1933), and codling moth (Garlick, 1948) showed that a particular photoperiod was most effective at a certain temperature, and these combinations corresponded to conditions found in nature at the time when diapause usually appeared in these insects. The larvae of the oriental fruit moth (Laspeyresia molesta) which developed slowly as autumn approached, usually entered diapause instead of pupating. According to Dickson, (1949 : Page 536) "- - - certain individuals are on the fence, the factors pushing them towards immediate pupation just about equalling the factors pushing towards diapause. The duration of the period that oriental fruit moth larvae remain in diapause, once they have entered, is determined by the temperature at which they are held. The higher the temperature, the shorter the period of inactivity". When reared at a constant temperature of 21°C in a photoperiod varying from 6 hours to 12 hours each, 90-100 percent of the caterpillars entered diapause but of those reared at the same temperature in a photoperiod of more than 12 hours each day an almost in-significant number of larvae entered diapause. At 21°C in a 9-hour photoperiod all the larvae entered diapause but at 27°C in a 12-hour photoperiod only 93 percent could enter diapause (Dickson and Saunders, 1945). This showed that a particular photoperiod had its preferential effect at certain levels of temperature.

(d) Effect of quality of food.

(i) Physiological stage of development of the host plant.

On senescent leaves of cabbage development was very poor and all larvae died before reaching the third instar. Larvae fed on white leaves from the heart and the young, quick-growing green leaves developed more quickly than those fed on leaves that were healthy and green, but mature. The difference was significant at $P < 0.001$ (Expt. 1, Table 1 a, b,). It was observed consistently throughout all the experiments that larvae which were reared on white leaves developed less rapidly than those reared on young green leaves; but the difference was always small and was not significant in any single experiment.

The slow speed of development due to the poorer quality food was associated with a decrease in body weight and silk production and an increase in the ratio of dry matter to live body weight, thus suggesting a nutritional deficiency (Expt. 1, Tables 2, 3, 4, 5). Moreover, very slow speed of development on senescent leaves was associated with the high death rate.

The incidence of attacks of the European cornborer *Pyrausta nubilalis* on different varieties of corn varied according to certain physiological differences in the plants as induced by the stage of development, percentage of sucrose or certain physical characteristics. A high death rate was associated with the slow speed of development and reduced body weight (Ficht, 1931, 1936; Polivka, 1931; Bottger and Kent, 1931). On the same variety of corn the number of larvae that survived was in direct correlation with earliness of planting and also the earliness of silking. The difference in development on a single variety planted on two different dates was equivalent to the difference obtained on two different varieties planted on the same date (Kelsheimer and Polivka, 1931). Larvae of the beetle Epitrix tuberus developed best on potato plants; development was very poor on wild tomato, marsh elder etc. Also, the adults lived longer and laid more eggs when they had been reared on potato. The difference between the various diets in their influence on E. tuberus was believed to be associated with different nutritive values of the foliage (Hill, 1946).

Similar effects of diet have also been observed in carnivorous species. When Trichogramma evanescens laid its eggs into the eggs of Tenebrio molitor which were less than a day old the resulting larvae died at the prepupal stage; if the eggs of T. molitor were 4-5 days old when parasitized T. evanescens reached the pupal stage but no adults emerged. Larvae of this parasite which developed in their natural host (eggs of Ephestia) were cream coloured and opaque, but those which developed in the eggs of Benchus were colourless and transparent suggesting some deficiency in food (Salt, 1935, 1936, 1937 a and b, 1938 a and b). Survival rate and speed of development of ladybirds on liver or meat was not as good as on aphids (Szumkowski, 1952), but when fed on liver plus an excess of vitamin C both speed of development and survival rate were very much improved. A mixture of vitamin E with liver had a favourable effect on fecundity and the hatching of eggs, but liver with vitamin E and aphids was the best for healthy development and fecundity which showed that the aphids contained some nutrient which was essential for the normal development of the beetles.

The speed of development of insects is affected in a similar manner whether they feed on different species of host plants, different varieties, or on plants of the same variety in different stages of development. If food is deficient in certain nutrients which are required by the insects that feed on it, their speed of development is retarded and the death rate increased. Attempts have been made to determine the nature of the factors that influence growth but these were mostly on carnivorous or scavenging species. For example, it was found that in the moth

Ephestia kuehniella development was retarded and certain body deformities appeared if a suitable quantity of linoleic acid was not present in its food (Fraenkel and Blewett, 1945). Similarly, the speed of development of the larvae of the rat flea was slowed down if there was some deficiency in the food. The blood serum of the host had all the essential proteins for normal development of the larva, but if the required amount of iron was lacking the death rate increased and development was delayed. The red blood corpuscles or haemoglobin are rich in iron but lack some other proteins necessary for normal development. When insects fed on these their development was prolonged and the death rate increased (Sharif, 1937). For many such insects nutritional formulae have been given to rear them artificially, e.g. Tribolium confusum (Lemonde and Bernard, 1951), Drosophila melanogaster (Schultz et al, 1946.

In phytophagous insects, on the other hand, such direct attempts to study the growth-affecting factors have not been so successful. Webster et al (1948) could not correlate any differences in chemical composition of the varieties of sorghum to the injury of the chinch bug. It is logical to believe that the differences in speed of development as influenced by different related species or varieties of host plants would be due to the presence of different quantities of certain nutrients in them, whereas the speed of development as influenced by plants in different physiological stages of development would be due to the change in the ratio of various nutrients. Since in both cases the ultimate effect is the same it appears that for normal development of the insects what is needed is a right proportion of nutrients in their food.

Thus there arise two aspects of study; firstly, to know what factors cause physiological changes in the host plants of insects and how these changes are caused; secondly, to know what sort of physiological changes appear in the cell sap of plants which affect the speed of development of the insects that feed on them. Since speed of development is only an outward sign of what is happening inside the insect body and death is the extreme effect of undesirable food, it would not be surprising that other functions of the body, like the excretion of certain materials (silk etc), the capacity to lay eggs and also, perhaps, the inception of diapause or similar functions may be influenced by different qualities of food. To study the physiological changes that take place in the plants it is necessary to study the effect of various factors responsible for these changes. Of these factors, age of the plant, composition of the soil, temperature and photoperiod are the most important. The influence of these factors on the host-plant cabbage and its subsequent effect on the speed of development, fecundity and the quantity of silk produced by Plutella is discussed in this chapter as tested by experiments.

(ii) Physiological difference in plants grown in different photoperiods.

Although caterpillars developed slightly more slowly when fed on cabbages grown under 15 hours of light per day than on cabbages grown under 9 hours of light, there was no significant difference in the time (Expt. 2, Table 6 b, c).

Evans (1938) found that Pieris brassicae larvae fed on food grown under normal light conditions grew more rapidly during the first half of the growth period than those fed on food grown under subnormal light conditions (low intensity), but during the last larval instar the latter made up some of the lost ground so that at pupation the difference of weight between the two types of larvae was small. It was thought that under low intensity of light a lower quantity of carbohydrates was produced in the cabbage leaves so that the larvae fed on them developed more slowly, but the relation of chemical composition of the leaves to the speed of development of the larvae was not clear. There was an indication that the physiological differences in cell sap affected the speed of development.

In these experiments cabbages were grown under long and short photoperiods assuming that certain physiological differences might appear in the leaves which in turn might affect the speed of development of the Plutella caterpillars feeding on them. Apparently there was not much difference in the speeds of development on the two types of leaves. Perhaps the physiological differences in the cell sap were not so great as to be able to affect the development , or perhaps the minimum level of nutrients required for satisfactory development were present in both types of food.

(iii) Effect of fertilizers given to plants.

Larvae developed equally quickly on leaves from plants which had received additional nitrogen or potassium; they developed more slowly (with a difference of more than a day when compared with the control) on leaves from plants which had received extra phosphorus. The difference was not significant (Expt. 6, Table 13a).

The influence of plants grown in mediums deficient in certain nutrients on the development of some insects feeding on them has been studied. The grasshopper Melanoplus mexicanus mexicanus, fed on wheat of high nitrogen-content, developed more quickly than those which ate wheat having a low nitrogen content (Smith and Northcott, 1951). However, when chinch bugs were fed on corn plants grown in a nutrient solution deficient in nitrogen they matured faster, lived longer and produced more offspring than when they were fed on plants grown on complete nutrients (Hasemann, 1946). Albama argillacea showed delayed development and suffered a high death rate on plants which were deficient in zinc and copper (Creighton, 1938).

In Experiment 6 different fertilizers were given in excess to two varieties of cabbage plants to see if they produced any immunity against the insect. Crops grown on the Waite Institute soil usually respond to phosphorus. The cabbages grown in pots as controls were as good in general appearance and size as those which received additional fertilizers. Phosphorus caused a slow speed of development through both varieties. There is an indication that, in this respect, the effect of nitrogen through variety "Succession" was more pronounced than through the variety "Sugarloaf", but due to high variability in the experiment none of these effects proved to be significant. The slow speed of development caused by the phosphorus application was associated with high death rate in both varieties but no such relationship was observed between the death rate and the effect of nitrogen differentially through the varieties, as discussed elsewhere. It seems that certain changes appeared in cell sap of the plants which received additional phosphorus and that the caterpillars which fed on them developed rather slowly (Expt. 5. See "Remarks").

(e) Interaction of food and photoperiod.

When plants which had been exposed to 9 hours of light each day were used as food there was an indication that the larvae would develop more quickly if they were exposed to 15 hours of light each day than if exposed to 9 hours of light daily. On the other hand when plants which had been exposed to 15 hours of light each day during their growth were used as food there was no difference in the speed of development of the larvae exposed to 9 or 15 hours of light each day. The interaction between food and photoperiod was just significant at the 5 percent level (Expt. 2, Table 6 a, b, c). There was also an indication that pieces of leaf from plants which had been grown exposed to a 9-hour photoperiod deteriorated rather quickly in the incubators when they were exposed to a 15-hour photoperiod.

It was seen above (Discussion I, b,) that caterpillars exposed to 9 hours' light daily developed rather slowly in an experiment done in the summer. It may be noticed that in the same experiment (2, Table 6) this effect was accentuated when the caterpillars were fed on food grown in a 9-hour photoperiod. This may mean that short photoperiod, apart from having a direct influence on the speed of development of larvae, also has a similar effect on them through the food. Since the differences in the length of larval life were not large enough it is not possible to say very definitely whether conditions of short photoperiod are suitable to cause an incipient diapause in Plutella. With other insects which undergo an intense diapause caused by photoperiod, it has been shown that by artificially creating the appropriate environment they can be induced to enter diapause at any time of the year.

(f) Interaction of food and temperature.

The speed of development of caterpillars feeding on mature leaves was slower than those feeding on young green leaves or white leaves of cabbage. This might be expected to happen if the caterpillars which were reared on the younger leaves ate more, taking in a greater quantity of food in a shorter time than those reared on the mature leaves; the greater weight of dry matter in their bodies would confirm this suggestion. Larvae which were reared on mature leaves spent a longer time in the larval and pupal stages than those reared on the other sorts of food both at 25°C and at 18°C, but the relative increase in the time required for development was greater at 18°C than at 25°C (Expt. 1, Table 1 a, b). This interaction was unexpected: if the slowness of development was due to the maturity of the leaves and if the processes of maturation went on faster at 25°C than at 18°C then one might have expected the opposite result. A possible explanation for the result which was demonstrated might be that in nature the mature leaves would be found in the hotter season. Thus a higher temperature may be more compatible with the mature leaves and a lower temperature more so with the younger and more tender leaves. The above contention is further confirmed by the fact that with mature leaves the live weight of the pupa was reduced more at a lower than at a higher temperature; significant at 5 percent level (Table 2 a, b). It is clear that temperature and maturity of cabbage leaves have a definite relationship and as far as their combined effect on the biology of Plutella is concerned, these two factors interact in a characteristic way.

(g) Previous state of eggs and speed of development.

In Experiment 3, caterpillars hatched on the 26th and 28th October, 1952, developed more quickly ($P < 0.001$ - Table 8 a, b, c) than those hatched on the 24th and 25th October. Since there was no difference in food this could not have been the cause. Temperature and light conditions of rearing were similar at all corresponding treatments. The possible causes of this difference in the speed of development might have been:

(i) Influence of photoperiod on eggs

(ii) Difference in physiology of the females

For starting the experiment (3) eggs were incubated at 20°C during night and 24°C during day time. The eggs hatched on October 24th were not exposed to any artificial light; those on the 25th got a constant exposure to electric light during the last 24 hours of their embryonic life. However, the eggs which hatched on the 26th and 28th were constantly in the light either for the whole or during most of their embryonic stage. It has been noticed that normally the caterpillars hatch during day-time and very few or none at all during the night or in complete darkness, which suggests that light acts as a sort of stimulus to the developing embryo. It may be that eggs laid by moths of over-wintering generations are in a condition of incipient diapause so that when they are exposed to continuous light (or long photoperiod) this condition is broken down. Kogure (1933) observed a somewhat similar influence of light on the eggs and pre-imaginal stages in the production of hibernating or non-hibernating eggs of the silkworm.

The majority of the moths collected from the field died after laying eggs for two or three days; thus most of the eggs which hatched on the 24th and 25th October were from short-lived females, whereas the remainder came from females which lived longer and perhaps had a higher vitality. There may have been a difference in the physiological condition of the moths which might have been impressed on their eggs, resulting in different speeds of development of their progeny.

Some of the moths were collected from cabbages and some from swedes but they were not kept separately in the laboratory. If, by chance, most of the eggs which hatched on the 24th and 25th had been laid by moths from swedes then there is the possibility that the cabbage is less suitable as food for progeny of insects which fed on swedes than for those that fed on cabbages in the field. There is no evidence that this is so with Plutella but for certain other species it is known that the progeny tend to prefer the food eaten by their mothers, e.g. sawfly Pontania salicis (Harrison, 1927), Ichneumonid Nemeritis canescens (Thorpe and Jones, 1937), and stick insect Carausius morosus (Sladden and Hewer, 1938).

(h) Difference between sexes.

Irrespective of temperature and the quality of their food, females developed more slowly than males and since they also had more dry matter and a higher live weight in the pupal stage, it appears that this extra time is utilized for eating more food. If the influence of temperature and food on the weight of pupae and their water content is considered in relation to the differences between the sexes with respect to the weight of the pupae and their water content, it appears that the female may fulfil its requirements better from a good quality food at moderately lower temperatures, whereas a male may be better able to develop on poorer food and at higher temperatures. (Expt. 1, Tables 1,2,4,5).

In Lucilia sericata and L. cuprina development of the reproductive organs in females was completed only if the adults had a diet that contained adequate protein whereas in the males it was independent of diet in the adult stage because the sperms were present within two hours of emergence (Mackerras, 1933). Herms (1928) with Lucilia and Weidling (1938) with mosquitoes observed that more females reached the adult stage when given larger quantities of food whereas, in cases of underfeeing, males increased in number. But Ullyett (1950) and other workers before him did not find any such effect of the quantity of food. However, it is probable that in the presence of different qualities of food, both sexes may show a selective survival rate. In Agrotis orthogonia, an insect feeding on many species of plants, more female pupae were produced on foods which were favourable for survival and speed of development and thus better in quality, and more males on poorer quality of foods although viability of pupae was not consistent in all cases (Seamans and MacMillan, 1935). Females of Bombyx store more glycogen and males more fat - this difference is noticeable in the larval stage but is more pronounced with the adult (Vaney and Maignon, 1905).

(i) General.

The speed of development of an insect varies according to the temperature of rearing as influenced by the metabolic activity of the body. It was seen above that either alone, or combined with temperature, light plays an important part. Photoperiod may influence the speed of development and the effect of a particular photoperiod may be more pronounced at one than at the other temperature. The effect of photoperiod on some insects is so pronounced that a state of diapause may be caused. The way in which normal functions of the body cease to continue is not known yet. In such a case if the insects are subjected to appropriate conditions of light artificially, they resume normal activities. For example, the nymphs of the grouse locust Acrydium arenosum angustum subjected to continuous light as compared with those kept in ordinary day-light of winter, grew quicker and showed a lower death rate and ultimately developed into a midwinter generation, whereas the control did not produce any offspring (Sabrosky et al, 1933). It has been noticed that photoperiod may affect the quality of the food-plant and in turn the speed of development of the insects that feed on it may be influenced (Section I; Discussion d - ii). Some other factors such as the physiological stage of development of the plant and the composition of the soil in which it grew may also affect its quality with respect to its nutritive value to the insects. Whenever some nutrients required by an insect for its normal development are not present in the food in adequate quantities the speed is retarded. The ultimate result of such an effect depends upon the nature of the nutrients missing from the diet.

While rearing Plutella caterpillars it was observed that during the very hot part of the summer when few larvae were in the field, the death rate of the caterpillars reared in the laboratory was very high even at optimum temperatures (Expt. 6. See "Remarks"). It was also observed that larvae could be reared in the incubators without any visible injury to them at a temperature higher in summer than in winter. It could not be proved because the numbers of larvae reared in the laboratory were not large enough. High mortality was associated with slow speed of development. If the observed differences were real ones, it would appear that temperature and photoperiod influenced the development of caterpillars through food probably by changing its quality or through some other unknown way.

It may be that the speed of development in insects is related to adaptations to the local conditions. The type of food available may play an important part in the evolution of a species.

It was found that more eggs of the spruce budworm (Choristoneura fumiferana) were found on the flowering balsam fir trees and such trees were found to harbour higher populations than the non-flowering trees. Larvae fed in the laboratory as well as in the field on foliage and pollen developed more rapidly than the ones that fed exclusively on foliage (Blais, 1952).

The European cornborer was introduced into the United States at two separate localities, viz. Toledo and New Haven. Local conditions being different at these places, two separate strains developed. The one in Toledo is a homozygus single generation strain which develops more slowly than the one in New Haven which is a homozygus multiple generation strain. Some time later the multiple generation strain was introduced into Toledo. It has been observed that these individuals entered the pupal stage more slowly than the multiple generation insects from New Haven (Arbuthnot, 1944).

In Java the soybean beetle Phaedonia inclusa originally fed on indigenous plants like Desmodium spp. and Pueraria etc. but later a strain developed which was adapted to soybean, a crop not indigenous in Java but introduced three to four hundred years ago. This adaptation occurred shortly before 1909 in Central Java. The new strain spread towards areas where the soybean was grown (Ankersmit, 1952).

Certainly food and other factors associated with it have a profound influence on the activity of insects and perhaps on their evolution too. It seems that temperature, food and photoperiod contribute a great deal to the variability found in the biological functions of the insect body. Many of the observations discussed here lead me to believe that the variance could be reduced a great deal if due caution is taken in rearing insects. As discussed in the next section, food alone has the greatest effect on fecundity.

Section II.

F E C U N D I T Y O F P L U T E L L A

(a) Effect of temperature.

(i) Constant temperature throughout the life-cycle.

Insects bred at 18°C produced more eggs than those at 21°C, the difference being significant at the 1 percent level (Expt. 2, Table 6 a, b). It was seen earlier (Tables 2, 4) that larvae which were reared at 25°C developed more rapidly and weighed less as pupae than those reared at 18°C. Thus the greater fecundity was associated with the greater weight, which in turn was associated with the slower rate of development. But it should be remembered that speed of development can also be slower due to some deficiency in food. The two, healthy and unhealthy conditions of slow development, should not be confused with each other.

The association of reproductive capacity with body weight may perhaps be universal among insects. The number of ova a blowfly can produce at one time is dependent on its size and thus on the amount of food obtained during its larval stage (Mackerras, 1933).

Burnett (1949) studied trends in greenhouse populations of the whitefly Trialeurodes vaporariorum and its internal parasite Encarsia formosa and found that with the rise and fall in temperature the fecundity and rate of development of the two species was affected. This effect of temperature was more important than the other effects of temperature in the autecology of the two species. At a higher temperature fecundity of the host decreased whereas that of the parasite was not much affected at the same temperature. He concluded that factors other than temperature had a great influence on the relative numbers of the two populations. For example, the longevity and fecundity of the host were greatly reduced when they fed on mature leaves, whereas the longevity and fecundity of the parasites were greatly reduced by a deficiency of the host larvae of a certain stage of development required for parasitization.

The moths which were kept at 18°C during their oviposition period lived longer than those kept at 21°C. At both temperatures there was a gradual decline in the number of eggs as females became older, (Fig. 1) which showed that those reared and kept at 18°C had an inherent capacity to lay a higher number of eggs than those which were reared at 21°C and were kept at the same temperature in the incubator.

(ii) Change of temperature within a life-cycle.

Moths which were transferred from 18°C to 21°C laid fewer eggs than the controls which were reared and kept continuously at 18°C (P   .01). It appeared that the moths lived for a shorter time when they were transferred to a higher temperature and that they died before they could lay all the eggs that they had in their bodies. No other treatment gave results that differed significantly from the controls. (Expt. 2, Table 7).

(b) Effect of photoperiod.

Moths reared from caterpillars exposed to 15 hours' light each day laid, on an average, 32 more eggs per female than those reared from caterpillars which had been exposed to 9 hours' light each day. The difference was significant at 5 percent (Expt. 2, Table 6 a, b). In this experiment (2, Table 6 a, b, c), the larvae developed more slowly at the shorter photoperiod. This is contrary to the results of an earlier experiment (1) in which high fecundity was associated with a longer time spent healthily as a larva. It was concluded from the earlier experiment that the greater fecundity of the moth resulted from a greater consumption of food as a larva. But this experiment (2) was done during the summer and the cabbages were grown out-of-doors in bright light and high temperature, whereas the previous conclusions were based on an experiment done during late autumn (April-May : Expt. 1). It may be that the larvae growing slowly in the 9-hour photoperiod on summer-grown food (Expt. 2) were in an unhealthy state and perhaps the larvae in fact did not consume more of the food than those kept in a 15-hour photoperiod. Or, it may be that food, grown during the summer, lasted better in the laboratory when it was exposed to 15-hours' light. These two conditions might have been complementary. In a similar experiment done in the winter (Expt. 5) at almost the same temperatures the moths which had experienced a 9-hour photoperiod when they were larvae laid more eggs than those which had been exposed to a 15-hour photoperiod, but none of the differences in this experiment were significant because the variances were high. Since the size of the effects was not impressively high in either case, the likelihood that the observed differences were merely due to chance is increased but that should not mean that such complicated relations between a photoperiod and a relative temperature do not exist at all, and it might be possible to demonstrate them if the experiment were repeated on a larger scale.

It is quite well known that different forms of aphids can be artificially produced by exposing them to certain photoperiods (Marcovitch, 1924; Shull, 1929) and that their fecundity is also influenced by such conditions of light (Davidsons, 1929). This problem has been studied more thoroughly in connection with diapause. Length of photoperiod in conjunction with a certain temperature is known to be the cause of diapause in many insects.

In Bombyx females that developed from eggs incubated at a low temperature (15°C - 20°C) and in continuous darkness produced non-hibernating eggs but those from eggs incubated at a high temperature (24°C - 28°C) in 15 hours' photoperiod each day or in continuous light produced hibernating eggs. Caterpillars which had completed their embryonic development in the latter circumstances, and which were reared at low temperatures in continuous darkness, developed into adults which again produced hibernating eggs (Kogure, 1933). In a series of experiments Kogure incubated eggs at different temperatures (varying from 15°C - 28°C) in continuous darkness and different photoperiods (including continuous light) and the caterpillars hatched from each of these treatments were reared at different temperatures both in continuous light and continuous darkness to see the influence of these factors in different stages of development within a life-cycle. It was seen that eggs incubated at a high temperature whether in continuous darkness or in continuous light, and irrespective of any subsequent treatments under which caterpillars were reared, gave rise to females all of which laid hibernating eggs which showed that under all circumstances incubation of eggs at a high temperature imparted characteristics of hibernation to the eggs of the next generation. Eggs which were incubated at intermediate temperatures and in continuous darkness developed into adults which mostly laid non-hibernating eggs. But eggs which were kept in continuous light at the same temperature developed into adults which laid hibernating eggs. If the caterpillars hatched from eggs which had been incubated in continuous darkness were reared at a lower temperature in the dark a higher percentage of females laid non-hibernating eggs as compared with those reared at the same temperature as that of incubation. On the other hand if caterpillars which hatched from eggs which had been incubated in continuous light were reared at a temperature lower than that of incubation a small percentage of females laid non-hibernating eggs and if this rearing was done in continuous darkness the percentage was rather higher but not so high as in the former treatments. At a still lower temperature of incubation (15°C) both in continuous darkness as well as in continuous light during that period, the resulting females laid non-hibernating eggs. Thus if the eggs were incubated at a high temperature (28°C) whether in continuous darkness or in light (which would be expected to give rise to females laying hibernating eggs) and subsequently even if the caterpillars were reared at a lower temperature in continuous darkness, moths laid hibernating eggs: which means once the future behaviour had been firmly determined during incubation, the conditions of rearing in the larval stage could not change it. On the other hand the behaviour of adults which developed from eggs which had been incubated at intermediate temperatures in continuous darkness, or at a low temperature (15°C) both in continuous darkness and light (all of which would be expected to give rise to females laying non-hibernating eggs) could be modified during the larval stage. When such larvae were reared at a low temperature in continuous light many more of them developed into moths which laid non-hibernating eggs than was the case with similar larvae reared at a higher temperature in continuous light. This means that if the eggs were incubated in conditions inducing the moths to lay non-hibernating eggs and the caterpillars were also reared in similar conditions (low temperature and continuous dark) the percentage of moths laying non-hibernating eggs was increased. In other words incubation conditions of a high temperature (25°C - 28°C) and more than 15-hours' photoperiod per day or continuous light go hand in hand to induce the moths to lay hibernating eggs whereas the incubation conditions of a low temperature (15°C - 18°C or so) and a short photoperiod of less than 12 hours each day or continuous darkness go together to induce the females to lay non-hibernating eggs. Comparing these combinations of the levels of the two factors with the favourable time of the year for rearing and the unfavourable season during which <u>Bombyx mori</u> needs going into a stage of quiescence, it would appear that the behaviour of this insect expressed in the experiments synchronizes with the seasonal requirements.

(c) <u>Interaction of temperature and photoperiod.</u>

The interaction did not produce any significant effect. Since at a lower temperature (18°C) fecundity was greater than at 21°C (Expt. 2) and the short photoperiod of 9 hours depressed egg laying capacity relative to the longer photoperiod of 15 hours, these two factors in combination (corresponding to autumn conditions in nature) resulted in moderate fecundity. Similarly the combination which is likely to occur in nature during summer, namely high temperature and long photoperiod, resulted in moderate fecundity because the two influences tended to counteract each other. The larvae took longer to develop when exposed to 9 hours' light each day but those that were exposed to 15 hours' light each day laid more eggs when they became adults. Longer larval life in a healthy condition is good for fecundity as presumably more food is eaten. It appears, therefore, that the insect may be adapted in nature in such a way that the factors of the environment (temperature, food, light) at any time of the year tend to compensate each other with the result that the insect may remain actively reproducing throughout the year.

(d) Effect of quality of food.

(i) The Physiological stage of development of plant.

In Experiment 4 moths which were fed on white leaves from the hearts of cabbage plants during their larval life produced the highest number of eggs, the average being 274 per female (Expt. 4, Table 10a) ; on the outer quick-growing, young, green leaves the average was 201 eggs per moth. The difference between these two types of food was not quite significant at the 5 percent level.

When white leaves were given to the first two instars and young green leaves in the second two, the number of eggs per moth was 221, which is in between the value of these two foods separately but nearer to the value expected were young green leaves given throughout the larval life. It shows that the effect of food eaten in the last two larval instars is dominant over that eaten in the first two instars.

In those cases where it was desired to use the mature leaves it was necessary to rear the larvae for the first two instars on white or young green leaves and then change to mature leaves for the later instars. Irrespective of whether the food during the first two instars was white or young green leaves, the change to mature leaves for later instars resulted in fewer eggs from the adults. The differences were significant ($P < .001$). Slightly more eggs were laid on the combination of white followed by mature leaves.

The favourable effect of good quality food appears to be accumulative when fed during a part of the larval life. As may be expected, perhaps the effect of food eaten during the last two instars is dominant over that taken in the first two instars. If the supply of a better quality food is extended to the third instar as well it imparts a cumulative good effect (Expt. 4 , Table 10a; treats. (2), (5), (7)) . However, in one treatment in which caterpillars after feeding on white leaves in the first three instars were given young green leaves in the fourth (Expt. 4, Table 10a; treat.(2)), the egg laying capacity was not as high as would have been expected due to the desirable effect of white leaves. This may have been accidental or some unnoticed factor might have had its influence.

Moths which were reared on a good quality food and which laid a high total number of eggs showed regular curves of oviposition whereas those reared on an inferior food showed great variation in the number of eggs laid on different days of their lives (Fig. 2).

Quality of food eaten is known to influence the fecundity in many insects. Reproductive capacity varied with the species of host plant in Melanoplus differentialis (Sanderson, 1939), Aphis rumicis (Davidson, 1922), Heliothis armigera (Isely, 1935), Leptinotarsa decemlineata (Trouvelot & Grison, 1935) and that of chinch bug with different varieties of sorghum (Dahms, Snelling, Fenton, 1936). The cotton leafworm Alabama argillacea laid fewer eggs when it was reared for seven to eight generations on fruit, but subsequent generations which were fed on a better diet regained their normal capacity for egg-production (Creighton, 1938). The tuber flea beetles Epitrix tuberis which were living on buffalo burr laid more eggs as the plants became older (Hill, 1946). One female of Aphis rumicis which was feedong on a young plant from which the top had been cut off, produced, during 14 days, 105 offspring. During the same period another aphis which was feeding on a young bean plant which was intact, produced 235 offspring. A high proportion of the progeny of the first one was winged but only a small proportion of the progeny of the second one was winged (Davidson, 1929).

When tea leaves of different ages, containing different proportions of carbohydrates to albuminoids, were fed to various species of insects, it was found that as the quantity of the carbohydrates in the food diminished the fertility of Epilachna, Tinolius and Toxoptera decreased, but that of Diacrisia and Helopeltis increased up to a certain proportion, and after that decreased. It was seen that the ratio between the carbohydrates and the albuminoids in the food played an important role and that somewhere there seemed to be an optimum, different for each separate species, on which the insects throve best (Jong, 1938).

Evans (1938) correlated nitrogen-content of the host plant with the rate of reporduction of aphis Brevicoryne brassicae. Hasemann (1946) found that on nitrogen-deficient corn the chinch bug matured faster and produced more offspring. On the other hand, nitrogen-content of food stimulated the reproduction of Melanoplus m. mexicanus (Smith and Northcott, 1951). This contradiction may mean that the effect of the quantity of nitrogen present in food is not quite straightforward work.

In Loxostege sticticalis the unsaturated fatty acid content of body fat was directly related to sterility; linoleic acid was essential for development and reproduction. This cannot be synthesized in sufficient quantity and must, therefore, be obtained from fatty material in plant foliage (Pepper and Hastings, 1943).

Records of infestation of apterous Aphis fabae on potted sugar beets showed that the leaves were very suitable when young but became unsuitable as they matured; became suitable again just after maturity and then unsuitable once more as they senesced (Ibbotson and Kennedy, 1950). The clustered distribution of aphids within the boundaries of the leaves of spindle and sugar beet was not a matter of chance but involved active aggregations; it was due primarily to intrinsic differences between leaves, but was aided by gregariousness (Ibbotson and Kennedy, 1951). Among the leaves on the same kind of plant the aphids preferred to feed and reproduced faster, on the whole, on young and early senescent leaves than on mature ones: they reproduced better on spindle than on beet leaves. On the basis of these findings Kennedy and Booth (1951) propounded a dual discrimination theory of host selection, "which assumes that aphids respond behaviourally to at least two main classes of leaf property: one associated with the age of the leaf and the other with the kind of plant".

The effect of the physiological condition of the plant (Solanum tuberosum) was studied on the fecundity of Leptinotarsa decemlineata which showed that the egg-laying capacity of the insect was less when it was feeding on old leaves than when it was feeding on young leaves. Grison (1952) obtained the following results: on young leaves 139 eggs per female (average life 39 days); on old leaves 12 eggs (20 days); on old leaves plus lecithine 2 percent, 228 eggs (49 days); old leaves with amiden 5 percent, 88 eggs (28 days); old leaves plus glucose 10 percent, 28 eggs (19 days).

It appeared that when excessive glucose was added the harmful effect of some nutrient deficient in old leaves was overshadowed (Grison, 1952). This may be due to a higher percentage of lecithin in young leaves: beetles fed on this type of food laid more eggs than those fed on old leaves (Grison, 1948).

The flea _Xenopsylla cheopis_ fed well and lived normally on baby mice, but they laid an abnormally small number of eggs. If the fleas were first fed for a few hours on an adult mouse and thereafter on baby mice they laid more eggs than those not fed on the adult mouse at first (Buxton, 1948).

It appears that certain nutrients in the food of an insect species are either absolutely essential or more desirable than others for the production of eggs. The quantity or proportions of these nutrients may vary from food to food (species to species) or within different qualities of the same type of food, (that is, different physiological stages of development of a plant or animal). It is doubtful whether the same nutrients are favourable for fecundity in insects belonging to related groups or that certain specific nutrients are required by every insect. It is very likely that the proportion of such a nutrient or group of nutrients to the rest of the nutrients of food, is more important than the actual quantity itself.

(ii) _The Physiological difference in plants grown in different photoperiods._

In Experiment 2 plants growing during summer were exposed to 9 hours and 15 hours of light daily: and in Experiment 5 plants growing during winter were exposed to the same photoperiods. In each case slightly more eggs were laid by moths which had been reared as larvae on the plants exposed to the longer photoperiod (Tables 6 a,b ; 11 a,b). But in neither case was the difference significant. The fact that the difference was in the same direction in each experiment suggests that it might be possible to demonstrate a small effect by using more replicates.

It used to be thought that the reproductive capacity of _Aphis rumicis_ towards September-October (Northern Hemisphere) declined as a result of lower temperature; but in cultures carried on throughout winter in a warm greenhouse the females also produced fewer offspring at this time of the year than they did in June; this lower fecundity might have been caused by the short photoperiod (Davidson, 1929).

As organic matter increases during the day time (Pigorini, 1915; Sacchi, 1921), mulberry leaves cut in the evening proved best for silk production (Bergmann, 1940). Of the individual substances isolated from mulberry leaf, adenine, asparagine (Misaroto, 1912), cystine and crysteine (Kishi, 1935), the last two were comparatively rare in young leaves but their quality increased with the growth of the leaf, being maximum at places where photosynthesis was most active.

(e) Interaction of food and photoperiod.

As tested by the number of eggs laid in experiments (2 & 5; Tables 6,11), the interaction was not significant. In general it appears that the food kept better when it was exposed to the same photoperiod as that in which it had been grown. In Experiment 5 caterpillars fed on food grown in 9 hours' light laid more eggs when exposed to 9 hours' photoperiod than to 15 hours (in the latter case the leaves in the incubator became yellow earlier than in the former case), with a difference of 28 eggs per female. Moreover moths laid in a very irregular manner (Fig. 5, (2).). However, cabbages grown in 15-hour photoperiod proved better than the above food for egg-production irrespective of the photoperiod to which the larvae were exposed in the incubator.

When the speed of development was measured the interaction between food and photoperiod was the same as when it was judged by the number of eggs laid. But since 15 hours' light per day was better for egg production in one experiment (2) and 9 hours' light in the other (5), it is difficult to say whether prolongation of larval life in 9 hours' light with food grown in 9 hours' photoperiod would be likely to result in the production of more eggs, especially because in Experiment 5 the length of larval life was not recorded.

Sexual forms of Aphis forbesi normally appear in November, but Marcovitch (1924) produced them early in the spring by giving 8 hours' daylight to the food plants. It was seen above that in Aphis rumicis the production of winged forms was connected with fecundity as influenced by the quality of food (Davidson, 1929). According to Shull (1928 & 1929) the offspring of wingless parthenogenetic females may be winged or wingless depending upon the exposure to light, which perhaps affects the nutritive condition of the plant. In some species of aphids the carbohydrate content of plants might play a critical part in determining the rate of reproduction during the short dull days of early spring and late autumn. Evans (1938) found that there was a low limit of carbohydrate content of cabbage plants at which reproduction was just possible; with the increase in carbohydrate content the rate rapidly increased till it reached a maximum, after which it declined or remained constant according to the light conditions.

It has been found that as a result of the photoperiod a substance of a catalytic character in the nature of a 'hormone' is formed which is responsible, directly or indirectly, for the induction of floral primordia (Murneek and Whyte, 1948), but the production of photoperiodic impulse probably has no direct relation to photosynthesis (Potapenko, 1944).

Diapause is imposed upon Euproctis (Grison, 1947) by seasonal changes in the quality of food (perennial deciduous host) caused by differences in temperature and photoperiod.

Since short photoperiod at lower temperatures may cause such an important change in the quality of plants, it is feasible that certain opposite reactions might appear in the plants if they are subjected to reversed conditions of photoperiod suddenly and thus the fecundity of the insects feeding on them might be affected. In other words some of the results which I have recorded in my experiments in which speed of development or fecundity has been influenced by the food, and especially food grown at different photoperiods at different seasons of the year, may reflect abnormal conditions in plants which have been grown at combinations of photoperiod and temperature which they never experience in nature.

(f) Relation between longevity and fecundity of moths.

It was observed in the experiments that generally the female moths which lived longer laid a higher number of eggs. As a rule a greater number of such long-lived moths was produced on white or young green leaves of cabbage than on mature green leaves. The females which lived for a longer period usually laid eggs regularly whereas the short-lived moths produced from poor quality food laid eggs in a very irregular manner (Fig. 2, (6),(8)). When the total number of eggs of 10 females reared on poor food was plotted as laid on different days of their lives the graphs showed that their laying sharply fluctuated from day to day, whereas those females which were reared on better quality food did not fluctuate so much in their laying and their graphs showed normal curves. Moreover, a greater proportion of living females reared on good quality food laid eggs every day than those reared on a poorer diet (Fig. 2, (1),(5),(7)).

(g) Sterility in males.

Fertile males can mate more than once. A female does not lay eggs without fertilization: quite often it mates more than once during its life. In the only experiment done with males there was an indication that the males which were reared as larvae on mature leaves tended to be sterile, while those that were reared on young white or young green leaves were fertile. But the experiment contained too few replicates to demonstrate the significance of the differences (Expt. 8).

(h) General.

Plutella reared at 18°C produced more eggs than at 21°C; moreover the greater fecundity was associated with the greater weight. The association of reproductive capacity with body weight is perhaps universal among insects. The influence of photoperiod on the speed of development is rather characteristic in the experiments and has also a significant effect on the fecundity. Perhaps the caterpillars respond to photoperiod by eating for a longer or a shorter period each day when exposed to the different photoperiods. Or photoperiod may influence the secretion of digestive enzymes. Pradhan (1939) claimed on histological evidence that the enzyme secretion was continuous in phytoplageous and discontinuous in carnivorous Coccinellids. In leaf eating Tettigonia enzymes are secreted when feeding is in progress but in field locusts Stenobothrus secretion is continuous (Schlottke, 1937).

Fertility of an adult insect depends in whole or part upon the adequacy of its nutrition during the pre-imaginal stages. A moderate limitation of the quantity of food available to a growing insect ordinarily results in the formation of an adult of reduced size but essentially of normal physiology and function (Trager, 1953). But if the food is deficient in some nutrients both the speed of development and the fecundity of the insect may be adversely affected. Such nutrients may be entirely different from the ones needed by the vertebrates. For example, the presence of cholestrol in the diet is neccesary for normal growth in insects (Fraenkel and Blewett, 1943), whereas vertebrates can synthesize it in their bodies.

Davidson (1921) reared Aphis rumicis on broadbeans, peas, mangolds, sugarbeet, red beet and poppies, and found that they did best on broadbeans, but on the other plants the speed of development was slow and there was lower rate of reproduction connected with smaller size.

The larvae of spruce budworm fed partially on pollen and partially on foliage developed more quickly than the ones fed exclusively on foliage. Pollen as a food did not appear to have any direct effect on survival or fecundity. It was observed that during the earlier stages of infestation, younger foliage was available but later on when the insects had to feed on old foliage mortality among them increased, their development was retarded and fecundity was reduced (Blais, 1952).

The aphid infestations on 'Katahdin' and on a seedling resistant to Myzus persicae were studied with two dates of planting. It was found that in the early planted pots the number of aphids per plant was five times greater on 'Katahdin' than on the resistant seedling (Bradley and Ganong, 1951).

Hasemann (1946) in his experiments found that insects reared on plants grown in mineral-deficient soils were not affected as far as their vitality and reproduction were concerned; instead the shortage of certain minerals actually proved beneficial. The greenhouse whitefly throve best on those petunia plants which were grown in full nutrients and did not develop normally on plants grown in the shortage of iron or potassium, but the tomato plants grown on full nutrients were less attractive than those on either a phosphorus or magnesium deficiency. The grain aphis, Toxoptera gramium bred more uniformly and quickly on wheat plants grown on full nutrients; shortages of either sulphur, potassium, magnesium or iron had no apparent ill effects on them, and for the first six generations the females actually produced more offspring than did those on the full nutrients. It seems that the aphis needs ample nitrogen in its diet and when certain elements like calcium, phosphorus or potassium are withheld from the host plant, it produces as well as on plants grown on full nutrients. In nature also the corn crops grown on soils which are deficient in nitrogen are found to have greater infestations of the pest. Thus, when soil deficiencies may have an unfavourable effect on the development of vertebrates, insects may not be greatly affected and in some cases they may even thrive on plants grown on soils deficient in some chemicals.

Section III.

PRODUCTION OF SILK.

Caterpillars reared at 18°C produced more silk than those reared at 25°C; the difference was significant at .1 percent (Expt. 1, Table 3).

Poorer quality of food, that is mature leaves, as compared with white or young green leaves of cabbage, depressed the quantity of silk produced; the difference was significant at .1 percent level. It may be seen that conditions which cause a lower body weight and lower fecundity also result in less silk. Larger insects produce more silk perhaps because they need a bigger cocoon.

Males produce less silk than females. They also develop more quickly, are lighter in body weight and have a higher ratio of dry matter to water.

In silkworms, the foods tried as substitutes of mulberry (e.g. Osage orange _Maclura aurantiaca_) were found to be of inferior quality because they resulted in a higher mortality, slower development and lower body weight and less silk of an inferior quality.(Vecchi, 1926, 1927, 1930). _Scorzonera hispanica_ (black salsify) in Europe was considered a suitable substitute but the mortality was very high; Damjanovskij et al (1933) found that high acidity in the leaves (pH 5.5-6.1) was the cause. Wild silkworms were not so restricted to one food - even among them there existed a close relationship between the type of leaves, the growth of the worms and the quality and quantity of the silk produced (Bito, 1931; Kitzawa, 1932). Nutritional value of the mulberry leaves was conditioned by age, climate, season, exposure to light and composition of soil; Kellner et al (1884) pointed out the importance of chemical changes in leaves with age. Within a period of one month changes in the chemical composition of leaves were noticed: dry matter steadily increased, protein and fat of the dry matter decreased, while its nitrogen free extracts, ash and fibrous material, increased. During the process of growth the proportion of different types of proteins in leaves changed; those present in the older leaves were less digestible by the gastric fluid of the silkworm (Kishi, 1933, 1935). When the silkworms were fed on young leaves the protein content of the dry weight of the body was increased and the absolute weight of the silk gland and its relative weight in comparison with the total weight of the body was also increased. Hence the silk production of worms raised on young leaves was greater than that of the worms raised on older leaves. The superiority of younger leaves over older ones also depends on their higher content of cell sap which contains most of the easily digested proteins (Kishi, 1932, 1935, 1937). Very young mulberry leaves were not so suitable for silk production as they contained less soluble carbohydrates (Kato, 1934). Caterpillars feeding on such leaves excreted more of uric acid which showed a high rate of metabolism (Kishi, 1935); as there are less digestible carbohydrates the worms are compelled to utilize the protein resources. This protein consumption can be decreased by supplementing the diet of very young leaves by an addition of sugar. Demjanooski et al (1933 a,b) found that a diet of top mulberry leaves (3-4 days old) reduced the larval period and the silkworms were strong and healthy, producing heavy cocoons of long, strong silk. Middle leaves (30-40 days old) proved like an average mixture and bottom leaves (90-100 days old) prolonged the larval stage, increased mortality and led to a low yield of cocoons of inferior grade.

The effect of cabbage leaves of different ages on silk production and body weight of <u>Plutella</u> is similar to that of mulberry leaves on <u>Bombyx</u>. It is possible that somewhat similar general changes in the chemical composition of cabbage leaves take place with growth as have been found in mulberry leaves, although there would be a variation in the individual substances found in the two types.

The influence of quality of food may be equally evident in the case of other excretions of various insect species. For example, Mahdihassan (1936 a,b) found that the quality of food was the most important factor in lac production.

Section IV.

D I A P A U S E.

Seasonal incidence of diapause is quite well known in many insects. Various environmental factors like temperature, food or photoperiod etc. are closely related to the inception of diapause in different species. In some insects like Pyrausta this phenomenon may be governed by genetical constitution which in itself may have been influenced by any of the above factors. Usually diapause is associated with slow growth, especially towards the later stages of larval development. It is thought that the outcome of slow rate of development may be to cause the larvas to mature with a reduced water content especially in insects in which diapause appears with the approach of autumn, a time when all the growth-retarding factors like lowering temperature, maturing food and less favourable humidity are prevalent. In other cases (as in Spalongia) it is determined by physiological condition of the mother; and this supports the view that slow rate of development and diapause may not have any causal relationship and that both of them may be caused by temperature, food or light (Andrewartha, 1952).

It was seen above (Discussion: Sec. I, II) that temperature in itself, though it affects the speed of development and total body weight, does not affect the ratio of dry-matter: water, (which is important for normal activity). Quality of food, on the other hand, affects all these three characteristics: and temperature and photoperiod have a great influence on growing food in changing its quality.

In insects in which temperature or light (photoperiod) is the direct cause of diapause the nutrients stored in their bodies must play an important part both in determining the onset and cessation of 'diapause-development' as the energy required for that time would be obtained from this source (e.g. fat body in diapausing insects). It appears that the storage of these nutrients, if not wholly, to a great extent, is influenced by the quality of food eaten. Thus it seems that of all the factors of the environment, food probably plays a dominant role even though apparently some other factor may appear to be doing so.

Pepper (1937) demonstrated that the diapause in sugarbeet webworm could be readily broken if the individuals were subjected to low concentration of vapours of certain fat-soluble chemicals. But these chemicals did not influence the diapause condition of codling moth larvae (Hastings and Pepper, 1944). The fat reserve in codling moth prepupae is over 20 percent greater than in the webworm prepupae. Over 98 percent of the moisture-free materials in the webworm prepupae consisted of protein and fat while only 84 percent of the dry material in the codling moth larvae could be attributed to these materials. This difference was supposed to be due to a higher percentage of unknown carbohydrates in codling moth than in the webworm. Moreover webworm prepupae contained more free fatty acids and had a smaller percentage of unsaturated acids than the codling moth prepupae. But in the webworm it was noticed that the quantity of unsaturated acids had increased during the period of five months of diapause (Pepper and Hastings, 1943). The comparison of the chemical composition of fats of these two species could not account for the observed difference in the behaviour of their diapausing forms to the action of various fat solvents. The authors suggested that a knowledge of the composition of the unidentified materials in codling moth larvae (supposed to be carbohydrates) may provide an explanation for the difference in behaviour between the two species (Hastings and Pepper, 1944).

There is an indication that Plutella undergoes an incipient diapause which condition is regulated by certain interactions of temperature and photoperiod (Discussion: Sec. I (b)). A similar symptom of slow speed of development is caused if caterpillars are fed on food grown in corresponding conditions of photoperiod (Expt. 2, Table 6). Although the difference is not large it is in the same direction as the direct effect of photoperiod on speed of development.

Section V.

SURVIVAL RATE OF PLUTELLA.

(a) Quality of food.

On senescent leaves of cabbage, caterpillars did not survive even when this food was given after feeding them on white or young green leaves in the first two instars (Expts. 1,4). Since during senescence there is very little photosynthesis going on in the leaves, the amount of carbohydrates present would be very low. Such a food may be inadequate as a diet. Moreover the proteins present in the tissues of a leaf are broken down and are utilized as a source of energy with the result that the percentage of water in the cell sap is increased. Perhaps the larvae did not get full nourishment when fed on this food; or perhaps during the break-down process some injurious by-products are produced in the sap which cause death.

Newly-hatched caterpillars failed to eat mature leaves (probably the cuticle is too hard), but when they were fed on tender young leaves in the first instar and mature leaves in the second instar, they remained weak, development was slow and large numbers died during larval life. If this food was given only in the third and fourth instars, the speed of development was not so slow and mortality was also reduced. But those which pupated were lighter in body weight and contained relatively more water than the pupae which were fed on tender young leaves throughout their larval period (Expt. 1, Table 5).

White and young green leaves from the same cabbage plant given throughout larval life were most suitable for development and on these survival and fecundity were much higher as compared with the other two foods. The moths reared on these foods lived for a long time and a high percentage of the females living laid eggs every day (Fig. 2).

The slower development and smaller populations of Tribolium on patent wheat flour and similar products than on whole-wheat flour was probably due in part to the low phosphorus content of the food (Nelson and Palmer, 1935). By the addition of wheat to vegetable mold from grassland in the diet of the Japanese beetle, its cold-hardiness was increased (Payne, 1929).

Kennedy et al (1950) studied leaf-by-leaf distribution of free infestations of viviparous Myzus persicae and Aphis fabae on sugarbeet and spindle plants in pots in the greenhouse and the distribution of the various seasonal forms of A. fabae on the same plants growing naturally outdoors. In each case the distribution was related to the age of the leaf; growing and senescing leaves were more susceptible to colonization than maturing, mature and dying leaves. When both insect species were infesting the same plant at the same time their distributions were broadly alike, but M.persicae was more closely confined to both younger and older leaves as compared with A. fabae. They reached the conclusion that the degree of adaptation of a given aphid to a given plant may be gauged by the extent to which the aphid can colonize the plant leaves not only when they are growing and senescing but also when they are mature and fully functional.

In the field the availability of young and tender leaves of cabbage to the newly hatched caterpillars of Plutella is very important for their survival. Congestion of too many larvae on a unit surface area may also result in the spoiled condition of the fresh leaf. During the first two instars the caterpillars, because of their small size, cannot go very far in search of better food, so they are especially vulnerable in this early stage of their development. High mortality, therefore, may occur due to a change in the quality of food by the feeding of caterpillars themselves. The larger larvae are not only more motile but they can also overcome this harmful effect of bad food with a greater ease if they move to better quality.

A mature crop of cabbage is, therefore, of no use to Plutella unless enough tender leaves are present for newly-hatched caterpillars to mine in; and the greater the surface area of mature leaves the smaller the chance that moths would lay enough eggs on the tender leaves. It has been noticed in the field that the population tends to increase most in a field of young cabbages. In young plants the insects tend to concentrate towards the centre, with the result that if they are numerous, the heart may not be formed. But if the heart has already formed at the time when most of the eggs are being laid, it becomes bigger from within, forming a covering of mature leaves on the top so that the plant does not suffer a severe loss from insect attack although the caterpillars go on feeding on the outer layers of the heart. In such advanced cases, dew forms on the centre of the cabbage; this moist condition is not suitable for the spinning and attachment of cocoons. The majority of caterpillars are seen feeding in the heart for the first three instars and in the fourth they move out to feed on maturer leaves and pupate there. It is in the centre of the plants that the larval parasite Horogenes (Angitia) searches for caterpillars, whereas the pupal parasite Diadromus is more commonly observed in between the large mature leaves. Ullyett pointed out the importance of the growth factor in cabbage plants in the study of the relationship of Plutella and its parasite Horogenes (Angitia). He found that in the field the percentage of hosts in which superparasitism was found varied directly with the number of host larvae per plant. This increase of superparasitism with increased host density is difficult to understand as it is the reverse of what would be expected when a discriminative ability is possessed by the parasite. A similar relationship existed between superparasitism and the ratio of hosts to female parasites. Where there were two hosts to every parasite superparasitism was highest: when the proportions were reversed and there were five parasites to every host, it was lowest. These two observations seemed anomalous. The plants on which the hosts were distributed for feeding and which were required to be searched by the parasites, were increasing in size during the period of observation, and that was the most important of the environmental changes. Thus when the field data were adjusted to show superparasitism per unit area rather than per plant, the percentage of superparasitism varied as would be expected. So when the parasite has fewest units to search the relative host density is high, therefore there is no difficulty in finding hosts as they are concentrated on a comparatively small area, and thus there is a greater chance of a host being found and parasitized. Since the parasites search at random (Ullyett, 1936 a) the degree of superparasitism would be increased. When the host density is low the number of parasites for a certain number of hosts is increased and the chance of superparasitism does not increase in the same proportion; as in random searching five parasites per unit area do not search that area five times as efficiently as one parasite alone (Ullyett, 1943).

Considering these cases it may be seen that when the cabbage plants are young and the weather has already warmed up there are greater chances of their being overpowered by the pest, firstly, because the moths will lay eggs on tender leaves and, secondly, because the parasites will not be quite active (Ullyett, 1947). But with the increase in surface area of the crop there will be a tendency towards moderation in density of the host insect. A practical use of this observation can be made by sowing the spring cabbages early so that their hearts may be formed before the expected time of the appearance of Plutella.

(b) Resistance in plants.

The survival rate of caterpillars fed on plants given nitrogenous and potassic fertilizers was not different from that of those on the controls, but the addition of phosphate caused a higher mortality; the difference was significant at .1 percent level (Expt. 6, Table 12). The leaves of the plants receiving additional phosphate seemed to be stouter than the others.

More caterpillars reached adult stage on the variety Sugarloaf than on Succession, but the difference was not quite significant at the 5 percent level. On the other hand the application of phosphorus as manure caused a higher death rate in the former than in the latter variety. (Expt. 6, Table 12 a,b).

Unfortunately, in this experiment there were unusually high death rates in all the treatments which I could not account for. Caterpillars died gradually. Though the leaves in the incubator (at the same temperature at which they were grown) turned yellowish earlier than what was normally observed in the previous experiments the mortality was not related to this characteristic as in many cases survival on such leaves was better than on quite green ones. The change in the colour of the leaf was not related to the variety of the cabbage or to manurial treatment.

Plants were grown in a temperature-control room during the summer at 70-80°F. This temperature corresponds to late winter or spring conditions in nature when days for photosynthesis are short. In this case low temperature combined with long-day for photosynthesis of plants may not have produced a quality of food which was not suitable for the insect.

Moreover, plants were grown within double glass walls which evidently did not permit the penetration of ultraviolet rays: in fact, the plants were never exposed to the direct rays of the sun because the leaves were brought to the laboratory in glass jars and were fed to the insects in the incubator. This might have been the cause of some undesirable changes in the plants.

The addition of nitrogenous fertilizer to mulberry trees and their interculture improved the quality of the food and the silkworms fed on that produced more silk (Bergman, 1940, Review). It seems from the above observations that the appearance or size of a plant is not indicative of resistance to insects. No chemical differences could be correlated to the resistance of sorghum varieties to chinch bug attack (Webster, et al, 1948). The effect of a fertilizer on a plant may be no more than merely to change the ratio of water to dry matter. According to Mumford and Hey (1930), the nitrogen content and water content of plants are interdependent and they suggest that this relation may be important for insect fecundity as well as resistance of plants to insects. A water relationship was also noticed by Tauber, et al (1945). The nitrogen content of the cell sap of plants is an important factor in their susceptibility to the attack of chinch bug (Dahms, 1948) and aphids (Davidson, 1922 & 1923). It was seen above (Kennedy et al, 1950) that the physiological stage of development of the leaves on host plant was closely related to aphis attack.

The physiological condition of the plant as influenced by age, type of soil and other factors of the environment forms, therefore, a very important basis for the study of its resistance to insect attack. It may be true that a plant which looks weak in health may be easily attacked by insect pests, but the insects can live on it only if it provides adequate nourishment. On the other hand a plant may look quite healthy but may contain an excess of some nutrient which may impart immunity to it against the attack of insects as, for example, cabbages getting excess of phosphate manure cause a high mortality among Plutella caterpillars feeding on them.

Schaefer (1936) put forward a hypothesis that the resistance among red locusts to infection of white fungal disease (Beauveria bassiana) was correlated with the general health and vitality of the individuals. Unfavourable climatic or environmental conditions lowered the resistance of the insect by an adverse effect on its vitality and hence such conditions indirectly favoured the spread of disease. But Ullyett and Schonken (1940) criticized this hypothesis and stated that since the disease did not appear every year it applied to special cases only. They noticed, however, that 4th instar Plutella caterpillars were more susceptible to fungus disease (Entomophthora sphaerosperma) than the early instars, which they thought might be due to the difference in composition of the body fluids. In this connection the physiological condition of food plants may have some influence on the health of caterpillars. While rearing Plutella caterpillars in the laboratory it was noticed that the adverse effect of undesirable food was always more pronounced in the 4th instar and that the caterpillars feeding on unhealthy cabbage leaves or leaves of undesirable quality, were more prone to disease fungi and bacteria than the ones feeding on good quality food (Expt. 8).

(c) Sexes : survival.

It has been shown above that the two sexes respond differently to different foods (Expt. 1) ; it is possible that at a given temperature (high) and certain quality of food (poorer) females may not be able to draw their nutritional requirements and relatively more of them may die whereas males may do better in those conditions.

Trager (1947) criticized the sole application of germinal theory of sex determination and pointed out that the ultimate outcome might be open to modification by quantity and quality of food eaten: as is shown in rotifers (Whitney, 1914, 1916); nematode parasites in grasshopper (Cobb et al, 1927; Christie, 1929); selective survival of one sex in insects (Herms, 1928; Salt, 1936); selective fertilization of eggs depending on size etc. of host (Chewyreuv, 1913; Clausen, 1939), and effect of starvation in larvae of Tribolium confusum (Holdaway and Smith, 1933). Herms (1928) found that in Lucilia sericata relatively more females reached the adult stage when food was plentiful and when food was scarce relatively more males survived. Weidling (1928) made similar deductions. But Ullyett (1950) objected that the size of the sample in these cases was not large enough and in his experiments on the same insect he did not find any difference. But quality and quantity of food in combination with some other factors, such as temperature or differential nutritional requirements of the two sexes, could affect their survival rate as is indicated by my experiments.

(d) Body-form : survival.

The insects that were reared on the poorer quality food (such as the mature leaves of cabbage) were small. Many of them died prematurely, and some showed deformities in wings and antennae. The wings were stumpy and the antennae drooped. When the larvae were reared at high temperatures, again many moths were found with non-erectile antennae but this cause should be differentiated from the effect of quality of food. In this case the insects were also unable to balance their bodies properly.

Caterpillars showed a tendency to stop feeding and moult if the food started to decay, and depending upon the quantity of such food eaten, they either died in the pupal stage or emerged into abnormal moths with or without the above-mentioned deformities.

Females from any of the above groups were found to be most variable in length of life and egg-laying: graphs presenting the number of eggs laid on different days of life show great flustuations whereas graphs of groups of females fed on good food (white or young green) in favourable conditions of photoperiod and temperature show fits nearest to bell-shaped curves of normal distribution (Fig. 2).

A small percentage of the larvae especially in the winter experiments, lingered behind the others so that sometimes they took even double the normal time; usually, with these individuals the durations of the pre-pupal and pupal stages were also longer. These "slow" caterpillars were usually sluggish and did not spin normal cocoons. A large proportion of the females which failed to lay eggs came from these "tailenders". On dissection they were usually found to be full of eggs. The cause of their failure to lay eggs could not be found: there is little doubt that they got a fertile male.

The quality of food is known to influence size in the clothesmoth (Titschack, 1926); eye-colour and wing proportions in Ephestia (Kohler, 1940); size of antennae in Drosophila (Gordon and Samg, 1941); and polymorphism in the honey-bee, white ants and other insects. The larvae of the Mediterranean flour moth Ephestia kuehniella fed on highly milled flour, developed slowly into moths of lighter weight than those fed on flour made from the entire wheat kernel (Richardson, 1926).

(e) General.

It was seen above (Discussion: Sec. I (a)) that at a higher temperature the speed of development in Plutella was quickened but body weight was reduced which presumably was the cause of reduced fecundity (Discussion: Sec. II (a) ; Expt. 2, Table 6 (a),(b)). Moreover, the interaction of temperature and different qualities of food showed that mature leaves of cabbage (which would be found in nature in the warmer season) were relatively more harmful at lower temperatures than at higher ones as measured by the reduction of body weight (Expt. 1): which in other words meant reduction in fecundity. Apart from the direct effect of quality of food on survival, the reduced reproductive capacity also results in smaller populations.

Ullyett (1950) bred several species of blowflies together in a controlled medium and found that in inter-specific competition fecundity was in direct proportion to the intensity of competition --intense competition produced small flies which laid few eggs. In this respect Lucilia suffered less than other species (as it has the smallest maximum normal-growth weight and hence required less food than the others). Thus in competition it outgrew other species found nearby. In all species the first reaction of larval population was to effect a reduction in the average size of the individuals so that they sacrificed size in favour of numbers. The total mortality increased at the same time as the reduction in size was proceeding.

Section VI.

LONGEVITY AND FECUNDITY OF TWO PARASITES OF PLUTELLA, AND DISPERSAL OF HOROGENES.

(a) Effect of temperature and number of hosts available on Diadromus.

Although the females of Diadromus lived longer at 18°C than at 25°C ($P < .01$ percent) both when offered 4 hosts and 8 hosts daily, neither temperature nor the number of hosts present made any significant difference to the total number of eggs laid; in other words, at a higher temperature the parasite lives for a shorter time but is more efficient in parasitization (Expt. 9, Tables 14,15,16).

The number of eggs laid at 18°C was slightly higher than at 25°C but this difference was not significant. At 18°C females laid eggs more regularly from day to day than at 25°C (Fig. 4). Giving females 8 host pupae instead of 4, did not induce them to lay more eggs. Rather fewer eggs were laid in the tubes where there were 8 pupae. But this difference was not significant and it must have been due to chance because it is most improbable that the presence of more hosts would cause the females to lay fewer eggs.

The number of eggs laid per female per day of life and the number of eggs per female per pupa were not significantly different in the treatments. When the females were given 8 host pupae each day some of them were superparasitized even if all the eight were not used to lay eggs. Maybe some of the pupae were not suitable and the females did not lay eggs in them, or perhaps the ones superparasitized were too attractive. Since there was no difference between the total number of eggs laid by the females offered eight or four host pupae a day, it would seem that the degree of superparasitization was higher in the latter case (the data have not been analysed as yet to test the chance of distribution of eggs at random). Lloyd (1940) also observed that this parasite superparasitized even in the presence of more host pupae although the distribution of eggs was not quite at random.

(b) Fecundity of Horogenes.

Twelve females which emerged from parasitized pupae collected in the field laid an average of 51 eggs at 25°C, the numbers varied from 1-194 eggs per female. The average life of the adults from emergence to death was 6 days, varying from 3-12 days (Expt. 10, Table 17).

(c) Dispersal of parasites and selection of host.

The adults of Horogenes, when released from a central point, had a tendency to spread outwardly in all directions, their density thinning out progressively away from the centre (Expt. 11, Table 19). It appeared that the parasites flew in any direction until they came near a cabbage plant; then they concentrated their attention around it. Since some of the host larvae on those plants were parasitized it would seem that the parasites searched for their hosts.

Wind definitely affected the direction of flight (Table 18). In the experiment, wind was blowing from west to east and a far greater number of parasites were taken east of the point of release than to the west, though they were recorded up to 5-feet distance in every direction. Moreover, most of the parasites were lost or were perhaps blown away without finding a plant.

Both in the presence and absence of wind quite a number of parasites were found sitting inactive on the pots underneath the plants (Tables 18, 19). The reason for the inactivity might be that since they had never experienced outdoor life they were getting used to the environment before starting a regular active life of parasitization within a few hours of release.

As to whether the parasites stopped at the plants taking them as cabbage or they stopped there finding any green vegetation above the ground, is difficult to say. It is also difficult to ascertain from these observations as to how the parasites perceived that Plutella caterpillars were there on the plants even though they had never searched for them before. It may be that a parasite female, while flying around on the leaves, by chance came across a caterpillar which, on touch, wriggled and the female followed it instinctively to lay an egg in it. And, after some time perhaps it encountered another and then another which made her remain in the vicinity. Most probably, many caterpillars were lost in the grass because they were chased in this way. This reaction to each other is a normal, instinctive behaviour of the parasite and the host.

Section VII.

GENERAL DISCUSSION.

(a) Synchronization of the activity of the insects with the seasons.

(i) Physical factors of the environment.

Within an optimum zone the effect of temperature on the speed of development of *Plutella* in the experiments was apparent in two ways: firstly, due to higher rate of metabolism and shorter life at the higher temperatures relatively smaller quantities of nutrients were stored in the body so that the inherent reproductive capacity was reduced; secondly, as the adult life was shortened the chance of dying without laying all the eggs was increased. On the whole, in *Plutella* at higher temperatures the length of the life-cycle and the fecundity were decreased.

In the experiments both speed of development and fecundity tended to be greater when the larvae were exposed, during their development, to particular combinations of temperature and photoperiod, namely when long photoperiod was associated with higher temperature and short photoperiod was associated with lower temperature, as they are in nature during early summer and autumn respectively. These factors interact in rather a complex way. It appears that at extremes, temperature is a dominant factor but within a range of optimum temperatures, photoperiod or ratio of light-hours to darkness has a profound effect. Speed of development is regulated in such a way that the harmful effect of one factor is counteracted by the beneficial effect of the other, thus providing a sort of balanced conditions: somewhat similar interactions were observed in the case of fecundity.

Interestingly enough a similar effect was observed indirectly through the food. Food grown at a certain photoperiod tended to be most efficacious when it was fed to larvae which were exposed to the same photoperiod. Also, food grown at certain temperatures tended to be more efficacious when fed to larvae which were exposed to appropriate photoperiods.

Thus food grown at a high temperature was best when fed to larvae experiencing a long photoperiod, and food grown at a low temperature was best fed to larvae experiencing a short photoperiod.

(ii) Influence of quality of food.

In experiments in which the influence of temperature and photoperiod was eliminated it was shown that caterpillars grew more quickly on young green leaves than on mature ones and that moths reared, during their larval stage, on the former food laid more eggs. Also the influence of food was accentuated at lower temperatures. The maturer food was more harmful at a lower temperature than at a higher one. In nature, mature food would be found in the hotter season. It was seen in Experiment 1 that at both temperatures, viz. 18°C and 25°C, the ratio of dry matter : water in the insect body remained constant; probably it holds good at all temperatures within the optimum zone and maybe that this characteristic is important for normal activity. Since on mature food this ratio is upset by reduction in dry matter and a relative increase in water, and the total body weight is also reduced, it may mean that at any one time in nature the reproductive capacity of the insect would be determined by the quality of food available. Thus Plutella may be adapted in such a way that when outdoor temperatures are higher as in summer (life-cycle is shortened) and more food of a maturer or undesirable type is available (on which the speed of development is slower and thus the life-cycle is lengthened), the insect body has a tendency to strike at a correct balance of dry matter : water ratio. But both of these factors lead to a lower body weight which, in other words, means lower fecundity. Thus environmental factors (such as temperature, etc.) promoting a short life-cycle, after some time create conditions (by maturing food), which reduce the reproductive capacity. It may appear in the field that the crop has finished and the food is exhausted but at the same time the inherent rate of reproduction in the insect has already been depleted.

(iii) Sex ratio.

Comparing the constitution of the female body with the conditions of temperature and quality of food providing these requirements (Discussion:

Secs. I (g), IV (c)), it should be noticed that whereas a female may get adequate nourishment only from a good quality food at a moderately lower temperature, a male can do as well at a higher temperature on a poorer quality food. It is, therefore, probable that in nature during favourable conditions of food and temperature there is an opportunity for a greater number of females to survive and in rather unfavourable conditions, a higher proportion of females may die so that males may increase proportionately. In the former case there will be a tendency for the population to increase in density thus increasing the chance of mating so that fewer males would be sufficient but in the latter case there would be a decrease in the density of the population so that a greater number of males would be required to provide an adequate chance of mating. Since actual counts were not made in the field, this is purely a hypothetical consideration.

As mentioned above Seamans and MacMillan (1935) also observed the effect of the quality of food on sex-ratio based on pupal counts, but they did not draw any conclusion because the ratio after emergence was not consistent with the one observed in the pupal stage. In the case of some foods (different species of host plants) the ratio was even reversed on the emergence of adults. That is, when insects were reared on a particular food males predominated in the pupal stage but more females than males emerged from them; the reverse was true on some other food. These differences might have been due to chance or to some difference in the nutrients present in various species of host plants. It has been seen that the cabbage leaves in different physiological stages of development have a different influence on both the speed of development and the fecundity of Plutella. It is quite likely that in a similar way the development of the two sexes may also be influenced. Marcovitch (1924) showed that sexproduction and migration in the Aphididae could be controlled experimentally by subjecting the hosts to definite hours of daily light exposure which effect was independent of temperature (in Temperate Zones). According to him 'the experiments with Aphis sorbi would indicate that just as the short days of fall stimulate the production of fall migrants, so the lengthening days of spring stimulate the production of spring migrants to take their abode on the plantain'. It seems that the activity of the aphids is regulated by the seasons of the year.

(iv). General.

On the basis of the experiments that I or other workers have done, I have given above my interpretation in the form of a hypothesis of 'Synchronization of the activity of the insects with the seasons'. Seasonal rhythm in population of multivoltine insects is well known. In the past in the study of the natural increase in animal populations too much emphasis has been laid on the direct effect of factors of the environment like temperature, light and food etc. But the indirect effect of these factors may be equally important. The presence or absence of food in nature is easily seen but the change in its quality may not be so apparent, although its effect on the population as a whole may be very important. It is hoped that in future due care will be taken in evaluating the effect of the different factors on animal populations.

(b) Balance of nutrients required by insects.

From the above account and work done on other insects, it would appear that the quality of food alone has a direct influence on the speed of development, survival rate, general activity and fecundity of insects. The difference in quality may be as found in different host species for a polyphagous insect or due to difference in the physiological stage of development of the host in a monophagous insect.

In the presence of optimum levels of physical factors of environment the population of an insect species cannot increase unless the available food is also of a desirable quality: sporadic appearance of an insect pest usually follows the fulfilment of these conditions. Due to a temporary change in physical factors to unfavourable levels there may appear a corresponding change in the quality of food (e.g. wilting or turgidity in plants, etc.) which may prove as harmful for insect survival as the direct effect of those factors. The effect of a more gradual change in the quality of food as found in different seasons of the year would be even more pronounced and would affect the entire population.

At any one time insects feeding on a poor quality of food (such as a less suitable species of host or a certain part of host less suitable than others for development etc.) develop slowly, showing a high mortality which is suggestive that some nutritional factor is absent in the food or not present in adequate quantities. Towards autumn, the temperature falls, the day-length becomes short and food of insects becomes drier and consequently different in quality as compared with early summer or spring food. During the adjustment of dry to wet ratio in this food some of the constituents may increase out of proportion to others (e.g. carbohydrates to proteins) which may be stored as such in the body of insects feeding on it. In the beginning of winter diapause appears in many insects in association with increased fat body which helps them to pass the coming unfavourable conditions.

It appears that for normal metabolism an insect requires a certain optimum quality of food containing the right proportion of nutrients. Since growing food is subject to the influence of external environment, such an optimum quality may or may not be available throughout the year. With change in environment (especially physical) certain corresponding changes in the constituents of food would be expected. Some of the nutrients in the food may be present but not in sufficient quantity relative to the others (as found in different species or varieties of a host plant) or some may be present in amounts that are too large relative to the others; in neither case would there be a proper balance of nutrients required for normal activity and reproduction; and certain abnormalities may appear in insects feeding on them.

If certain nutrients are deficient in its food, the normal metabolism of the insect may be upset and it may have to eat more in order to make up the deficiency or may not be able to feed normally at all: slow larval development may be followed by abnormal pupation. Deformed adults may emerge from them which may be short-lived and may have a poor reproductive capacity. If, however, food is very deficient in those nutrients or some harmful constituent is present in it (as, probably, in senescent or decaying leaves) insects feeding on it may die early in life.

In the other case when no vital nutritive factor be deficient in food but some of the constituents may be in a greater proportion to others the insect feeding on it in an attempt to keep up normal metabolism may end by storing an excess of some nutrients (e.g. increased fat body in diapausing insects). During this process the speed of development may be slowed down and in the long run this excessive material stored in the body in itself may upset the normal metabolism. This is, of course, considering that the insect body in such cases is not able to utilize selectively the nutrients present in the food, either because there is no such inherent capacity in that species to do so, or because that faculty has been temporarily affected adversely due to the influence of some other factor of the environment, e.g. the changing length of day may affect certain neuron cells of the insect and thus may cause the secretion of certain hormones which, in turn, may affect the secretion of digestive enzymes etc. If it happens at a time of the year from when on conditions outside are not suitable for normal activity (as low temperature in winter), the insect may enter into a prolonged or intense diapause. On the other hand, if outside conditions are not altogether unfavourable and further development is possible, the normal metabolism may be affected for a short time and after the excessive food store is used up by metabolism and a correct ratio of nutrients is set up within the body, normal activity may be resumed; this may be a case of incipient diapause.

In this hypothesis of 'balance of nutrients required by insects for normal activity', I have made an attempt to explain that for the normal activities of the insect body like healthy development and reproduction, the nutrients are required in certain proportion. If, due to some cause, that proportion is upset, certain abnormalities appear in the metabolism or form of the insect, such as deformities in wings and shape of body, slow speed of development, reduction or impediment in egg-laying capacity or diapause etc. Andrewartha (1952) in giving a hypothesis of 'food mobilization' also pointed out that the metabolic process associated with food reserves stored in the fat body or egg-yolk has a central position as regards the cause of diapause.

S U M M A R Y

The caterpillars of Plutella developed more quickly at 25°C than at 18°C; and they weighed less at pupation at 25°C than at 18°C, but the ratio of dry matter to water was the same at both temperatures.

The exposure of caterpillars to different photoperiods influenced their speed of development. There was an indication that the influence of light was different at different temperatures and perhaps at different seasons of the year.

The larvae reared on white or young green leaves of cabbage developed more quickly than those reared on green but mature or senescing leaves. In this respect the slow speed of development was associated with a higher death-rate among them and a lower body weight combined with a higher water content of the pupae. The harmful effect of the poorer quality food was accentuated at a lower temperature.

The larvae which fed on leaves from cabbages which had received extra phosphorus developed more slowly than the controls, and the death-rate was higher. There was no difference in the speed of development of larvae in the controls and those reared on leaves from plants which had received extra nitrogen or potash.

Irrespective of temperature and the quality of their food females developed more slowly than males and they also had more dry matter and a higher live weight in the pupal stage. Since the interaction of quality of food and sex and the interaction of quality of food and temperature were significant it appeared that the female fulfilled its requirements better from a good quality food at moderately lower temperatures, whereas the male was better able to develop on poorer food and at higher temperatures. It showed that there was differential survival of the sexes.

The insects bred at 18°C produced more eggs than those at 21°C which is thought to be due to the lower body weight at the higher temperature. Photoperiod also influenced fecundity but the effect was not so clear because in two experiments carried out at different seasons of the year light in combination with other factors showed contradicting results.

The quality of food eaten by the caterpillars had a profound influence on their fecundity. Those reared on white or young green leaves of cabbage laid significantly more eggs as compared with those reared on green but mature leaves. Similarly, when larvae were reared on the better quality food they produced more silk, the resulting moths lived longer and a higher proportion of the males were fertile.

The caterpillars reared on plants grown in 15 hours of light each day were more fecund in the adult stage than those reared on plants grown in 9 hours of light daily. The same result was shown by two experiments done in summer and winter, but in both cases the differences were not quite significant at the 5 percent level.

From the effect of temperature and photoperiod and their interaction on the speed of development of Plutella it appears that this insect may be undergoing an incipient diapause in winter.

Although the females of Diadromus lived longer at 18°C than at 25°C, both when offered 4 hosts and 8 hosts daily, neither temperature nor the number of hosts present made any significant difference to the total number of eggs laid.

A preliminary study was made of the dispersal of Horogenes (Angitia) adults in the field. It appeared that immediately after release they spread outwards in all directions. When they came across a cabbage plant they searched for hosts. In this experiment cabbages had been arranged at certain distances apart and a certain number of hosts had been placed on each plant. Routine observations of the presence of parasites were made.

Two general conclusions were reached, firstly, that in Plutella there is 'synchronization of the activity of the insect with seasons', and secondly, that for the normal activities of Plutella a 'balance of nutrients is required by the insect'. It is the author's opinion that these conclusions may also apply broadly to other insects and this may be a useful hypothesis on which to base further work.

ACKNOWLEDGEMENTS.

My sincere thanks are due to Dr. H. G. Andrewartha for his kind guidance and supervision of this work.

I am grateful to the Commonwealth of Australia and the Government of the Union of India for the award of a Fellowship under the Colombo Plan, and to the University of Adelaide for the assistance which made it possible for me to conduct the work at the Waite Agricultural Research Institute. The University of Adelaide also provided an additional grant of money which allowed me to extend my period of work for several months.

I am thankful to Mr. D. C. Swan for the provision of apparatus and for other help given by his department. My thanks are due to Professor J. A. Prescott (Director of the Waite Institute) for the use of the Temperature Control Room and for his helpful consideration of other needs. I am also thankful to Dr. T. C. Browning for his ungrudging help from time to time and to Mr. P. E. Madge for his constructive criticism of the manuscript.

To Mrs. I. Matheson I am indebted for her advice and checkings of the calculations, and to Mr. K. P. Phillips for photographing the figures and plates given in the thesis. Mrs. B. Passey very kindly identified the species of bacteria and Dr. J. H. Warcup the moulds.

I acknowledge with much appreciation the efforts Miss E. H. Hosking has put in to prepare the typescript of the thesis.

A P P E N D I X

EXPERIMENT 12.

The speed of development of Plutella as influenced by different photoperiods during incubation and rearing at 17°C.

In Experiment 3 (pages 19-23) caterpillars hatched on the 26th and 28th October, 1952, developed more quickly than those hatched on the 24th and 25th, and it was thought that it might have been due to the exposure of the eggs to light for different lengths of time (Table 8,a,b,c). This experiment was repeated on the same dates (caterpillars hatched on the 23rd, 24th and 25th October, 1953), to see if there was any influence of photoperiod during the incubation of eggs from overwintering moths on their subsequent development in the larval period.

Third instar Plutella caterpillars were collected from the field (Waite Institute) and were reared in the laboratory at 17°C. As moths they laid eggs at the same temperature. The eggs were incubated at 17°C, half of them being exposed to 9 hours' electric light (1 foot away from 'Mazda' globe 40 w.) each day, and the other half to 15 hours' light daily. As they hatched the larvae from both lots were reared in 9-hour and 15-hour photoperiod each day.

The caterpillars hatched only during exposure to light and within 2-4 hours of their hatching they were distributed at random in the respective treatments. They were reared individually on young green leaves of cabbage in glass specimen tubes 2" x 13/16". The first change of food was done on the fourth day of hatching but subsequently the food was changed on every third day.

To note the time of pupation observations were taken three times a day after every eight hours. Two days after pupation the pupae were separated from their cocoons and the sexes segregated. The weights of both pupae and silk were taken. For their dry matter the pupae were desiccated at 102°C and were kept at that temperature for 24 hours, after which they were weighed.

The following table shows the summary of results and the analysis of variance of the data relating to larval plus prepupal life in days.

Table 20.

(a) Duration of life in days from hatching to pupation (mean based on 25 observations in each treatment), at 17°C at different photoperiods during incubation and rearing.

Rearing	Incubation		Mean
	9 Hours	15 Hours	
S. D.	(± 0.23)		(± 0.16)
9 hours	17.7	18.0	17.8
15 hours	15.3	15.6	15.4
S. D.	(± 0.16)		G. Mean
Mean	16.5	16.8	16.6

Least significant differences (d.f. 96) :

	5%	1%	0.1%
Body of table	0.6	0.9	1.1
Margins	0.5	0.6	0.8

(b) Analysis of variance :

Variance due to	d.f.	S.S.	M.S.
Total	99	272.27	
Treatments	3	144.98	
Incubation	1	2.17	2.17
Rearing	1	142.81	142.81 ***
Interaction	1	0.0	
Error	96	127.29	1.326

Conclusion.

The larvae from eggs exposed to 15 hours of light each day during incubation developed at the same speed as those from eggs exposed to 9 hours of light daily. But the larvae exposed to a 15-hour photoperiod while rearing developed more quickly than those exposed to a 9-hour photoperiod ($P < .001$). This would mean that in Experiment 3 the speed of development of the larvae was not influenced because they were exposed during their embryonic stage to different durations of light, but some other unknown factor was showing its influence (see Discussion : Section I (g), p.55). The caterpillars in this experiment were reared at 17°C whereas in Experiment 3 they were reared at 20°C and 24°C. As the larvae were reared at different temperatures in the two experiments, photoperiod might have influenced the developing embryos differently. Unless it is proved that photoperiod has a differential influence at different levels of temperature I cannot explain the difference in the behaviour of larvae hatched on different dates in Experiment 3; this may be the influence of some factor other than photoperiod.

B I B L I O G R A P H Y

* Papers not read in the original; only their summaries were cited from the reviews.

Andrewartha, H. G. (1952). Diapause in relation to the ecology of insects. Biol. Rev. 27: 50-107.

Ankersmit, G. W. (1952). Local differences in food plants of Phaedonia inclusa (Stal.). 'The soyabean beetle'. (Col. Chrysomelidae). Trans. IXth. Internat. Cong. Ent. 1 : 800-804.

Arbuthnot, K. D. (1944). Strains of the European cornborer in the United States. U.S. Dep. Agric. Tech. Bull. No. 869.

Bergmann, W. (1940). Relations between the food and silk of silkworms. Textile Res. 10 : 462-475. (The Japanese references given below were taken from this paper.)

Bito, S. Bull. Sericult. Silk Ind. (1932).

Demjanovskij, S., Galcova, R., and Demjanovskij, N. Zool. Z. 12 : 59 (1933). Ber. Wiss. Biol. 27 : 788 (1933).

Demjanovskij S., Prokofeva, F., and Fillippov, L. Zool. Z. 12 : 3 (1933). Ber. Wiss. Biol. 26 : 33 (1933).

Kato, K. J. Agric. Chem. Soc. Japan. 9 : 691 (1934). Bull. Agric. Chem. Japan. 18 : 102 (1934).

Kellner, O., Sako, T., and Sawano, J. Landwirtsch. Versuchsta. 30 : 59 (1884).

Kishi, T. J. Agric. Chem. Soc. Japan. 8 : 397 (1933). Ibid. 8 (1933) ; 8 (1933) ; 9 (1934) ; 9 (1934) ; 10 (1934) ; 10 (1934) ; 11 (1935) ; 11 (1935) ; 11 (1935) ; 11 (1935) ; 11 (1935).

Kitzawa, K. Bull. Sericult. Silk. Ind. Japan. 5, 6 (1938).

Mimuroto, Z. J. Coll. Agric. Tokyo, 5 : 63 (1912).

Pigorini, L. Ann. Staz. bacol. sper. Padova 41 (1915).

Vecchi, A. Bull. Soc. entomol. ital. 58 : 132 (1926).

Blais, J. R. (1952). The relationship of the spruce budworm (Choristoneura fumiferana Clem.) to the flowering condition of balsam fir (Abies balsamea (L) Mill.). Canad. J. Zool. 30 : 1-29.

Bottger, G. T. (1940). Preliminary studies of the nutritive requirements of the European cornborer. J. Agric. Res. 60 : 249-257.

Bottger, G. T. and Kent, V. F. (1931). Seasonal history studies on the European cornborer in Michigan. J. Econ. Ent. 24 : 372-379.

Bradley, R. H. E. and Ganong, R. Y. (1951). Aphid infestation on Katahdin and on a seedling resistant to Myzus persicae (Sulz.) with two dates of planting. Canad. J. Zool. 29 : 329 - 338.

Breitenbrecher, J. K. (1918). The relation of water to the behaviour of the potato beetle in a desert. Publ. Carneg. Instn. No. 263, pp. 341 - 384.

Burnett, T. (1949). Effect of temperature on insect host-parasite population. Ecology. 30 : 113-134.

Buxton, P. A. (1948). Experiments with mice and fleas. Parasitology 39 : 119- 124.

*Chan, (Konyit) (1940). Notes on vegetable insect pests in Hong Kong. Part II. Hong Kong Nat. 10 : No. 2, pp. 98-101.

*Chewyreuv, L. (1913). Le role des femelles dans la determination du sexe de leur descendance dans la groupe des Ichneumonides. C.R. Soc. Biol., Paris. 74 : 695.

Christie, J. R. (1929). Some observations on sex in Mermithoidae. J. Expt. Zool. 53 : 59-76.

*Clausen, C. P. (1939). The effect of host size upon the sex ratio of hymenopterous parasites and its relation to methods of rearing and colonization. J.N.Y. Ent. Soc. 47 : 1-9.

_______ (1940). Entomophagous insects. N.Y. : McGraw-Hill.

*Cobb, N. A., Steiner, G. and Christie, J.R. (1927). When and how does sex arise? Off. Rec. U.S. Dep. Agric. 6 (43).

*Cousin, G. (1932). Etude experimentale de la diapause des Insects. Bull. Biol., Fr. Suppl. 15 : 341.

Creighton, J. T. (1938). Factors influencing insect abundance. J. Econ. Ent. 31 : 735-739.

Dahms, R. G. (1948). Effect of different varieties and ages of sorghum on the biology of the chinch bug. J. Agr. Res. 76 : 271-288.

Dahms, R. G., Snelling, R. O. and Fenton, F. A. (1936). Effect of several varieties of sorghum and other host plants on biology of the chinch bug. J. Econ. Ent. 29 : 1147-1153.

Davidson, J. (1921). Biological studies of Aphis rumicis Linn. Ann. Appl. Biol. 8 : 51-65.

_______ (1922). Biological studies of Aphis rumicis Linn. Reproduction on varieties of Vicia faba. Ann. Appl. Biol 9 : 135-149.

_______ (1923). Biological studies of Aphis rumicis Linn. The penetration of plant tissues and the source of food supply of aphids. Ann. Appl. Biol. 10 : 35-54.

_______ (1929). On the occurrence of the parthenogenetic and sexual forms in Aphis rumicis Linn. with special reference to the influence of environmental factors. Ann. Appl. Biol. 16 : 104-134.

_______ (1942). On the speed of development of insect eggs at constant temperatures. Aust. J. Expt. Biol. & Med. Sci. 20 : 233-239.

Dawson, R. W. (1931). The problems of voltanism and dormancy in Telea polyphemus. J. Expt. Zool. 59 : 87-131.

Dickson, R. C. (1949). Factors governing the induction of diapause in the oriental fruit moth. Ann. Ent. Soc. Am. 42 : 511-537.

Dickson, R. C. and Saunders, E. (1945). Factors inducing diapause in oriental fruit moth. J. Econ. Ent. 38 : 605-6.

Evans, A. C. (1938). Physiological relationships between insects and their host plants. I Effect of the chemical composition of the plant on reproduction and production of winged forms in Brevicoryne brassicae L. (Aphididae). Ann. Appl. Biol. 25: 558-572.

Evans, A. C. (1939a). The utilization of food by certain lepidopterous larvae. Trans. R. Ent. Soc. Lond. 89 : 13-22.

Ficht, G. A. (1931). Some observations on the planting date of corn and its relation to European cornborer population. J. Econ. Ent. 24 : 380-386.

__________ (1936). The European cornborer in Indiana. Bull. Ind. Agric. Expt. Sta. No. 406.

Fraenkel, G. and Blewett, M. (1943b). The sterol requirements of several insects. Biochem. J. 37 : 686- 692 - 695.

__________ __________ (1945). Linoleic acid, L-tocopherol and other fat soluble substances as nutritional factors for insects. Nature 155 : 392.

Garlick, W. G. (1948). A five year field study of codlin moth larval habits and adult emergence. Sci. Agric. 28 : 273-292.

Gorden, C. and Sang, H. (1941). The relation between nutrition and exhibition of the gene Antennaless (Drosophila melanogaster) Proc. Roy. Soc. B. 130 : 151-184.

*Grison, P. (1947b). Development sans diapause des chenilles Euproctis phaeorrhaea. C.R. Acad. Sci., Paris. 225 : 1185-1186.

* __________ (1948). VIIIe Cong. int. Ent. Stockholm. pp. 226-234.

__________ (1952). Relations entre letat physiologique de la plantehote, Solenum tuberosum et la fecondite du doryphore, Leptinotarsa decemlineata Say Trans. IXth. Internat. Cong. Ent. Versailles. 1 : 331-337.

Hardy, J. E. (1938). Plutella maculipennis, Curtis, its natural and biological control in England. Bull. ent. Res. 29 : 343-372.

Harrison, J. W. H. (1927). Experiments on the egg-laying instincts of the sawfly Pontania salicis Christ. and their bearing on the inheritance of required characters; with some remarks on a new principle in evolution. Proc. Roy. Soc. B. 101 : 115.

Hasemann, W. (1946). Influence of soil minerals on insects. J. Econ. Ent. 39 : 8-11.

Hasting, E. and Pepper, J. H. (1944). The fatty materials in diapausing codling moth larvae (Carpocapsa pomonella L.). Arch. Biochem. 4 : 89-96.

*Heller, J. (1926). Chemische Untersuchungen über die Metamorphose der Insekten. III Ueber che 'subitane' und 'latente'. Entwicklung Biochem. Z. 169 : 208-234.

Herms, W. B. (1928). Effect of different quantities of foods during larval period on the sex-ratio and size of Lucilia sericata Meigen and Theobaldia incidens Thomas. J. Econ. Ent. 21 : 720-729.

Hill, R. E. (1946). Influence of food plants on fecundity, larval development and abundance of the tuber flea beetle in Nebraska. Nebr. Agric. Expt. Sta. Res. Bull. No. 143.

Hodge, C. (1933). Growth and nutrition of Melanoplus differentialis Thomas. (Acridiidae). Growth on a satisfactory mixed diet and on diets of single food plants. Physiol. Zool. 6 : 306-328.

Holdaway, F. G. and Smith, H. F. (1933). Alteration of sex ratio in the flour beetle Tribolium confusum Duval, following starvation of newly hatched larvae. Aust. J. Expt. Biol. Med. Sci. 11 : 35

Ibbotson, A. and Kennedy, J. S. (1950). The distribution of Aphis fabae Scop. infestations in relation to leafage. II. The progress of the aphis infestations on sugar beet in pots. Ann. Appl. Biol. 37 : 680-696.

__________ __________ (1951). Aggregation in Aphis fabae Scop. I. Aggregation on plants. Ann. Appl. Biol. 38 : 65-78.

Iseley, D. (1935). Relation of hosts to abundance of cotton-boll-worm. Ark. Agric. Expt. Sta. Bull. No. 320.

Jong, J. K. de (1938). The influence of the quality of the food on the egg production in some insects. Treubia. 16 : 445-468.

Kelsheimer, E. G. and Polivka, J. B. (1931). Correlation of cornborer survival with maturity of corn. J. Econ. Ent. 24 : 386-388.

Kennedy, J. S. and Booth, C. O. (1951). Host alternation in Aphis fabae Scop. I. Feeding preferences and fecundity in relation to the age and kind of leaves. Ann. Appl. Biol. 38 : 25-64.

Kennedy, J. S., Ibbotson, A. and Booth, C. O. (1950). The distribution of aphid infestations in relation to leaf-age. I. Myzus persicae (Sulz.) and Aphis fabae Scop. on spindle trees and sugar beet plants. Ann. Appl. Biol. 37 : 651-679.

Kogure, M. (1933). The influence of light and temperature on certain characters of the silkworm, Bombyx mori. Kyushu Imp. Univ. Dep. Agric. J. 4 : 1-93.

*Kohler, W. (1940). Der Einfluss verschiedenen Ernahsungsgrades auf aussere Korpermerkmale, auf die Entwicklungsgeschwindigkeit, Lebensdauer und Fortpflanzungsfahigkeit von Ephestia kuehniella Zeller. Biol. Zbl. 60 : 34-69.

Lemonde, P. A. and Bernard, R. (1951). Nutrition des larves de Tribolium confusum Duval. I. Recherche Dan Regime synthetique basal satisfaisant leurs besoins nutrities. Canad. J. Zoo. 29 : 71-83.

Lloyd, D. C. (1940). Host selection by hymenopterous parasites of the moth Plutella maculipennis Curtis. Proc. Roy. Soc. Lond. B. 128 : 451-483.

Ludwig, D. (1932). The effect of temperature on the growth curves of Popillia japonica. Physiol. Zool. 5 : 431-447.

Mackerras, M. J. (1933). Observations on the life-histories, nutritional requirements and fecundity of blowflies. Bull. Ent. Res. 24 : 353-362.

*Mahdihassan, S. (1936a). Predisposing factors and infection by lac and other scale insects. Z. angew. Ent. 23 : 265-280.

* __________ (1936b). The range of host selection and the specific differentiation of lac and other parasites. Arch. Naturgesch. N. F. 5 : 1-22.

Marcovitch, S. (1924). The migration of the Aphididae and the appearance of the sexual forms as affected by the relative length of daily light exposure. J. Agric. Res. 27 : 513-522.

Marsh, H. O. (1917). Life-history of _Plutella maculipennis_. Jr. Agric. Res. 1 : 1-10.

Mumford, E. P. and Hey, D. H. (1930). Water balance of plants and resistance to insect pests. Nature. 125 : 411-412.

Murneek, A. E. and Whyte, R. O. (1948). Vernalization and photosynthesis -- a symposium. Waltham, Mass., U.S.A., Chronica Botanica Co. (pp. 53-54.)

Nelson, J. W. and Palmer, L. S. (1935). The phosphorus content and requirement of the flour beetle _Tribolium confusum_ Duv., and a study of its needs for vitamin D. J. Agric. Res. 50 : 849-852.

Painter, R. H. (1936). The food of insects and its relation to resistance of plants to insect attack. Amer. Nat. 70 : 547-566.

Payne, N. M. (1929). Absolute humidity as a factor in insect cold-hardiness, with a note on the effect of nutrition on cold-hardiness. Ann. Ent. Soc. Amer. 22 : 601-620.

Pepper, J. H. (1937). Breaking dormancy in _Loxostege sticticalis_. J. Econ. Ent. 30 : 380.

____________ (1938). The effect of certain climatic factors on the distribution of _Loxostege sticticalis_. Ecology 19 : 565-571.

Pepper, J. H. and Hastings, E. (1943). Biochemical studies on the sugar beet webworm (_Loxostege sticticalis_ L.) with special reference to the fatty acids and their relations to diapause and sterility. Tech. Bull. Montana Agric. Expt. Sta. No. 413.

*Picard, F. (1926). Recherches sur la biologie de l'Altise de la vigne (_Halicta ampelophaga_). Ann. Epiphyt. 12 : 177-196.

Polivka, J. B. (1931). The effects of physiological change in the corn plant on cornborer survival. J. Econ. Ent. 24 : 394-395.

*Potapenko, A. I. (1944). Compt. Rend. Acad. Sci. U.S.S.R. 45 : 84-85.

Pradhan, S. (1939). Regeneration of gut epithelium, Coccinellids. Quart. J. Microscop. Sci. 81 : 451-478.

Readio, P. A. (1931). Dormancy in _Reduvius personatus_. Ann. Ent. Soc. Amer. 24 : 19-39.

Richardson, C. H. (1926). A physiological study of the growth of the Mediterranean flour moth (_Ephestia kuehniella_ Zeller) in wheat flour. J. Agric. Res. 32 : 895-929.

Robertson, P. L. (1939). Diamond back moth investigation in New Zealand. N.Z. J. Sci. Tech. (A). 20 : 330-364.

Roeder, K. D. (1953). Insect physiology. Edited by Wiley, N.Y.

*Romanova, V. P. (Tzedeler, O. E.) (1931). The cabbage moth in connection with mustard cultivation. Zb. Opinton. Agron. 1/n - Vostoka IX, Nos. 2. pp. 165-195.

Sabrosky, C. W., Larson, I. and Nabours, R. K. (1933). Experiments with light on reproduction, growth and diapause in grouse locusts (Acridiidae). Kans. Acad. Sci. Trans. 36 : 298-300.

Salt, G. (1935). Experimental studies in insect parasitism. III. Host selection. Proc. Roy. Soc. B. 117 : 413-435.

_______ (1936). Experimental studies in insect parasitism. IV. The effect of superparasitism on populations of Trichogramma evanescens. J. Expt. Biol. 13 : 363.

_______ (1937a). The sense used by Trichogramma to distinguish between parasitized and unparasitized hosts. Proc. Roy. Soc. B. 122 : 57-75.

_______ (1937b). The egg parasite of Sialis lutaria : a study of the influence of the host upon a dimorphic parasite. Parasitology. 29 : 539.

_______ (1938a). Experimental studies in insect parasitism. VI. Host suitability. Bull. Ent. Res. 29 : 223-246.

_______ (1938b). Further notes on Trichogramma semblidis. Parasitology. 30 : 511-522.

Sanderson, M. W. (1939). Crop replacement in relation to grasshopper abundance. J. econ. Ent. 32 : 484-486.

Schaefer, E. E. (1936). The white fungus disease (Beauveria bassiana) among red locusts in South Africa and some observations on the grey fungus disease (Empusa grylli). Union S.Afr. Dep. Agric. Sci. Bull No. 160.

Schlottke, E. (1937). Digestive enzymes and diet, carnivorous beetles, grasshoppers, roach. Zeitschr. Vergleich. Physiol. 24 : 210-247, 422-50, 463-490.

Schultz, J., St. Lawrence, P. and Newmeyer, D. (1946). A chemically defined medium for the growth of Drosophila melanogaster. Anat. Rec. 96 : 44.

Seamans, H. L. and McMillan, E. (1935). The effect of food plants on the development of pale western cutworm (Agrotis orthogonia Mou.) J. Econ. Ent. 28 : 421-425.

Sharif, M. (1937b). On the life history and the biology of the rat flea, Nosopsyllus fasciatus (Bosc.). Parasitology. 29 : 225-238.

Shull, A. F. (1928). Duration of light and the wings of the aphid Macrosiphum solanifolii Roux. Arch. Entev. Mech. Organ 113 : 210.

_______ (1929). Determination of types of individuals in aphids, rotifers, and cladocera. Biol. Rev. 4 : 218-248.

Simmonds, F. J. (1948). The influence of maternal physiology on the incidence of diapause. Philos. Trans. B. 233 : 385-414.

Sladden, D. E. and Hewer, H. R. (1938). Transference of induced food habit from parent to offspring. III. Proc. Roy. Soc. B. 126 : 30-44.

Smith, D. S. and Northcott, F. E. (1951). The effects on the grasshopper Melanoplus mexicanus mexicanus of varying the nitrogen content in its food plant. Canad. J. Zool. 29 : 297-304.

Szumkowski, W. (1952). Observations on Coccinellidae. I. Coccinellids as predators of lepidopterous eggs and larvae in Venezuela. II. Experimental rearing of Coleomegilla on a non-insect diet. Trans. IXth Internat. Cong. Ent. 1 : 778-785.

Tauber, O. E., Drake, C. J., and Decker, G. C. (1945). Effect of different food plants in egg production and adult survival of grasshopper Melanoplus bivittatis Say. Iowa State Coll. J. Sci. 19 : 343-359.

Theodor, O. (1934). Observations on the hibernation of Phlebotomus papatasii. Bull. ent. Res. 25 : 459-472.

Thorpe, W. H. (1939). Further studies on pre-imaginal olfactory conditioning in insects. Proc. Roy. Soc. B. 127 : 424-433.

Thorpe, W. H. and Jones, F. G. W. (1937). Olfactory conditioning in a parasitic insect and its relation to the problem of host selection. Proc. Roy. Soc. B. 124 : 56.

*Titschack, E. (1926). Untersuchungen uber das Wachstum, den Nahrungsverbrauch und die Eirzeugung. II. Tineola bisselliella Hum. Gleichzeitig ein Beitrag zur Klarung der Insektenhautung. Z. Wiss. Zool. 128 : 508-569.

Trager, W. (1947). Insect nutrition. Biol. Rev. 22 : 148-177.

__________ (1953). Nutrition. Chapt. 14. Insect Physiology edited by K. D. Roeder. Wiley, N.Y.

*Trouvelot, B. and Grison, P. (1935). Variations de fecondite du Leptinotarsa decemlineata avec les Solanum tuberiferes consommes par l'insecte. C. R. Acad. Sci., Paris. 201 : 1053.

*Trouvelot, B., Lacotte, Dussy and Thenard (1933). Les qualities elementaires des plantes nourricieres du L. decemlineata et leur influence sur le comportement de l'insecte. C. R. Acad. Sci., Paris. 197 : 355-356.

Ullyett, G. C. (1936a). Host density and the success of entomophagous parasites. Nature, Lond. 137 : 742.

__________ (1943). Some aspects of parasitism in field populations of Plutella maculipennis Curt. J. Ent. Soc. S. Afr. 6 : 65-80.

__________ (1947). Mortality factors in populations of Plutella maculipennis Curtis (Tineidae : Lep.), and their relation to the problem of control. Dep. Agric. Forest Ent. Mem. Vol. 2 (6).

__________ (1950). Competition for food and allied phenomena in sheep blowfly populations. Phil. Trans. Roy. Soc., Lond. B. 234 : 77-174.

Ullyett, G. C. and Schonken, D. B. (1940). A fungus disease of Plutella maculipennis in S. Africa with notes on the use of entomogenous fungi in insect control. Sci. Bull. Dep. Agric. No. 218.

Uvarov, B. P. (1928). Insect nutrition and metabolism. Trans. Ent. Soc. Lond. 76 : 255-343.

Vaney, C. and Maignon, F. (1905). Chemical changes during metamorphosis : Bombyx mori. C.R. Acad. Sci. 140 : 1192-1195.

Vowels, D. M. (1950). Sensitivity of ants to polarized light. Nature. 165 : 282-283.

Webster, J. E., Sieglinger, J. and Davies, F. (1948). Chemical composition of sorghum plants at various stages of growth and relation of composition to chinch bug injury. Tech. Bull. Okl. Agric. Expt. Sta. No. T-30.

*Weidling, K. (1928). Die Beeinflussung von Eirchrenzahl undgrosse einiger Dipteren durch Hunger im Larval-stadium mit eingen Beobachtungen uber die Chaetotaxis der Hungertiere und uber den Einfluss verschiedener physikalischer und chemischer Einwirkungen auf den Entovicklungsgang dieser Tiere (Calliphora erythrocephala, Stegomyia fasciata und Anopheles maculipennis). Z. angew. Ent. 14 : 69-85.

Whitney, D. D. (1914). The influence of food in controlling sex in Hydratina senta. J. Expt. Zool. 17 : 545.

_______________ (1916). The control of sex by food in 5 species of rotifers. J. Expt. Zool. 20 : 263.

Wigglesworth, V. B. (1939). Principles of insect physiology. Lond. Methuen.

*Zolotarev, E. Kh. (1938). Summer and autumn rearing of Antherea pernyi as influencing the diapause of the pupa. Zool. Z. 17 : 622-633. (In Russian : English summary).