BIOLOGICAL AND ECOLOGICAL STUDIES ON THE CODLING MOTH (CARPOCAPSA POMONELLA L.) IN ISRAEL[1])

By

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INTRODUCTION

The investigation was undertaken with the object of supplementing the still fragmentary knowledge of the life history of the Codling Moth in Israel. *Bodenheimer* and *Naim* (4) and *Schweig* (13) studied the bionomics of this pest and succeeded in elucidating many details, but various biological and ecological aspects remained unknown. An extensive research project was therefore undertaken in 1941 and continued for ten years in the orchard of Mikveh-Israel and in the laboratory at Rehovot. Some of the results obtained during the first three years of study, which have already been published (*Klein* and *Vavolsky*, 10), are incorporated in this paper, so as to provide a more complete picture.

WORKING PROCEDURE

a. *In the orchard.* In an orchard which received the customary sprays, moths were trapped in dishes suspended from the branches and containing a bait of a 10 per cent water-solution of molasses, with a small addition of yeast. The moths caught were counted each morning. In addition, burlap-bands placed on the trunks of the apple trees were examined weekly, and all larvae and pupae found in them were transferred into breeding-jars.

b. *In the laboratory.* The Codling Moth was bred through its successive stages and generations. Longevity and ovipostion studies were conducted in large jars, while jars of medium size were employed for the breeding of individual larvae and pupae. Transfers of larvae onto the fruit were made on the day of hatching. The moths were fed on pieces of cotton-wool soaked in sugared water.

THE MOTH

Emergence

Considerable differences in the date of the first catch in the bait-traps, which amounted to five weeks between the extremes, were noted over the ten-year period.

Balachovsky (2) succeeded in breaking the diapause by sudden transfer of larvae from one temperature extreme to another (from -10^{0} C to -25^{0} C). *Harpaz* (8) found that prolonged exposure of the larvae to a low temperature of -3^{0} C followed by a transfer to 16^{0} C did not provide a sufficiently great shock to affect the diapause.

Since sufficiently sharp fluctuations of temperature rarely occur in Israel, it would seem that the breaking of the diapause is controlled by a certain temperature trend rather than by sudden changes in temperature. In this respect, a striking correlation

1) Abridged translation from Hebrew.

exists between the dates of the first catch of moths and the average temperatures prevailing during the preceding months (Table 1, p. 157).[1]) With the exception of the year 1944, the earliness of appearance of the moths follows fairly closely the average temperature level for February-March.

Since the moths are mainly active during the night and especially at dusk, much work has been done on the effect of dusk temperature. It appears from the work of *Glenn* (6) and *Webster* (16) that the moths remain motionless if twilight temperature does not exceed 12° C, while copulation and oviposition only take place if the temperature is above 15° C. *Balachowsky* and *Biennot-Bourgin* (3) confirm that there is no flight under 15° C and that the moths die without offspring if cold nights prevail during the first few weeks after emergence. The general trend of Table 1 (p. 157) suggests that the higher the twilight temperatures during the early spring months the earlier the appearance of the moths.

Bodenheimer and *Naim* (4) calculated on the basis of biological data supplied by *Glenn* (6) and *Shelford* (14) that the threshold of development of the Codling Moth lies at 10° C and that the effective temperature required for the completion of the development of one generation amounts to 625 day-degrees. The results of breeding of the summer generations show that the pupa requires 30 to 35 per cent of the total effective temperature, i. e. 187 to 220 day-degrees.

The amount of effective temperature supplied during the post-hibernation period from rise of temperature following the coldest month till the first appearance of the moths, was calculated for each year (Table 2, p. 158). If we exclude the exceptional year of 1944, we may conclude that the effective temperature accounted for by the post-diapause development averages between 220 and 230 day-degrees. Thus the temperature records of February and March provide a general clue as to the probable time of appearance of the moths.

Results of laboratory experiments referred to in the chapter dealing with pupal development show that the pupation of the larvae in the laboratory takes only about twenty days. Excluding the year 1944, the duration of the pupation period under field conditions varies between 30 and 62 days. The divergence is probably due to the inaccuracy of field observations as compared with laboratory findings, though it should be noted that the dates of emergence recorded in the laboratory approximated to those indicated by trapping. It is of course possible that a number of days may pass between the emergence of the moths and their first occurrence in the traps. Calculation on the basis of monthly averages also introduces an artificial factor which may be at variance with the biological trends. According to *Balachowsky* (2), 16 days pass between the date of transfer from low to high temperature and the beginning of pupation, whereas pupation itself lasts only 10 days. It should be remembered that the figures in Table 2 include the pre-pupation period.

No phenological correlation was observed between the moth and the apple tree. In this connection it is worth mentioning that all the commercial varieties grown in this country are foreign introductions. It is likely that the date of blossoming in the experimental orchard were affected by the winter spray which is applied annually in Israel to assist in the breaking of dormancy. The spraying is timed to precede the flowering of the early varieties by about two weeks, but the estimates often prove to be wrong. An indication of this is given by some phenological data supplied for the Calville de San Sauveur variety (Table 3, p. 159). No correlation is indicated between

1) Page numbers in parentheses refer to the Hebrew text.

the flowering dates and the time of the appearance of the first moths. It follows therefore that flowering cannot be used as a guide to spraying against Codling Moth.

One of the factors which may account for the lack of correlation between flowering and moth appearance, is the difference in response to mid-winter temperatures. According to *Weldon* (15) the dormancy of deciduous fruit trees is prolonged if the average temperature of December and January is above 10° C. *Harpaz* (8) proved, on the other hand, that hibernating larvae kept in mid-winter in a refrigerator at 3° C did not emerge before those which had been overwintered at a room-temperature of 16° C.

The sex ratios in the first generation of moths (Table 4, p. 161) show a certain tendency towards protandry, but the data so far collected are not sufficiently significant.

We designate the moths encountered during the period from the beginning of appearance to the first decline in their numbers, as parents of the first generation. The total catches of these parent moths varied considerably from year to year. The numbers represented by weekly catches (Table 5, p. 162) rose steeply to a maximum situated around the middle of the period of occurrence and then declined again more or less rapidly.

In the year of maximum catch the number of moths was three and a half times higher than during the year of minimum catch. The total annual captures also showed great variation. The following annual totals include the moths which emerged from pupae formed in the burlap-bands in relation to those found in the traps.

Year	1942	1943	1944	1945	1946	1947	1948	1949	1950
Number of moths	131	228	54	73	103	142	200	183	119

The curves of recorded monthly totals as shown in Figure 2 (p. 163), indicate roughly four seasonal waves which can be classified as follows:

1. The parents of the first generation—from first appearance till about mid-May.
2. The parents of the second generation—till early July.
3. The parents of the third generation—till the end of August.
4. Left-overs of the previous class, frequently reinforced by infecund moths produced the same summer by some of the larvae of the third generation.

On the average, nearly half of the parents of the first generation were caught on the wild pear, presumably owing to the fact that the blossoming and fruit-setting of this tree is considerably in advance of all the apple varieties (Table 8, p. 165). It is noteworthy, however, that the smallest number of moths was attracted to the local Hashabi apple, although it is the first to blossom among the apple varieties. The highest number of moths was found on Reinette grise and the smallest on Rome Beauty which is the latest variety to blossom.

The Sex Ratio

The sex counts of trapped moths, carried out over a period of four years (1947—1950) gave consistently higher monthly figures for females (Table 9, p. 116). Over the whole the females constituted on the average 58 per cent of the total number of moths caught. The relative monthly catch of females increased up to June and, after a drop in July, went up again August.

Among the moths which were reared in the laboratory from larvae recovered from the burlap-bands (Table 9, p. 166), the seasonal average numbers of males and females were almost equal over a period of eight years. A heavy preponderance of males at the beginning of the season gave way to a gradual trend in favour of the females which attained the highest percentage in July, after which their relative numbers decreased again. The females of the July emergence give rise to the July and August larvae which are generally responsible for the worst damage to fruit.

Adult Longevity

Throughout the season, the females live longer on the average than the males (Table 10, p. 167). The respective life-span of males and females is 5 compared with 6 weeks in the spring, 3 against 4 weeks towards the end of summer, and 2 against 3 weeks in the autumn.

The longevity decreases in both sexes with rising temperature, although a rise over 26° C makes for a renewed trend towards longer life (Table 11, p. 167).

The longevity of females increases with rising air humidity. No such correlation has been established for males (Table 12, p. 168).

The Female Moth

The preoviposition period of the parents of the first generation averages 8 to 11 days; in the summer it amounts to only about 5 days (Table 14, p. 169). The preoviposition is longest at low temperatures, shortens with an increase of temperature to 24—25° C, and again increases slightly if temperature rises to 26—27° C. A rise in air humidity shortens the preoviposition period.

The average oviposition period does not vary much through the season, though the maximum values increase gradually during the summer months (Table 14, p. 169). The shortest period of oviposition was recorded at the temperature of 24—25° C and air humidity of 72—74 per cent. These ranges seem to indicate the optimum conditions since they lead to an acceleration of the process of oviposition.

Most females die soon after cessation of oviposition. The average period of senescence does not exceed 2 days in April; during the remainder of the season it amounts to about 4 days, although in the summer some senescent females continue to live for about a fortnight.

The preoviposition period constitutes, on the whole, the relatively longest period in the female's life. The particularly long preoviposition period in April (64 per cent of the female's total life-span) is probably due to the low temperature of that month, which delays copulation. There is little difference between the relative duration of the oviposition and senescence periods, except at the beginning and at the end of the season, when the period of senescence is relatively much shorter (Table 16, p. 170).

THE EGG

Out of 178 laboratory-bred females, only 97 i. e. 54.5 per cent were found to be fertile. The proportion of fecund females is lowest in April; it graduallly increases with the rise of temperature through the season, reaching maximum in August (Table 17, p. 171).

Observations indicate that in this country the great majority of the eggs is always laid on the leaves. In the spring and early summer a small number of eggs can be found on the twigs, and later in the season on the fruit. In the laboratory, eggs are mostly laid on the walls and occasionally on the bottom of the breeding-jars, but not on fruit suspended into the jars. They are usually laid singly, although, on account of the limited space in the jars, they are frequently found close together. No arrangement in rows or any other regular pattern of egg-laying can be discerned.

The average number of eggs laid by a female in the laboratory was found to be around 33, while the average calculated for the fecund females only was 61. The lowest number of eggs was laid in April. The highest average number of eggs per female was laid in June, while the maximum was recorded in August: 228 eggs per fecund female (Table 18, p. 172).

Some females lay their eggs during a very short time and continue to live for a number of days afterwards, while others are slow in laying and did immediately after the completion of oviposition. The highest rate of laying may occur at any time during the period of oviposition.

Incubation takes, on the average, one week at the beginning of the season, and 5 to 6 days in the summer. Shortest incubation periods were recorded at the temperature of 21—22^0 C and air humidity of 66—72 per cent, i.e. intermediate values for the season.

No losses were recorded among the eggs in the laboratory. There is no information available concerning egg mortality in nature.

THE LARVA

Larvae hatched in the breeding-jars never settle on the fruits provided for them, but invariably try get out of the jar through the muslin cover. This indicates a tendency for wandering about before settling down in the fruit which constitutes the natural habitat. By tracing the course of larvae shortly after hatching, it was established that the young larva is capable of covering a distance of 15 meters in 6 hours. It follows that it can reach the fruit even if the egg was laid some distance away.

If placed on a fruit, the larva may begin gnawing within a few minutes of hatching. The penetration into the fruit takes about two and a half hours. If no fruit can be reached within a few hours, the larva enters a leaf through the under-surface at some point close to the principal vein and feeds on the leaf tissue.

Larvae of the first generation habitually leave the original apples after feeding upon them for 9—10 days and migrate to new ones. There they complete their development and pupate. A second migration has never been observed. Larvae of later generations, which usually have larger fruits at their disposal, frequently complete their development in the same fruit.

The average development period of the larvae is shortest in the second generation (less than 19 days), somewhat longer in the third (20 days), and longest in the first generation (23 days). The diapause extends over 7 to 9 months. It can be assumed that the climatic conditions of the early summer (temperature of 24—25^0 C and air humidity 67—78 per cent) provide the optimum environment for the development of the larvae (Table 22, p. 176).

In the laboratory, about two thirds of the larvae died before completing their development (Table 23, p. 177). Field observations indicated that the mortality rate among the larvae is high before penetration into the fruit and again during the cocoon-spinning stage. Very few larvae die while inside the fruit.

The mortality of larvae appears to be higher in summer than in spring (Table 23, p. 177). The high summer temperatures are undoubtedly responsible for a high rate of mortality among the young crawling larvae before they reach the safety of the fruit.

The number of *khamsin* days during the summer was found to be of decisive importance in controlling the population of larvae (Table 25, p. 178). There is a consistent reversed relationship between the number of *khamsin* days during the season and the level of the annual catch of larvae.

In addition to the high temperature, the low air humidity which prevails during the *khamsin* constitutes, no doubt, an important factor in reducing the larval population. It is likely that the relatively low humidity in the Jordan Valley accounts partly for the fact that Codling Moth infestations in that region are generally less serious than in the Coastal Plain.

The weekly captures of larvae are shown in Figure 3 (p. 179). The general trend of the curves and their infrequent approach to the nil level indicates a constant overlapping of the different generations. With the exception of the year 1945, three fairly well defined peaks can be discerned in the curves. The periods of abundant catches, represented by these peaks, extended in most years over the first half of June, the second half of July, and again from mid-August till the beginning of September. No larvae could be found after September in most years.

Table 26 (p. 180) details the emergence of moths derived from larvae captured in the bands, on the basis of nine years of laboratory records. The overall emergence amounted to only 27 per cent. It has already been indicated that the climatic conditions prevailing in June appear to be optimal for larval development. A considerable decrease in emergence occurs in August, with the rise of temperature above 26° C. It can be assumed that the low percentage of emergence in May and again in September is largely due to the severe *khamsins* which frequently occur during these months. It seems that during the cocoon-spinning stage (which corresponds to the first few days under the burlap-bands) the larvae are particularly sensitive and that the climatic conditions prevailing at that time decide their fate.

Table 27 (p. 181) shows that the number of moths emerging the following spring constitutes only 4.4 per cent of the total number of moths and accounts for only just over 1 per cent of the trapped larvae. On three occasions, the transfer of larvae for breeding was incomplete (see foot-notes to Table 27) and, consequently, appropriate corrections were made in Table 28 (p. 182). The effect of *khamsins* is again indicated. The general trend is for the percentage of emergence to decrease with increasing number of *khamsin* days.

The experimental orchard, which was planted in 1938, yielded its first crop in 1941. In that year the burlap-bands were arranged on the stems of 24 trees which stood in two east-west rows. The number of banded trees of each variety is indicated by bracketed figures in the list of varieties. The yearly average numbers of larvae trapped per tree of different varieties are given in Table 29 (p. 182) and the averages per tree calculated for all the years of observation are listed below:

Hashabi (local apple)	20.4 (2)	Malus seedling	9.7 (1)
Calville de San Sauveur	19.6 (6)	Reine de Reinette	7.7 (2)
Belle de Boskoop	16.7 (2)	Rome Beauty	7.7 (2)
Reinette Bowman	13.5 (1)	Reinette grise	7.7 (4)
Peasgood Nonsuch	11.1 (2)	Cox's Orange Pippin	2.5 (2)

The relative abundance of catches is in close conformity with local horticultural experience. Besides Winter Banana which was not represented in the observation plot, the first three varieties listed have a reputation for being subject to heavy infestations by Codling Moth, while Rome Beauty and the late-ripening Reinettes are known to be relatively less susceptible. Cox's Orange Pippin is not a commercial variety in Israel and no competent information is available about its susceptibility in practice.

According to the observations of *Bodenheimer* and *Naim* (4) in the Coastal Plain in 1926 and 1927, some of the larvae recovered from bands entered diapause during the second half of July 1926, while by the end of August all larvae had entered diapause in both years.

Our observations from 1942 till 1950 on captured larvae showed that the diapause normally began in July. The number of larvae which pupated after July differed from year to year, but never exceeded 25 per cent. All larvae which were found under the bands from August onwards were in diapause. The nine-year averages of summer month temperatures were: June — 24° C, July — 26° C, August — 26.5° C, with fluctuations in ranges of monthly averages during the nine years: 22.5 — 25.3° C, 25.1 — 27.0° C and 25.7 — 27.3° C, respectively. The nine-year averages of maximum monthly temperature were: June — 30.5° C, July — 32.0° C, August — 32.5° C. A relatively high summer humidity prevailed during all the experimental years: 66 to 77 per cent. It seems, however, that no decisive importance in inducing diapause can be attached to air humidity, as the development of the larvae up to the stage of cocoon-spinning takes place inside the fruit, in a constantly humid environment.

There is a wide-spread opinion that shortening day-lenght constitutes a decisive diapause-inducing factor. The average daily number of light-hours in this country is: June — 14^{15}, July — 13^{35}, August — 12^{55}. According to observations of Prof. *F.S. Bodenheimer* (oral communication), the Codling Moth in the neighbourhood of Baghdad has only one generation during the year, and larvae enter diapause about the middle of May. According to *Clayton* (5) the average temperature in Baghdad is about 22° C in April, 28° C in May and 32° C in June. Humidity in Baghdad is much lower than in the Coastal Plain of Israel. The average number of daylight hours along the latitude of Baghdad is: April — 12^{55}, May — 13^{35}, June — 14^{15}.

Harpaz (8) studied the influence of temperature on pupation of laboratory-bred larvae. Larvae hatched during the first half of April which had penetrated fruits, were transferred partly into an incubator set at 27° C and partly into a cellar with an average temperature of 23° C. All the larvae in the incubator entered diapause, while those in the cellar gave rise to moths at the beginning of July. From a batch of larvae hatched during the second half of June, all those placed in the incubator entered diapause, while those in the cellar, in which an average temperature of 24.5° C prevailed at the time, developed into moths by the end of July. In a third series of these observations fruits infested with partly or fully developed larvae were collected in the orchard in the middle of May. Of the larvae kept in the incubator, 42 per cent entered diapause, while the remainder developed into moths during the second half of June. 29 per cent of the larvae kept in the cellar (average temperature 24° C) entered diapause and the rest gave rise to moths in June. Humidity in both places was at least as high as outdoors.

From the information surveyed in the above paragraphs the following conclusions can be drawn:

1. In Israel diapause takes place during a period of decreasing day-length, whereas in Iraq diapause is connected with lengthening photoperiods.
2. Entrance into diapause appears to be determined by the conditions prevailing throughout the duration of larval development and not only those obtaining during the last development stages.

3. When the average temperature does not exceed 25° C, only part of the larvae enter diapause. With temperatures rising above 26° C diapause becomes general. Temperature seems to be the main factor controlling diapause in countries in which Codling Moth develops several generations during the year.

THE PUPA

There is a definite correlation between the pupation period and the air temperature (Table 30, p. 185). The average period of pupation decreases steadily with rising temperature from 18 days in early spring (counted from the end of the diapause) to less than 10 at the height of summer.

Humidity seems to have no influence on the duration of pupal development. This might be expected, since for the purpose of cocoon-spinning the larva either crawls into some well protected part of the tree or else remains inside the fruit, while the cocoon also offers protection against acute fluctuations of humidity.

The mortality rate of pupae under laboratory conditions (Table 31, p. 185) averages 41 per cent and is thus considerably lower compared with the 64 per cent mortality rate among larvae. The mortality rate of pupae formed by hibernating larvae is very low. The gradual rise in the rate of mortality through the season parallels a similar rise in the case of larvae.

THE ANNUAL DEVELOPMENT CYCLE

Table 33 (p. 186), summarizing the average results of the breeding experiments, indicates a cycle of two generations (52 + 299 = 351 days) and a cycle of three. There are two possibilities of a three-generation cycle: one extending over 52 + 41 + 258 = 351 days, the larvae of the third generation hibernating; the other comprising 52 + 41 + 40 = 133 days and lasting from April to August. The three generation development does not establish a complete cycle, as the moths of the last generation do not normally engage in oviposition and even if a few eggs are laid, the larvae hatched from them mostly perish at an early stage.

From the epidemiological point of view, a cycle consisting of three full generations per year can be regarded as the dominant one under the conditions of the Coastal Plain. Although a small number of early moths may give rise to four generations during the season, the last generation of such an extended cycle is of no epidemiological importance. On the other hand, part of the larvae of the second generation enter diapause, thus confining the cycle to two generations.

Data on natural mortality at the various stages of development are summarized in Table 34 (p. 187). Since in the laboratory breedings hatching from all the fertilized eggs was complete, the number of eggs can be taken to equal that of the larvae. If we consider May-June, June-July and July-August to correspond roughly to the development periods of the first, second and third generation respectively, a steady rise in mortality rate with each successive generation becomes apparent,

On the basis of the various laboratory results, such as the percentage of females in the total population, the percentage of fecund females, the number of eggs laid and the mortality rate in the different generations, a calculation has been made of the annual reproductive potential of one pair of parent moths emerging in the spring (Table 35, p. 187). It appears that a pair of fertile moths may give rise to about 17 fertile pairs in the following year. Of course, this calculation, being based on the results of laboratory breeding, does not represent the reproduction rate under natural conditions. In the orchard, large numbers of individuals are undoubtedly destroyed (especially in the egg and early larval stage) by natural enemies about which we know as yet very little in this country. Moreover, in the laboratory the moths are protected against the effects of extreme weather conditions, viz. khamsin, high temperatures, rains, etc. It is therefore obvious that under field conditions the reproduction rate is very much lower.