30. Observations on the Life-History, Biology, and Genetics of the Lady-bird Beetle, *Adalia bipunctata* (Mulsant).

By ONÈRA A. MERRITT HAWKES, M.Sc. (Birm.), B.Sc. (Lond.) *.

[Received July 3, 1920: Read November 2, 1920.]

CONTENTS.

	Page
1. Introduction	475
2. The Food and Feeding of *Adalia bipunctata*	477
3. Notes on the Life-History	480
a. Mating	480
b. The Eggs	481
c. The Larvæ	482
d. The Pupæ	482
e. The Imagines	483
f. The Enemies of the Lady-bird	483
g. Hibernation	484
4. The Genetical Relations of the Varieties	485
5. Summary	488

1. *Introduction.*

During three years of breeding pure and hybrid silkworms (*Philosamia*), I have been increasingly impressed by the apparent reasonableness of what would be regarded as fluctuating varieties; and by reasonableness, I mean a genetic relation between the variations of the parents and those of the offspring. To understand such variations, what appears to be needed is a large number of exhaustive studies of normally occurring varieties in animals untouched by Man. Insects present a large number of variations, but little or nothing is known of their inheritance. The Japanese have made extensive studies of silkworms (largely domesticated), and in America, Roswell Johnson (**13**) has made a wide study of *Hippodamia*, as a result of which he has been able to make the following important statement (**13**):—"Every variety or noticeable variation of *Hippodamia* that has been tested is inheritable in some degree." Miriam Palmer (**21**, **21***a*) has also made successful studies of the American varieties of *Adalia* and other Coccinellids. Meissner (**19**, **20**) and Schröder (**23**), in Germany, have made a small number of breeding experiments with some of the varieties of *Adalia bipunctata*.

Work of this kind would have the added advantage that in some cases the sciences of genetics and classification would be able to go hand in hand, instead of, as is too usual, being mere bowing acquaintances.

Adalia is highly suitable for work of this character, as there

* Communicated by E. GREEN, F.Z.S., F.E.S.

are many easily procurable varieties, which, as far as is known, are not regional.

Palmer (**21**) worked for some time at *Adalia*, but she had only a few varieties to deal with, as in America there occurs only the "type" and three varieties, whilst in Europe there are more than twenty-six named varieties. It would be impossible to get as quick results here as in America, as two generations per annum are the most one can obtain in England under natural conditions, whereas Palmer succeeded in obtaining four and five during the long American summer. Our erratic climate also makes the food-supply (aphides) more uncertain than under more stable climatic conditions.

Coccinellids have been extensively studied in the United States, as they are there recognised to be of considerable economic importance; but in England there has been little careful study of their habits, their distribution, or the genetical and possibly regional relations of the varieties which are so numerous in some of the species. Donisthorpe (**6**) has published the only complete history of any species, *Coccinella distincta*. The following observations were made in the course of genetical experiments which are still in progress.

The varieties of *Adalia* have been determined chiefly by Meissner and Schröder, who based their determination principally upon the variations in the colour of the elytra, but neglected the very considerable variations of the thorax. Schröder believes that the varieties from pure red elytra at the one extreme to pure black at the other are modifications of a scheme of seven spots and a scutellar mark. This is an interesting matter of speculation, but we do know that in Europe there are two principal forms: (1) "type," in which the elytra are a reddish brown with an approximately round black spot in the middle of each elytron; and (2) a black form with either two or three red spots in each elytron: when two are present, an upper lateral and a mid-dorsal, the variety is known as var. 4-*maculata*; when three are present, an anal red spot being added to the above two, the variety is named 6-*pustulata*. All other varieties, none of which occur in large numbers, can probably be grouped about these two main forms.

The Red varieties are generally acknowledged to be commoner than the Black, though very few accurate statistics have been recorded. Meissner found 35·2 per cent. Black in Summerfeld and 42·3 in Potsdam. In Staffordshire and Warwickshire I found 29 per cent. Black in 1918, 25 per cent. in 1919. In 1920 I found 2·75 per cent. Black at Crouch Hill, London, N., 42·7 per cent. Black on hops at Bishop's Frome, Herefordshire, 11·7 per cent. at Enville, Staffordshire, and, very much to my surprise, 78·5 per cent. Black in the Edgbaston district of Birmingham. Further observations will show whether localities are characterised by certain varieties or whether the prevalent varieties vary from time to time. If the varieties remain the same, will it mean that

there is little or no migration, that hibernation takes place locally, and that the varieties breed true? Or, does the particular environment allow only certain varieties to survive?

Two, possibly four, factors have to be considered in a genetic study of the Black and Red forms:—

1. Pattern: that is, the shape and distribution of the spots.
2. Colour: (*a*) black, which is the same in both "type" and black varieties;
   (*b*) red, which, contrary to accepted opinion, I believe different in the Red and Black forms.
3. Size: there is great range in size in the Coccinellidæ, which Johnson believes is chiefly adaptational, but the mean size of the varieties under consideration is different, and perhaps constitutes a definite character.
4. There may be a physiological factor in the reaction of these varieties to heat.

Microscopical examination by transmitted light shows that the reddish colour in both varieties is due to a clear yellow, to which brownish-red, semi-transparent particles are added in the Red form and red-brown and carmine in the Black variety.

There is probably a physiological factor to account for the seasonal appearances of the two forms, in England the Black usually appearing later and disappearing earlier than the Red. I have also observed that when the breeding-boxes were overheated, the Black could live at a higher temperature than the Red.

2. *The Food and Feeding of* Adalia bipunctata.

There is considerable difficulty in feeding *Adalia* with its food, living aphis. The occurrence of aphis is very erratic, being much affected by sudden climatic changes, such as cold, wind, and heavy rains. At times they disappear inexplicably.

Adalia will eat many but not all species of aphis. During two years' breeding I have found three species which are not acceptable:—(1) *Aphis rumicis*, the black bean aphis which is found on broad beans in early summer. The young of this species are eaten to a small extent, but the large only under stress of circumstances. One may continually find a bean-row black with this destructive aphid, but very few lady-birds upon them when, on a bed of nettles a few yards away, can be found large numbers of Coccinellidæ—*C. septempunctata*, *C. variabilis*, *A. bipunctata*, *Halyzia* 14-*guttata*, *H.* 22-*punctata*, and *H.* 14-*punctata*,—even when the aphids are not obviously numerous. (2) A bluish-green aphis (*Macrosiphum aconitum* (Van der Goot)), which I have found only on Monkshood. This has never been eaten by *Adalia*. Johnson says "several of the highly-coloured aphis cannot be successfully fed to Coccinellids." (3) *Hyalopterus pruni*: this aphis

has a grey-green mealy exudation, which fills the stomata of the larvæ and so kills them. When a Victoria plum was covered with this aphis, no larvæ or imagines were ever found among them, and very few larvæ of the Hover-fly, which is probably an even more prolific eater of aphis than the Coccinellidæ.

The presence of large numbers of Coccinellidæ on the Stinging Nettle may be due to the fact that these insects are not universally carnivorous. *C. septempunctata* certainly eats the abundant pollen and possibly other products of this plant. Donisthorpe found that *C. distincta* ate the honey supplied to ants, and I have found *C. septempunctata* eat the exudation from bean plants and Jerusalem artichokes in the autumn. During the summer I have observed *A. bipunctata* apparently eating the juice of raspberries and split plums.

The *Adalia* larvæ in the first two instars have to be fed with minute aphis, as, although sufficiently pugnacious to attack large aphis, the latter can easily shake them off.

Any species of aphis were used in 1918, but in 1919 practically two species only —in early summer *Aphis pruni* Fab., which attacks damson-trees; and for the remainder of the year *Aphis fagi*, which lives only on the beech. Although the latter is slightly woolly when full grown, it is in the earlier stages very acceptable to *bipunctata*. The copper-beech is attacked more frequently than the green beech, and on the former numbers of *bipunctata* are to be found all the summer. The supply of beech aphis has the advantage of being fairly constant, as the leaves and branches are so flat and so close together that it takes a great deal of cold and rain to clean the aphis off the tree. The flat leaves, which do not wither readily, are very suitable in boxes. The aphis of the rose (*Siphonora rosæ*) and of the nettle (*Aphis urticia*) both die quickly in boxes, presumably owing to the wilting of the thin leaves of the food-plants.

In August 1920, after a variety of experiments, I found that the adults will eagerly eat pounded dates, upon which they can live for months. The newly hatched larvæ cannot use this food at all, but I succeeded in bringing one larva from the second instar to the perfect insect on dates alone, the imago being of average size. Most of the older larvæ kept alive on this diet for some time, but did not grow much and ultimately died.

I have obtained the best results by feeding in closed boxes. The boxes must be opened every day, not only to introduce fresh food but also fresh air, which is of paramount importance to this species. Great care has also to be taken to remove all mouldy leaves. A mould (probably *Cladosporium aphidis* Jhüm) quickly grows on the honey-dew produced by the aphis, especially that found on beech and sycamore leaves. This mould fatally attacks the larvæ. It first appears on the thorax, but its method of producing death is undetermined.

The main difficulty of rearing is the cannibalistic habit of not only *A. bipunctata*, but also *C. septempunctata*, *C. variabilis*, and *H.* 14-*punctata*. The larvæ eat eggs and one another in either

the larval or pupal stages. This phenomenon is not due to confinement or lack of food, as it takes place in the presence of abundant food and in normal natural conditions. One can easily watch what appears to be a form of Coccinellid degeneracy among the larvæ which frequent red and black currant bushes. I have seen adult *bipunctata* and *septempunctata* eat their own eggs in boxes and on the trunks of trees, but never eat either larvæ or pupæ. This habit was also observed (**6**) in *C. distincta* in confinement. Palmer has, however, observed the imagines eating larvæ when there was no other food in the cages. On one occasion I watched a *bipunctata* eat the abdomen of a small fly caught in a spider's web. After a period of experimental starvation, two *Adalia bipunctata* feasted upon a small weak relation. Cannibalism has also been noticed by Palmer, Johnson, Burgess, etc.

On hatching, the almost colourless larvæ remain clinging to the empty egg-shells, part (never all) of which forms their first meal. They next fall upon one another. This same early habit of cannibalism also occurs in *Epilachna* (**27**), the vegetarian Lady-bird. If by chance an egg lags behind the others, it never hatches, for it is eaten by a larva which was born a little earlier. The larvæ remain on the egg-mass until fully coloured, and then suddenly and simultaneously disperse. Approximately a quarter of the larvæ are eaten before this dispersal.

During the first instar there is great mortality, partly owing to lack of sufficiently small aphis and partly to cannibalism. The young larvæ do best in small boxes, as they seem incapable of wandering far at this stage to find food, which, I believe, is chiefly obtained by good luck and persistent wandering. As early as possible the larvæ were isolated in separate boxes, but I was inclined to think cannibalism in the early stages a physiologically highly suitable diet, and, with this in view, I fed the *bipunctata* with small larvæ of other species. This practice was not, however, always successful, as sometimes the eater became the eaten. Partially successful attempts were made to feed the larvæ on cooked and raw hen's egg. Coccinellid eggs were always eaten when put in the boxes, but this is not a suitable proceeding in the early instars, as an odd egg may escape and hatch. During 1918, 21 of 22 families were reduced to one, as the full significance of cannibalism was not then recognised.

It is interesting to consider the intermittent competition between larvæ of the same batch of eggs. It is not the larva which first starts in the race which necessarily first reaches the winning-post. It may be the first to reach the end of the first instar, but during the short quiescent period which precedes ecdysis, it becomes a defenceless prey to those who have lagged behind. This special danger recurs at the end of each of the four instars.

The method of attacking the pupa is always the same, the larva beginning on the ventral side near the anal point of attachment and eating its way upwards and forwards, half

burying itself in the process. The head, the thorax, and the tough dorsal skin are frequently left untouched.

There is, however, no special mode of attacking the aphis, and certainly no painless method of dining. The *bipunctata* catches hold of a passing aphis and at once proceeds to devour it in spite of its struggles, which continue far into the meal. The legs, the wings, the head, and part of the cuticle of abdomen and thorax are usually left. The meal may take as long as five minutes.

The mother *bipunctata* is not very wise in her choice of a position for her eggs—many are laid on leaves, but also many on the branches and trunks of trees. I have even found them on wooden palings and on stones by the side of garden-paths. As the young larvæ cannot wander far in search of food, and as the parent is lacking in the instinct to lay eggs where there would be an adequate larder, the capacity for eating eggs and one another may be of considerable biological value. Indeed, knowing what we do of aphis, one realises that it would indeed be a wise Lady-bird that could guarantee aphis for its newly-hatched young. The period of incubation varies from three to nine days, and in that time the aphis might have disappeared. In May 1918 the damson-trees were covered with aphis for three weeks; without any apparent change in the weather, the aphis began suddenly to descend the tree-trunks in myriads, and at the end of two days hardly an aphis could be found. I have found eggs laid on the petals of a rose, but the petals fell before the eggs hatched.

The use of cannibalism was well demonstrated in July 1920. An isolated gooseberry-bush had every shoot attacked by aphis, upon which large numbers of *bipunctata* larvæ were feeding. At the time when the larvæ were beginning to pupate, a few cold rainy days caused the aphis to completely disappear. At once the larvæ began to attack each other and the pupæ, and, finally, themselves pupated on an entirely cannibal diet. I saw no signs of migration from this bush on account of shortage of aphis.

Cannibalism is probably of use in preserving the race during periods of aphis famine, as the larvæ, unlike the adults, cannot live long without food. Cannibalism is not of the same biological use to the imago, as its power of flight gives it a large range, and, when necessary, it can remain long periods without food. I have starved Lady-birds for three weeks, and at the end some of the males were capable of successful fertilization.

3. *Notes on the Life-History.*

a. *Mating.*

Mating takes place in captivity in the presence of plenty of light, especially direct sunlight. The response to light is very rapid. Immediately a box containing a number of Lady-birds is put in the sunlight, they begin to move quickly, fly, and mate. The same activity does not take place if the box is warmed without light. Fresh air, especially moving air, is also conducive to mating.

A. bipunctata is both polyandrous and polygamous. When a

male and female are isolated in a box, mating takes place at intervals during a period of two to nine weeks. Copulation lasts from half to three-quarters of an hour. It takes place when no eggs are laid and when the egg-laying period of the female is finished. Palmer states that the female lays fertile eggs three weeks after fertilization. Mating takes place in Staffordshire and Warwickshire during the whole summer, but the principal season is May to June, with a subsidiary season from the middle to the end of August. Probably only a very few of the newly emerged Lady-birds breed until the following year. The insects have been found mating on sunny days in late September, but at that time no eggs were laid.

b. *The Eggs.*

TABLE I.

Detailed Record of Family, 33 (1919).

Dates of Oviposition.	Number of Eggs and Colour.	Incubation. (Days.)	Larval life. (Days.)	Pupation. (Days.)	Number of Imagines.
(1) 22. 7. 19	16 (yellow) }	5	25	8	6
(2) 22. 7. 19	24 (orange) }				
(3) 23. 7. 19	8 (deep orange).	9	16	7	1
(4) 27. 7. 19	8 („ „).	6	—	—	—
(5) 27. 7. 19	11 („ „).	6	17	13	3
(6) 27. 7. 19	3 (yellow base, orange tip).	6	24	7	1
(7) 28. 7. 19	21 (orange).	7	17	8	2
(8) 29. 7. 19	25 (yellow base, orange tip).	5	22	9	1
(9) 1. 8. 19	25 (deep orange).	—	—	—	—
(10) 3. 8. 19	24 („ „).	6	19	—	—
(11) 7. 8. 19	12 („ „).	3	18	7	9
(12) 9. 8. 19	8 („ „).	3	24	7	1
	Total 185	Av. 5·6	Av. 20·2	Av. 8·2	Total 24

Mating took place on 17.7.19 between two Red "type" *Adalias*. In batches (1) and (8) the larvæ had light rings around all the abdominal and thoracic tubercles: hence these larvæ appeared much lighter than the larvæ of the remaining batches, which only had light rings around the lower lateral tubercles. The resulting imagines were all red, those from these two batches being indistinguishable from the others.

The eggs are spindle-shaped and laid in batches of from three to fifty. The outer shell is colourless and covered with numerous protuberances. The colour of the egg is due to the yolk, which is usually yellow but may be orange—a range of shades similar to those of the yolk of the hen's egg. Usually the whole batch of eggs laid on a single occasion is of the same uniform colour, but they may vary (see Table I.). In several batches the eggs shaded from yellow at one end to orange at the other. The eggs do not change in colour until a few hours before the larvæ are to merge, when they become a greenish grey.

The average number of eggs laid was between 140 and 148, the largest numbers laid were 167 in 1918, 189 in 1919, and 418 in 1920. The largest number laid in twenty-four hours was 80. The Black and Red forms are not differentiated by the colour, size, or shape of the eggs or by the number of eggs laid. Clausen (**3**) found 190 the average number laid in America.

The eggs are usually laid on the under side of leaves, but may also be found in slight depressions on the trunk and branches; on the trunk they are usually on the north side or at the angle where a branch originates. The bright-coloured eggs are very conspicuous on the brown bark. On the lower three feet of the trunk of a plum-tree badly attacked by aphis, I found within a week 42 patches of Coccinellid eggs—*A. bipunctata*, *H.* 14-*guttata*, *H.* 14-*punctata*, *C.* 11-*punctata*, and *C. variabilis*. Evidently there is a tendency to lay the eggs away from the light, but I have watched a *septempunctata* lay her eggs on a stone in bright sunlight. The usual period of incubation is three days, but it may extend to nine. The average laying period of the first two years' observations was 24 days. Incubation varied from 3 to 13 days, the average being 5 days in 1918, 4 in 1919, and $7\frac{1}{4}$ in 1920. Clausen (United States) finds the average incubation 5 days and the average egg-laying 28·2 days.

c. *The Larvæ.*

The larvæ when about to pupate are of a blackish-brown colour. The first upper lateral abdominal tubercle is always orange, and an orange patch extends across the abdomen between the fourth dorsal abdominal tubercles. This orange patch may be succeeded by similar patches of decreasing size and colour-intensity in the 5th, 6th, and 7th abdominal segments. In many cases there may be orange on the lower lateral tubercles of the fourth abdominal segment. The lower lateral tubercles may be surrounded by a cream-coloured ring (see note to Table I.). There is great variation in the depth of colour of the orange patches.

I have made many unsuccessful attempts to determine the differences in the larvæ and pupæ which are destined to become respectively Red and Black imagines. In 1918 the average larval period was 27 days, the minimum 22 and the maximum 27. In 1919 the average was 23, the minimum 16 and the maximum 39. Clausen found the average 16·1 days for the United States. In 1920 the average larval period was 35 days, the minimum 23, and the maximum 37.

d. *The Pupæ.*

The larvæ usually pupate on the under side of leaves, especially where the edge is curled up by aphis or drought. Pupæ are sometimes found on the upper side. In 1918 very few pupæ were found on the upper side of leaves, but in the early part of 1919,

when there was a great deal of wet and cloudy weather, a much larger proportion was found on the more exposed surface. During the sunny part of July and August 1919 the pupæ were again rarely found on the upper side. I have found no special orientation of *bipunctata* pupæ, such as is so striking in *Anatis ocellata*, which both on the trunk and needles of the pine normally faces upwards.

The average length of pupation in 1919 was 13 days, the minimum 9 and the maximum 21. In 1919 the average was 17, the minimum 3 and the maximum 28. In 1920 the average was 20 days, the minimum 16, and the maximum 22. Clausen and Girault (**10***a*) both found the American average 6 days. The very short period of three days was produced by placing the pupæ in a temperature of 101° F.

e. *The Imagines.*

On emergence the imagines vary from palest yellow to orange. Air and light usually produce the normal colour in a couple of days, but at times the original orange may persist for weeks. At certain seasons when *bipunctata* are emerging the majority caught are of an orange rather than the typical red colour. This observation applies also to *septempunctata* and *variabilis*. The variations of colour so obvious in some collections are not all true variations, but many are probably due to the development being still incomplete when the specimens were taken.

Although the Lady-bird which emerges in August or September may live to the following June, a period of ten months, its longevity during the summer is much shorter, the male sometimes dying after a mating-period of three weeks, although the female has lived two months after laying her eggs. Captivity would no doubt greatly modify this character.

The combined duration of incubation, larval life, and pupation varied from 28 to 56 days. The shortest period occurred during the very hot weather subsequent to July 22, 1919. Burgess (**1**) gives the complete period as 28 days in America, where the temperature would be very similar to that during this particular period in 1919.

Only a small percentage, 8 per cent. to 17 per cent., of the eggs laid became imagines. Palmer's results were better, as she obtained from 13 per cent. to 25 per cent. of imagines.

f. *The Enemies of the Lady-bird.*

The colour of the Coccinellids is supposed to be protective, and it is stated that they are not eaten by Insectivores. The yellow excretion produced by both larvæ and imagines is supposed to protect them from predaceous enemies. The latter contention appears to be partly based upon the fact that the excretion is disagreeable to Man both as regards taste and smell. Certainly

the Lady-bird has some enemies besides parasitic flies. In this country the larvæ are eaten to some extent by Syrphid larvæ, for which reason it was imperative to examine carefully all leaves put in the breeding-boxes, as if any of these voracious Syrphids were inadvertently introduced, they soon made an end of the Coccinellid larvæ as well as the aphis. Spiders also eat these larvæ, as they have been found sucked dry in spider's webs on several occasions. In England I have observed Flycatchers and Sparrows taking *septempunctata* and *bipunctata*, and also found considerable numbers of the elytra of *septempunctata* in the droppings of Sea-Gulls when that Coccinellid was abundant on the coast. Elytra of *bipunctata* and *septempunctata* have been seen in the pellets of the Brown Owl. In America, Flycatchers and young Swallows are stated to eat Lady-birds. There also all stages of the Coccinellidæ are eaten by *Mantis religiosa* and a Wood-Bug, *Podisus serieventris* (1).

g. Hibernation.

The periodical appearance of vast numbers of various Coccinellids has long been known. These appearances are of two types: (1) increased numbers of the insects in various districts of the country during the spring or summer, in places where there were or had been large numbers of aphis; and (2) large numbers of the insects at specified places, usually in the spring or autumn, where there was or had been no food. In the latter case the insects are in close juxtaposition, and may occur in such quantities that the term "masses," used by Johnson, most fitly describes the case.

Septempunctata have occurred in masses by the seaside in England in the autumn, and Fabre (10) has observed them on Mount Ventoux in the Vaucluse Alps at a height of 4500 feet in June and October. This is a condition similar to *Hippodamia*, which is constantly found in large masses on the western American Mountains, where it is known that they gather to hibernate. The same phenomenon possibly also occurs in the Alps and other European mountains. The masses by the sea are probably pre- and post-hibernation gatherings. Johnson suggests that the yellow excretion may play some part in gathering these numbers together. If this is so at the time of hibernation, it may also be a factor in gathering Coccinellidæ together for feeding purposes.

In Staffordshire I have found hundreds of *septempunctata* swarming over sand-hillocks by the roads and on the commons, on warm days in April, at a time when they are beginning to emerge, in places where there is no sign of aphis. I have never found *bipunctata* in large quantities, although they do collect in small groups under bark for the winter hibernation. Mr. Alfred Priest reported to me the presence of large numbers of *bipunctata* in the neighbourhood of a disused chimney-stack in

September 1919. Early in 1920 he visited this place, and found large numbers of the insects lying massed upon one another in the cracks between the bricks where there was practically no shelter. The Lady-birds were on all sides of the chimney.

In September 1919 large numbers of *septempunctata* were reported from various parts of England, but in Staffordshire there were at the same time large numbers of *bipunctata* and *C. 11-punctata*, which, on account of their small size, were much less obvious. This abundance was entirely accounted for by the weather-conditions. Early in August there had been a period of warm fine weather during which aphis and Coccinellid larvæ flourished: this was succeeded by a wet, cold period, which no doubt retarded the pupæ; but when a second period of hot weather supervened, the retarded pupæ responded, as my breeding experiments show they will do, and simultaneously, instead of over a protracted period, the adults appeared.

4. *The Genetical Relations of the Varieties.*

Matings were made during the summers of 1918 and 1919. During the first year, only 22 of the 57 fertile matings produced a complete generation, the family in each case being reduced to one imago. In 1919, 23 complete generations were produced from 35 matings.

Eleven of these successful matings were Red × Red, and with the exception of one, Mating 32, produced only Red offspring, among which there occurred small variations from their parents and from "type." The Red bred true, producing none of the Black variety.

The exceptional mating (32) consisted of two Reds taken when mating. The female laid one small batch of eggs (7), from which two Black imagines were produced. Clearly the female was at the end of her productive period, and had probably mated with a Black before she was caught.

Six matings of Black × Black were made, five of which produced both Red and Black imagines, a phenomenon quite different from the Red × Red matings; but as it was not possible to guarantee that the females had not had partners previous to the scheduled one, it cannot at present be deduced that the genetic constitution of the Black as regards the purity of the genes is different from that of the Red.

The sixth mating (24), which produced only Blacks, was as follows:— ♂ var. 4-maculata × ♀ 4-maculata produced five 4-maculata and one 6-pustulata. The female had certainly had no previous mate.

The five matings of Black × Black produced 8 Blacks and 4 Reds. It must be noted that these Reds were all variations from "Type" and not exactly like the Red parent. The problem therefore arises—are these variations heterozygous forms with an intermediate appearance? Similar varieties have, however, been

found in the pure Red families, where, moreover, the variations of the offspring appear related to those of the parents; if, however, these variations are the heterozygous forms, one would expect to find some Blacks appearing when these Reds are mated together, but, so far, that has not been the case. A large number of matings will have to be made, as the numerical proportions in which the varieties occur in nature indicates that there are certain points of genetic stability, and that many of the intermediate varieties, if such there are, must have a definite relation to certain parent types.

The condition in *bipunctata* may be similar to that observed by Lutz (17) in *Crioceris asparagi*. He says: "Thus we have a good case of a perfectly graded variation (from spots discrete to spots joined) obeying Mendel's law. Spots joined even lightly and on one elytron only make a "pure" recessive individual. One of these intermediate forms seems characteristic of the (DR) heterozygous form."

Six matings as follows were made between Black and Red :—

m. 20 ♂ Red × ♀ 6-pustulata produced one Red.
m. 21 ♂ Red × ♀ 6-pustulata produced one 4-maculata, one 6-pustulata, two Red.
m. 22 ♂ Red × ♀ 4-maculata produced five 6-pustulata, three Red.
m. 23 ♂ Red × ♀ 6-pustulata produced four 4-maculata, five 6-pustulata, two Red.
m. 25 ♂ 4-maculata × ♀ Red produced one 4-maculata.
m. 29 ♂ Red × ♀ 6-pustulata produced one 4-maculata, two 6-pustulata, one Red.

There is here no sign of dominance, but there is a large proportion of Blacks (20) to the Reds (9). This proportion is surprising, as the Blacks are normally in the minority according to data so far collected. If the larvæ destined to become Black imagines have the same physiological response to heat as the Black imagines (see section 1), their large proportion might be accounted for.

So far, only two matings (m. 57 in 1918 and m. 25 in 1919) were made between a Black ♂ and a Red ♀; both these produced Black offspring only, so that not sufficient data is yet at hand to judge if there is a sex factor in the inheritance.

There are usually two medium posterior whitish spots on the pronotum of the Red form. These may be absent, or the two may be large enough to fuse in the middle line. So far, no regular method of inheritance of these spots has been determined. Palmer (1911) found "the presence of the whitish basal markings on the pronotum (of *annectans* and *melanopleura*) dominate over its absence in *coloradensis* and *humeralis*." The degree of the development of these spots is not related to the degree of the development of the black dorsal spot in any way; these white spots are absent in the Black form, the pronotum of the Black

and Red differing thus in degree of pigmentation. But those Red forms, in which the black spot even stretches as a band across the elytra, do not necessarily have a more pigmented pronotum than in "type." If an increase in the size of the black spot of "type" means a step forward in a melanistic direction, one would expect this tendency also to affect the pronotum.

C. variabilis.

C. variabilis has two forms of imagines, which in general colour arrangement are similar to the two principal forms of *A. bipunctata*. There is a Black form with ten red-ochreous spots and a Red (ochreous) form with fourteen black spots. The difference in the shade of the red between the two forms is much more marked than in *Adalia*. The red spots on the Black frequently tend to carmine at the edges, but the red ground-colour of the Red form would more accurately be described as ochreous; it is never as deep a red as occurs in *A. bipunctata* (type). I have no information of the percentages in which these types occur. The Black form of *variabilis* is the "type," but whether this indicates that it is the more common is unknown.

The dimorphism in *bipunctata* and *variabilis* is not equivalent to that of *Lina* (**18**), in which there is a spotted and a melanic form, for in that species there is certainly only one colour-pattern, as the spots can be sometimes seen in the melanic form by holding the wings up to the light. MacCracken (**18**) found the melanism recessive.

Two matings of *variabilis* were made: (1) mating 17, ♂ Black × ♀ Red produced 4 Red imagines; and (2) mating 18, ♂ Red × ♀ Black produced 4 Black and two Reds. As in *bipunctata*, there is no sign of dominance.

A third mating (10) was made between a ♂ Red *bipunctata* and a ♀ Black *variabilis*, the result of which was 7 Red *variabilis* and 5 Black *variabilis*. The two mated at intervals from May 29 to June 26, and during that period laid eggs as follows:— 15 on June 3, 16 on June 4, 24 on June 12, 6 on June 18, and 15 on June 26; a total of 76. As the results were all *variabilis*, one cannot but suppose that the female was satisfactorily fertilised by a male of her own species before she was caught. This, however, involves the necessity that some of the spermatozoa remained capable of fertilization for 29 days at least; but Palmer states, p. 235 (**21**): "A female *Adalia* would not seem to be able to lay fertile eggs for more than three weeks after being isolated from a male."

On one point these two species differ considerably, for it is the Black form of *bipunctata* which is the more variable in the number of spots, whilst in *variabilis* it is the Red form which is the more variable. The recurrence of the same type of variation in species so nearly related and which constantly occur together, makes an understanding of the one imperative to a satisfactory understanding of the other.

5. *Summary.*

1. *Adalia bipunctata* has so many varieties that it is highly suitable for the needed study of inheritance of normally occurring variations.

2. *Adalia* can be mated in captivity with ease, but their cannibalistic habit makes it very difficult to rear them satisfactorily in large numbers.

3. The time passed in the various stages is variable, depending not only on the food, but also on the temperature, to which all stages, but especially the pupal, make a rapid response.

4. Little is known of either hibernation or migration, but apparently both *septempunctata* and *bipunctata* tend to collect in numbers in the spring and autumn, and may at times be found hibernating, piled upon one another, similar to the "masses" of *Hippodamia* found in the western U.S.A.

5. There is no evidence of dominance in crosses between the two main forms—the Red "type" and the Black (var. 4-maculata and var. 6-pustulata).

6. Eleven matings of Red × Red produced only the Red type.

7. Black and Red forms also occur in *C. variabilis*, and, as in *bipunctata*, neither is dominant.

8. The pronotum of the Black form is darker than that of the Red, but there is no progressive blackening of the pronotum of the Red coincidentally with the increase in the size of the black spots of the elytra.

9. Although it is possible to make a series from pure red elytra on the one hand through various patterns to pure black on the other, this cannot be regarded as proof that the variations are merely fluctuating. The percentages of the variations is, as far as is known, approximately stable, and certain types are far more common than others. These facts, combined with the observation that the children tend to show the variations of the parents, strongly suggest that there are probably certain points of genetic stability, and that only analysis is needed to show that there is some regular method of inheritance.

I have much pleasure in thanking Dr. A. D. Imms for naming several of the aphis species and Mr. W. B. Grove for naming the mould, *Cladosporium aphidis*, which he believes has never before been recorded as British.

Literature.

1. Burgess, A. F. 1903.—Economic Notes on the Family Coccinellidæ. U.S. Dept. Agric. Div. Ent., Bull. 40 (New Series), pp. 25–32.

2. Burgess, A. F., & Collins, C. W. 1911.—The Value of Predaceous Beetles in destroying Insect Pests. U.S. Dept. Agric. Year-Book, pp. 453–466.

3. Clausen, C. D. 1915.—A Comparative Study of a Series of Aphis-Feeding Coccinellidæ. Journ. Econ. Ent. vol. viii. pp. 487–491.
4. Chyzer, Bela. 1886.—Note on Cannibalism of Coccinellidæ. Revatani Lapok. vol. iii. p. 107.
5. Curtis, John. 1860.—Farm Insects. London: pp. 71–73.
6. Donisthorpe, H. 1919.—Myrmecophilous Lady-bird, *Coccinella distincta* Fald.: its life-history and association with Ants. The Entom. Record, 1919, vol. xxxi. No. 12, pp. 214–222, & 1920, vol. xxxii. No. 1, pp. 1–3.
7. Dunning. 1869.—Discussion on swarms of Coccinellæ, Nov. 1869 by Mr. Dunning. Trans. Ent. Soc. London, p. xxv.
8. Ewing, H. E. 1914.—Some Coccinellid Statistics. Journ. Econ. Ent. vol. vii. pp. 440–443.
9. Ewing, H. E. 1913.—Notes on Oregon Coccinellidæ. Journ. Econ. Ent. vol. vi. pp. 404–407.
10. Fabre, Henri. 1897.—'Souvenirs Entomologiques.' The chapter entitled "Les Emigrantes."
10 *a*. Girault, A. A. 1914.—Pupal Stages of *Adalia bipunctata*. Ent. News, vol. xxv. p. 155.
11. Holtz, Martin. 1907.—Ueber *Adalia bipunctata* L. typ. und deren Varietat sex-pustulata L. Ent. Woch., 24 Jahrg. pp. 181–182.
12. Johnson, Roswell. 1907.—Economic Notes on Aphids and Coccinellids. Ent. News, vol. xviii. pp. 171–174.
13. Johnson, Roswell. 1910.—Determinate Evolution in the Colour-pattern of Lady-beetles. Carnegie Inst., No. 122
14. Johnson, Roswell. 1912.—Heredity of Colour-Pattern in Coccinnellid Beetles (abstract). Proc. 7th Int. Zool. Congress, Cambridge, Mass., pp. 409–410.
15. Krause, A. H. 1904.—*Adalia bipunctata* Varietaten aus Nord-Thüringen. Ent. Zeits. vol. xviii. p. 112.
16. Lutz, K. G. 1888.—Hibernation of the Two-spotted Lady-bird. (Correspondence.) Insect Life, vol. i. p. 56.
17. Lutz, F. E. 1908.—Notes on the Inheritance of Variations in the Colour-pattern of *Crioceris asparagi*. 'Psyche,' Boston, vol. xv. pp. 50–52.
18. McCracken, I. 1906.—Inheritance of Dichromatism in *Lina* and *Gastroidea*. Journ. Exp. Zool. vol. iii. pp. 331–336.
19. Meissner, Otto. 1912.—Statistik und Biologie von *Adalia bipunctata*. Ent. Zeits. vol. xxvi. pp. 82–83, 87–88, 94–95.
20. Meissner, Otto. 1912.—Cannibalismus bei Coccinelliden. Wien. Ent. Zeit. vol. xxvi. p. 322.
21. Palmer, Miriam A. 1911.—Some Notes on Heredity in the Coccinellid genus *Adalia* (Mulsant). Ann. Ent. Soc. America, vol. iv. pp. 283–302, 4 pls.
21 *a*. Palmer, Miriam A. 1914.—Some Notes on the Life-history of Lady-beetles. Ann. Ent. Soc. America, vol. vii. pp. 213–237, 2 pls.

22. REICHART, A. 1904.—*Adalia bipunctata* (L.) varietaten. Ent. Jahrb. Leipzig, vol. xiii. pp. 179–181, 1 Taf.
23. SCHRÖDER, CHR. 1901 & 1902.—Die Variabilitat der *Adalia bipunctata*, gleichzeitig ein Beitrag zur Descendez-Theorie. Allg. Zeits. für Ent., Bd. vi. (1901), Nos. 23 & 24, pp. 355, 371; Bd. vii. (1902), pp. 5, 37, 65, mit Tafel 5 und 5 Textabbildungen.
24. SCHRÖDER, CHR. 1904.—Selektions und der Theorie der Zeichungs-phylogenie bei den Lepidoptera. Allg. Zeits. für Ent., Bd. ix. pp. 215, 249, 281.
25. SCHRÖDER, CHR. 1909.—Die Erscheinungen der Zeichnungsvererbung bei *A. bipunctata* und ihren ab. 6-pustulata u. 4-maculata. Zeits. wiss. Inseckten biol. Berlin, vol. iv. pp. 132–134.
26. SLATER, J. W. 1889.—Cannibalism with Lady-birds. Insect Life, vol. ii. p. 55.
27. SMITH, J. B. 1892—General Notes: *Epilachna borealis*. Insect Life, vol. v. Nov., p. 98.
28. SMITH, J. B. 1893.—Carnivorous and Herbivorous Insects. Ent. News, vol. iv. p. 123, figs. 1 & 2.

Birmingham, November, 1920.