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Life-history of Melittobia acasta

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The insect first came under my notice in 1918 when I was watching the habits of and making experiments with certain solitary bees and wasps in my garden in Cambridge. I had started there a small colony of *Odynerus spinipes* by bringing home pieces of an old mud wall containing larvae from a ruined cottage at Histon and I had attracted various other wasps and bees by providing glass and elder tubes arranged on shelves attached to my garden fence.

On the 30th May of that year I noticed that a minute Chalcid was swarming over one of the pieces of the mud wall and later freely entering tubes which were being occupied by bees and wasps and, in the case of glass tubes so occupied, I noticed that numbers of this minute insect became sealed up in the cells constructed by the bees or wasps.

At first I thought that these imprisoned individuals had been caught accidentally in the cells and that they would quickly perish but, on watching them, I noticed certain acts which caused me to form a different opinion.

I therefore began to investigate the life-history and by the autumn of that year I had worked it out and it was not until I was describing some of the curious habits of this little parasite to my friend Dr Keilin that he referred me to Malyshev's paper which he very kindly translated for me. I then found that, although in the main my observations agreed with those of the Russian author there were various points upon which I differed from him and I therefore decided to work out the life-history again and to make some further experiments.

It was not until January 1921 that I was again able to obtain the necessary material as I had allowed all my stock to die out after completing my observations in 1918.

(*b*) *Technique.*

In order to watch the life-history of and to experiment with this minute insect I made a number of cells by cutting pieces of glass tube of about 8 mm. diameter gauge into 3 inch lengths and fixing these horizontally to small pieces of cardboard by means of thin wires (Pl. XXVI, fig. 9). Into the middle of such a piece of tube a wad of cotton wool was pushed and rammed tight, the wad being about half an inch long. Each end of the tube plugged with a similar wad gave me two cells to each tube. I found that these cotton-wool plugs were sufficient to prevent the escape of the insects under ordinary circumstances since, if the female is placed under conditions which give her suitable food and suitable material for the reception of her eggs, she makes no effort to escape. If however females were retained in such a cell without food they frequently attacked the plugs and when they were numerous—as when a whole brood hatched out and was left in a cell, they frequently bit their way out. It is curious to notice that under these circumstances, the central plug was seldom, if ever, attacked and presumably the insects were guided to the end plug by air currents through the wool. The cardboard to which the tubes were attached made them stable and upon it numbers and dates referring to the imprisoned insects were written.

The food-material, in the form of resting larvae and of pupae of various species, was placed in the cell and every movement of the parasite on its host could be watched under a Zeiss binocular dissecting microscope. The tube could be rotated so as to cause the host larva or pupa to roll over so that *Melittobia* eggs and larvae could be seen and even counted, if not numerous, without removing the host from the cell. As a rule however the cell was opened and the host tipped out whenever a count of eggs and larvae of the parasite was to be made and at these times the parasite sometimes remained in the tube and sometimes came out upon the host. In the latter case she frequently remained upon the host the whole time that her eggs and larvae were being removed and usually showed no signs of fear or annoyance even when pushed out of the way by the brush or needle.

Occasionally the cells required cleaning as the glass became dulled by the excreta of the female.

The cotton-wool plugs seemed to permit the passage of all necessary air and in every way these cells were most convenient to handle. Most of my experiments were made with the larvae of species of *Odynerus* and of *Osmia rufa* but, as will be seen later on, the latter was, for some unknown reason, not an ideal host, so that most of my results were obtained from experiments with the wasp larvae.

II. The Hosts of *Melittobia*.

Melittobia is parasitic upon a number of kinds of bees and wasps. Howard (1892) gives a list of 14 different genera which are attacked by it. Malyshev (1911) adds three more and Girault (1912) adds another two. It was also known to be parasitic upon various flies of which it attacks the pupa.

Experiment however shows that almost any larva or pupa of bee or wasp is attacked by it under laboratory conditions and even beetle larvae and pupae served as food for both imago and larva.

But although almost any insect larva or spider in a quiescent condition—such as those paralyzed and stored up by various fossorial and Eumenid wasps, or larvae about to pupate—seemed to be regarded as suitable for oviposition and as food for the resulting larvae, in many cases such larvae failed to mature, mainly, I believe, because the food material dried up and the parasites conquently starved.

The following is a list of the genera of hosts previously recorded:

Anthophora	*Ceratina*	*Pison*
Osmia	*Prosopis*	*Sceliphron*
Chalicodoma	*Stelis*	*Chrysis*
Heriades	*Odynerus*	*Monodontomerus*
Anthidium	*Trypoxylon*	*Leucospis*
Bombus	*Agenia*	*Musca* and other fly pupae.
Megachile		

I have experimented with the following hosts:

Osmia rufa	*Chrysis ignita*	
Megachile spp.	Ichneumonid parasite of larvae of *Hypera variabilis*	
Odynerus spinipes	Paralyzed larvae of *Hypera variabilis*	From cells of solitary wasps
,, *antilope*	,, Tineid caterpillars	
,, *callosus*	,, spiders	
Vespa sp.	*Donacia* pupae	
Trypoxylon figulus	*Calliphora*, *Musca*, etc., puparia	
Crabro sp.	*Urophora solstitialis* (Muscid) pupae	
Psen sp.		

In every case, excepting the paralyzed spiders and larvae from the cells of solitary wasps, I have succeeded in rearing the parasite on these hosts but, as will be seen later, in one case, that of *Osmia rufa*, the food seemed very unsatisfactory (*v.* Chap. XI).

III. Male and Female Characters.

The male and female imagines are very different from one another. The former (Plate XXVI, fig. 1) is of a dark brown colour, even reddish, with minute wings quite useless for flight. The anterior pair, which are the larger, are only about one-third the length of the insect and, when lying at rest on the dorsum, only reach just beyond the first visible abdominal segment, the posterior pair not extending more than two-thirds of the way across this segment.

The head bears on each side, instead of the usual compound eyes, a single ocellus and there are also three ocelli in a group in the usual position on the vertex.

The antennae are very peculiar. They consist of what are apparently eight segments but the apical one is two or three segments compressed to form a club. The scape consists of one very large segment which forms about half the total length of the antenna. This large segment is broad and triangular in shape, attached to the head by one angle, the flagellum being attached to it at one of the others, the inner one when the antenna is viewed from above. On the under side of the scape at its distal end and between the two angles is a hollow space (Plate XXVI, fig. 1 *a*, *b*).

The female (Plate XXVI, fig. 2) is darker in appearance, being usually pitchy brown, has compound eyes and the normal chalcid elbowed antennae. The wings, which overlap when at rest, extend almost to or slightly beyond the apex of the abdomen, this depending upon whether the latter is full of eggs or otherwise.

The only published figures, so far as I can find, are those of Graham Smith (1915–16 and 1918–19) who illustrates male and female in both his papers, but as the figures in the two papers are so different and as, in my opinion, they do not give a correct idea of the insect, I have made drawings for this paper.

Waterston (1917) gives figures of certain parts of the adult insects such as the male antenna and the metasternum and first abdominal segment on a larger scale than in my drawings.

IV. LIFE-HISTORY.

(a) *General statement.*

Various facts in the life-history have been given by different authors but there are only two accounts which are in any way complete, those of Malyshev (1911) and of Graham Smith (1915–16 and 1917–18). The former author deals with the species as a parasite of *Odynerus*, a genus of solitary diplopterous wasps, while the latter deals with it as a parasite of certain Diptera.

Malyshev's observations and experiments go farther than those of Graham Smith but in one or two important points they are incomplete. In view of the fact that Malyshev's paper is in Russian, I offer no excuse for giving here a detailed account of the life-history.

So far as I have observed, the imagines first appear under natural conditions some time after the middle of May and they can be found in their haunts as late as September. Under laboratory conditions, by keeping the species in an incubator at summer temperatures, it is possible to continue to produce successive generations throughout the winter, and this fact has enabled me to complete and repeat certain experiments which otherwise would have taken perhaps six or seven months (see Chap. XII, "Winter rearing of *Melittobia*," p. 367).

Although occasional over-wintering pupae are to be found the species normally winters in the larval condition and although, as I have said, the imagines may appear in May, overwintered larvae may remain as larvae until June, the imagines not appearing until July, even when kept in the laboratory. These hibernating larvae are not always full-grown but as many batches of such larvae have completely finished their food supply before commencing hibernation, they either complete their growth by feeding upon their neighbours in the mass or perhaps in some cases pupate prematurely.

It might also be reasonably assumed that any food left over would be unfit for consumption by the time the larvae became active again but this is not necessarily the case as the host larva remains alive for a long time during the process of "deflation."

Under natural conditions, shortly after emergence, the females, having mated, break out of the cells in which they have developed. At this stage they show a definitely positive heliotropism. Such individuals, released in front of a window in the laboratory, move directly towards the light and, if confined in a horizontal glass tube closed at one end, they will remain in the tube if the open end is turned away from the source of light. If such a tube is turned round, the females at once stream out towards the light.

This positive phototropism lasts for a considerable time but it is apparently eventually overcome by a chemiotropism when the insects seek the cells of their hosts, primarily for nourishment.

The first tendency of the female on entering the cell of a host is to feed, although oviposition upon the host may commence very soon.

But females can delay oviposition apparently almost indefinitely, even when their abdomens are swelled almost to bursting point, if the host is not in a suitable condition or, as will be seen later, if mating has not taken place. Thus I have had females laying within 24 hours of emerging from the pupal stage, when placed upon suitable material, and I have had other females which had not oviposited 50 and even 60 days after emergence, when placed in a cell with an unhatched egg of the host-species, these females having waited for the host to reach the full grown larval condition before commencing oviposition.

(*b*) *The egg.* (Plate XXVI, fig. 5.)

The eggs, which are hyaline and almost transparent, vary somewhat in shape and in size. The smallest eggs measured were about ·33 mm. in length while the largest were about ·37 mm. They are elongated and taper somewhat towards one pole and measure about ·1 mm. across at the widest part. Some taper more strongly than others and as these were scarcer I assumed at first that they were destined to produce males, but experiment showed that this was not the case and that there is no visible difference between male and female eggs.

The egg is not firmly fastened to the host but adheres very slightly as if it were just damp. It is quite easily lifted off by means of a needle point or fine brush but as a rule it will not fall off if the host is turned over. If, however, in the process of turning over the host, the egg comes in contact with the glass cell it adheres more readily to the latter.

Incubation varies from 2 to 9 days and the emergence of the larva from the egg is almost impossible to determine. The chorion is extremely thin and the larva apparently begins to feed through it, as I have observed is the case in some other hymenoptera, for instance *Trypoxylon figulus*. Sooner or later this thin "shell" splits and contracts.

(*c*) *The larva.* (Plate XXVI, figs. 6 and 7.)

The newly emerged larva is transparent and is composed of a head and thirteen segments. The tracheal system shows only four pairs of spiracles, one on the mesothorax and one on each of the first three abdominal segments, though the branches from the lateral trunks in the three or four succeeding abdominal segments indicate where, at a later stage, additional spiracles will appear.

The larva remains in the first stage from two to six days or even longer and then a moult takes place and five additional pairs of spiracles appear, one on the metathorax and the others on the fourth to the seventh abdominal segments. I have never actually seen a moult take place but, by examining numbers of larvae ·60 to ·70 mm. in length, it is possible to find individuals about to moult in which the additional spiracles are faintly visible subcutaneously.

A second moult takes place before the final larval stage is reached but no further change takes place in the number of spiracles.

The full-grown larva attains a length of about 1·7 to 1·9 mm. and is usually smooth, the constrictions between the segments having disappeared during growth.

It has been said that the larva feeds without puncturing its host but this does not seem to be strictly accurate. The larva possesses a minute pair of mandibles which, in the first stage, are more or less triangular in shape, the free angle being sharply pointed; but in larger larvae this point is greatly lengthened (Plate XXVI, figs. 3 and 4). I imagine that these points are driven in subcutaneously and serve to hold the mouth of the parasite to the host and at the same time allow the "blood" of the host to pass out. The minuteness of the punctures can be gathered from the fact that, on the removal of a feeding larva the spot at which it has been feeding is not recognisable, even under high magnification. On the other hand if a large number of feeding larvae are gently removed from a host the surface of the latter appears as if it were gently perspiring, though of course this might be due to exudation of fluid from the mouths of the larvae at the moment of removal.

The larva is full grown, under the most favourable conditions of food and temperature, in eight or nine days, and only then does it begin to produce excrement. This habit of not producing excrement until feeding has ceased seems to occur in a large number of Hymenopterous larvae though there are others, such as *Osmia*, *Megachile*, *Sapyga*, etc., which begin to produce faecal pellets when about half grown.

Shortly after completing this cleansing process the *Melittobia* larvae become pupae.

It is interesting to note that the larvae take the colour of the host upon which they feed, as do other "blood" sucking Hymenoptera, *e.g. Odynerus*, *Chrysis*, etc. By feeding the *Melittobia* larvae upon the salmon-red coloured larvae of a small *Crabro* sp., the larvae became salmon-red. Fed on larvae of *Odynerus spinipes* the larvae are yellow, while if fed upon larvae of *O. antilope* they are creamy white and this colour depends upon the blood colour of the host, which in turn depends upon the blood colour of the beetle- or moth-larva or spider upon which it fed. By feeding larvae for a few days on *Crabro* and then transferring them to *Odynerus*, the colour of the parasite changes from salmon-red to yellow or cream.

As soon as the larva begins to cast out excrement, the colour begins to disappear and all *Melittobia* larvae, however they have been fed, ultimately become a pale transparent creamy-white colour.

(*d*) *The pupa.*

As soon as the pupa appears it is possible to decide the sex of the individual since, in the female pupa, the compound eyes are visible, though at first without colour, while no eyes are at first visible in the male pupa. In the course of time the eyes of the female pupa become red and shortly before the emergence of the imago, the whole pupa becomes black while that of the male becomes reddish brown. The duration of the pupal period under the most advantageous conditions is about seven days.

But both larval and pupal periods vary very considerably in their duration under different conditions. So far as I know, the species normally hibernates in the larval stage and such larvae, as I have already mentioned, may not pupate until the following July, so that we have the shortest larval period as eight days and the longest as about eleven months. The pupal period also varies between about seven days and perhaps ten months.

V. The Habits of the Female.

(*a*) *Food and method of feeding.*

The female feeds upon the blood of her host which she obtains by puncturing with her ovipositor. A hungry female walks about upon the host, be it egg, larva or pupa, tapping it with the apices of her antennae until she selects a suitable spot. She then bends the apex of her abdomen downwards and thus brings the point of her ovipositor into contact with the surface of the host (Plate XXVI, fig. 8 *a*). The ovipositor is then released from its sheath by the abdomen straightening again and the insect by a steady or, may be, a slightly jerky pressure of the body forces the apex of the ovipositor through the "skin" of the host (Plate XXVI, fig. 8 *b*). The stylet may be driven in deeply, even to its base, or it may merely penetrate but, after a short interval, it is withdrawn and the insect rapidly moves backwards, feeling about with her antennae until the puncture is discovered, when the mouth is at once applied to it (Plate XXVI, fig. 8 *c*). After sucking for a short time, the insect moves away and may at once repeat the process at some other spot.

One would scarcely expect that the egg or young larva of a bee or a wasp could suffer this treatment and survive and yet I have had many examples of eggs punctured, even so that a globular effusion of "blood" appeared upon the surface, without the vitality being, to all appearance, affected. I have placed as many as 15 *Melittobia* females in a cell with a newly hatched larva of *Osmia* and have allowed them to feed freely upon the host for a fortnight, and yet ultimately these heavily taxed hosts have pupated and emerged as adults.

In the same way *Melittobia* females placed in cells with older host larvae produced no ill-effects so long as they were only feeding and I am therefore quite satisfied that the feeding habits of this parasite are not necessarily injurious to the host.

(*b*) *Preparation of food for the larvae.*

On the other hand, once a *Melittobia* female lays an egg upon its host, whether the latter is in the egg, larva or pupa stage, the host is apparently doomed. This seemed at first a most extraordinary thing. It was difficult to believe that the mere fact of the parasite egg being in contact with the body of the host could cause the destruction of the latter and the experiment of removing eggs from one host and placing them upon another with which no *Melittobia* female had come into contact proved that the parasite egg itself in no way affected the host.

This point puzzled me for some time as it seemed that the only explanation was that the *Melittobia* possessed some subtle instinct by which it knew when a host was moribund and that, in such a case, the parasite oviposited on what was really an unsuitable host. What seems to be the real explanation came to me accidentally. With a high power binocular microscope, I was watching a *Melittobia* female puncturing a mature *Odynerus* larva and I happened to notice a fluid oscillating in the semi-transparent ovipositor. Gradually the ovipositor was buried to its base in the host and after an interval of about two minutes it was withdrawn and I was surprised to see the insect move away without making any attempt to find or to suck the puncture. This, then, appeared to be a different process from the feeding one and I made a number of experiments with ripe female *Melittobias*, *i.e.* females which had already begun to oviposit, isolating individuals in glass cells each with a host suitable for oviposition, the host in every case being a resting larva of either an *Osmia*, an *Odynerus* or a *Chrysis*.

By watching these females it was easy to establish the fact that they frequently made punctures without afterwards sucking them and occasionally it was possible to imagine a fluid passing down the ovipositor into the wound[1].

As soon as I saw a host larva punctured in such a manner, I transferred it to a separate cell and left it, with the object of seeing whether it would ultimately become a pupa and emerge in the normal manner. In some cases these larvae may have been thus punctured only once and in other cases they may have been punctured a number of times but they were always removed from the parasite before the latter laid any eggs upon them. All but one of these larvae, numbering thirty-eight, failed to develop.

In another set of experiments, involving twenty *Odynerus* larvae in the resting stage, I allowed *Melittobias* to lay a few eggs upon them, always removing the eggs before they hatched and removing the females after a few days and in all these cases again the *Odynerus* larvae failed to pupate.

It seems therefore that the *Melittobia* female punctures her host for two different purposes, one in order that she may feed upon its "blood" and the other in order that she may inject something so as to stop the development of the host for the benefit of her offspring.

[1] I have used the word "imagine" here because it is extremely difficult to make the observation, it being necessary to get the parasite in a particular position with regard to the light and, of course, to see the ovipositor before it is driven in to its base. The only case of which I am absolutely certain that I saw a movement of fluid in the ovipositor from parasite to host was one in which a female was puncturing a fly puparium but, as in the case of fly puparia the parasite lays its egg on the fly pupa contained within the puparium, I may have been watching the passage of eggs.

Malyshev (1911) had observed the puncturing in connection with oviposition and he regarded its function as twofold: first to paralyse the host and secondly to preserve it, but here, I think, he went too far. He only mentions one case, in which he saw a larva of *Odynerus antilope* receive three punctures in the beginning of September and he remarks that it remained soft and fresh, without showing any other sign of life, until the following May, when it dried up. Had this larva not been punctured at all it would have remained soft and fresh until the following May when it would have pupated. There seems to me to be no need to imagine any preservative effect, apart from which there is good reason for believing that there is none, since in every case where eggs were laid upon eggs or immature larvae of a host, these host eggs and larvae quickly collapsed and showed all the usual signs of decay.

It is sufficient then to regard this preparation of the host by the injection of some paralysing fluid as similar to that seen in those solitary wasps which store up living food for their progeny.

So far as my observations go, this "stinging" by *Melittobia* always takes place at least once, and sometimes frequently, before any eggs are laid, although Malyshev asserts that oviposition may be commenced before any "stinging" takes place, though this is less usual.

(c) *Oviposition.*

Melittobia is in all cases ectoparasitic and the statement of Malyshev that, under certain circumstances, it is an endoparasite is misleading. Thus he speaks of it as becoming endoparasitic when it oviposits through the cocoon of an hymenopterous host or the puparium of a fly.

I have opened numbers of fly puparia after having observed *Melittobias* puncturing them but in no case did I find any eggs except on the enclosed pupa.

When a female is about to lay her eggs she moves over the host, tapping with her antennae until she finds a suitable spot. Such a spot is usually, though not always, upon the upper side of the host larva or pupa as it lies in the cell, whether it be dorsum or venter uppermost and, if there is any choice of position, of which I am doubtful, the head end is more favoured than the apex of the abdomen.

Having selected the spot the female brings the apex of her abdomen into contact with the surface of the host and, having fixed the apex of the ovipositor in the chitin, the apex of the abdomen withdraws to its normal position. So far the action has been that of a feeding or a "stinging" female but, for oviposition, the ovipositor is not driven into the host, merely remaining fixed by its apex.

The abdomen can now be seen slowly expanding and contracting until, after a few such movements, a slight bulge appears at the base of the ovipositor on its anterior side and this bulge rapidly passes downwards and the egg suddenly shoots out near the apex. It is a most extraordinary sight and looks like a conjuring trick to see the comparatively enormous egg appear from the exceedingly fine tube.

The egg shoots out more or less horizontally and lies on the surface of the host, its long axis, as it lies, corresponding more or less closely with that of the *Melittobia*. Sometimes one of the middle legs seems to be used to guide the egg as it emerges.

Within about half a minute another egg may be laid alongside the first and as many as 7 or 8 eggs may be laid in one spot within 5 or 6 minutes. A large number of eggs may ultimately become massed together at one spot or the female may scatter her eggs over the surface, but where she is ovipositing through a cocoon or puparium the eggs are almost invariably laid in heaps.

VI. THE HABITS OF THE MALE.

(*a*) *General habits.*

I have said that, as a rule, the males emerge first in the cells. These males are very active; they creep over and amongst the larvae and pupae, even seizing them in their jaws and thus moving them about, though I have never seen a male injure a larva or pupa.

Two males, on meeting, usually engage in mortal combat, though when a cell is very full of emerging females the males are so busy that they seem to pay less attention to one another.

So far as I can find the males do not feed.

I have paid but little attention to the length of life of the male, but in those cases where a male has been introduced into a cell containing a female, the former has usually succumbed within seven days. In these cases, however, I have no record of the age of the male when he was introduced into the female cell but in one case I found a male alive twenty days after introduction, the female having died—or having been killed by the male—within 24 hours after his introduction. It is possible that inability to fulfil the sexual function may prolong life as in the case of the female. (See section upon "Longevity of the Female," p. 363.) Smith, F. (1853) says that the male usually lives about seven weeks.

The killing of the female by the male was, unfortunately, a not uncommon occurrence and on several occasions stopped experiments of some importance. Whether or not this is a phenomenon caused by the experimental conditions it is, of course, impossible to say.

(*b*) *Courting.*

Courting is a strange phenomenon in that a special contact is made between the antennae of the male and female as a preliminary to copulation. The male mounts upon the back of the female and moves forward, seeking for her antennae, the apices of which he ultimately succeeds in getting into the pocket on the underside of the long scape segment of his antennae (*v.* Plate XXVI, fig. 1 *a* and *b*).

Coïtus is very rapid and the male immediately seeks for another mate. He quickly decides whether a female is willing or unwilling and wastes very little time over the latter.

VII. The Numerical Proportion of the Sexes.

There seems to be no reliable way of determining the proportion of the sexes in a family, since the male and female eggs are indistinguishable, as I have already said, and the larvae are more or less cannibals, so that sometimes quite large numbers of individuals disappear during the larval period. By counting pupae one gets more reliable results than by counting the imagines since the males in the latter stage destroy one another, and, under laboratory conditions, also sometimes destroy females.

Graham Smith gives results of counts of imagines which range from less than one to more than fifty males per hundred females but, since a female may lay more than a thousand eggs and his figures are all for small batches, they give us no reliable criterion.

By counting pupae I found that, in any one batch of eggs, the males ran from about one to four or five per cent. of the females.

Now, as will be shown later, a female normally lays two, and perhaps three, batches of eggs and she mates with a male before each bout of egg-laying. If she is unfertilized or if, after laying a batch of eggs she is not permitted to mate again, she can only lay male eggs, that is, the eggs can only develop into males. Presumably therefore unfertilized eggs produced males and fertilized produce females, as in many other Hymenoptera. As therefore she produces both male and female offspring after mating and before she has exhausted her supply of spermatozoa, it is reasonable to conclude that she can control the flow of spermatozoa from her spermotheca and thus determine the sex of her offspring—as Fabre has shown is the case with certain species of *Osmia* and *Chalicodoma* (*v. Bramble Bees and Others*, Chaps. IV and V). It might also be concluded from the fact that males usually emerge first in a brood, that the first eggs laid by the female are male eggs, but it may be that males develop more rapidly than females, a point I have so far omitted to investigate.

If therefore the sex is determined by the mother at the time of oviposition the proportion may well vary for each female according to circumstances.

VIII. Fecundity.

I have already mentioned that oviposition may commence within twenty-four hours of the emergence of the female but it is often, perhaps usually, a very prolonged process.

Malyshev states that the females lay 200 to 300 eggs and perhaps more during four or five weeks but he does not say how he obtained his figures. I have, however, obtained results in my experiments which seem to indicate that the females are much more prolific than this author has shown.

In order to test the fecundity of individuals I placed in separate cells five freshly emerged females which had mated, supplying each with a resting *Odynerus* larva and, at intervals, removing from the latter the eggs and larvae, keeping a record of the totals for each female. In this way I found that the egg-laying capacity of the females varied considerably, the total number of eggs laid by each being: 961, 529, 1217, 1086 and 598. It will be noted however that the lowest total exceeds considerably the figures given by previous observers.

The eggs and larvae were removed and counted, usually at intervals of seven days after the first few weeks, and at the end of six or seven weeks the females had almost ceased to lay eggs. The few eggs laid by each at this period were placed upon fresh hosts and allowed to hatch out in order that pupae might be obtained to determine the sex. They all proved to be males, indicating that the mother had come to the end of her supply of spermatozoa. A male was therefore introduced into each of the cells containing the females and, during the following week, the number of eggs laid in four out of the five cases ran into three figures.

Although the number of individuals experimented with is too small to justify any definite statement, these experiments seem to indicate that the female normally lays about half her eggs after her first mating, the totals being 439, 270, 680, 348 and 597 and, in three out of the five examples, she had exhausted her egg-laying capacity after the results of a second mating, the numbers of eggs in the second broods being 522, 259, 333, 738 and 1 respectively.

The last few eggs of these second broods were allowed to hatch and the larvae reared in order to test their sex and, with the exception of a single individual, all were males, so that, at the same time as the female exhausted her supply of eggs she had exhausted her second supply of spermatozoa.

The following table (p. 362) gives details of all the results referred to above:

As to the rate of oviposition I have made no daily counts and at first I adopted a somewhat rough method of estimating which gave some very divergent results. Thus in August, in 17 days, out of a batch of four females the lowest yield was 152 eggs while one female gave 213 eggs. Of another batch of six females in the same month, one laid 92 eggs in 12 days while another laid 218 in the same period. These figures give averages per day of 9, 12·5, 7·6 and 18·1.

In December I began to go into this question more carefully, using the five females already referred to, and Table II shows the days upon which the counts of eggs were made and the average number of eggs laid per day as worked out from these counts. This table thus shows that the productivity of the female, when at her best, may reach 31 eggs per day and that she is at her best from 7 to 14 days after mating. I shall refer to the fecundity of the unfertilized female later on.

Table I. ***Showing the number of eggs laid by fertilized females kept in the incubator at a temperature of about* 21° C. (*about* 70° F.). *On the dates given all eggs and larvae were counted and removed.***

	Dec.	January						February				March				April					May		
	31st	6th	9th	12th	15th	22nd	29th	5th	12th	19th	26th	5th	12th	19th	26th	2nd	9th	16th	23rd	30th	7th	14th	
FF 1	|	107	64	61	41	55	107	4 |	131	210	130	47	3	D	**961**	—	—	—	—	—			
FF 2	|	61	91	55	50	6	2	5 |	10 |	103	30	12	50	51	0 |	D	**529**	—					
FF 3	|	117	156	105	79	165	50	8 |	170	141	10	3	6	3 |	79	116	9 D	**1217**					
FF 4	—	—	—	—	—	—	—	—	|	186	131	29	2 |	166	153	109	126	—	159	18	7	D	**1086**
FF 5	—	—	—	—	—	—	—	—	|	189	156	130	117	4	1 |	1 D	**598**						

D = ♀ dead. The dark lines indicate mating dates.

Table II. ***Showing the dates upon which eggs and larvae were counted and removed and the average number of eggs laid per day by each female.***

	January						February				March				April				May
	6th	9th	12th	15th	22nd	29th	5th	12th	19th	26th	5th	12th	19th	26th	2nd	9th	23rd	30th	7th
FF 1	| 17·8	19	19	18	7·9	15	·5 |	18·7	30	18·5	6·8	·4	D	—					
FF 2	| 10	17	17	17	·8	·3	·7 |	1·4 |	14·7	4·3	1·7	7·1	7·3	0 |	D				
FF 3	| 19·5	30	31	30	23·5	7·1	1·1 |	24·3	20·1	1·4	·4	·8	·4 |	11·3	16·5	1·3	D		
FF 4	—	—	—	—	—	—	—	—	| 26·5	18·7	4·1	·3 |	23·7	21·8	15·5	18·0	11·3	1·0	D
FF 5	—	—	—	—	—	—	—	—	| 27	22·3	18·5	16·7	·5	·1 |	D				

D = death of the female *Melittobia*. The dark lines indicate mating dates.

IX. Longevity of the Female.

Table I, already referred to, shows that, in the cases of the four females which produced second broods, the length of life varied from twelve to sixteen weeks, *i.e.* 84 to 112 days, and that, during all this time, they were actively ovipositing. Graham Smith (1918–19) records having seen one female ovipositing over a period of 18 days and another over a period of 37 days but it is possible that his observations were upon females which had no chance of a second mating and had therefore ceased to lay eggs because they had exhausted their supplies of spermatozoa.

I have several other records of ovipositing females which survived for periods exceeding 90 days and it seems, therefore, that, under normal conditions, this would be about the average length of life of the female.

If, however, unfertilized females are prevented from mating, the length of life is enormously increased, eight such females having lived as follows: 211, 204, 225, 223, 209, 195, 202, 202 days. This will be referred to further in the next chapter where full details are given in Table III, p. 365.

X. The Unfertilized Female.

I have already mentioned that, under natural conditions, the males never leave their natal cells, so that mating takes place there; and I believe that it is not until after mating has taken place that the females become positively heliotropic. I have never, under natural conditions, come across an unfertilized female; that is, every female which has been allowed to emerge from the pupal stage in the cell where it grew up mates before leaving that cell. It is quite easy, however, to obtain unfertilized females by simply removing female pupae from the cells and allowing them to hatch out without a male having access to them.

Several authors mention the results of experiments with unfertilized females. Such a female, when placed in a cell with suitable food material will, sooner or later, lay a small number of eggs—it may be only one but is more usually four or six, though occasionally there are a few more. The female takes great interest in these eggs and in the larvae which hatch from them, patting them with her antennae and returning to them again and again. She takes, perhaps, greater interest in the resulting pupae and may even be said to show excitement when one of them is about to become an imago. All the resulting imagines are males and she mates with the first one to emerge and within a very short time commences to lay freely, twenty or thirty eggs sometimes being deposited within twenty-four hours of the appearance of the male.

At first sight this habit of the unfertilized female of producing her own mate when another is unobtainable seems a somewhat extraordinary phenomenon and yet, from what I have shown by experiment, it appears to be a normal phase in the life-history of the insect after she has exhausted her first supply of spermatozoa and preparatory to producing her second brood. It is mainly conjecture, but I believe that the female imprisoned in the host's cell develops a desire to break out of the cell only when she has her spermatheca full, so that once the female has produced her first brood she waits patiently for her second mating and then passes on to another cell to produce her second brood. My only evidence in support of this belief lies in the fact that in my glass cells the female was often to be seen on the cotton-wool plug after her second mating especially when the host larva within the cell was already fully stocked or was almost reduced to an empty skin.

It is interesting to notice that inbreeding is the rule with this species, the first mating being between brother and sister and the subsequent ones between mother and son. Exceptions to this rule may occur when two females together enter a host cell and both produce a brood but as in such a case the two females must frequently come from the same cell, they will usually be sisters and the second mating would in this case be between nephew and aunt.

I made a number of experiments with a view to seeing what an unfertilized female would do if I prevented her from mating by removing her eggs or larvae so that no male could develop, and these experiments have given somewhat interesting results.

In the first place, as I have already mentioned, the life of the female is greatly prolonged, the ninety days, which I believe to be about the average life of the normal female, being, in a number of cases, more than doubled and in my eighteen experiments averaging 174·8 days.

In the second place, whereas under normal conditions no imago is to be found after about the end of October, unfertilized females remained alive all through the winter, withstanding at times temperatures below freezing-point and only died in the second week of March after living 202 days—in fact, longer than many similar females kept at summer temperatures in the incubator.

In the third place the female can be induced to lay many more male eggs under experimental conditions than she would probably do under natural ones—although it must be remembered that we have no definite knowledge of the number of male eggs laid by a female under natural conditions.

Of eighteen cases, the average number of eggs laid per female was 35·6, one individual laying as many as 93 eggs, others 70 and 61, while one individual only laid 7 eggs in 131 days. In all these cases the experiment was kept going until the female died, so that the number of eggs obtained from each female was the total number she laid during her life. The following Table (III) gives the details of these experiments.

Table III. *The unfertilized female. Oviposition induced by frequent removal of eggs.*

	August								Oct.			December							January						February				March				April		
	20	22	23	25	26	27	28	29	17	6		10	14	18	21	24	27	31	6	9	12	15	22	29	5	12	19	26	5	12	19	26	2		
		2	1	2	1	1	1	1	49	50		4	4	4	3	3	3	4	6	3	3	40	10	7	7	7	7	7	7	7	7	7	7		
	×	0	1	1	1	0	0	0	6	3	Placed in incubator	2	2	3	1	1	2	1	0	4	4	—	0	4	2	2	2	10	6	5	7	◗	—	211 days	70 eggs
	×	0	1	0	1	0	0	0	10	3		8	0	1	1	0	6	2	2	6	2	—	2	1	0	0	0	0	0	◗	—		—	204 ..	46 ..
	×	0	0	0	1	0	1	0	3	0		4	0	3	1	1	0	0	3	4	2	—	2	2	1	0	0	0	0	0	1	0	◗	225 ..	29 ..
	×	0	0	0	1	1	1	2	6	3		2	1	6	2	1	3	2	2	2	1	—	7	2	1	1	1	0	0	◗	—	—	—	204 ..	48 ..
M 5		×	1	3	3	0	1	0	5	0		3	3	2	2	1	1	1	0	0	1		0	0	1	0	0	0	0	0	2	0	◗	223 ..	30 ..
M 6		×	0	5	0	0	1	0	6	2		7	6	7	2	0	0	0	1	1	2		0	0	1	1	1	3	0	0	◗		—	209 ..	46 ..
M 7		×	0	1	0	5	1	0	6	1		7	4	4	2	0	4	2	5	1	4		0	1	4	10	10	21	◗	—	—		—	195 ..	99 ..
M 8		×	0	2	1	1	1	2	8	4		—	—	—	—	—	—	—	—	—	—	6	—	0	0	0	0	0	0	◗			—	202 ..	25 ..
M 9		×	1	1	0	0	0	2	7	1		—	—	—	—	—	—	—	—	—	—	0	—	0	0	0	0	0	0	◗				202 ..	12 ..

wo top transverse columns refer to the month and the day. The next refers to the number of days' interval since the previous inspection.
) M 9 are the 9 unfertilized females used in this experiment and the transverse columns show the number of eggs laid by each of them and removed at short or long
ntervals. M 1 to M 7 were placed in an incubator at a temperature of about 21° C. (70° F.) on December 6th. ◗ = death of the female *Melittobia*.

XI. *Osmia rufa* Larvae and Pupae used as Hosts.

I have already said something about the apparently indefinite variety of hosts which *Melittobia* will attack but I have had one very curious experience in this matter.

In a large number of my earlier experiments the larvae and pupae of the red *Osmia* (*O. rufa*) were used because it was one of the commonest species at my garden fence and, although *Melittobia* eggs were laid in the normal way upon the resting larvae and pupae in the laboratory, the eggs often failed to hatch out and frequently the larvae died before they were full grown, in fact it was rather exceptional to rear a *Melittobia* from egg to adult using this species as the host.

At the time that my garden fence was infested with the parasite I opened more than 130 cells of *Osmia rufa* which had been constructed in tubes placed upon shelves attached to the fence and in only one case did I find any sign of the *Melittobia* and in that one cell were two half-grown larvae. And yet in the laboratory the resting larvae and pupae of the *Osmia* were readily accepted by the parasite which fed and oviposited upon them—but the majority of the brood died.

Another interesting point in the relationship of *Osmia rufa* to *Melittobia* is that in the number of cases in which I have allowed one or more of the parasites to enter the cell of the growing larva, the parasites have invariably perished when the *Osmia* larva began to spin its cocoon, being caught amongst the outer threads—and yet *Melittobia*, in similar relationship with any of the three species of *Odynerus* with which I have worked, always survived and destroyed its host.

In a number of cases I placed *Melittobia* females in cells with *Osmia rufa* pupae enclosed in cocoons and in almost every case the parasite failed to destroy the bee. In these cases it was evidently because the *Osmia* cocoon was too tough for the parasite to penetrate, since pupae removed from their cocoons were invariably oviposited upon and in such cases the female *Melittobia* lived for many weeks, feeding upon the blood of the pupa, while those placed with *Osmia* cocoons died after three or four weeks, evidently from starvation.

This is the only host which so far I have found, upon which *Melittobia* does not really flourish and it seems as if there is some quality in the blood which has a deleterious effect upon the parasite.

That the toughness of the cocoon should be an additional safeguard is worthy of remark since Malyshev suggests that some species may escape the parasite because of the nature of the building materials used in the construction of the cells. Thus he mentions some of the *Heriades* which build the cell-walls of resin in which *Melittobia* gets caught and he suggests that *Odynerus alpestris* possibly escapes to some extent for the same reason.

These few facts serve to emphasise the peculiarities of the relationship between parasite and host and to give an idea of the apparent triviality of the things which make all the difference in that relationship. Another example of this is to be seen in the life-history of the fossorial wasp *Sapyga quinquepunctata* which I have recently investigated.

In this case the usual host of this parasite in my garden in Cambridge was the Blue Osmia (*O. aenea* (*caerulescens*)) while *Osmia rufa* was immune and it appeared that the latter species owed its immunity to the fact that the pollen paste stored in the cells by the mother bee was too dry for the larvae of the parasite. Eggs of *Sapyga* were occasionally laid in the cells of this species but the larvae always perished and, in laboratory experiments, where the *Sapyga* eggs were placed in the cells of *O. rufa*, the result was always the same. If, however, the pollen paste was made suitably moist by the addition of honey or even treacle—the latter, as experiment showed, being quite useless as a food for the *Sapyga* larva—the parasite could be brought to maturity without any difficulty.

XII. Winter rearing of *Melittobia*.

I have already said that by keeping the species during the winter in an incubator at a summer temperature 20–22 C. (about 70 F.) it was possible to raise successive generations.

I first tried this because I was held up in the autumn in the middle of experiments which I was very anxious to continue and I therefore placed batches of hibernating larvae in glass cells in an incubator early in December.

Different batches of larvae behaved differently. Some responded within a few days to the warmth and began to void excrement preparatory to pupation; others remained apparently quite unaffected by the warmth for much longer periods. Moreover a whole batch of larvae did not necessarily behave in the same way and a few extreme examples will make this point clear.

Batch 1.

Placed in incubator	10. xii. 21
Some casting excrement	26. xii. 21
A few pupae	31. xii. 21
A few imagines	5. ii. 22
Mostly pupae, a few larvae	15. i. 22

Pupation period 31 days and upwards

Batch 2.

In incubator	10. xii. 21
One pupa	24. xii. 21
All pupae	31. xii. 21

Pupation period 50 days and upwards

Batch 3.

In incubator	10. xii. 21
One pupa and the male appeared	6. i. 2
About half have pupated	5. ii. 22
Many still larvae	19. ii. 22

During the summer, the normal pupal period is only about seven days and females hatched in the incubator at summer temperatures gave rise to generations which had pupal periods of about the normal summer duration and yet in the case of those hibernating larvae which pupated in the incubator, the pupal period varied from 18 to 57 days in duration. Now a long pupal period is not an innovation to the species, since over-wintering pupae do occur under natural conditions and therefore the explanation of the long pupal period in the case of these incubated hibernating larvae seems to be that the effects of the incubator are gradual and that it takes some time before the insect reacts to the increased temperature, or it may be that the reaction of a larva or pupa to change of temperature is slight but that of the imago is more marked, since once the imago appeared she behaved exactly like a summer individual and passed on her activity to her eggs, larvae and pupae.

The apparent irregularity of the action of increased temperature on different individuals in the same batch (*e.g.* 21 to more than 67 days in Batch 1) is perhaps to be accounted for on the assumption that the individuals in a batch differ considerably in age.

XIII. Means of Dispersal of *Melittobia*.

In the course of the season there may be two to five and even more generations of *Melittobia* so that, but for the cannibalism amongst the larvae and the poor means of distribution available for the species, this parasite would be a very serious menace to a very large number of species of bees and wasps.

Yet, as a matter of fact, in the Cambridge district I have only succeeded in finding one old clay wall of a few square yards in extent from which I have been able to get my supplies of material and even from this wall, after three or four years, there are still *Odynerus spinipes* emerging, although what used to be a very large and flourishing colony is now reduced to very small numbers.

Now the females can apparently only fly an inch or two at a time and, for the most part, they do not use their wings. I have never lost a specimen by letting her run about upon the laboratory table when I have wished to clean out her glass cell.

These females run about fairly rapidly and are active and it is quite easy to see how they might quickly overwhelm a colony of a host species once they reached it but it is the passage from one colony to another that is difficult to understand.

Walker mentions that the species occurs "on windows" and although I have not so far found it in such situations, this suggests to me a possible means of dispersal. I cannot imagine *Melittobia* deliberately walking into a house and then becoming positively heliotropic, but, when wandering about the haunts of solitary wasps and bees it may occasionally mount upon these, and thus be transported to other haunts whereby it would occasionally be bumped off against the window-pane.

XIV. Summary.

Melittobia is a chalcid, ectoparasitic upon a number of species of Hymenoptera and upon the pupae of certain flies. The insect was bred in the laboratory and the life-history is described in detail.

A number of experiments were made with regard to possible hosts and as to feeding and reproduction and certain points are of some interest.

For instance, the male apparently does not feed but the female uses her ovipositor with which she punctures the eggs, larvae or pupae of various insects, afterwards sucking the blood which oozes from the puncture. Such eggs, larvae or pupae, in spite of repeated punctures, may continue to develop.

Before beginning oviposition upon the surface of a suitable host, the female punctures the host one or more times with her ovipositor and apparently injects an anaesthetizing fluid, since insect larvae and pupae, upon which eggs have been laid, very rarely develop farther and yet remain fresh for a considerable time extending to many months.

With regard to reproduction, inbreeding appears to be normal, mating usually taking place between two individuals of the same brood and later between the female and one of her own offspring. Virgin females, unable to find a male, lay a few eggs, which always produce males, the first of which to emerge mates with the female.

The female is very prolific and may lay as many as twelve hundred eggs in two or three batches, mating taking place before each batch is laid. The last eggs of a batch are almost invariably male eggs, indicating that the female has exhausted her supply of spermatozoa.

A virgin female, whose eggs are removed so that she cannot rear a mate, may lay as many as ninety eggs during her life-time, her length of life being more than doubled, and such a female will survive through the winter, even withstanding frost, whereas fertilized females apparently all die in October or November at the latest.

All the eggs of a virgin female are apparently capable of developing and all such eggs produce males.

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EXPLANATION OF PLATE XXVI.

Fig. 1. ***Melittobia acasta*** ♂. Dorsal view. *sp.* =spiracle of first abdominal segment. *cx*3 = base of coxa of third pair of legs attached at posterior end of the pleural suture, the epimeron not being separated by a suture from the first abdominal segment. *a* and *b* = dorsal and ventral views of antenna.

Fig. 2. *Melittobia acasta* ♀. Dorsal view.

Fig. 3. Third stage larva—ventral view of head showing mouth (*m.*); head skeleton (*t.*); mandibles (*m.*), retracted within mouth but capable of being protruded, and salivary ducts (*sd.*) *Ant.* = antennae.

Fig. 4. Third stage larva; mandible (ventral view).

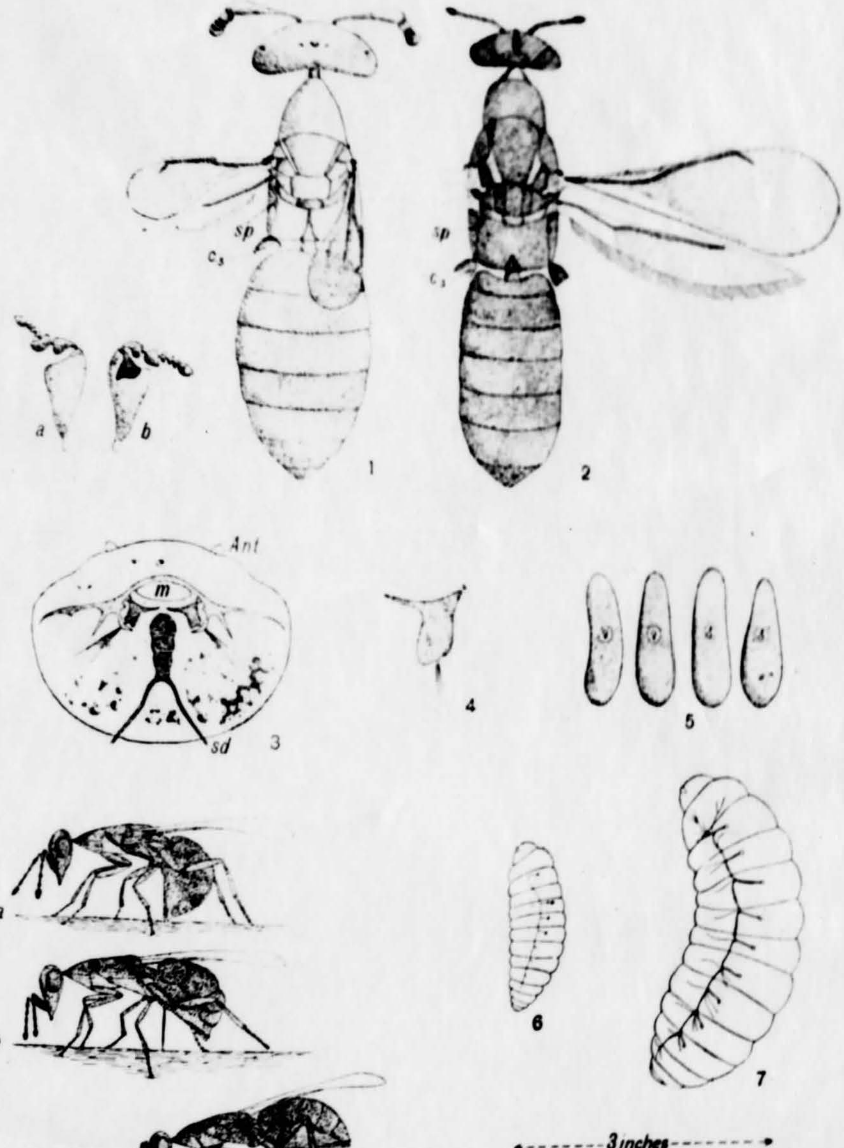
Fig. 5. Egg. Two eggs which produced females and two which produced males.

Fig. 6. First stage larva; lateral view.

Fig. 7. Second stage larva; lateral view.

Fig. 8. The female feeding upon its host. Diagrammatic figures made from sketches showing the insect placing the ovipositor in position, (*a*): drawing in the ovipositor, (*b*): licking the puncture (*c*).

Fig. 9. Glass cells used in breeding *Melittobia*. *C.* = plugs of cotton-wool. The tube is held down to a piece of cardboard by wires.



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