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Biology. — *Sex-ratio variability and the problems of reproduction among lac-insects.* By S. MAHDIHASSAN. (From the Zoological Institute, Giessen. Direktor Prof. W. J. SCHMIDT.) (Communicated by Prof. H. F. NIERSTRASZ).

(Communicated at the meeting of March 25, 1933).

From the standpoint of plant-pathology scale insects may be divided into two classes, with and without parthenogenesis. A typical coccid is imagined as unisexual where each individual born is able to reproduce its kind and the species therefore capable of multiplying twice as fast as when males were to be in equal numbers. In this case it is easy to assume the wind as a simple distributing agent. However where pathenogenesis does not occur, it has to be understood, that a male and a female larva are transported together or in some way come to lie near each other which would make the wind an improbable means of distribution. The second hypothesis is that two or more larvae are transported by a fly and that both sexes are represented; this is not difficult to grant if it is known that the sex-ratio approaches equality. The chances of sexual reproduction, however, would tend to be reduced as the sex-ratio would deviate from it. The third possibility is that the wind scatters the individual larvae wide apart, for the wind cannot do otherwise, but that the adult male seeks out the female through its sense of smell as is known in other insects. It is proposed to examine these fundamental questions with particular reference to the lac producing coccid, *Lakshadia communis*.

CARTER (1) was the first to make the suggestion that the lac insect, like

the aphid, may multiply parthenogenetically but the idea was entirely forgotten until I found a new form of the adult female lac cell, resembling a crown, which I believed to be a parthenogenetic insect (5). Later observations made me change this view (9). The verdict of E. SHRADER is further quoted in favour of sexual reproduction among coccids: „I have been unable to find any evidence that previous investigators have considered the possibility that parthenogenesis may occur... despite the fact that most entomologists concerned with coccidae have strongly suspected that parthenogenesis may play an important role in the reproduction of the group" (14).

In the literature on coccids the natural means of distribution is very casually touched or entirely omitted. The problem gains an extra importance where insects were presumed to be parthenogenetic but observations could not substantiate it. The following considerations exclude the wind as a distributing agency of the lac insect. Most coccids leave their dead skins attached to the twigs so that the old range of infection can also be ascertained. This is particularly easy with lac insects which form visible encrustations and the dead colonies may be collected and sold as stick-lac. In Bangalore *L. communis* thrives on some very common trees: *Ficus mysorensis* is a regular avenue tree; *Anona squamosa* yields edible fruits and is also very plentiful, encrustations of lac are thus easily noticed on it when fruits are gathered; *Guazuma tomentosa* is, likewise, a frequent avenue tree. When lac is collected from these trees and the localities plotted on a map no kind of order is found; infection is not found on two or three neighbouring trees but spontaneously on trees scattered far and wide. With wind as a distributing agency it was expected the trees infected would show the direction in which it usually blows during the season of larval swarming. Briefly, all observations point to prove that the young insects are transported by some kind of fly, a theory first applied to the biology of the lac insect by the French lac-expert, M. HAUTEFEUILLE (2).

When we are prepared to consider the possibility of a fly carrying two or more larvae we are confronted with the rare chances of the sexes being different. In Bangalore there are two life cycles of *L. communis*. The mother insects growing during the rainy season produce offspring in October but the larvae develop, one and all, into winged males. The non-monsoon generation consists normally of scattered crown shaped cells which deliver larvae in May; the progeny consists of about 11 females to 1 male which is always wingless. In the first case the problem is not how two larvae are carried but how the lac insect can ever multiply in the entire absence of females. The only conclusion is that the labile sex-complex changes into a bisexual nature and the early stages of the hermaphrodite have been already illustrated (9). The crown shaped cell is nothing else than the larva of the winged male transformed to display the functions of both the sexes. The fine cytological work of Mrs.

SCHRADER explains a similar case in another coccid (13). When the ratio is 11 females to 1 male there are likewise 5 chances of two larvae of the same sex being carried to only 1 of their being different. My observations show that the larvae are transported singly for crown shaped cells are found one on each twig; and very likely only one or two larvae from each swarm are thus carried to other trees.

The last possibility to be explained is that the sexes have been scattered wide apart but that the adult male has the power of seeking out its female. We have to estimate in this case the powers of flight on the part of the male and the average distance separating the sexes. The solution is very simplified by the consideration that when the males are winged there are no normal females anywhere and when the latter occur the male is wingless and has to cover 11 females in the same colony before it can seek others at a distance.

It is evident the importance attached to the problems of reproduction arise principally from sex-ratio determinations which in itself implies identification of the sexes in the earliest larval stage. It is sufficient to find the sex-ratio of the larvae as they swarm out of the mother cells; those which have died within, without seeing the light of the day, would never have been otherwise distributed. Likewise such colonies where deaths have occurred cannot give the necessary sex-ratio, for it has been actually found that mortality is relatively higher among the males.

Attempt to determine the sex of young lac and other scale insects was made by IMMS and CHATTERJEE without success (3). No less an authority on coccids than Šulc, likewise, mentions: „Erste Larvae. Sie weist keine ausseren Geschlechtsunterschiede aus" (15). Nevertheless a long paper, with 26 Figures differentiating the sexes in the first stage accompanied by two macrophotographs of young colonies has been already published where the sex ratios have also been determined (6). The larvae shortly before and after the first moult have been further illustrated (8); the first stage larvae of the female, the winged and wingless male are again figured in another communication (10). The ventral views of the male and female crawling larvae have also been illustrated (7). These communications are mentioned to remove all doubts regarding the probability of early sex-ratio determinations.

By brood lac is meant encrustation of lac with living insects about to deliver swarms of young ones and as such used for propagation. In Bangalore this is obtained only at the end of the monsoons; the pieces are invariably small as previously illustrated (12) and contain each a crown shaped cell which is dry, indicating it as the mother cell which gave rise to the offspring forming the chunk of lac. Now these insects growing during the rainy season give rise only to winged males as has been already mentioned. In the second larval stage they form long cells differentiating themselves from those of the female and the wingless male, all of which have been previously figured (11). Since the lac insects have been studied

by a number of famous scientists and no one has recorded an excess of males much less their exclusive preponderence Fig. 1, Pl. 1 is reproduced in its support. The specimen belongs to *L. communis* growing on *Butea frondosa,* Lingal, Hyderabad State, July 1919 and the picture shows the insects magnified about 2 diameters. It represents the top portion of a long, vertically growing twig, encrusted with cells of winged male lac insects. The encrustation, not the twig, shows a gradual thickening towards the top being the direction in which all insects have been facing. The settlement has been so thick that the anterior portions of the cells are hidden and only their posterior regions are visible. The male leaves its cell through the opercular opening, marked O with an arrow in white ink, this opening is covered before its exit by the opercular lid, marked L with an arrow in black ink, Fig. 1. This is mentioned to indicate the direction in which the cells have been fixed as is evident from the photograph. With the encrustation in hand it would be easy to convince the cells belong to winged males, the photograph, so far described, however, only shows that the cells, which are individually indistinct, belong to males. The larvae of winged males, however, as distinct from those of the wingless male and the female, show high phototropism ; they thirst, so to speak, for light and crowd themselves competing with one another for front seats. As we get towards the top we are nearing the source of light and crowding is proportionally heavier. The twig freed from the encrustation would naturally show the basal portion thicker than the top end. I must mention, upto now, I have not seen a better example of phototropism among lac insects than shown in Fig. 1, so that the larvae of winged males are thereby easily distinguished.

As larvae are abundant only during October and scarce during May it follows distribution from tree to tree occurs solely at the end of the rainy season. The mother insects which form the chunks of broodlac also give rise to excreta containing both glucose and fructose and on this honey thrive bacteria which form esters of butyric acid and attract flies feeding on slimy products ultimately enabling the young ones to be carried to other trees. The larva belonging to the winged male must, however, become bisexual for which it is necessary each to be singly distributed. On the same tree crowded along with other winged males this transformation never occurs. That the crown shaped cells are derived from the winged males is easily proved by the fact that during the other season, when both females and wingless males are found, the bisexual forms are never found either in the same colony or scattered singly. Briefly then, from October till May the generation is carried by the crownshaped cell while its contemporaries have all died as bachelors. The transformation is accompanied by an enlargement in its size, the crown shaped cell is almost twice the size of the normal female cell. The latter delivers as a rule some 700 larvae ; the former has been observed to give once 1435 females and 114 males, the counting was done in the second larval stage

PLATE I.

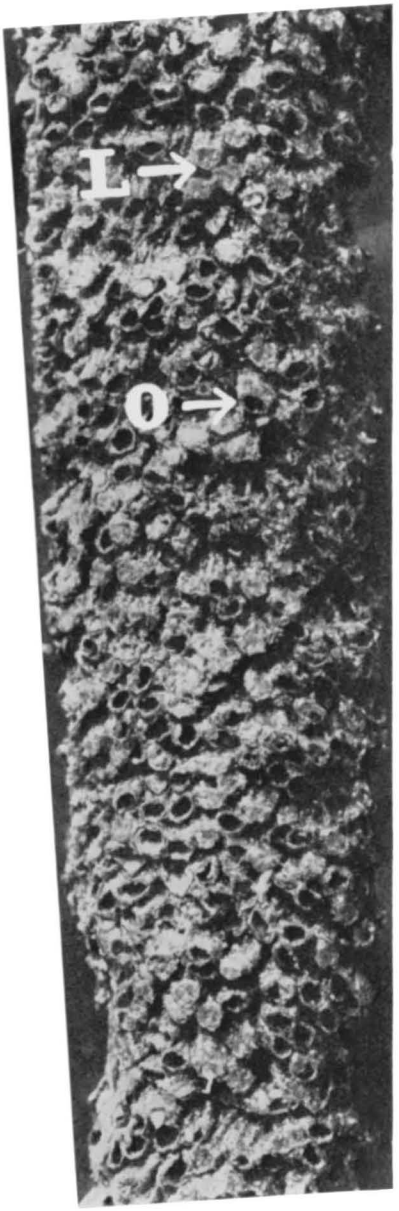

Fig. 1

Fig. 2

Fig. 3

where deaths had been noticed, hence the actual number of larvae born must have been higher. The crown shaped cell thus functions as more than two individuals. In order to bring 1500 larvae into the world the cooperation of at least two females and one male would be necessary besides the natural difficulty of transporting two or more different larvae at the same time.

Fig. 2, Pl. 1, shows a crownshaped mother cell, marked C, showing half the progeny, of some 1500 larvae in the second larval stage, on one side of the twig. It represents 10 : 9 natural size and was a vertical twig hanging downwards from a horizontal branch of *Nephelium Litchi*, Botanical Gardens, Bangalore, June 1923. The crownshaped cell was nearer the joint with a horizontal branch so that the larval settlement has occurred most at the other end of the twig. Light falling from above the end with the crown shaped cell had more share of it than its growing end and yet the larvae have settled in the direction away from light. The young lac insects exhibit geotropism so that on a vertical twig growing upwards its basal end, which is nearer the earth, would be the more thickly populated ; the fully developed encrustation would therefore show a gradual tapering shape thinning towards the top as illustated in Figs. 4 and 6 (9). A vertical twig growing downwards has its basal portion attached to a horizontal branch and away from the earth and larvae reacting to geotropism would now prefer the growing end of the twig ; the fully grown encrustation would appear club-shaped thickening as we proceed away from the base of the twig although this in itself is thinner at the growing end. Such an illustration would be reproduced in another communication on photo- and geotropism among lac insects. It interests us here to observe that apart from the fact that the crown shaped cell gives rise invariably to females and wingless males the picture reproduced in Fig. 2, Pl. 1, is characteristic of a generation where both the sexes are present. Fig. 1 was selected to show an extreme case of phototropism in order to distinguish, thereby, the winged males, Fig. 2 likewise represents, an extreme case of geotropism indicating the presence of both the sexes among the larvae. That females predominate in such a generation is not as yet evident from Fig. 2.

As already mentioned the total progeny arising from all the crown shaped cells is very small on account of the scarcity of the mother cells. These are really so scarce that during the eight years in Bangalore I could observe only a few cells where the larvae were swarming or had swarmed a month ago. They are however easily collected along with the encrustrations formed at the end of the monsoon season, when the former are empty. During 1923 the monsoons in Bangalore failed and the temperature went upto 103 F., a record for the previous thirty years. Under these circumstances chunks of brood lac obtained during November, for the delayed monsoons had lengthened the time of maturation, gave rise to abnormal sex ratios the following generation. As usual lac was infected on different trees and records kept. Many of them showed a mixed generation ; the

winged males predominated, while the wingless males and females were also present. In May 1924 brood lac of the non-monsoon season was obtained for the first time in Bangalore and the offsprings contained the same sex ratio as delivered by the crown shaped cells. Mother-insects growing during the dry season, normal or otherwise, give progeny with the same sex ratio. Fig. 3, Pl. 1, is specially reproduced for it shows hardly any dead larvae in the colony, as the reader can verify for himself. Five cells of wingless males are numbered, N$^{os.}$ 1 and 5 in white and the rest in black ink; all the rest belong to the female. A portion of the colony with the male larval cell, N^{o}. 3, is further enlarged in Fig. 4, Pl. 2. The male in the second larval stage is distinctly larger than the female of the same age, contrary to the finding of IMMS and CHATTERJEE. The female cell which has just moulted for the second time with its moulted skin marked s., is seen in the female cell marked III; most female cells are in the early third stage. A couple of cells are still in the second stage, one of which is marked II. The picture has been retouched to bring out the outline of the cells.

In Fig. 3, Pl. 1, it would be noticed that all the male cells point in one direction. The insects had settled all around an upwards growing twig, of *Guazuma tomentosa* yet the male larvae do not show eagerness to press forwards and to acquire illuminated seats. It must be remarked, however, they, one and all, point in the direction of light. The numerous female cells on the contrary show two directions of settlement, some facing the source of light while others the very reverse. Only female larvae show this poverty of phototropism. Fortunately this phenomenon has been unwittingly illustrated by IMMS and CHATTERJEE in their Fig. 3, Pl. 2, where 8 female cells are figured, 5 facing one direction and 3 the very contrary. This is said to suggest that when larval settlement shows the cells to have fixed themselves in different directions it is a rough indication of females predominating. Although Fig. 4, Pl. 2, represents only a small number of cells still it also bears out this phenomenon which is better seen in Fig. 3, Pl. 1. It is thus clear that the generation issuing from mothers growing during the non-monsoon season contains some 11 females to 1 male as Fig. 2 would verify and this contrasts itself with Fig. 1 where all are males.

CARTER, of all previous writers, alone gives a sex-ratio finding. The generation issuing at the end of the monsoons has an equal number of males and they are all winged. The other generation has two females to one male which here is wingless. He was thus the first to establish an alternation of generation among males towards which WEBER rightly draws the attention of his reader, saying, that the lac insect, "zeigt sogar einen mit Flügelpolymorphismus verbundenen Generationswechsel. In der ersten Generation dieser Lackschildlaus gibt es nach IMMS und CHATTERJEE geflügelte und ungeflügelte Männchen, die zweite Generation hat nur ungeflügelte. Dieser regelmässige Wechsel erinnert etwas an die bei den Aphidenen vorliegenden Verhältnisse, wenn wir auch nicht sicher sagen

PLATE II.

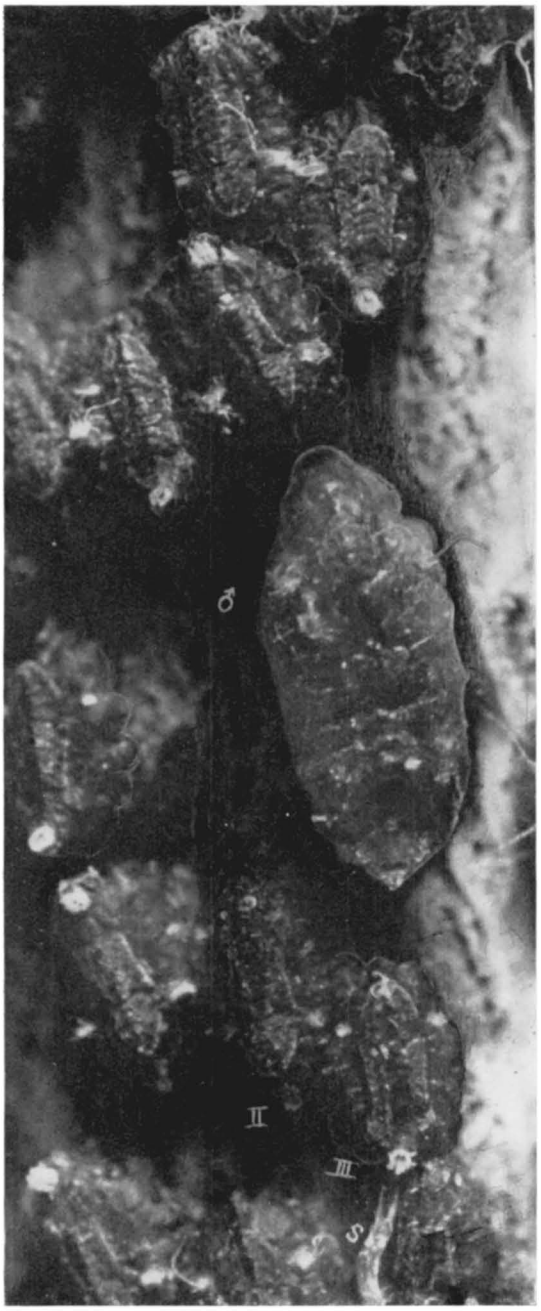

Fig 4

können ob diese Ähnlichkeit nicht nur oberflächlich ist, ob die Flügelreduktion bei den Cocciden nicht in Wirklichkeit nach den bei den pterygopolymorphen Wanzen gültigen Regeln eintritt" (16). Where females occur wingless males occur; CARTER casually mentions this fact and its confirmation has been the particular contribution of IMMS and CHATTERJEE. How the sex ratios depend on the weather was not observed before. Upto now the two life-cycles have been called the winter and the summer crops. To show the great influence of moisture on the life of the lac insects I have introduced the terms monsoon and non-monsoon crops. Similarly the existence of crown shaped cells, the occurrence of pure colonies of winged males, as well as the great preponderance of females at the other season, 11 or more females to 1 male, has been overlooked.

The important fact to be borne is the influence of water on sex ratios of lac insects. The generation containing 11 females to 1 male may be imagined as not conducive for sexual reproduction. It may be supposed that one male is not enough for all the 11 females to be fertilised. But among their progeny year after year no other result has been obtained than pure colonies of winged males; at least some females could be imagined as being fertilised so that the coming generation ought to be mixed. The usual ratio between the sexes under drought conditions of 1923 gave a mixed generation the following season. The importance of the climatic factors as different from that of sex-ratio is thereby very apparent.

The supply of water increases the growth of mother insects, the size is greater, the number of larvae born is higher, also mortality is less; but inspite of all these favourable conditions the next generation is predisposed to be males. Among aphids the reverse is known, viz. conditions of plant growth are helpful for the female sex determination. Among lac insects it has been definitely established that conditions of growth and female sex determination are opposite to each other.

In 1919, I published a paper on the cultivation of lac from a physiological standpoint (4) giving results of observations concentrated mainly on the plants infected by the lac insects. No account could then be taken either of the different species of lac insects or of sex ratio variability. Yet the conclusion was arrived at that the lac parasite plays a very passive role in the attack; the trees have first to prepare slimy products and then invite the insect to suck out the undesirable byproducts. Here the same conclusion is independantly arrived at: the tree in vigourous growth with good supply of water is so able to change the sex ratio of the lac insects that not one female is left for the species to continue upon it in the future. A better illustration of the passivity of the parasite cannot be imagined. Such sudden disappearances of other scale insects are also known and attributed to the weather, or in the words of MITCHEL to, "a mysterious something, an occult quality of the atmosphere". It is proposed to show elsewhere how these insect epidemics may sometimes be

explained by sex-ratio variability in favour of the female and their spontaneous natural regulation by a preponderance of males.

Grateful acknowledgement is made of the kind interest of Dr. h. c. NAVAB SIR HYDER NAVAZ JUNG, Kt., L. L. D., Finance Minister, Hyderabad State, but for whose encouragement the work could never have been carried to the present stage.

EXPLANATION OF THE FIGURES.

Pl. 1, Fig. 1. Colonies of cells formed solely by the larvae of winged males. The encrustation is gradually thickening towards the top indicating more intense colonisation due to phototropism.

Fig. 2. A hermaphrodite crownshaped cell, C., with its offspring consisting of both sexes; half the population lies on the other side of the twig and is hidden from view.

Fig. 3. Mother insects growing during the non-rainy season give rise to more females than males, the latter being wingless. Male cells are numbered and face one direction. The remainder are females which have settled in mixed directions.

Pl. 2, Fig. 4. A portion of Fig. 3 enlarged with the wingless male cell N^0. 3 which has not yet moulted for the second time. The female cells are mostly in early 3rd larval stage e.g. the cell marked III and the second moult skin, S.; Cell II has not yet moulted for the second time.

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Anatomy. — *Ueber die basale Opticuswurzel und die caudalen Verbindungen der Commissura transversa Gudden der Vögel.* Von EUGEN FREY (Zürich). (Communicated by Prof. C. U. ARIËNS KAPPERS.)

(Communicated at the meeting of March 25, 1933).

Für diese Untersuchung wurden die folgenden Präparate des Niederländischen Zentralinstituts für Hirnforschung in Amsterdam benutzt: Markscheidenserien von Passer domesticus, Melopsittacus undulatus, Columbia domestica, Cacatua roseicapilla, und andere. Vereinzelt wurden auch einige nach Nissl, Heidenhain oder Cox gefärbte Serien untersucht. Ausser den Transversalserien wurden auch in einigen Fällen Sagital- und Horizontalschnittserien verwendet.

Ein Frontalschnitt durch den Thalamus eines Melopsittacusgehirns, etwas frontal von der Commissura anterior, gibt ein sehr übersichtliches Bild aller Decussationssysteme an der Basis des Thalamus. Ganz dorsal ist die Commissura supra-optica dorsalis (Commissura Meynert), die ein ziemlich mächtiges Bündel von relativ dicken Fasern darstellt, zu sehen. Da sie eine ausgesprochene caudo-dorsale Richtung einnimmt, ist nur ein relativ kurzer Abschnitt derselben am Frontalschnitt zu sehen. Unmittelbar ventral von der Commissura Meynert liegt ein viel schmaleres Bündel feiner schwach myelinisierter Fasern, das nicht so stark caudalwärts strebt und deswegen am Schnitt ein länglicheres Gebilde als die Commissura supra-optica dorsalis darstellt. Ventral von der Commissura transversa, nach einem deutlichen Zwischenraum, tritt die mächtige Kreuzung der Optici hervor.

Die Betrachtung der weiteren Schnitte caudalwärts zeigt, dass die Entfernung zwischen der Commissura transversa und dem Chiasma noch deutlicher wird. Am Schnitt durch die Ebene der Commissura anterior ist die Commissura Meynert bereits aus der Mitte verschwunden und ist beiderseits in der mittleren Höhe des Thalamus, sich fächerförmig ausbreitend und in der Richtung des Tractus thalamo-frontalis und des Tractus occipito-mesencephalicus strebend und gleichzeitig aufsplitternd, zu sehen. Die Commissura transversa behält ihre zentrale Lage bei deutlicher Entfernung