

Parasitism in an outbreak of the coconut moth (*Artona catoxantha* (Hamps.)) in Java (Lep.)

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Much information on the ecology of the coconut moth in Java has been collected since the late Dr S. LEEFMANS (1928) laid the foundations of our knowledge of this pest during his career as agricultural entomologist in Indonesia. From a practical point of view it was of particular importance to study conditions under which outbreaks of this pest are likely to develop, and for this purpose population studies were made during a number of years on a coconut estate in Central Java (VAN DER VECHT, 1950 a).

It proved much more difficult to investigate the factors responsible for the termination of outbreaks, for in most outbreaks reported since 1928 the pest was controlled by mechanical or chemical methods. Some smaller outbreaks where control was unnecessary were either reported too late or they were too far away from the main laboratory at Bogor. When in December 1939 an outbreak was discovered in a coconut area of minor economic importance in the neighbourhood of Djakarta, only 30 miles from Bogor, this was a welcome opportunity to make a detailed study of the influence of parasites, hyperparasites and possible other factors. As it was very unlikely that the outbreak would assume serious proportions, the owners of the trees agreed to abstain from application of control measures.

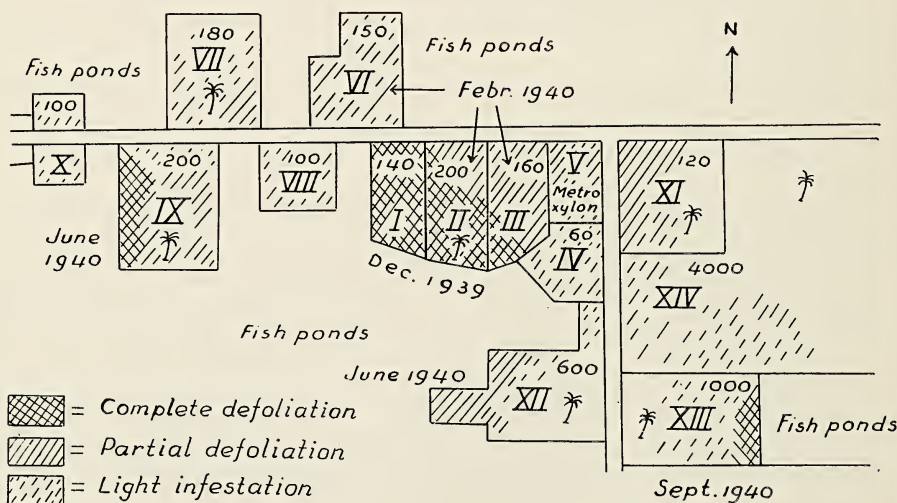


Fig. 1. Sketch of an area near Djakarta, where an outbreak of *Artona catoxantha* occurred in 1939—1940. Scale 1 : 10,000.

I—XIV = coconut groves, numbered in order of attack by *Artona*.

100, 120, etc. = numbers of coconut trees in each grove.

Dec. 1939, Febr. 1940, etc. = time of maximum damage.

The area in which the outbreak had developed is shown in fig. 1. It consisted of irregular groups of a few hundreds to some thousands of coconut trees separated by fish ponds and marshy areas with *Metroxylon*-vegetation. In the groves I—III some hundreds of trees had been seriously damaged (all leaves brown to dry) in the second half of the month of December.

From 28 December 1939 samples of infested leaves were collected each week at various places. The material was studied in the laboratory at Bogor and daily records were kept of the development of the stages of *Artona* and of the primary and secondary parasites. The most important parasites occurring in this area were *Neoplectrus bicarinatus* Ferr. (Hym., Eulophidae), *Apanteles artonae* Rohw. (Hym., Braconidae), and the two Tachinids *Ptychomyia remota* Aldr. and *Cadurcia leefmansii* Bar. Notes on the bionomics of these species in Java have been given in an earlier paper (VAN DER VECHT, 1950 b).

Until the end of May 1940 the samples were collected in the groves I—IV, where the insect still occurred in considerable numbers in January and February. In these months the surrounding plots received only a light infestation from the outbreak centre, but in the following months, a few secondary outbreaks developed here, leading to complete defoliation of some small groups of trees in June and

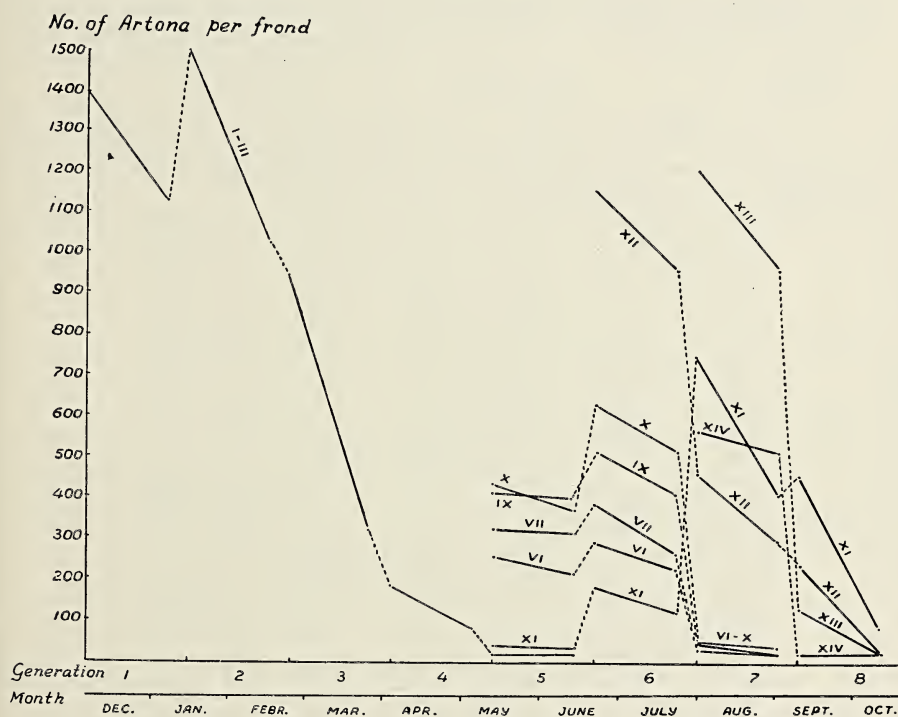


Fig. 2. Graph showing the estimated population density of *Artona* in different groves during the period December 1939–October 1940. The periods of the moth flights are indicated by broken lines; the beginning of each solid line represents the number of eggs, the end presents the number of unparasitized pupae. The degree of sloping of the solid lines indicates the extent to which the population density was reduced by parasites.

July. From the beginning of June samples were also collected in groves VI—IX, and in July also in grove XII. Not until September was it discovered that another small secondary outbreak had developed in grove XIII. The further spread of these secondary infestations was negligible and in October 1940 repeated investigations did not reveal the presence of living *Artona* anywhere in the area.

Population density. As is normally the case in *Artona*-outbreaks, the successive generations of *Artona* were sharply separated (compare VAN DER VECHT, 1950 a). Moth flights occurred once per 5—6 weeks and lasted for about two weeks. Data on the population density had to be restricted to the periods when no moths were present (3—4 figures for each generation); they are summarized in fig. 2.

During the development of each generation the density decreased to a varying degree, dependent on the activity of the parasites and on the mortality due to other causes. The influence of the parasites is indicated by the degree of sloping of the drawn lines, but the other causes of mortality could not be analyzed sufficiently to be expressed in the figure.

The graph shows a strong decline of the density in groves I—III during the period January—March; this is partly caused by migration of the moths, partly

Table 1. Distribution of *Artona* stages, observed at weekly intervals during 5 successive generations, expressed in % of total numbers of specimens of each generation.

Collection		Egg	Larval stages					Full cocoon		Moths ¹⁾
Date	No.		I	II	III	IV	V	(0—5 days)	(6—10 days)	
28 Dec. '39	1	—	—	—	18	27	12	42	1	—
4 Jan. '40	2	—	—	—	—	10	8	36	26	—
11 „	3	10	—	—	—	—	1	13	48	38
18 „	4	80	7	—	—	—	—	—	3	97
25 „	5	+ ²⁾	3	15	34	39	9	—	—	—
31 „	6	—	—	1	13	30	32	24	—	—
8 Feb.	7	—	—	—	1	6	4	57	27	4
15 „	8	5	—	—	+	+	+	14	35	51
22 „	9	63	17	—	—	—	+	1	8	91
29 „	10	—	18	35	33	14	—	—	—	—
7 March	11	—	—	—	18	42	33	7	—	—
14 „	12	—	—	—	2	16	17	65	—	—
21 „	13	—	—	—	—	+	1	19	67	13
28 „	14	52	—	—	—	—	+	3	25	72
4 April	15	29	42	18	5	—	—	—	2	98
11 „	16	—	—	—	19	44	37	—	—	—
18 „	17	—	—	—	14	42	27	17	—	—
25 „	18	—	—	—	—	8	10	67	15	—
2 May	19	—	—	—	—	—	+	7	49	44
9 „	20	±60	+	—	—	—	+	1	7	92
16 „	21	3	30	42	25	—	—	—	+	—
23 „	22	—	—	2	25	66	7	—	—	—
30 „	23	—	—	—	7	59	31	3	—	—
6 June	24	—	—	—	—	16	34	43	7	—

¹⁾ These figures indicate only the percentage of moths of a certain generation that had emerged at the time of collecting; how many of these were alive at that moment could not be ascertained.

²⁾ + = one or a few specimens, less than 1% of total population.

by increasing parasitization. When samples were taken in groves VI—X, there were about 200—400 *Artona* stages per leaf and these were scarcely parasitized. After a slight increase in the sixth generation, however, the infestation disappeared in the seventh generation. In the groves XII and XIII the pest disappeared in the 8th generation. The infestation in XIV emanated from the secondary outbreak in XIII.

Composition of the population. — Data on this subject are brought together in table 1. For each set of samples the figures indicate by which percentage of the total population the successive stages of the insect were represented. The figures for each stage include also the parasitized specimens present on the leaves when the samples were taken. For pupae of *Neoplectrus*, cocoons of *Apanteles* and puparia of the Tachinids the age of the parasitized host larva could be determined approximately from the dates of emergence and the known average duration of development of each of these parasites.

The table shows, that the difference in age between the youngest and oldest specimens of one generation is about 16 days¹). A measure for the degree of discontinuity of the population may be obtained by expressing the numbers of individuals of two predominant stages (representing a group in which the age differs at most 8—9 days) in percentages of the total numbers present. The figures thus obtained are given in table 2; they show a distinctly increasing discontinuity in the successive generations.

Table 2. Degree of discontinuity in five successive generations of *Artona*.

Generation	Predominant stages	Percentage of total population	Do. per generation
1	larvae V + young cocoons	54	} 59
	„ „	64	
2	larvae III + IV	73	} 67
	„ IV + V	62	
3	larvae II + III	68	} 75
	„ IV + V	75	
	„ V + young cocoons	82	
4	eggs + larvae I	71	} 74
	larvae III + IV	81	
	„ IV + V	69	
	„ V + young cocoons	77	
5	larvae I + II	72	} 82
	„ III + IV	91	
	„ IV + V	90	
	„ V + young cocoons	77	

Duration of the generations. — By comparison of the corresponding stages of development of the successive generations, a fairly accurate determination

¹) Duration of egg stage = 5 days; do. of larval stages each $3\frac{1}{2}$ —4 days; cocoon = 10—11 days.

of the duration of each generation is possible. If we take, for instance, as a criterion the day on which 50% of the larvae have spun a cocoon, we find the following comparable dates for the successive apparent generations: 30 Dec., 4 Febr., 12 March, 23 April and 6 June. The intervals are resp. 36, 37, 42 and 44 days and demonstrate a gradual lengthening of the duration of development per generation. For further discussion of this phenomenon see p. 131.

Egg production and sex ratio of *Artona*. — Since *Artona* does not readily oviposit under laboratory conditions, no detailed study of possible changes in the reproductive capacity of the insect could be made. Comparison of the observed numbers of healthy pupae with the numbers of eggs of each following generation appears to indicate, however, that there was a marked decrease in the reproductive capacity of the moths, particularly in the later phases of both the primary and the secondary outbreaks.

Reduction of the population density was found to be accompanied by changes in the sex ratio. In the original outbreak area the percentage of females decreased from 50 in the first observed generation to 44 in the second and 37 in the third (numbers of specimens examined: 4011, 2358 and 1156, respectively). In the secondary outbreaks the percentage of females varied somewhat irregularly from 34—47, but the mean of all observations in the 5th—7th generations was only 40 (specimens examined: 6489).

Neoplectrus bicarinatus Ferr. — This parasite attacks the *Artona*-larvae in the second instar and develops in 9—12 days; the wasps thus emerge at a time when the non-parasitized larvae of the same age are in the fourth or fifth instar. When *Neoplectrus* is attacked by the *Pleurotropis*, the adults of this secondary parasite emerge a few days after normal emergence of *Neoplectrus*.

Table 3. Relationship between *Artona*, the parasite *Neoplectrus* and the secondary parasite *Pleurotropis* during 5 successive generations of *Artona*.

Predominant stage of host at time of collecting	1 st generation			2 nd generation			3 rd generation			4 th generation			5 th generation		
	Larvae II—IV	% <i>Neopl.</i>	% sec. par.	Larvae II—IV	% <i>Neopl.</i>	% sec. par.	Larvae II—IV	% <i>Neopl.</i>	% sec. par.	Larvae II—IV	% <i>Neopl.</i>	% sec. par.	Larvae II—IV	% <i>Neopl.</i>	% sec. par.
Larvae I	—	—	—	—	—	—	—	—	—	142	35	0	—	—	—
„ II-III	—	—	—	1794	0.2	0	665	11	48	580	21	29	163	3	0
„ IV-V	415	4	67	923	5	66	743	34	49	480	32	79	379	6	43
Pupae 2-4 days	311	0.3	0	191	28	89	444	24	70	109	29	78	8	(12)	0
Pupae 8-10 days	12	0	—	16	31	100	16	19	33	3	0	—	—	—	—
Moths and eggs	12	0	—	1	0	—	2	0	—	1	0	—	—	—	—
Totals	750	2%	62%	2925	4%	77%	1870	23%	54%	1315	27%	51%	550	5%	34%

The data on the parasitism by *Neoplectrus* in the groves I—IV are summarized in table 3. For each of the five observed generations this table shows the *Artona*-stages predominant at the time of collecting, the number of larvae which were examined, the percentage of these which were attacked by *Neoplectrus*, and the

extent to which the latter were parasitized by *Pleurotropis*. To determine the percentage of *Artona*-larvae parasitized by *Neoplectrus*, only the larvae which were in the second, third and fourth instars at the time of collecting have been taken into account. The exclusion of the older larvae tends to render the percentages too high, but on the other hand the totals include a certain number of second instar larvae which would have been parasitized if they had not been collected. We may assume, therefore, that the figures give a fairly reliable impression of the importance of this parasite.

In the first observed generation *Neoplectrus* was of little importance, the parasitism then being only 2%. In the following three generations the parasitism was rather irregular, as a rule starting at a low level when the host generation was still young and reaching a maximum of about 30% as the generation progressed. In the fifth generation the conditions were apparently less favourable for *Neoplectrus*; very probably both the greater scarcity of the host and the more pronounced discontinuity of the population have been detrimental to the parasite.

When old pupae or moths were the predominant stages of the host, only a small percentage of the few suitable host larvae then present were attacked by *Neoplectrus* (altogether 8 out of 63 larvae). In *Neoplectrus* the capacity to discover its host when the latter is present in very small numbers only, is distinctly less pronounced than in *Apanteles* (see below, p. 128).

The secondary parasite, *Pleurotropis detrimentosus* Gah., was already active during the first observed generation (10 out of the 16 collected *Neoplectrus* specimens were attacked by it). In the second and following generations *Pleurotropis* restricted the growth of the *Neoplectrus* population very seriously. In the third and fourth generations the secondary parasitism was already 48 and 29% respectively when second and third instar larvae were the predominant stages of *Artona*; as the *Artona* generation progressed, the percentage of parasitized *Neoplectrus* increased rapidly to 70 or more. When the percentages, observed during an *Artona* generation, are compared with the total for that generation, it appears that the most reliable impression of the importance of the secondary parasite can be obtained by collecting material at the time when the fourth larval instar of *Artona* is the predominant stage. Earlier observations give a too low figure, at a later date the influence of the secondary parasite may be overestimated.

It seems remarkable that *Neoplectrus*, although seriously attacked by secondary parasites, is nevertheless able to exert an important degree of control in a discontinuous host population. The main factor appears to be the very short life cycle of the parasite, which is only 9—11 days when second instar *Artona* larvae are attacked. Since suitable host larvae are generally available during a longer period, the parasite may pass through two generations (perhaps sometimes even three) in one of the generations of the host. In the samples, collected at Djakarta, larvae and pupae of *Artona* were usually present during three or four successive weeks, illustrating that the development of a second generation of *Neoplectrus* was of common occurrence in this outbreak.

Apanteles artonae Rohw. — This parasite usually oviposits in the host in the second instar. The life cycle is about two weeks. A comparison of the observed *Apanteles* population with the numbers of *Artona* larvae of the second, third and

fourth instar, present at the time of collecting, gives again a reasonable picture of the degree of control exerted by the parasite.

A compilation of the available data on the parasitism by *Apanteles* meets with certain difficulties. When an *Apanteles* cocoon is attacked by a secondary parasite, a few weeks may elapse before the progeny of the latter emerges from the cocoon. Such cocoons will therefore have a much greater chance to be recorded as "full" than the unparasitized ones. If they are included in the counts, the importance of the secondary parasites would be strongly overestimated. In order to avoid this error and to obtain a reliable basis for comparison between healthy and parasitized *Apanteles* cocoons, we have not counted the *Apanteles* cocoons from which secondary parasites emerged within 12 days after the date of collecting.

Table 4. Relationship between *Artona*, the parasite *Apanteles*, and the secondary parasites which attack *Apanteles*, during five successive generations of *Artona*.

Predominant stage of host at time of collecting	1 st generation			2 nd generation			3 rd generation			4 th generation			5 th generation		
	Larvae II-IV	% <i>Apanteles</i>	% sec. par.	Larvae II-IV	% <i>Apanteles</i>	% sec. par.	Larvae II-IV	% <i>Apanteles</i>	% sec. par.	Larvae II-IV	% <i>Apanteles</i>	% sec. par.	Larvae II-IV	% <i>Apanteles</i>	% sec. par.
Larvae I	—	—	—	—	—	—	—	—	—	142	6	(0)	—	—	—
" II-III	—	—	—	1794	3	24	665	3	0	580	3	0	163	6	(0)
" IV-V	415	1	(0)	923	2	40	743	3	40	480	0	—	379	1	(50)
Pupae 2-4 days	311	4	8	191	6	0	444	0.2	(100)	109	0	—	8	0.5	(0)
Pupae 8-10 days	12	100	50	16	69	82	16	81	31	3	(100)	(0)	—	—	—
Moths and eggs	12	100	58	1	(100)	(100)	2	(100)	(0)	1	(100)	(0)	—	—	—
Totals	750	5	35	2925	3	31	1870	3	24	1315	2	0	550	2	8

() indicate percentages of *Apanteles* and secondary parasites which are based on examination of less than 10 *Artona* larvae or *Apanteles* cocoons.

The data of table 4 show that the total parasitism by *Apanteles* was only 5% in the first observed generation and even less during the following months. An interesting fact is that the *Apanteles* population was never able to increase considerably. Even when host larvae in the suitable stage for attack by the parasite were abundant, the parasitism did not rise above 5%. Partly this may be due to the activities of the secondary parasites which attacked altogether about 25% of the larvae or pupae in the cocoons and showed a tendency to become more numerous as the *Artona* generation progressed.

When we compare the weekly records of the occurrence of *Apanteles* with those of *Neoplectrus*, a striking difference may be observed. The latter was almost absent in collections made at a time when old pupae or moths were the predominant stages of the host, but *Apanteles* was obtained from almost every suitable host larva collected in such a period (altogether 55 *Apanteles* from 63 *Artona* larvae). This demonstrates its extraordinary capacity to discover the host when present in small numbers only.

The control of the host, exerted by *Apanteles* under the conditions of this

outbreak, was of little importance. The parasite was perhaps of greater significance because of its influence on the composition of the host population. *Apan-teles* eliminates a high percentage of the individuals which deviate in age from the majority of which the population is composed. Although present in small numbers only, this parasite yet plays an important role: it maintains or stimulates the discontinuity of the host population and thus hampers its own development as well as that of the other parasites.

The Tachinids. — The data on the occurrence of the Tachinids are summarized in table 5. They illustrate a rapid increase of the parasitism by these flies from 2% in the first to 55% in the third generation. In the fourth generation, when the host was much less numerous than in the third, the percentage decreased to 34, and in the fifth the Tachinids were no longer important.

Table 5. The importance of the Tachinids in groves I—IV.

Observed generation	Number of <i>Artona</i> cocoons examined	Prepupa or pupa died, cause unknown	Moths	<i>Cadurcia</i>	<i>Ptychomyia</i>	Total Tachinids
1	4636	518 = 11%	4014 = 87%	84	20	104 = 2%
2	3557	357 = 10%	2358 = 66%	422	420	842 = 24%
3	5299	528 = 10%	1835 = 35%	1235	1701	2936 = 55%
4	2168	276 = 13%	1155 = 53%	209	528	735 = 34%
5	101	16 = 16%	81 = 80%	2	2	4 = 4%

These figures are in agreement with the repeatedly made observation, that the "searching ability" of the Tachinids with regard to *Artona* is not very well developed. These flies do not exert an important degree of control unless the host is very numerous.

Secondary parasites of the Tachinids were of very little importance in this outbreak, the secondary parasitism being never higher than 2%.

In order to study the influence of the Tachinids with relation to the degree of development of the *Artona*-population, the available figures have again been arranged according to the predominant stage of the host at the time of collecting (table 6).

Table 6. Relation between the age of an *Artona* generation and the degree of parasitism by the Tachinids (4 generations).

Predominant stage of host at time of collecting	Percentages of <i>Artona</i> cocoons containing Tachinid puparia				
	Gen. 1	Gen. 2	Gen. 3	Gen. 4	Average
Larvae IV and V	3%	23%	3%	58%	39%
Cocoons 2-4 days old	1%	28%	7%	31%	32%
Cocoons 8-10 days old	3%	12%	2%	35%	25%
Moths and eggs	11%	7%	0%	22%	20%

The table indicates that the parasitism decreased slowly as the host population grew older. The first specimens to reach the suitable stage for infection by the

flies were as a rule more heavily parasitized than the younger larvae. This circumstance tended to alter the composition of the population and to prolong the duration of its development as a whole. Sometimes (gen. 1) the youngest specimens of a generation (the last to reach the susceptible stage) were more strongly parasitized than their immediate predecessors; this happened when the first flies emerged early enough to attack these stragglers.

Regarding the relative abundance of the two species of Tachinids the following conclusions may be drawn (table 5). During the first observed generation *Cadurcia* was more numerous than *Ptychomyia*. The latter, however, increased more rapidly in numbers and in the fourth generation it made up more than 70% of all the Tachinids collected.

In the secondary outbreaks in the groves VI—XIII, where material was collected during the 5th—7th generations of the pest, *Cadurcia* was without exception more numerous than *Ptychomyia* (groves VI—XI: 757 *Cad.*: 288 *Pt.* = 2.6 : 1; groves XII—XIII: 490 *Cad.*: 202 *Pt.* = 2.4 : 1). This could either indicate that *Cadurcia* spreads more rapidly than *Ptychomyia*, or that it normally occurs in greater number in places where *Artana* is scarce or absent.

Collective influence of the parasites. — Besides the parasites discussed above some other Hymenoptera attacked *Artana* in this outbreak, viz. *Eurytoma*, *Brachymeria* and a few *Goryphus* species. These were always so rare that their influence on the host population was negligible.

As *Neoplectrus* and *Apanteles* attack the host in the same stage, the percentages of larvae killed by them may be added; the Tachinids can only attack the remaining larvae and therefore the total percent. of parasitism (P) must be calculated as:

$$P = A + N + (T \times \frac{(100 - A - N)}{100}),$$

in which A = percent. *Apanteles*, N = percent. *Neoplectrus* and T = percent. Tachinids.

Table 7. Collective influence of the parasites in 5 successive *Artana* generations.

Observed generation	Average no. of <i>Artana</i> stages per leaf	Parasitized by <i>Neoplectrus</i>	Parasitized by <i>Apanteles</i>	Remainder per 100 <i>Artana</i> larvae	Parasitized by Tachinids	Remainder per 100 <i>Artana</i> larvae	Total % killed by parasites
1	1400	2%	5%	93	2% = 2	91	9%
2	1500	4%	3%	93	24% = 22	71	29%
3	950	23%	3%	74	55% = 41	33	67%
4	190	27%	2%	71	34% = 24	47	53%
5	8	5%	2%	93	4% = 4	89	11%

The figures thus obtained for the five observed generations are summarized in table 7. They show an increase in parasitism up to a maximum of 67% in the third generation; in the two following generations the percentages were 53 and 11, respectively. The decrease in parasitism after the third generation is certainly due to the greater scarcity of the host and perhaps also to the more pronounced discontinuity of its population.

Discussion. — In recent studies on insect outbreaks it has been observed that in the final phase the decrease in numbers of the insect was accompanied by a reduction in reproductive rate (WELLENSTEIN, 1942). Among the symptoms of a declining physiological condition in the nun moth, observed near the end of an outbreak, H. MORS (in WELLENSTEIN, l.c.) mentioned the slower rate of development of the larvae, increased larval mortality, lowered egg production, shortened life of adults, and reduced percentage of females.

Very little is known concerning the occurrence of such symptoms in insect outbreaks in the tropics. Changes in the sex ratio of *Helopeltis theivora* Waterh., the notorious tea pest, were reported long ago to be associated with fluctuations in population density, the percentage of females being lower as the insect was scarcer and "the conditions more adverse" (MANN, 1907). Other insects have rarely been studied in this respect.

The present study shows that it would be desirable to pay more attention to this aspect in future investigations, for although the available data are far from complete, there are some distinct indications of a reduced vigor of the *Artona* population in the final phase of the outbreak. The gradually increasing duration of the successive generations (36, 37, 42 and 44 days) is an indication of a reduced rate of development. Such differences could also result from irregularities in parasitism (elimination of older specimens of a host population), but since the longest duration was observed when the parasitism was already on the decline, this is hardly a plausible explanation. The decreases or relatively slight increases in population density after each moth flight (see fig. 2) point to a low egg production. Finally, there was a distinct reduction in the percentage of females as the outbreak progressed.

Since our observations point to a reduction in the physiological condition of the *Artona* population in the final phase of the outbreak, it would be incorrect to ascribe the decline of the population density exclusively to the influence of parasites. It should be kept in mind that the percentage of parasitism is favourably influenced by a slackening of the rate of reproduction of the host.

In the present outbreak the tendency of the infestation to spread from the first defoliated centre towards the surrounding plantations was much less pronounced than in the majority of outbreaks observed in Central Java. This may be due to differences in the size and the location of the coconut groves and in parasitism, but the possible existence of differences in the reproductive capacity of the insect should not be overlooked.

Summary. — The relationship between the populations of the coconut moth *Artona catoxantha* (Hamps.) and of some of its primary and secondary parasites was studied during an outbreak of this pest near Djakarta, West Java. In the coconut groves first attacked the pest disappeared within a few generations; in the following months a few secondary outbreaks developed in neighbouring plantations, but none of these reached serious proportions.

The decrease in the *Artona* population was accompanied by increasing parasitism by *Neoplectrus bicarinatus* Ferr. and the Tachinids *Ptychomyia remota* Aldr. and *Cadurcia leefmansii* Bar. The larval parasite *Apanteles artonae* Rohw. was unable to increase in numbers under the existing conditions (sharply separated generations

of the host and serious influence of secondary parasites). The maximum total parasitism (67%) was observed one generation after the host reached maximum density.

The available data point to the possibility that the termination of the outbreak must at least partly be ascribed to a decline in the physiological condition of the *Artona* population.

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Het rapport bevat een vrij groot aantal afbeeldingen en verschillende grafieken en is op een onderhoudende wijze geschreven. — LPK.

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