SYSTEMATICS BIONOMICS AND DISTRIBUTION

OF THE PLANT BUG

Nysius huttoni WHITE

(HETEROPTERA : LYGAEIDAE)

A Thesis Presented in Partial Fulfilment
of the Requirements for the Degree of
Master of Agricultural Science
in the University of New Zealand

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Alan Charles Eyles

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INTRODUCTION

> "No locality seems too remote for the species of this genus. Whether it be the icy wastes of Greenland, the coral islands of the Pacific, or the upper slopes of the Himalayas, Nysius is certain to be represented. It occurs from Tierra del Fuego to Siberia, from Greenland to New Zealand."
>
> - W.E. China

Nysius huttoni White, endemic to New Zealand is a member of an almost cosmopolitan genus which shows remarkable adaptation throughout the world. As it is the only Nysius species so far recorded from this country, some attention to it is surely due, if for no other reason.

There are, however, other valid reasons which prompted this study, and these are as follows. Relatively little work has been carried out on N. huttoni, there being only one study (by Gurr, 1957) specifically on this insect; the immature stages have not been described; no illustrations of any of the instars either nymphal or imaginal have been published, except for one photomicrograph by Blair and Morrison (1949) of a balsam-mounted imago, but it is so distorted as to be unrecognisable; the systematics of the insect has not been fully studied, for Usinger (1943) states that two species may be represented; the number of broods per year is not known, but Myers (1926) states that there is probably more than one. An attempt has been made to elucidate the subject along these lines.

Further, the insect occurs in large numbers and is easily caught, which two factors contribute much to the suitability of the insect for study material. Thus N. huttoni presents ample scope for a general study on the bionomics of an animal.

ACKNOWLEDGEMENTS

Grateful acknowledgement is made to Mr. L. Gurr for his encouragement and guidance in the supervision of this study, and for helpful criticisms in the preparation of this thesis.

The author is also indebted to Dr. E.A. Cumber, Entomology Division of the D.S.I.R. for information, and the use of some insect material, from a survey of insects of grasslands in the North Island, to Dr. T.E. Woodward of the University of Queensland for information on the subfamilies of the Lygaeidae represented in New Zealand, and to Miss E.C. Campbell of the Botany Staff for the identification of a moss.

Thanks are also due to Mr. H. Drake for photographic work in the reproduction of the drawings, to Mr. J.E. van Paahuys for the translation of certain German literature, and to Mrs. A.W. Warren for typing this thesis.

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REVIEW OF LITERATURE

(a) Systematics

Nysius huttoni White was described in 1878 by Buchanan White from adult specimens collected by Hutton and Wakefield. Hutton (1897) gave a brief description, sufficient to identify imagines, in a list of Hemiptera then known in New Zealand. A key to the New Zealand Lygaeid genera and species, is included in his paper. Myers (1926), unable to identify four species of *Nysius* other than *N. huttoni*, sent specimens to Dr. Bergroth for description, but the outcome does not appear in the literature. In 1943, however, Usinger on examining eleven *N. huttoni* specimens, noted variability "in colour and even to some extent in structure that two species may be represented." The paper comprises a history of the tribe Orsillini in New Zealand, and descriptions of five new species including *Brachynysius convexus* Usinger, which genus he here also erects.

(b) Bionomics

Myers (1926) in a general study on the biology of New Zealand Heteroptera, gives, for *N. huttoni*, very brief notes on some host plants, and the final ecdysis. It was not until Gurr's paper in 1957 that the life history of the insect was published. He showed that:

(1) there are five nymphal instars, and gives the duration of each;

(2) unlike other species of *Nysius* which oviposit in grass glumes or composite flowers, *N. huttoni* oviposites in the soil. Total individual egg production by nine females is given

(3) newly emerged adults are pale buff in colour, but darken to full colour in twelve hours

(4) greatest activity coincides with the highest day temperature; the bugs conceal themselves under clods or debris on the ground as soon as the temperature begins to fall in the evening

(5) rain induces sluggishness

(6) adults overwinter at the bases of weeds and grasses and under vegetable debris.

(c) Distribution

Evidence that N. huttoni occurs throughout the North and South Islands is given by Myers (1926), Usinger (1943) and Gurr (1957). Alfken (1905) and Kirkaldy (1908) have both recorded it from the Chatham Islands whilst Woodward (1954) recorded it from the Three Kings Islands.

(d) Economic Importance

(i) Lucerne and Red Clover: Amongst harmful insects on lucerne Myers (1921) mentions "Nysius huttoni (very common)." The bug reached phenomenal numbers on lucerne (near Wellington) especially in dry patches where there were gaps in the crop. N. huttoni is also listed by Myers amongst harmful insects on red clover. "Perhaps the commonest insect in the field, both of lucerne and red clover, is the ... plant bug Nysius huttoni ... a close relative of the destructive chinch bug of North America and of the Rutherglen bug of New South Wales." Whilst in Blenheim, the crops were more advanced, but the bug was common throughout, and, although there was no apparent damage, Myers considered the continual sucking by the insects must be a factor of some importance.

(ii) Wheat: Certain lines of wheat from North Otago and South Canterbury produced "sticky dough" or "slimy gluten" when the flour was used for baking (Morrison 1939, Blair and Morrison 1949, Gurr 1957). They found Heteroptera present in large numbers in many wheat crops and in surrounding vegetation. Morrison (1939) caged samples of the most abundant species of plant bug, Stenotus binotatus Fabr., N. huttoni and Hudsona anceps (White) Evans, separately on developing wheat crops at Lincoln Agricultural College. Wheat not confined with insects was not damaged. Results from his experiments are:

(1) All three plant bugs caused bugged wheat and therefore sticky dough.

(2) Plant bugs causing the damage in New Zealand are different from those

species (mainly Eurygaster and Aelia species) causing similar damage in Europe and Asia. E. bipotatus is cosmopolitan, but E. hattorni and E. anceps are native to New Zealand.

(3) Because the harmful species in New Zealand are widely distributed, and not confined to Otago or Canterbury where the trouble is most prevalent, and because the proportion of crops attacked to the quantity grown, is small, it is suggested that wheat is not the normal or preferred food of the bugs.

(4) Damage is more prone in certain wheat areas than in others, which suggests that the prevalence of certain weeds, the climatic conditions prevailing, the time of ripening of wheat, or a combination of those factors, may be closely linked up with the trouble.

(5) Damaged grains show a white, oval or round patch with a central black spot, the rostral puncture.

Gurr (1957) states that damaged grains may be shrunken and cuboid in shape as a result of prolonged or multiple feeding of the bugs. He explains that wheat is attacked in the milk ripe stage, a proteolytic enzyme being injected to facilitate ingestion of the plant juices by suction. Abnormal behaviour of the gluten is caused by enzymatic residues in the grain. The following additional information on the effect of bug feeding on wheat in New Zealand was contributed by Gurr:

(1) "As little as one per cent of bugged wheat used in the production of flour has made it unsuitable for baking .... Bugged wheat may be used for flour without affecting its baking qualities if at blending it is mixed in quantities of less than one per cent with unaffected lines."

(2) Bug damage in New Zealand does not affect germination of wheat.

(3) The bugs live on weeds at the edges of crops, but as the weeds die at the height of summer, in the dry subhumid South Canterbury and North Otago regions, the bugs are forced onto the ripening wheat.

The writer noted the following difference between wheat bugs in New Zealand and bugs attacking cereals in other countries.

(a) Bug damage in New Zealand does not affect germination of wheat (Gurr 1957), whereas cereal grains damaged by bugs in other countries suffer reduced germination (Malenotti 1931, Tordesillas 1955, Lefage 1937).

(b) N. huttoni attacks only the grain of wheat when it is at the milk-ripe stage (Morrison 1939, Blair and Morrison 1949, Gurr 1957), whereas overseas bugs also feed on the growing cereal plants (Scott 1929, Wölfer 1932, Tischler 1939, Kretovich et al 1943).

(c) In New Zealand, the proportion of wheat crops attacked to the quantity grown, is small (Morrison 1939) due to restriction of bug feeding to the edge of the crop (Gurr 1957). In other countries, however, the bugs spread throughout the crop and cause severe damage, often to the extent that the crop is not worth harvesting (Scott 1929, Malenotti 1931, Manninger & Manninger 1953).

There is a similarity in that both the New Zealand and the overseas cereal bugs rely on other plants, mainly weeds and grasses, as overwintering quarters, and as a source of food until the appearance of, and subsequent movement onto, the cereal crop.

(iii) Crucifers: "Greatest economic loss is caused by its damage to cruciferous seedlings" - Gurr (1957). The reason is that the whole area of the seedling crop provides suitable bug habitat, so that damage is not confined to the edge of the crop. Large numbers feeding around the young stems, suck much sap from the plants which then wilt; blockage of conducting vessels as a result of feeding punctures prevents recovery by the plants.

SECTION A - SYSTEMATICS

"... it appears likely that the New Zealand Orsilline fauna will prove to be just as unique, though possibly somewhat smaller, than that of the Hawaiian Islands."

- E.L. Usinger

CHAPTER 1

THE PLACE OF N. huttoni WITHIN THE FAMILY LYGAEIDAE

N. huttoni belongs to the tribe Orsillini (Stål)*; one of three tribes which comprise the sub-family Lygaeinae. As well as the genus Nysius Dallas, at least twenty other genera have been assigned to the Orsillini. The major divisions of the family Lygaeidae represented in New Zealand are given below, and in particular, of the sub-family Lygaeinae.

Family LYGAEIDAE

Sub-family Lygaeinae
Sub-family Heterogastrinae+
Sub-family Cyminae
Sub-family Megalonotinae++

Sub-Family LYGAEINAE

Tribe Lygaeini
Tribe Orsillini
Tribe Metrargini (exclusively Hawaiian)

* The tribe Orsillini is a taxonomic category and therefore has a description, the genus Orsillus Dallas being the type genus.

+ Heterogastrinae Stål, 1872 takes priority over Chauliopinae Breddin, 1907 which is a junior synonym.

++ Megalonotinae Slater, 1957 replaces Rhyparochrominae Stål, 1862, the type genus Rhyparochromus Curtis, 1836 falling as a junior homonym of Rhyparochromus Hahn, 1826.

The New Zealand Orsillini, comprising eight species representing four genera, are as follows:

Nysius huttoni White
Brachynysius convexus Usinger
Hudsona anceps (White) Evans
Rhypodes clavicornis (Fabr.) Evans
Rhypodes sericatus Usinger
Rhypodes myersi Usinger
Rhypodes chinai Usinger
Rhypodes stewartensis Usinger

The genera Rhypodes Stål, Hudsona Evans, and Brachynysius Usinger, are endemic to New Zealand, but the genus Nysius is cosmopolitan. Usinger (1943) says:-

> "The New Zealand Orsillini are so peculiar that no relatives of the endemic genera are known from elsewhere. N. huttoni, however, is allied to the Hawaiian Nysius blackburni White and to Nysius backstroemi Bergroth from Juan Fernandez. The new genus Brachynysius is apparently a remarkable offshoot from typical Nysius."

CHAPTER 2

DESCRIPTIONS OF STAGES

Egg (Plate 1)

Longer than broad, ratio length to width, 3:1; slightly concave ventrally, convex dorsally and laterally; blunt anteriorly, pointed posteriorly. Four to six papilliform micropylar processes surround cephalic pole; no operculum or pseudoperculum; external chorionic surface sculptured in anterior third with longitudinal grooves, almost converging at cephalic pole. Size: mean length 0.77 mm.; mean width 0.28 mm. Colour (soon after oviposition) straw yellow (Ostwald series X, 2 la)*, darker area at cephalic pole marigold orange (Ostwald series XIV, 4 pa).

Southwood (1956), on micropylar apparatus, supported two divisions of the Geocorisae:

(1) Pentatomomorpha - possessing micropyles, but no operculum, although some groups possess a pseudoperculum.

(2) Cimicomorpha - possessing pseudomicropyles and micropyles, and also possessing an operculum.

Lygaeoidea belong to the Pentatomomorpha and do not possess an operculum. Southwood also stated that the micropylar processes number three to six in the Orsillini, and from the literature showed that they are papilliform in Nysius. N. huttoni eggs are in agreement with these earlier findings. The micropylar processes on N. huttoni eggs were usually regularly spaced, although irregularities in spacing did occur. One to two days following oviposition, these processes became faintly white, and prior to hatching they became distinctly white in end view. During incubation, the grooves or wrinkles in the chorion may extend. The colour of the freshly laid egg has been described by Carr (1957) as "creamy-white" and that of Nysius coenosulus Stål by Usinger (1942) as "almost water white or colourless and

* Ostwald (1931) Colour Standards

shining, with a small amount of yellow yolk at the anterior or micropylar end". N. huttoni eggs observed at the moment of oviposition were very pale and were either (a) almost water white, or (b) a very pale yellowish orange. In both cases there was a small orange coloured region at the cephalic pole. The (b) type of colouring probably resulted from retention of the egg within the abdomen for a longer period before oviposition, a view which is supported by the fact that the eggs became progressively darker in colour during incubation.

Egg Dimensions

A total of 176 eggs were measured under a Zeiss low power stereoscopic microscope, using an eyepiece scale. Because of the shape of the egg, it was necessary to take three measurements of length and width on each egg. Most of the eggs were measured either on the day of oviposition or the following day, but it was found that even after one week there was no change in egg dimensions. All measurements taken on individual eggs are shown in Appendix IIa, and in Appendix IIb the sizes and wing form of some of the maternal parents are given

Length

The mean length, 0.77 mm, was obtained by averaging the means of the three measurements taken on individual eggs. The distribution of egg length is shown in Table 1, and graphically in Fig. 1.

TABLE 1

FREQUENCY DISTRIBUTION OF EGG LENGTH

All measurements are in eyepiece scale divisions: one scale division = 0.055 mm

Class Interval	Egg Length (class)	Frequency
	9.5	1
	10.0	1
11.0	10.8 - 11.2	25
11.5	11.3 - 11.7	28
12.0	11.8 - 12.2	38
12.5	12.3 - 12.7	25
13.0	12.8 - 13.2	44
13.5	13.3 - 13.7	12
14.0	13.8 - 14.2	2

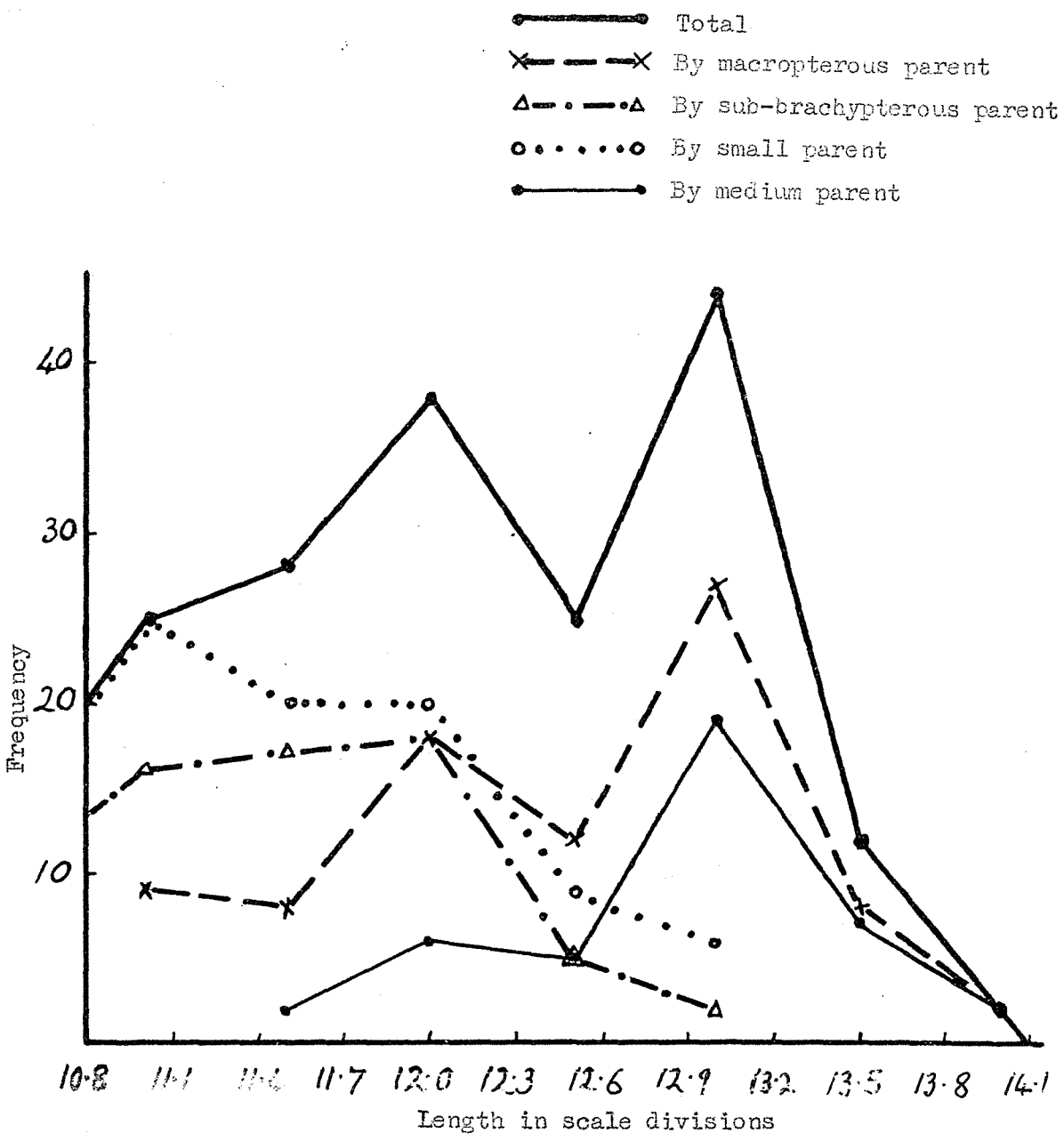


Fig. 1

Distribution of egg length

The distribution was not normal, for there were two peaks, one at 12 divisions, and one at 13 divisions. It seemed that two populations were involved. From the field, some adult specimens collected were macropterous, and some were sub-brachypterous. As eggs from both forms were included in the eggs measured, it was decided to investigate the possibility that a macropterous population laid eggs differing in size from those of a sub-brachypterous population. The data on egg length was reclassified according to the form of the maternal parent. The two distributions obtained are shown in Table 2, and graphically in Fig. 1.

TABLE 2

FREQUENCY DISTRIBUTIONS OF EGG LENGTH WHEN GROUPED ACCORDING TO FORM OF MATERNAL PARENT

All measurements are in eyepiece scale divisions: one scale division = 0.063mm

Class Interval	Egg Length (class)	Frequencies	
		Sub-brachypterous Parent	Macropterous Parent
	9.5	1	
	10.0	1	
11.0	10.8 - 11.2	16	9
11.5	11.3 - 11.7	17	7
12.0	11.8 - 12.2	18	12
12.5	12.3 - 12.7	5	11
13.0	12.8 - 13.2	2	26
13.5	13.3 - 13.7		8
14.0	13.8 - 14.2		2

As the wing form of one or two females was unknown there are slightly less total eggs than in Table 1. The eggs laid by the sub-brachypterous females seemed in the main, to be smaller than those laid by macropterous females, but the latter's eggs still showed a bimodal distribution which overlapped the sub-brachypterous distribution. The means of the (so called) two populations differed by one scale division or 0.063mm. The sub-brachypterous population eggs mean

length and standard deviation were, respectively (in scale divisions), 11.5 and 0.75, whereas the corresponding figures for eggs laid by the macropterous females were 12.5 and 0.63. The trial division into sub-brachypterous and macropterous populations on egg length, placed the former into a separate group, but in the latter the overlap may be explained by supposing a greater variation in egg length for this group. However, this arbitrary division does not explain the total bimodal distribution and is unsatisfactory because some sub-brachypterous females laid large eggs and some macropterous females laid small eggs.

Later, the author was able to distinguish three populations, each differing in size, among N. buttoni adults (see Chapter 3). The medium and small populations included several different winged forms from macropterous to brachypterous. From the sizes of the females given in Appendix IIb, it is clear that the large population was absent from the experiment under consideration.

Accordingly, the possibility that a medium sized population laid larger eggs than a smaller population was investigated. Where the size and form of the female was known, the egg data was re-classified as in Table 3, and the resulting distributions are shown graphically in Fig. 1.

TABLE 3

FREQUENCY DISTRIBUTIONS OF EGG LENGTH WHEN GROUPED ACCORDING TO SIZE OF MATERNAL PARENT

All measurements are in eyepiece scale divisions: one scale division = 0.063mm

Class Interval	Egg length (class)	Frequencies: Small Parent	Medium Parent
	9.5	1	
	10.0	1	
11.0	10.8 - 11.2	25	
11.5	11.3 - 11.7	20	2
12.0	11.8 - 12.2	20	6
12.5	12.3 - 12.7	9	5
13.0	12.8 - 13.2	6	19
13.5	13.3 - 13.7		7
14.0	13.8 - 14.2		2

The eggs laid by the small population fell into a separate group from those laid by the medium population. There was less overlap, and a more marked modal peak for each population. The means of the two populations differed by 1.4 scale divisions or 0.088mm. The mean and standard deviation (in scale divisions) of the small and medium populations were, respectively, 11.4 and 0.67, and 12.8 and 0.60.

The division into two populations according to size of adults compared with the grouping into two populations according to wing form of adults, gave a greater difference between the population means, a lesser difference between their standard deviations, and a better explanation of the bimodal graph for total eggs.

Width

The mean width, 0.20mm was obtained by averaging the means of the three measurements taken on individual eggs. The data on egg width received the same treatment as that on egg length. The results are shown in Table 4 and graphically in Fig. 2.

TABLE 4

FREQUENCY DISTRIBUTION OF EGG WIDTH

All measurements are in eyepiece scale divisions: one scale division = 0.063mm

Class Interval	Egg Width (class)	Frequencies				
		Total	Reclassified according to form		Reclassified according to size	
			Sub-brachypterous ♀ Parent	Macropterous ♀ Parent	Small ♀Parent	Medium ♀Parent
5.8	5.7-5.9	1	1		1	
4.1	4.0-4.2	47	24	16	30	2
4.4	4.3-4.5	83	30	33	37	26
4.7	4.6-4.8	38	6	24	7	14
5.0	4.9-5.1	4	1	2	1	2

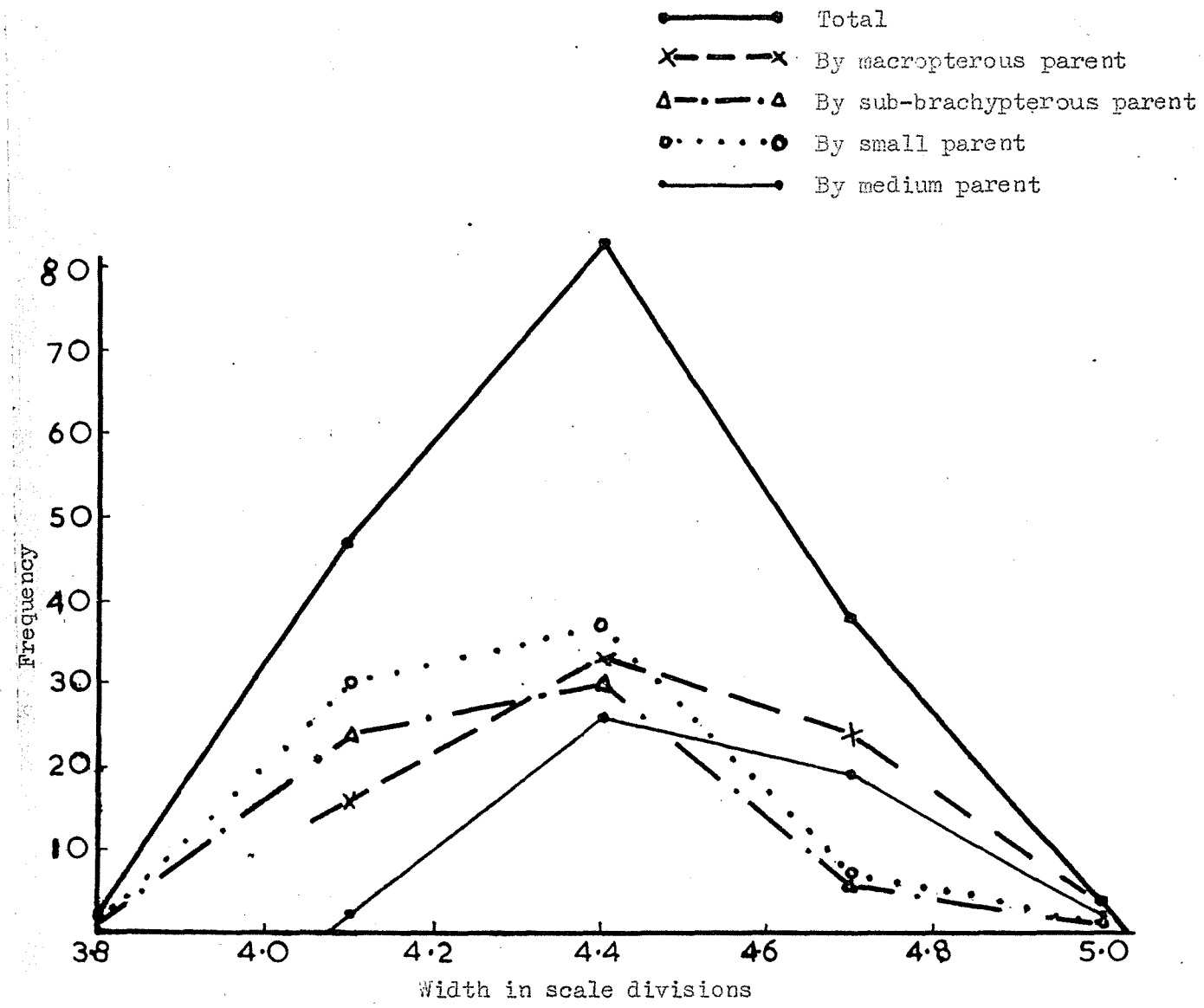
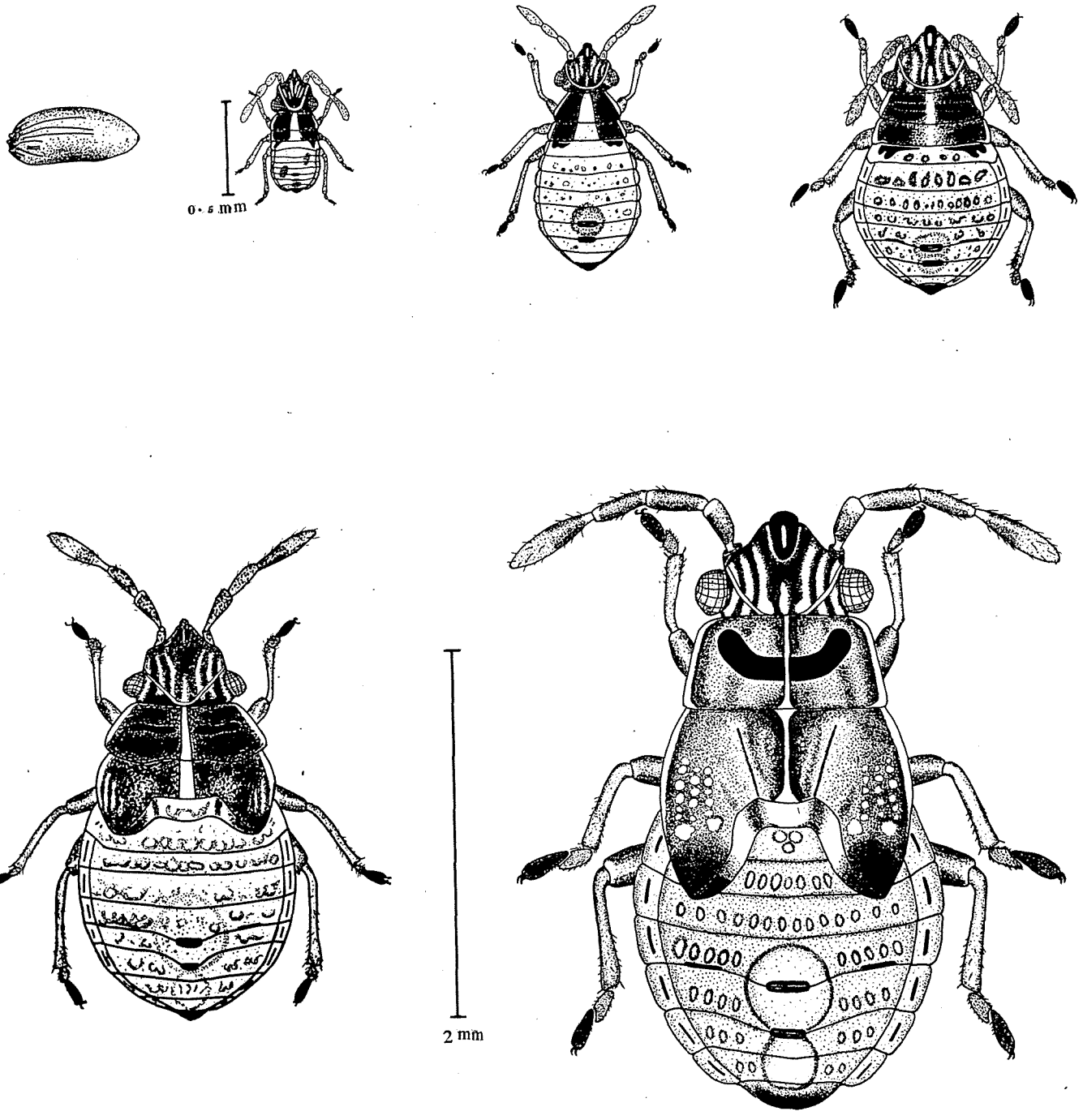


Fig. 2

Distribution of egg width

PLATE 1

Egg and nymphal instars of *Aysius huttoni*



longer than mesonotum. Mesonotum slightly longer t an metanotum. A narrow strip extending slightly on both sides of midline on pronotum, and more so on mesonotum, lacks black pigmentation. Metanotum devoid of black pigmentation except for a narrow, oblique line extending full length of segment on each side. Pleura of thorax narrow, flattened, transparent.

Abdomen: shorter than head and thorax together, 4:6; slightly wider than head, 5:4.5.0. Two distinct mid-dorsal abdominal scent gland openings inter-segmentally disposed between segments four and five, and five and six. Pleura narrow, flattened, opaque. Eight abdominal segments.

Tarsi: two segmented, distal segment longer than proximal, 1.8:0.7 (hind tarsus).

Size:(When fed): Mean length 0.84mm: mean width (head) 0.28mm: (abdomen) 0.84mm.

Colour:*

Head: brownish black, (Ostwald series IV, 4 pl)+; seven head stripes and ecdysial suture of head, orange (O.XII, 3pc.) giving impression of portions not darkened; eyes red (O. XIV, 7 pa); antennae and rostrum grey-black (O. II, 1 li.); distal rostal segment black (O. series O,n).

Thorax: Pro- and meso-nota brownish black (O.IV, 4 pl), the undarkened, mid-dorsal strip, orange (O.XII, 5 na). Metanotum basically orange as abdomen; two narrow oblique lateral, black markings extend length of segment. Pleura undarkened, as abdomen. Ventral thorax: subcoxal plates, only, darkened, rest orange. Legs lighter than head, grey-black (O.II, 1 li).

* At eclosion, the nymph is pale orange in colour, but darkening occurs gradually over a period of seven hours until definitive colouration (as described above) is assumed. A description of the colour changes occurring at intervals during the darkening process is given in Chapter 6.

+ Throughout the descriptions, Ostwald's (1951) Colour Standards are referred to, and each reference is abbreviated on the pattern (O.IV, 4 pl).

TABLE 5

BODY AND SEGMENTS OF FIRST STAGE NYMPHS

All measurements are in eyepiece scale divisions; one scale division = 0.035mm. S.D. = Standard Deviation

Insect No.	Head Length	Head Width	Inter-ocular width	Eye Width	Eye Length	Rostral Segments				Antennal Segments				Body length		Abdomen Width		Rostrum extends to
						1	2	3	4	1	2	3	4	Unfed	Fed	Unfed	Fed	
1	3.0	4.5	3.0	0.7	1.0	1.7	1.8	1.5	2.0	1.0	1.0	1.6	2.7	9.5		5.0		hind coxa
2	3.0	4.5	3.0	0.7	1.0	2.0	1.8	1.4	2.0	1.0	1.0	1.5	2.5	10.0		5.0		"
3	3.5	4.5	3.5	0.5	1.0	2.0	1.8	1.2	2.0	1.0	1.0	1.7	2.9	10.0		5.0		"
4	3.0	4.5	3.5	0.7	1.0	1.7	2.0	1.5	2.0	1.0	1.0	1.6	2.7	11.0		5.0		"
5	4.0	4.5	3.3	0.6	1.0	2.0	1.8	1.2	2.2	1.0	1.1	1.5	2.9	11.0		5.0		"
6	3.0	4.5	3.4	0.5	1.0	2.0	2.0	1.0	2.5	1.0	1.0	1.5	2.8		13.0		4.8	"
7	4.0	4.4	3.3	0.5	1.0	2.1	1.5	1.7	2.0	1.0	1.0	1.5	2.9	11.0		5.0		"
8	3.7	4.5	3.0	0.7	1.0	2.0	2.0	1.4	2.0	1.0	1.0	1.6	2.7		14.0		6.0	"
9	3.0	4.5	3.1	0.7	1.0	2.0	1.8	1.5	2.5	1.0	1.0	1.5	3.0		14.5		6.0	"
10	3.7	5.0	3.4	0.8	1.0	2.0	2.0	1.6	2.2	1.0	1.0	1.6	3.0		12.5		6.0	"
11	3.5	4.2	3.0	0.6	1.0	2.0	2.0	1.4	2.1	1.0	1.1	1.6	2.7		13.0		4.0	"
Mean	3.4	4.5	3.2	0.64	1.0	2.0	1.9	1.4	2.1	1.0	1.0	1.6	2.8	10.4	13.4	5.0	5.4	hind coxa
Range	3.0-4.0	4.2-5.0	3.0-3.5	0.5-0.8	1.0	1.7-2.1	1.5-2.0	1.0-1.7	2.0-2.5	1.0	1.0-1.1	1.5-1.7	2.7-3.0	9.5-14.5		4.0-6.0		"
S.D.	0.42	0.18	0.21	0.45	0	0.13	0.16	0.20	0.20	0	0.045	0.071	0.16	0.66	0.82	0	0.82	

Abdomen: basically orange (O. XII, 5 na); abdominal scent gland openings dark; three red (Q XIV, 6 pa) spots occur on dorsum, two laterally, and one towards anus; anus black (O. series 0, n).

Second Nymphal Instar: (Plate 1 and Table 6)

Head: broader than long, 6.4:5.0; eyes approximately one fourth as wide as interocular space, 1.0:4.4, and approximately one third as long as head, 1.5:5.0. Rostrum extending beyond posterior coxae, the first segment one half length of head, 2.5:5.0; total length almost half length of body, 9.8:19.5; segments one to four 2.5-2.5-2.0-2.8. Antennae one and a third times as long as width of head, 8.4:6.4; less than half length of body, 8.4:19.5; segments one to four 1.6-1.7-1.8-3.3.

Thorax: Pronotum slightly longer than mesonotum; broader than long; broader posteriorly than anteriorly; sides straight or slightly arcuate, rounded posteriorly. Metanotum approximately same length as mesonotum; black pigmentation slightly extended on first stage, two semi-lunar patches visible on each side, reaching to one half to two thirds length of metanotum. Black pigmentation absent from narrow strip on midline of pro- and mesonota. Pleura of thorax, narrow, flattened, transparent. Femora longer than tibiae, 4:3; tarsi two jointed, possessing bi-lobed ampullae; proximal segment shorter than distal, 1.0:1.9 (hind tarsus).

Abdomen: same length as head and thorax together, 10:10; one and a half times as wide as head, 9.6:6.4. Two distinct mid-dorsal scent gland openings intersegmentally disposed between segments four and five, and five and six. Pleura narrow, flattened, opaque. Eight abdominal segments.

Size: mean length 1.23mm mean width (head) 0.40mm (abdomen) 0.62mm.

Colour:

Anterior half of body similar to first stage except that black

TABLE 6

BODY MEASUREMENTS OF SECOND STAGE NYMPHS

All measurements are in eyepiece scale divisions; one scale division = 0.063mm. S.D. = Standard Deviation

Insect Number	Head Length	Head Width	Inter-ocular Width	Eye Width	Eye Length	Rostral Segments				Antennal Segments				Body Length	Abdomen Width	Rostrum extends to
						1	2	3	4	1	2	3	4			
1	5.6	6.5	4.5	1.0	1.6	2.5	2.6	2.0	3.0	1.6	1.6	1.9	3.4	20.0	10.0	hind coxae
2	5.9	6.6	4.6	1.0	1.9	2.5	2.8	2.0	3.0	1.5	1.8	1.8	3.5	18.5	9.0	"
3	4.5	6.4	4.3	1.0	1.5	2.5	2.8	2.0	2.9	1.8	1.6	1.8	3.2	18.0	-	"
4	5.0	6.0	4.1	1.0	1.5	2.5	2.5	2.0	2.9	1.5	1.6	1.8	3.1	15.0	9.8	mid coxae
5	5.2	6.5	4.5	1.0	1.3	2.5	2.8	1.8	2.7	1.5	1.6	1.8	3.5	21.0	9.8	"
6	4.5	6.4	4.2	1.0	1.5	2.5	2.7	2.0	2.7	1.7	1.8	1.8	3.7	19.0	11.0	-
7	4.0	6.0	4.0	1.0	1.2	2.4	2.0	1.9	2.5	1.8	1.8	1.7	3.0	17.5	8.0	hind coxae
8	4.8	6.5	4.5	1.0	1.5	2.7	2.5	2.0	2.9	1.6	1.7	1.7	3.6	22.0	10.0	"
9	5.5	6.5	4.5	1.0	1.6	2.5	2.7	1.8	3.0	1.5	1.6	1.8	3.0	20.5	10.5	"
10	4.5	6.5	4.5	1.0	1.9	2.5	2.0	2.0	2.7	1.4	1.7	1.8	3.4	19.0	10.0	"
Mean	5.0	6.4	4.4	1.0	1.55	2.5	2.5	2.0	2.8	1.6	1.7	1.8	3.3	19.5	9.8	hind coxae
Range	4.0-5.9	6.0-6.6	4.0-4.6	1.0	1.2-1.9	2.4-2.7	2.0-2.8	1.8-2.0	2.5-3.0	1.4-1.8	1.6-1.8	1.7-1.9	3.0-3.7	18-22	9-11	
S.D.	0.60	0.21	0.21	0	0.22	0.075	0.31	0.082	0.17	0.14	0.094	0.087	0.25	1.44	0.88	

pigmentation on metanotum has extended. Pleura transparent to pale grey (O. IV 1 ea), flattened.

Abdomen: Dorsal surface basically dirty orange (O. XIV, 3 pa), offset by markings of red and white; red spots arranged irregularly; scent gland openings black; pleura grey. Ventral surface lacks markings except for lateral red streaks, black edges of two segments anterior to anus, and portions of viscera showing through cuticle. Anus black (O. II, 2 pn).

Third Nymphal Instar: (Plate 1 and Table 7)

Head: almost one third again as broad as long, 8.8:5.6; eyes a little more than one fourth as wide as interocular space, 1.4:5.1, and a little more than one third length of head, 2.0:5.6. Rostrum reaching posterior coxae, the first segment approximately two thirds length of head, 3.3:5.6; total length approximately half length of body, 11.8:25.0; segments one to four 3.3-3.0-2.3-3.2. Antennae longer than width of head, 10:8; not quite half length of body, 10:23; segments one to four 2.0-2.0-2.1-3.9.

Thorax: Pronotum broader than long; broader posteriorly than anteriorly; strongly convex dorsally; sides straight, rounded anteriorly and posteriorly. Pronotum longer than mesonotum, mesonotum longer than metanotum, 3:2:1. A dark black line now present across centre of pronotum. Black pigmentation absent from narrow strip on midline of pro- and mesonota. First signs of wing pad development appear as slight, rounded, laterally disposed projections on posterior margins of meso- and metanota, but less obvious on metanotum. Black pigmentation on metanotum further extended than in second stage, now bicornuate and almost reaching posterior of segment. Pleura narrow, flattened, opaque.

Abdomen: slightly shorter than head and thorax together, 10.8:12.1; one third again as wide as head, 11.8:8.0. Dorsal abdominal scent gland openings, and pleura as in first stage. Eight abdominal segments

Tarsi: proximal segment to distal segment, 1.5:2.5 (hind tarsus).

Size: Mean length 3.5mm; mean width (head) 0.8mm; (abdomen) 0.74mm.

TABLE 7

BODY MEASUREMENTS OF THIRD STAGE NYMPHS

All measurements are in eyepiece scale divisions: one scale division = 0.063mm. S.D. = Standard Deviation

Insect number	Head Length	Head Width	Inter-ocular width	Eye Width	Eye Length	Rostral Segments				Antennal Segments				Body Length	Abdomen Width	Ratio of length Abdomen : Head plus thorax		Rostrum extends to
						1	2	3	4	1	2	3	4					
1	6.0	8.0	5.0	1.6	2.0	3.0	3.0	2.5	3.6	2.0	2.0	3.5	3.7	24.9	13.0	13.0	12.0	hind coxae
2	5.0	8.0	5.0	1.6	1.8	3.0	3.0	2.5	3.1	2.0	2.0	2.0	3.4	24.0	10.0	12.0	12.5	"
3	6.0	7.9	5.0	1.5	2.0	3.0	3.0	2.5	3.0	2.0	2.0	2.0	4.0	21.0	10.0	8.0	13.0	"
4	5.0	7.8	5.0	1.4	2.0	3.5	3.0	2.5	3.0	2.0	1.8	2.0	4.0	20.0	11.0	-	-	"
5	6.5	6.0	5.5	1.2	2.0	3.5	3.0	2.5	3.0	2.0	2.2	2.0	4.0	26.0	11.0	-	-	"
6	5.8	8.0	5.0	1.5	2.0	3.1	2.8	2.5	3.0	2.0	2.0	2.0	4.0	25.0	12.5	-	-	-
7	5.2	8.1	5.2	1.2	1.9	3.5	2.8	2.0	3.0	2.0	2.0	2.0	4.0	24.0	14.0	12.0	12.0	-
8	6.0	8.0	5.2	1.2	2.2	3.5	3.0	2.0	3.5	2.0	2.0	2.2	4.0	24.0	11.0	12.0	12.0	hind coxae
9	4.7	7.8	5.0	1.4	1.9	3.0	3.2	2.0	3.0	1.8	1.9	2.0	4.0	18.0	11.0	8.5	9.5	"
10	6.0	8.1	5.5	1.3	1.9	3.6	3.1	2.4	3.5	2.0	2.5	2.5	4.1	24.0	14.0	12.0	13.5	"
Mean	5.6	8.0	5.1	1.4	2.0	3.3	3.0	2.3	3.2	2.0	2.0	2.1	3.9	23.0	11.8	10.6	12.1	hind coxae
Range	4.7-6.5	7.8-8.1	5.0-5.5	1.2-1.6	1.8-2.2	3.0-3.6	2.8-3.2	2.0-2.5	3.0-3.6	1.8-2.0	1.8-2.5	2.0-2.5	3.4-4.1	18-25	10-14	8.0-13.0	9.5-13.5	
S.D.	0.59	0.11	0.21	0.16	0.11	0.25	0.12	0.24	0.25	0.087	0.10	0.18	0.21	2.55	1.51	1.96	1.27	

Colour:

Head: black (O. II, 2 pn); seven head stripes and ecdysial suture of head, orange (O. XII, 3 pe); eyes dark red; antennae, rostrum and underside of head, lighter than dorsal surface of head, brownish black (O. IV, 2 pl).

Thorax: pro- and mesonota and pigmentation on metanotum, black (O. II, 2 pn); a dense black line across centre of pronotum; undarkened mid-dorsal strip, orange (O. XII, 3 pc); remainder of metanotum as abdomen; pleura pale grey (O. IV, 1 ea); coxae and subcoxal plates black (O. II, 2 pn); remainder of ventral thorax, pale orange to grey (O. II, 1 ge); legs brownish black. (O. IV, 2 pl).

Abdomen: white spots surrounded by red (O. XII, 7 pc) spots, extending almost length of segment, are regularly arranged in a row across each segment. Background colour, still orange, is paler than these markings. Dorsal pleura marked by one red (O. XII, 7 pc) bar along centre of each segment, whilst two parallel red bars occur ventrally on each segment. Dorsal scent gland openings black; two light fawn areas approximately one segment in diameter surround them; a dark line on each side of anterior scent gland opening. Anus black (O. II, 2 pn); two segments immediately anterior to anus, blackened on mid-ventral edges.

Fourth Nymphal Instar: (Plate 1 and Table 8)

Head: more than one third again as broad as long, 10.6:6.9; eyes almost one third as wide as interocular space, 2.0:6.5; eye length approximately three fourths anteocular length, 2.7:3.9 and approximately one third length of head, 2.7:6.9. Rostrum extending to posterior coxae, and resting, partially, in a very shallow groove on ventral surface of head and thorax; the first segment a little over two thirds length of head, 4.8:6.9; total length almost half length of body, 15.8:32.5;

segments one to four 4.8-4.0-3.0-4.0. Antennae almost one and a half times as long as width of head, 14.5:10.6; less than half length of body 14.5: 32.5; segments one to four 2.7-3.5-3.0-3.3.

Thorax: Pronotum broader than long; broader posteriorly than anteriorly; sides arcuate, rounded posteriorly; posterior edge may be slightly sinuate or straight; flattened dorsoventrally, slightly convex dorsally. Mesonotum at middle, four fifths length of pronotum, 3.8:4.8; posterior margin between hemelytral pads at middle, arcuate. length of mesonotum laterally to tip of mesonotal wing pad, one half as long again as mesonotum at middle, 6.0:3.8. Wing pad development considerably advanced on third stage; mesonotal pads overlap metanotal pads except at inner bases and sides; extending usually one third to one half length of first abdominal segment. Metanotum very short at middle, black pigmentation extended over wing pads but absent at middle.

Abdomen: slightly shorter than head and thorax together, 16.0:16.4; almost one and three fourths times width of head, 17.4:10.6. Scent gland openings and pleura as in earlier stages. Eight abdominal segments.

Size: Mean length 2.05mm; mean width (head) 0.67mm; (abdomen) 1.10mm.

Colour:

Head: black (Ostwald series II, 2 pn); seven head stripes and ecdysial suture of head, pale orange to yellow (O. VI, 3 ic); eyes brownish red (O. VIII, 6 pg); antennae black, white bands at joints, distal half of fourth segment brown. Rostrum orange-brown (O. X, 4 pe), fourth segment black.

Thorax: except for mid-dorsal strip and portion of metanotum between wing pads, black (O. II, 2 pn); dark band across centre of pronotum densely black (O. series o.p); narrow, pale orange (O. VI, 3 ic) mid-dorsal strip on thorax; two or three similar coloured lengthwise stripes on mesonotal wing pads, and one on each metanotal wing pad; pleura pale grey,

TABLE 8

BODY MEASUREMENTS OF PUPAL STAGE MALES

All measurements are in eyepiece scale divisions: one scale division = 0.005mm. S.D. = Standard Deviation

Insect Number	Head Length	Head Width	Inter-ocular width	Eye Width	Ante-ocular length	Eye Length	Rostral Segments 1	2	3	4	Antennal Segments 1	2	3	4
1	6.5	10.0	6.0	2.0	4.0	2.6	5.0	3.5	3.0	3.5	2.7	3.0	2.7	3.5
2	6.0	10.2	6.0	2.0	3.5	2.5	5.0	4.0	3.0	4.1	3.0	3.0	3.0	3.1
3	6.0	11.0	7.0	2.0	4.3	2.5	5.0	4.0	3.0	3.8	3.0	4.0	3.0	3.3
4	6.0	11.0	7.0	2.0	3.5	3.0	5.0	4.1	3.0	3.9	2.6	3.5	3.0	3.1
5	8.0	11.0	7.0	2.0	4.5	2.9	4.0	4.4	3.0	4.7	2.9	4.0	3.6	5.9
6	6.5	11.3	7.0	2.2	5.0	3.0	4.0	4.0	3.0	4.0	2.5	4.0	3.2	5.7
7	7.0	11.0	7.0	2.0	3.5	3.0	5.0	4.0	3.0	4.0	2.7	3.5	3.0	5.5
8	7.0	10.8	6.4	2.2	3.5	2.5	4.5	3.8	3.0	4.0	2.4	3.5	2.5	5.0
9	6.2	10.0	6.0	2.0	3.5	2.5	4.0	3.8	3.0	3.9	2.5	3.0	2.8	5.0
10	7.5	10.0	6.0	2.0	4.0	2.8	5.0	4.0	3.3	3.9	2.5	3.5	3.0	5.0
Mean	6.9	10.6	6.5	2.0	3.9	2.7	4.8	4.0	3.0	4.0	2.7	3.5	3.0	5.3
Range	6.0-8.5	10.0-11.3	6.0-7.0	2.0-2.2	3.5-5.0	2.5-3.0	4.0-5.0	3.5-4.4	3.0-3.3	3.5-4.7	2.4-3.0	3.0-4.0	2.5-3.6	5.0-5.9
S.D.	0.90	0.52	0.50	0.082	0.53	0.25	0.35	0.23	0.10	0.30	0.22	0.41	0.31	0.33

Insect Number	Length of mesonotum: At middle	To tip of wing pad	Body Length	Abdomen Width	Length of hind leg: Femur	Tibia	Tarsus 1	Tarsus 2	Ratio of length: Abdomen : Head plus thorax		Wing pads extend to	Rostrum extends to
1	3.3	5.0	30.0	16.0	7.0	7.0	2.0	3.0	14.0	16.0	½ segment 1	hind coxae
2	4.0	5.7	32.5	19.0	7.0	8.0	1.9	3.4	16.0	16.5	"	"
3	4.0	6.0	32.0	18.0	7.0	8.4	2.0	3.5	17.5	14.5	"	"
4	3.0	6.0	28.0	15.0	7.0	8.0	2.0	3.5	13.5	14.5	¾ segment 1	"
5	4.2	7.2	31.0	17.0	7.0	9.0	2.1	3.2	13.3	17.5	½ segment 2	"
6	4.5	7.0	37.0	20.5	6.5	8.0	2.0	3.5	20.0	17.0	⅓ segment 1	mid coxae
7	3.0	6.5	32.0	18.0	7.0	8.0	2.0	3.5	16.0	16.0	⅔ segment 1	hind coxae
8	4.0	6.1	38.0	16.5	7.0	7.8	2.0	3.5	19.0	19.0	½ segment 1	"
9	3.9	5.5	32.5	16.0	7.0	7.3	2.0	3.3	16.5	16.0	segment 1	"
10	3.9	5.0	31.5	17.5	7.5	8.0	2.0	3.0	15.0	16.5	"	"
Mean	3.8	6.0	32.5	17.4	7.0	8.0	2.0	3.3	16.0	16.4	½ segment 1	hind coxae
Range	3.0-4.5	5.0-7.2	28-38	15-20.5	6.5-7.5	7.0-9.0	1.9-2.1	3.0-3.5	13.3-19	14.5-19		
S.D.	0.51	0.75	3.00	1.62	0.24	0.55	0.045	0.21	1.33	1.35		

Thorax: Pronotum more than twice as broad at posterior as long, 15.7:7.0; sides straight, rounded anteriorly and flaring posteriorly to humeral angles; posterior edge may be sinuate or straight; flattened dorso-ventrally, slightly convex dorsally. Mesonotum at middle a little shorter than pronotum, 6.5:7.0; posterior margin between hemelytral pads at middle, arcuate. Length of mesonotum laterally to tip of mesonotal wing pad, twice as long as mesonotum at middle, 13.3:6.5. Mesonotal pads overlay metanotal pads, except at inner bases and sides, so that tips of both are level and extend, usually, to posterior of 2nd or 3rd abdominal segment. Metanotum at middle short, one fifth as long as mesonotum at middle, 1.3:6.5. Legs: forefemora shorter than midfemora, midfemora shorter than hindfemora, 7.4:7.9:10.0; foretibiae shorter than midtibiae, midtibiae shorter than hindtibiae, 7.7:7.8:10.9; tarsi two-jointed, second segment longer than first; foretarsus one shorter than midtarsus one shorter than hindtarsus one, 3.0:3.2:3.0; foretarsus two longer than midtarsus two, but shorter than hindtarsus two, 4.0:3.9:4.2.

Abdomen: approximately three fourths length of head and thorax together, 16.9:23.1; one and a half times width of head, 13:19.7. Two mid-dorsal abdominal scent gland openings intersegmentally disposed between segments four and five, and five and six; a dark line occurs laterally on each side of anterior scent gland. Pleura narrow, flattened, opaque. Eight abdominal segments, the eighth tergum platelike, projecting slightly beyond anus.

Ventral abdomen male: Sternites seven and eight darkened on mid-ventral line; external genitalia not evident.

Ventral abdomen female: Sternites six, seven and eight darkened on mid-ventral region, sternite six sometimes darkened on one border only; external genital rudiments evident as more heavily pigmented area on mid-ventral line of segments seven and eight.

almost transparent (O. series O. e); legs dark brown.

Abdomen: mainly a dirty orange (O. X, 3 nc); red (O.XII, 7 pc) markings; many have extended laterally to enclose parts of the whitish or pale grey background colour, resulting in a row of white spots with red borders; such markings confined to posterior half of each segment. Dorsal abdominal scent gland openings black; a dark line on each side of anterior opening (as in 3rd and 5th stages). A circular area, reddish throughout radiates from anterior scent gland opening to middle of third segment anteriorly, and anterior of sixth segment posteriorly; a smaller brown-edged circular area extends from posterior scent gland opening to anus. Pleura flattened, each segment marked by one red (O. XII, 7 pc) bar dorsally, and two parallel red bars ventrally. Ventral abdominal surface now marked similar to dorsal surface, but sometimes the red markings are orientated lengthwise across, and not along, the segments; anus black; segments six to eight black on ventral edges.

Fifth Nymphal Instar (Plate 1 and Table 9)

Head: more than half again as broad as long, 13.0:8.3*; eyes a little more than one fourth as wide as interocular space, 2.2:7.9; length of eye almost three fourths anteocular length, 3.1:4.5, and more than one third length of head, 3.1:8.3. Rostrum extending to posterior coxae, and resting, partially in a shallow groove on ventral surface of head and thorax; the first segment three fourths length of head, 6.0:8.3; total length half length of body, 20:40; segments one to four 6.0 - 5.3 - 4.1 - 4.7. Antennae one and a half times as long as width of head, 19.4:13.0; a little less than half length of body, 19.4:40.0; segments one to four 3.8 - 5.1 - 4.0 - 6.5.

*Although the mean head width shown in Table 9 is 12.4 scale divisions, the figure of 13.0, the mean head width of 100 nymphs, used in the calculation of the growth ratio (see Table 10) is more accurate and is therefore used in the description.

TABLE 9

BODY MEASUREMENTS OF FIFTH STAGE NYMPHS

All measurements are in eyepiece scale divisions: one scale division = 0.033mm. S.D. Standard Deviation

Insect Number	Head Length	Head Width	Inter-ocular Width	Eye Width	Ante-ocular length	Eye Length	Rostral Segments 1	2	3	4	Antennal Segments 1	2	3	4	Pronotum Length	Pronotum Width Posterior	Length of Mesonotu At middle	To tip o wing pad
1	7.0	11.2	7.0	1.8	4.5	3.1	6.0	5.0	3.5	4.5	4.0	4.7	3.7	6.0	6.7	14.8	7.0	13.0
2	7.0	12.0	7.5	2.1	3.8	3.0	5.2	5.0	4.0	4.6	4.0	4.7	3.7	6.0	7.0	14.0	6.1	13.0
3	8.0	13.0	8.2	2.0	4.5	3.0	6.0	6.0	4.5	5.0	3.8	5.5	4.0	6.1	7.0	16.0	6.0	16.0
4	7.5	12.9	8.0	2.1	4.6	3.0	5.8	5.0	5.0	5.0	4.0	5.6	4.0	6.8	7.2	16.0	6.7	14.5
5	9.0	12.0	8.0	2.0	4.0	2.8	6.0	6.0	4.0	5.0	4.0	5.0	4.0	7.0	7.0	15.5	6.5	12.5
6	8.0	13.0	8.0	2.8	5.0	3.5	6.5	6.0	4.0	5.0	4.0	5.7	4.5	7.7	8.0	17.0	6.0	14.0
7	11.5	13.0	8.5	3.0	5.7	3.2	6.0	5.5	4.5	4.5	4.0	5.0	4.5	6.5	6.0	15.0	6.5	13.0
8	7.5	12.2	8.0	2.1	4.8	3.3	6.0	4.8	4.4	4.8	3.5	5.0	4.0	6.8	8.0	15.0	7.0	14.0
9	9.0	12.0	7.5	2.2	5.0	3.1	6.0	5.0	4.0	5.0	3.0	4.5	3.5	7.0	6.8	15.0	5.7	11.7
10	9.5	13.0	9.0	2.0	5.8	3.5	5.6	4.0	4.0	4.0	3.5	6.0	4.0	6.7	7.2	16.0	6.0	14.0
11	10.0	13.5	9.0	2.0	4.0	3.0	6.0	5.0	4.0	5.0	3.6	4.5	4.0	6.2	6.7	15.0	7.0	13.0
12	10.8	12.8	8.5	2.1	4.0	2.9	6.5	5.5	4.5	4.0	4.0	5.6	4.4	6.5	7.5	16.0	5.5	13.0
13	11.0	12.0	7.1	2.8	4.0	2.9	6.0	5.5	4.0	4.0	4.0	5.0	4.0	6.5	7.0	15.5	6.0	13.0
14	6.0	12.0	7.8	2.2	4.0	3.0	6.0	5.0	4.0	5.0	4.0	5.0	4.0	6.6	6.0	14.0	7.2	13.0
15	6.0	12.2	8.0	2.1	4.0	3.0	7.0	5.5	3.5	4.9	3.2	5.0	4.2	6.5	7.0	16.2	7.0	14.0
16	7.0	11.8	7.2	2.2	4.0	2.9	5.5	5.1	3.8	4.8	4.0	4.6	4.0	6.5	6.2	15.0	6.1	12.0
17	6.5	11.4	7.5	2.2	4.0	2.9	6.0	5.5	4.0	5.0	4.0	4.9	4.0	6.0	7.0	15.5	7.0	13.0
Mean	8.3	12.4	7.9	2.2	4.5	3.1	6.0	5.3	4.1	4.7	3.8	5.1	4.0	6.5	7.0	15.7	6.5	13.3
Range	6.0-11.5	11.2-13.0	7.0-9.0	1.8-2.8	4.0-5.8	2.9-3.5	5.2-7.0	4.0-6.0	3.5-5.0	4.0-5.0	3.0-4.0	4.5-6.0	3.5-4.5	6.0-7.7	6.0-8.0	15.5-16.0	6.1-7.0	11.7-16.0
S.D.	1.76	0.65	0.60	0.33	0.62	0.197	0.40	0.53	0.36	0.38	0.32	0.46	0.26	0.45	0.37	0.32	0.75	1.01

Insect Number	Mesonotum Width	Metanotum length at middle	Length of Foreleg Femur	Tibia	Tarsus 1	Tarsus 2	Length of Midleg Femur	Tibia	Tarsus 1	Tarsus 2	Length of Hindleg Femur	Tibia	Tarsus 1	Tarsus 2	Rostrum extends to	Sex
1	18.0	1.2	7.0	7.0	2.2	4.0	7.0	7.5	3.5	3.8	10.0	9.8	3.0	4.0	-	Male
2	14.6	1.5	6.0	7.0	2.0	4.0	7.0	8.0	2.0	4.0	10.0	11.0	3.0	4.0	-	"
3	21.0	1.8	8.0	7.8	1.8	4.0	7.0	8.0	2.0	4.0	10.0	11.5	3.0	4.0	Hind coxae	"
4	23.0	1.1	8.0	8.0	2.0	4.0	9.0	8.0	2.5	3.8	11.0	11.8	3.0	4.0	"	Female
5	20.0	1.2	7.0	8.0	2.0	4.0	8.0	7.0	2.0	4.0	9.0	10.5	3.0	4.5	"	Male
6	21.5	1.0	8.0	8.4	2.0	4.0	9.0	8.0	2.5	4.0	11.0	12.0	4.0	4.8	-	Female
7	20.5	1.8	7.0	7.0	2.0	4.0	7.5	7.0	2.0	4.0	10.0	11.0	3.0	4.0	Hind coxae	Male
8	19.5	1.0	8.0	8.0	2.5	4.0	7.0	8.0	2.5	4.0	10.0	11.0	3.0	4.0	"	"
9	18.5	1.2	8.0	7.5	2.0	4.0	9.0	7.0	2.0	4.0	9.5	10.5	3.0	4.0	"	"
10	23.0	1.3	8.0	8.0	2.2	4.0	7.5	8.0	2.0	4.0	10.0	11.5	3.0	4.5	Mid coxae	Female
11	24.0	1.0	8.0	8.0	2.0	4.0	8.0	9.0	2.0	4.0	10.0	12.0	3.0	4.0	Hind coxae	"
12	20.0	1.2	8.0	8.0	2.0	3.8	8.0	8.0	2.0	3.8	10.5	11.0	3.0	4.0	"	"
13	19.0	1.2	7.0	7.5	2.0	4.0	8.0	7.8	2.0	4.0	10.0	10.5	3.0	4.0	"	"
14	17.2	1.2	7.0	7.8	2.0	3.8	8.0	7.0	2.0	4.0	9.0	10.0	3.0	4.5	"	"
15	20.5	1.8	7.2	8.0	2.0	4.2	8.0	8.1	2.0	3.8	10.0	11.4	3.0	4.5	"	Male
16	20.0	1.2	6.5	7.0	2.0	4.0	8.0	8.0	2.0	3.8	10.0	10.0	2.6	4.0	"	Female
17	20.0	1.1	7.0	7.4	2.0	4.0	7.5	7.5	2.0	4.0	9.0	10.0	3.0	4.5	"	Male
Mean	20.0	1.5	7.4	7.7	2.0	4.0	7.9	7.8	2.2	3.9	10.0	10.9	3.0	4.2	Hind coxae	
Range	14.6-24.0	1.0-1.8	6.0-8.0	7.0-8.4	1.8-2.5	3.8-4.2	7.0-9.0	7.0-9.0	2.0-3.5	3.8-4.0	9.0-12.0	9.8-12.0	2.6-4.0	4.0-4.8		
S.D.	2.27	0.27	0.65	0.45	0.15	0.097	0.68	0.54	0.39	0.10	0.77	0.72	0.27	0.28		

background more of a bluish or greenish tinge, and white spots and red markings not as regular. Mid-ventral markings on segments six to eight in females, and seven and eight in males, dark brown to black.

From the foregoing descriptions it is seen that each nymphal instar is readily distinguished by size, by characteristic black pigmentation on the metanotum in the first three instars, and by wing pad development in the fourth and fifth instars (see Plate 1). The shallow groove on the ventral surface of the thorax, in which the rostrum partially rests, was well developed in the fifth stage, was slight in the fourth stage, was very faintly visible on some third stage, but was absent in second and first stage nymphs. However, there was in all stages, a deeper rostral groove on the underside of the head.

It was noted that fourth and fifth stage nymphs caught in the late autumn were darker in colour, that is were a denser black on the head and thorax, and in some cases the abdomen was showing a blackish tinge at the sides.

Some material was preserved in Carle's fixative which was very satisfactory, because specimens, even after several months, were scarcely faded.

Progression in Growth

Dyar (as mentioned by Usinger, 1942) suggested that the sclerotized parts of the insect body increase in size in a more or less regular geometrical progression during successive instars, there being a growth factor for each species representing the increase in size at each moult. Przibram (Przibram and Megusar, 1912) has extended this principle and gives a theoretical progression factor of 1.26 (the cube root of 2) for insects in general.

Head widths of 100 nymphs of each instar were measured. The nymphs were taken at random from samples caught at Massey Agricultural College and Hokowhitu, and, in the case of the fourth and fifth instars, also from Marton and Havelock North. Individual head width measurements are shown in Appendix IIIa. The frequency distributions of head width are shown in Table 10, and graphically in Fig. 3.

Colour:

Head: black (Ostwald series II, 2 pn) seven dorsal head stripes and ecdysial suture of head pale orange to pale grey (O.II 1 ca); eyes reddish brown (O. IV, 6 pl); ventral surface of head dark brown to black except for white bases of antennae and a light grey (O. series O, e) area under eyes; antennae dark brown almost black, white bands at joints of segments, distal half of fourth segment lighter brown. Rostrum dark brown almost black, fourth segment black.

Thorax: black (O. II, 2 pn), not a deep black but denser on tips of wing pads; dark band across centre of pronotum densely black (O. series O, p); in places lighter pinkish to pale grey (O. II, 1 ca) markings on wing pads; narrow mid-dorsal, thoracic ecdysial suture line, white to pale grey (O. II 1 ca) - this strip, wider in earlier instars, is here reduced to a line; pleura pale grey (O. II, 1 ca). Legs: coxae and subcoxal plates black (O. II, 2 pa); trochanters dark brown; femora dark brown, tibiae lighter brown proximal tarsal segment dark brown, distal tarsal segment black.

Abdomen: To naked eye appears grey-brown but on closer examination appears mainly red; background colour of dorsal segments greyish blue (O. II, 14 ge); white spots in a row across each segment, each spot surrounded by a red (O. XII, 7 pe) border; abdominal scent gland openings black (O. II, 2 pn); a dark line on each side of anterior scent gland; a dark edged circular area, lighter in interior, encircles anterior scent gland opening and extends from segment four to segment six; a similar coloured but smaller circular area extends from posterior scent gland opening to anus; eighth tergite black (O. II, 2 pn); pleura flattened, white to grey (O. II, 1 ca), each segment marked by one red (O. XII 7 pe) bar dorsally and two parallel red bars ventrally. Ventral surface of abdomen similar in colour to dorsal surface except that

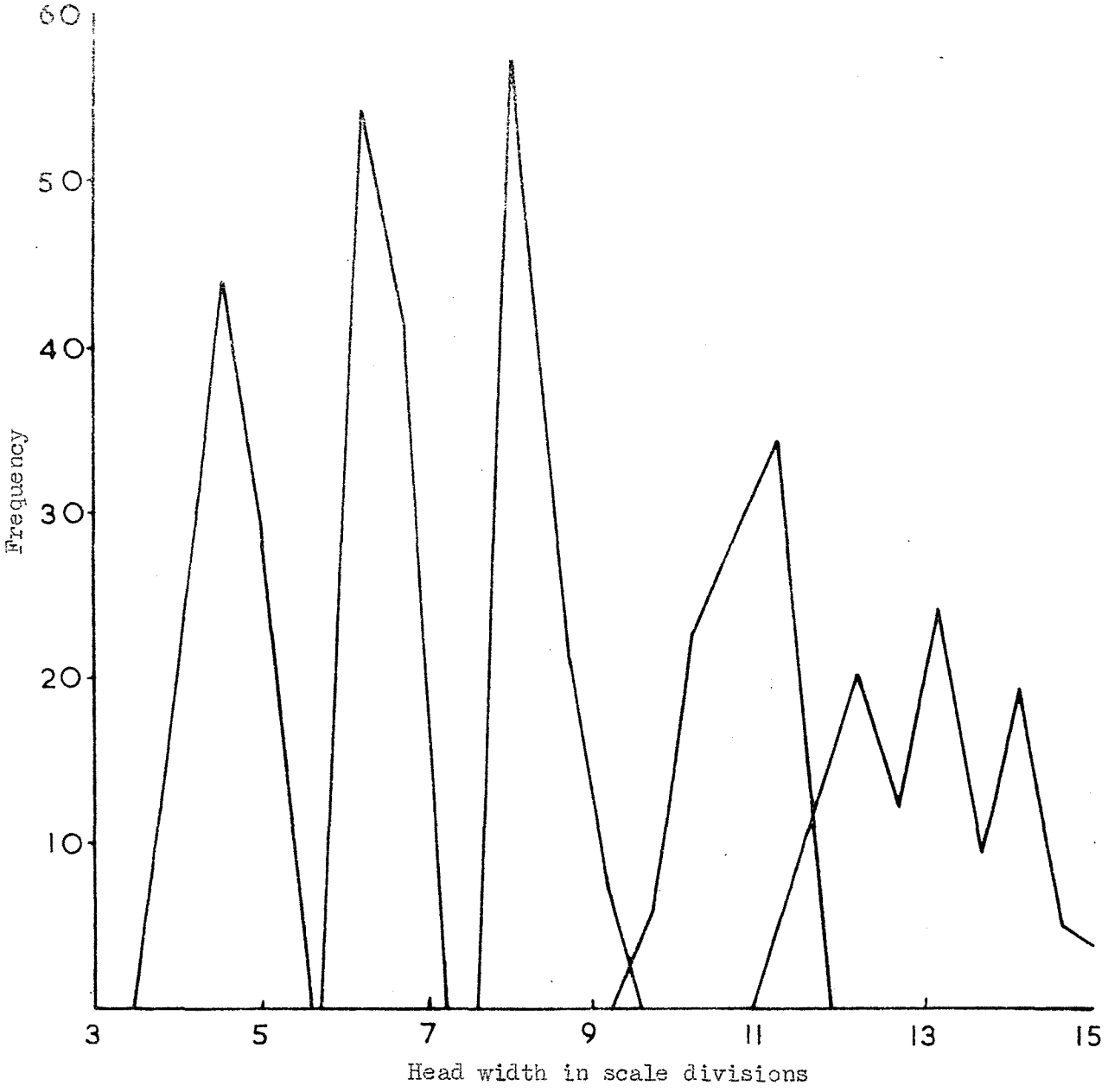


Fig. 3

Distribution of head width showing the five nymphal instars in Nysius huttoni

The five instars were shown to be distinct, but there was some overlapping of the third and fourth, and fourth and fifth instars. There was more spread in the fourth instar and greater spread in the fifth instar which exhibited a trimodal curve. A sex difference was expected because in the adults, males are smaller than females, but clearly more than a sex difference is represented. For Nysius coenosulus Stål, a bimodal distribution in the fifth nymphal stage was demonstrated by Usinger (1942). Although he could not distinguish their sex, he attributed the double peak to a sex difference. The author was able to distinguish the sex of fifth stage N. huttoni nymphs and considers that the trimodal curve may indicate three populations. Thus for eggs and nymphs, the distributions were not normal. The problem was further investigated in adults (see Chapter 3).

At this stage it was necessary to determine whether or not, a sex difference was involved. Accordingly, the body measurement data from Table 9 was divided into those for males and those for females, and the mean measurements for each morphological character in each sex, is shown in Table 11. Inspection of this data revealed that there were slight differences between the sexes in most characters. To elucidate this, analyses of variance were carried out on four main characters, namely head width, length of mesonotum at middle, width of pronotum and width of mesonotum, and are presented in Tables 12 - 15. In headwidth and length of mesonotum at middle there was no significant difference between the sexes. In width of pronotum, a difference between the sexes, significant at the five per cent level, was demonstrated. For width of mesonotum, however, the difference though measurable was not significant. Thus in three out of four characters, and in particular head width (on which the graph in question was drawn), no significant differences between the sexes could be demonstrated. Therefore, the trimodal graph has nothing to do with a sex difference, and it seems logical to conclude that three populations, differing in size, are represented. Further, in the preserved material, two groups of fifth stage nymphs were noted - short plump ones, which took on a greenish abdominal tinge in Carle's fixative, and larger, somewhat

narrower ones, which took on a yellowish abdominal tinge. A very small number were orange tinted. Also in all nymphal stages there did seem to be both short, plump individuals and longer, narrower individuals.

TABLE 10

FREQUENCY DISTRIBUTION OF HEAD WIDTH MEASUREMENTS FOR EACH MOULT INSTAR

All measurements are in eyepiece scale divisions: one scale division = 0.083 mm

Instar	Class Interval	Head Width (= class)	Frequency
1	3.5	3.2 - 3.7	1
	4.0	3.8 - 4.2	21
	4.5	4.3 - 4.7	44
	5.0	4.8 - 5.2	29
	5.5	5.3 - 5.7	5
			100
	Mean head width 4.5 (=0.38mm)		
2	5.7	5.5 - 5.9	2
	6.2	6.0 - 6.4	54
	6.7	6.5 - 6.9	41
	7.2	7.0 - 7.4	3
			100
	Mean head width 6.3 (= 0.40mm)		
3	7.7	7.5 - 7.9	14
	8.2	8.0 - 8.4	57
	8.7	8.5 - 8.9	21
	9.2	9.0 - 9.4	7
		9.5	1
			100
	Mean head width 8.2 (=0.50mm)		
4		<9.5	1
	9.7	9.5 - 9.9	6
	10.2	10.0 -10.4	23
	10.7	10.5 -10.9	29
	11.2	11.0 -11.4	34
	11.7	11.5 -11.9	8
			100
	Mean head width 10.7 (=0.67mm)		
5	11.2	11.0 -11.4	4
	11.7	11.5 -11.9	3
	12.2	12.0 -12.4	20
	12.7	12.5 -12.9	12
	13.2	13.0 -13.4	24
	13.7	13.5 -13.9	9
	14.2	14.0 -14.4	19
	14.7	14.5 -14.9	5
		15.0	4
			100
	Mean head width 13.1 (=0.85mm)		

TABLE 11

COMPARISON OF BODY MEASUREMENTS OF MALE AND FEMALE FIFTH STAGE NYMPHS

Morphological character	Mean measurement in scale divisions	
	Males	Females
Head length	7.9	8.7
Head width	12.1	12.6
Interocular width	7.8	8.1
Eye width	2.2	2.3
Anteocular length	4.5	4.4
Eye length	3.1	3.1
Rostral segment 1	6.0	6.0
" " 2	5.4	5.1
" " 3	4.1	4.2
" " 4	4.8	4.6
Antennal segment 1	3.7	3.9
" " 2	4.9	5.3
" " 3	4.0	4.1
" " 4	6.4	6.7
Pronotum length	6.9	7.0
Pronotum width	15.0	16.6
Mesonotum width at middle	6.8	6.2
Mesonotum length to tip of wing pad	13.4	13.3
Mesonotum width	19.2	21.3
Metanotum length	1.4	1.2
Forefemur	7.2	7.6
Foretibia	7.5	7.8
Foretarsus 1	2.1	2.0
Foretarsus 2	4.0	4.0
Midfemur	7.6	8.2
Midtibia	7.6	7.9
Midtarsus 1	2.2	2.1
Midtarsus 2	4.0	3.9
Hindfemur	9.9	10.2
Hindtibia	10.7	11.1
Hindtarsus 1	3.0	3.1
Hindtarsus 2	4.2	4.2
*Body length	41.0	39.2
*Abdomen width	18.5	21.1

*Not included in Table 9

TABLE 12

ANALYSIS OF VARIANCE FOR HEAD WIDTH

Source of Variation	Degrees of Freedom	Sums of Squares	Mean Square	F. value	F. required 5%	F. required 1%	Result
Sexes	1	1.08	1.08	2.92	4.54	8.86	N.S.
Remainder	15	5.62	0.37				
Total	16	6.70					

TABLE 13

ANALYSIS OF VARIANCE FOR LENGTH OF MESONOTUM AT MIDDLE

Source of Variation	Degrees of Freedom	Sums of Squares	Mean Square	F. value	F. required 5%	F. required 1%	Result
Sexes	1	1.44	1.44	2.89	4.54	8.86	N.S.
Remainder	15	7.53	0.50				
Total	16	8.97					

TABLE 14

ANALYSIS OF VARIANCE FOR WIDTH OF PRONOTUM AT POSTERIOR

Source of Variation	Degrees of Freedom	Sums of Squares	Mean Square	F. value	F. required 5%	F. required 1%	Result
Sexes	1	10.34	10.34	5.81	4.54	8.86	*
Remainder	15	26.70	1.78				
Total	16	37.04					

TABLE 15

ANALYSIS OF VARIANCE FOR WIDTH OF MESONOTUM

Source of Variation	Degrees of Freedom	Sums of Squares	Mean Square	F. value	F. required 5%	F. required 1%	Result
Sexes	1	13.49	13.49	2.95	4.54	8.86	N.S.
Remainder	15	68.75	4.58				
Total	16	82.24					

By dividing the mean head width for each instar by that of the previous instar, the growth ratio between any two successive instars was obtained. The calculation of the mean growth ratio is set out in Table 16.

TABLE 16

CALCULATION OF MEAN GROWTH RATIO

Instars		Mean Head Widths		Growth Ratios
2nd / 1st		6.3 / 4.5		1.40
3rd / 2nd		8.2 / 6.3		1.30
4th / 3rd		10.7 / 8.2		1.30
5th / 4th		13.1 / 10.7		1.22
		Mean growth ratio for nymphal stages,		1.31
Adult / 5th	Adult ♂ / 5th ♂	13.5 / 12.1	1.10	1.11
	Adult ♀ / 5th ♀	14.0 / 12.6	1.11	
		Overall mean growth ratio from first instar to adult		1.266

Usinger (1942 working on N. coenosulus nymphs obtained a mean growth ratio of 1.38 which is near Przibram's theoretical progression factor of 1.26. With N. huttoni, the mean growth ratio for the nymphal stages was 1.30 which is very near Przibram's factor. As the head width measurements of adults were also available, the growth ratio between the fifth stage nymph and the adult was calculated. Head width measurements of 100 adults are shown in Appendix IIIb. As the nymphs could be sexed in the fifth stage, and because there was a size difference between sexes in the adult, the ratio was calculated for each sex. The headwidths of the fifth stage nymphs used were those shown in Table 11. The ratios obtained, 1.10 and 1.11 were also in reasonable agreement with Przibram's factor and showed that there was the same relative increase in growth in males and females.

The overall mean growth ratio, from first instar to adult came to 1.266 correct to three decimal places, and this almost equals Przibram's factor. The ratio between the final nymphal instar and the adult should be included in the mean ratio because growth does occur between these two instars.

Image

The original description is reproduced here:

Nysius huttoni White (1879), Ent. Monthly Mag. 15 : 33

"Obovate, greyish-testaceous with grey pubescence and coarse fuscous punctures; head rather finely punctuate, black, the vertex and the antennae reddish-brown, the outside of the 1st joint of the antennae, the 2nd and 3rd towards the apex, and the 4th darker; pronotum with a transverse band near the front margin, a central longitudinal band abbreviated before and behind, the sides, and some spots within the hind angles, irregularly black, as is almost all the scutellum except the extreme apex. Elytra streaked more or less with black, the extreme front margin and three spots more or less confluent on the apical margin, always fuscous-black; membrane whitish, spotted with fuscous at the base; legs yellow-testaceous, spotted (especially the femora) and punctured with black; the 1st and 2nd joints of the tarsi at the base, and the whole of the 3rd, fuscous-black; body below black marked with yellow. Head sub-equal in length to the pronotum, and with the eyes somewhat broader than the apex of the latter the bucculae not reaching the base of the head, scarcely decreasing in height backwards and suddenly ending, about equal to the 1st joint of the rostrum; rostrum reaching the hind coxae; 1st joint of the antennae much, and the 2nd a little longer than the 3rd. Scutellum with a triradiate elevation in the middle. Elytra sub-parallel at the base, then dilated and reflexed along the front margin. Length, 3½-4mm.; breadth, 1⅝mm."

Although satisfactory for identification purposes, the above description does not conform to present day standards. Accordingly it is redescribed below. At this juncture, it is necessary to explain that what is now designated as N. huttoni can be demonstrated to comprise three size groups. This matter is considered in some detail in the second part of Chapter 3. From the sizes given in the original description, there can be no doubt that it applies to the large population, and accordingly, the redescription was made on that population.

Definitions of Terms Used

Measurements of adults were taken from specimens mounted on points. Antennae, rostrum and legs, were measured by tipping the insects so that the desired part was in the horizontal plane. All other measurements were taken from directly above

the insect, when it was in a normal horizontal position as depicted in Plate 3. Usinger (1942) said, "Specimens were measured by tipping the insects so that the desired parts were in the same plane". Thus, as the Orsilline head is somewhat declivous, head length measured after Usinger's method would be longer than when measured after the author's method. The latter method was considered more practicable, because the lengths of all parts could then be added together to equal the measurement obtained for the total length of the insect as defined below. The measurements used by Usinger have been followed, with some additions, and the alteration in head length. Some of the terms used in the descriptions and Tables are self-explanatory, but others needing further amplification are defined below.

Length of head from posterior of head to tip of tylus (measured from directly above the insect).

Width of head including eyes.

Anteocular length measured from level of front margins of eyes to apex of tylus (from directly above insect, as in head length).

Interocular width is the shortest distance between inner margins of eyes.

Antennae and rostrum each segment measured individually and then added together for the total length.

Length of pronotum on median line.

Length of membrane from apex of commissure clavus to posterior of membrane.

Length of membrane beyond level of apices of coria, measured from an imaginary line drawn across these apices, to posterior of membrane.

Length of membrane beyond posterior of abdomen. Usinger measured this from the dorsal surface, but the author found that inverting the specimen for this measurement gave greater accuracy, as many membranes were not clear.

Length of corium on a straight line from basal articulation at humeral angle to outer apical angle.

Width of insect is the distance across broadest part of hemelytra.

Length of insect measured in a single plane from apex of tylus to posterior of membrane in macropterous and sub-brachypterous forms, and to posterior of

abdomen in brachypterous forms.

The author included for following additional measurements

Legs, each segment measured individually, total length of forewing, and where possible, total length of hindwing, and length of hindwing exceeding posterior of abdomen.

One measurement, the point of branching of the vein R + M, mentioned by Usinger was not taken on N. huttoni because this point could not be readily ascertained.

The term macropterous refers to insects in which the wings exceed the posteric of the abdomen. Sub-brachypterous is a term taken from Woodward (1954), and refers to insects in which the posterior of the wings is level with the posterior of the abdomen. I have included in this group insects in which the wings scarcely exceed the posterior of the abdomens because in possessing convex and strongly rounded wings, they clearly belong here. The term brachypterous refers to insects in which the posterior of the wings does not reach the posterior of the abdomen.

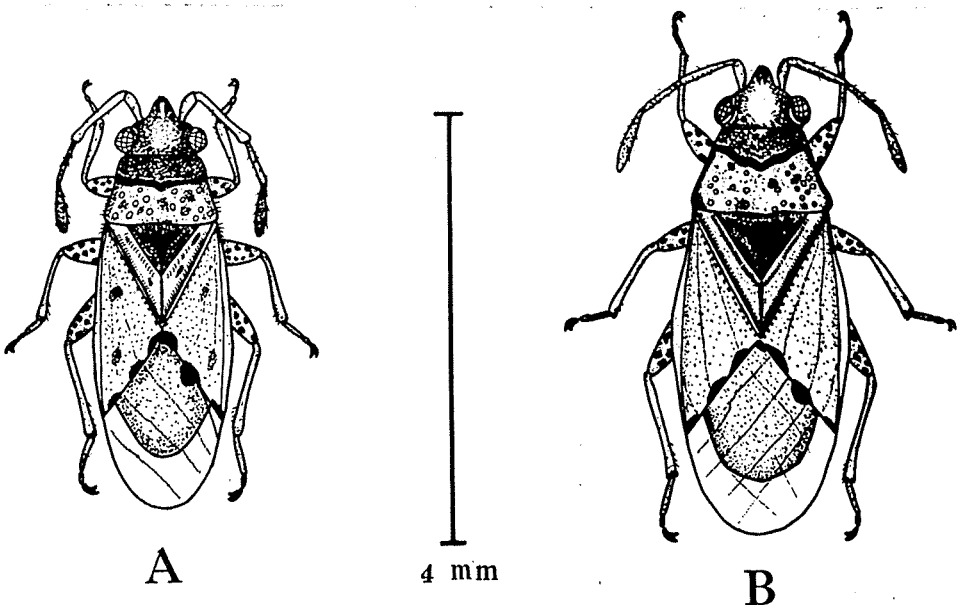
Imago redescription: (Plate 2 A and B, Plate 3 A and B, and Table 17)

Head: approximately two thirds broader than long, 3.6:2.3; extending well beyond middle of first antennal segment; covered by a fine pubescence; eyes less than half as wide as interocular space, 0.8:2.0; length of eye equal to anteocular length, 1.0:1.0. Bucculae scarcely decreasing in height posteriorly and suddenly ending before posterior margin of head. Rostrum extending to posterior coxae, and resting in a groove on underside of head, and partially in a shallow groove on ventral surface of thorax; first segment shorter than head, 2.0:2.2; segments one to four 2.0 - 1.9 - 1.7 - 1.4. Antennae a little more than twice width of head, 7.3:3.6; as long as head, pronotum and scutellum together, 7.3:7.3; segments one to four 1.2 - 2.3 - 1.7 - 2.1.

Thorax: Pronotum almost one third longer than head, 2.9:2.2; approximately as broad anteriorly as long, 3.1:2.9; two thirds broader posteriorly than

Nysius huttoni adults, dorsal.

A macropterous male, large population; B macropterous female, large population; C sub-brachypterous female, medium population; D brachypterous female, medium population; E sub-brachypterous male, small population; F sub-brachypterous female, small population.



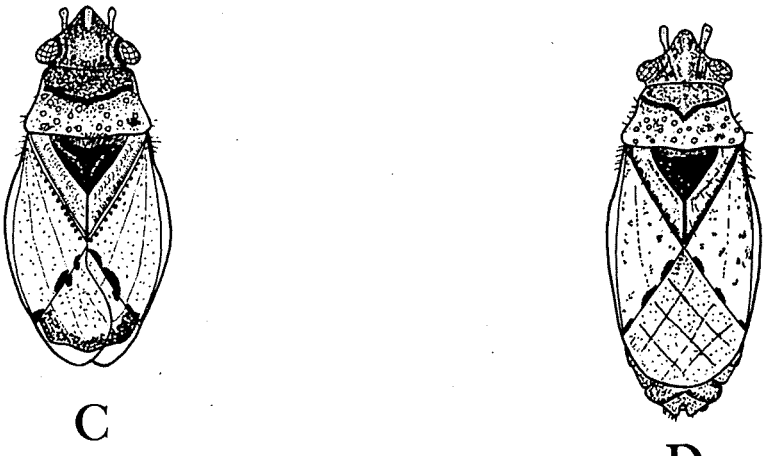
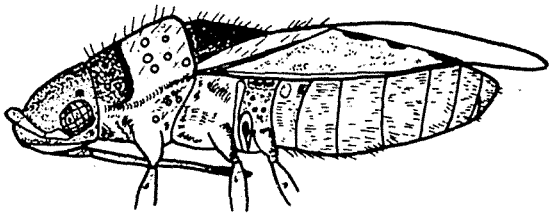


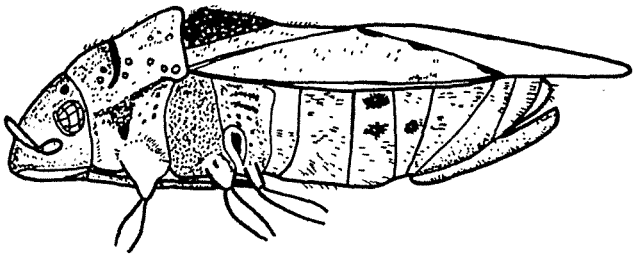
PLATE 3

Hyalus huttoni adults, lateral

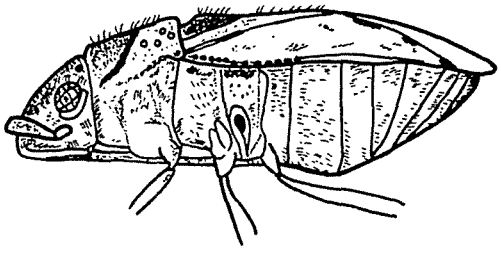
A - C as in Plate 2; D sub-brachypterous male, small population.



A

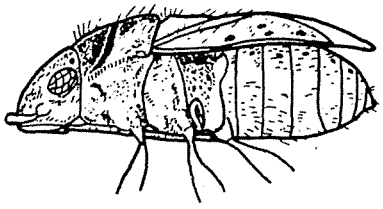


B



C

2 mm



D

long, 4.9:2.9; sides straight; posterior edge slightly convex; punctate, but sometimes only in paler, posterior portion. Scutellum broader than long, 3.2:2.2; with a triradiate elevation in the centre; sometimes very sparcely punctate. Pronotum and scutellum covered by coarse hairs, but in the female, only by a fine pubescence.

Hemelytra: scarcely to slightly convex; exceeding tip of abdomen by one fourth length of membrane, 1.5:6.2; membrane one seventh shorter than costal margin of corium, 6.2:7.2; the portion of membrane posterior to level of apices of coria approximately as long as the portion anterior to this, 3.2:3.0; costal margins straight but diverging almost to apex of scutellum and then arcuate. Three black blotches more or less confluent along suture between corium and membrane; embolium distinct, 0.5 scale divisions at greatest width; clavus and corium covered by a fine pubescence;membrane veined and opaque, but sometimes clear. Hindwings slightly shorter than fore wings, 9.6:10.6; usually extending a little beyond posterior of abdomen.

Legs: femora spotted, forefemora shorter than midfemora, midfemora shorter than hindfemora, 3.0:3.5:4.6; foretibiae shorter than midtibiae, midtibiae shorter than hindtibiae, 2.8:3.0:4.8; second tarsal segment shortest, 0.5; first and third tarsal segments of equal length on fore- and midlegs, 0.8; but first segment longer than third on hind tarsus, 1.3:0.9.

Female: larger in general, and in particular broader across hemelytra; ovipositor cleft more than half length of abdomen.

Size: Male: mean length 5.74 mm.; mean width (head) 0.86 mm.; (hemelytra) 1.37mm
Female: mean length 4.00 mm; mean width (head) 0.94 mm.; (hemelytra) 1.67 mm.

Colour:

Head:black (Ostwald series II, 2 pn) sometimes completely, but usually mid dorsal surface lighter in colour to reddish brown (varying in extent);

TABLE 17

[illegible] OF ADULTS

All measurements are in micrometer units : one micrometer unit = 0.[illegible] mm

Head Length	Head Width	Inter-ocular Width	Eye Width	Ante-ocular Length	Eye Length	Rostral Segments 1	2	3	4	Antennal Segments 1	2	3	4	Pronotum Length	Pronotum Width Anterior	Pronotum Width Posterior	Scutellum Length	Scutellum Width	Body Length	Body Width
2.3	3.5	2.0	0.8	1.1	1.1	2.1	2.0	1.8	1.5	1.2	2.4	1.7	[illegible]	3.6	4.1	4.6	3.5	3.1	10.1	5.0
2.2	3.6	2.0	0.9	1.0	1.0	2.0	1.8	1.6	1.3	1.4	2.4	2.6	[illegible]	3.0	4.1	[illegible]	3.3	3.4	13.9	[illegible].7
2.0	3.8	2.0	0.8	1.1	1.0	1.9	2.0	1.8	1.7	1.0	2.3	2.0	[illegible]	3.0	3.1	[illegible]	3.0	3.3	13.7	[illegible].6
2.4	3.7	2.0	0.8	1.0	1.0	2.0	1.8	1.5	1.3	1.2	2.0	1.6	[illegible]	2.9	3.1	[illegible]	3.1	3.0	13.7	[illegible].7
2.0	3.6	1.9	0.8	1.0	1.1	2.0	1.8	1.6	1.4	1.2	2.5	1.7	[illegible]	2.6	3.2	[illegible]	3.3	3.0	14.0	[illegible].5
2.2	3.6	2.0	0.8	1.0	1.0	2.0	1.9	1.7	1.4	1.2	2.5	1.7	2.1	2.9	3.1	[illegible]	[illegible].3	3.2	[illegible].6	[illegible].5
2.0-2.4	3.5-3.8	1.9-2.0	0.8-0.9	1.0-1.1	1.0-[illegible]	[illegible].3-2.1	1.6-[illegible].0	1.5-1.8	1.2-1.7	1.0-1.4	2.3-[illegible].0	1.6-[illegible].0	1.6-[illegible].3	2.6-3.0	3.1-[illegible].3	[illegible].[illegible]-[illegible].[illegible]	[illegible].[illegible]-[illegible].[illegible]	3.0-3.4	[illegible].[illegible]-[illegible].[illegible]	[illegible].[illegible]-[illegible].[illegible]
0.21	0.12	0.05	0.05	0.07	0.07	0.07	0.10	0.14	0.20	0.14	0.19	0.17	0.24	0.17	0.10	[illegible].1	[illegible].0	0.19	0.0	0.19
2.0	4.0	2.4	0.8	1.2	1.0	2.0	2.0	1.6	1.4	1.3	2.6	1.8	[illegible].2	3.5	3.4	[illegible]			13.3	[illegible].3
2.4	3.8	2.3	0.8	1.2	1.1	2.0	1.5	1.4	1.6	1.3	2.3	1.7	[illegible].2	3.0	3.3	[illegible].4			13.3	[illegible].7
2.5	4.0	2.4	0.8	1.3	1.1	2.0	1.6	1.4	1.4	1.2	2.4	1.7	[illegible].3	3.4	3.0	[illegible].0			13.0	[illegible].0
2.2	3.9	2.3	0.8	1.2	1.1	2.2	1.8	1.5	1.5	1.2	2.0	1.6	[illegible].3	[illegible].3	3.5	3.6			13.7	[illegible].9
2.1	4.0	2.4	[illegible].8	1.0	1.0	2.1	1.8	1.7	1.4	1.2	2.4	1.6	[illegible].2	3.0	3.7	3.9			13.[illegible]	[illegible].0
2.3	3.9	2.4	0.8	1.2	1.1	2.1	1.7	1.5	1.5	1.2	2.3	1.8	[illegible].6	[illegible].1	3.6	3.7			[illegible].7	[illegible].9
2.0-2.5	3.8-4.0	2.3-2.4	0.8	1.0-1.3	1.0-1.1	2.0-2.2	1.5-2.0	1.4-1.7	1.4-1.6	1.2-1.3	2.0-[illegible].6	1.7-1.8	[illegible].[illegible]-[illegible].[illegible]	[illegible].0-[illegible].4	3.3-3.9	5.4-5.9			[illegible].0-[illegible].[illegible]	[illegible].7-7.3
0.021	0.11	0.07	0	0.07	0.07	0.01	0.20	0.13	0.10	0.70	0.45	0.07	[illegible].37	0.20	0.25	0.20			[illegible].[illegible]	0.34

Hemelytra Length of Membrane Total	Beyond apices of coria	Beyond abdomen	Length of Corium	Total wing length	Hindwings Total wing length	Length beyond abdomen	Femora Fore	Mid	Hind	Tibiae Fore	Mid	Hind	Tarsi Fore 1	2	3	Mid 1	2	3	Hind 1	2	3
6.6	3.5	1.6	7.4	11.0			2.8	3.5	5.0	2.5	[illegible].8	[illegible].3	[illegible].[illegible]	[illegible].[illegible]	[illegible].9	0.7	0.5	0.7	1.1	0.5	0.8
6.4	3.3	1.7	7.8	11.0	9.7	0.4	3.0	3.5	[illegible].4	3.3	3.5	[illegible].4	[illegible].[illegible]	[illegible].[illegible]	[illegible].7	0.9	0.4	0.5	1.5	0.5	0.8
6.1	2.5	1.6	7.3	10.7			3.1	3.6	4.5	2.3	2.8	[illegible].8	0.3	[illegible].4	0.8	0.9	0.4	0.7	1.4	[illegible].6	[illegible].9
6.3	3.7	1.9	6.9	10.4			3.0	3.2	4.2	2.9	2.7	[illegible].0	0.7	0.5	0.9	0.8	0.4	0.8	1.2	0.4	0.9
5.8	2.8	0.8	6.8	9.9	9.4	0.3	3.0	3.5	4.8	3.0	3.0	[illegible].9	0.8	0.5	0.9	0.7	0.4	0.8	1.4	[illegible].5	0.9
6.2	3.2	1.5	7.2	10.6	9.6	0.4	3.0	3.5	4.6	2.8	[illegible].0	4.8	0.8	0.5	0.8	0.8	0.4	0.7	1.5	0.6	0.9
5.8-6.6	2.5-3.7	0.8-1.9	6.8-7.8	9.9-11.0	9.4-9.7	0.3-0.4	2.8-3.1	3.2-3.6	4.2-5.0	2.5-3.3	2.7-[illegible].5	4.0-[illegible].4	0.7-0.8	0.4-0.5	0.7-0.9	0.7-0.9	[illegible].4-[illegible].5	0.5-0.8	1.1-1.5	0.4-0.6	[illegible].8-0.9
0.31	0.50	0.38	0.41	0.46	0.31	0.31	0.11	0.16	0.91	0.40	[illegible].32	[illegible].38	0.05	0.05	0.10	[illegible].10	0.05	0.12	0.17	0.071	0.071
7.8	4.0	1.9	9.0	12.8			[illegible].5	[illegible].7	[illegible].5	[illegible].0	[illegible].[illegible]	[illegible].9	1.0	0.5	0.9	1.0	[illegible].5	[illegible].0	1.5	[illegible].7	1.3
6.8	3.4	1.8	7.9	10.2	9.7	1.5	[illegible].0	3.4	4.9	2.9	3.0	4.0	0.8	0.4	0.6	0.7	0.4	0.7	1.2	0.5	[illegible].8
6.5	3.0	1.4	8.4	11.4			[illegible].5	[illegible].5	[illegible].2	[illegible].2	[illegible].7	[illegible].0	0.6	0.4	0.9	[illegible].7	[illegible].4	[illegible].8	1.3	[illegible].4	0.7
6.8	3.4	1.7	8.2	11.5	10.8	1.0	[illegible].2	[illegible].6	[illegible].0	[illegible].0	[illegible].5	[illegible].5	0.6	0.4	0.8	[illegible].7	0.4	0.7	1.3	0.5	0.8
6.8	4.2	1.8	8.2	11.4	10.5	0.7	[illegible].0	[illegible].2	[illegible].3	[illegible].0	[illegible].2	[illegible].2	0.8	0.4	0.8	[illegible].6	[illegible].5	[illegible].9	1.5	0.5	[illegible].9
6.9	3.6	1.7	8.3	11.5	10.3	1.0	[illegible].2	[illegible].5	[illegible].2	[illegible].0	[illegible].4	[illegible].5	0.8	[illegible].4	0.7	[illegible].6	0.4	[illegible].0	1.6	0.5	0.9
6.5-7.8	3.0-4.2	1.4-1.9	7.9-9.0	10.2-12.8	9.7-10.8	0.7-1.3	[illegible].0-[illegible].5	[illegible].2-[illegible].7	[illegible].9-[illegible].5	[illegible].9-[illegible].2	[illegible].0-[illegible].7	[illegible].9-[illegible].0	0.6-0.1	[illegible].4-[illegible].5	[illegible].[illegible]-[illegible].9	[illegible].7-1.0	[illegible].4-[illegible].5	[illegible].7-[illegible].9	1.2-1.8	0.5-0.7	0.7-1.3
0.50	0.49	0.20	0.41	1.05	0.55	0.44	0.21	0.12	0.24	0.11	[illegible].28	[illegible].46	0.17	[illegible].35	0.19	0.12	0.071	[illegible].[illegible]	0.26	0.10	0.24

eyes reddish brown (O. IV, 5 pl); antennae yellowish brown (O.VIII, 4 lc) on first and second segments, third and fourth segments dark brown (O. IV, 4 pl); rostrum black (O. II, 2 pn).

Pronotum: has a densely black (O. series O, p) transverse band one third total length from anterior margin; usually black (O. II, 2 pn) in anterior half and mainly pale buff or dull straw yellow (O. IV, 2 gc) in posterior half, but sometimes completely black. Scutellum black (O. II, 2 pn).

Hemelytra: usually pale buff or dull straw yellow (O. IV, 2 gc) but sometimes variegated with black; membrane varies from pale buff to cloudy white to almost clear; three black blotches along each corial suture.

Legs: also pale buff, femora spotted black, third tarsal segment dark brown (O. IV, 4 pl).

Plesiotypes, males and females (Entomology Division of the D.S.I.R.), Nelson, January 1950, L. Gurr.

No short wing forms of the large population have been found. A possible explanation is that a reduction in wing length may be accompanied by a reduction in wing width in which case the shorter winged individuals would be placed in the medium population. If later, short wing forms are found, then this description will need to be extended to include all forms.

The redescription should be compared with the description of Brachynysius convexus Usinger (1945) which is probably the closest relative, and the Brachynysius genus description. The two species are very similar except for the wings. In both species, the antennal proportions are approximately the same, the ratio width of scutellum to length of scutellum is approximately the same, and the antennae are as long as head, pronotum and scutellum together. However, when head length is measured after Usinger's method, the latter ratio is altered slightly in N. huttoni but then the lengths of head and pronotum become equal. Of the Brachynysius head

Usinger (1943) said, "Head as in typical Mysius ..." No rostral proportions are given for B. convexus except the first segment which is similar to that of N. huttoni, as are also the bucculae. After consideration of the variation exhibited in N. huttoni (Chapter 3), the validity of B. convexus and of Brachymysius are discussed.

CHAPTER 3

WING-POLYMORPHISM AND SIZE VARIATION IN N. huttoni

From examination of 900 field specimens mounted on points, and at least another 1000 field specimens preserved in Carle's fixative, it was obvious that the range of variation within the species was great. Three forms, macropterous, sub-brachypterous and brachypterous were present (see Plate 2). At first, an attempt was made to determine the influence of temperature during nymphal development on the wing form expressed in the imago, because work by Wigglesworth (1952) on Rhodnius prolixus Stål, indicated that high temperature favoured macroptery, and low temperature, sub-brachyptery.

There are a few Hawaiian Orsilline species which have relatively short wings, but in almost every case one form only, occurs (Usinger, 1942). Nesosis (Trachynysius whitei brachypterous Usinger (1942), was made a separate sub-species because it had a shorter wing. It seemed likely that the three forms in N. huttoni were three different forms of the same species, for two forms occur in Cymus novaezelandiae Woodward (1954) which belongs to the subfamily Cyminae, and is also endemic to New Zealand. By interbreeding macropterous and sub- brachypterous forms (both ways), it was hoped to elucidate this problem.

The specimens also differed in size, and there seemed to be three size groups. Later, it became clear, that if any divisions were to be made, they would be on size and not wing form, because all three forms occurred in at least two of the size groups. The three methods (outlined above) of studying the variation within N. huttoni are discussed separately.

(a) VARIATION IN WING FORM

Effect of Temperature on Wing Form

The three forms seemed to occur naturally in both sexes. Wigglesworth (1952) showed with R. prolixus nymphs that a high temperature (34°C) in the fourth stage

produced larger than normal wing pads in the fifth stage, whereas a low temperature (18°C) produced smaller than normal wing pads. The optimum temperature for nymphal development was 28-30°C. Accordingly, fourth stage nymphs of M. huttoni were subjected to one of three temperature ranges, to test the possibility that high temperature favoured macroptery, and low temperature brachyptery. The temperatures chosen were: high, 34°C, in a controlled temperature cabinet; low, minimum 9.4-15.6°C, maximum 17-21°C, in the shade of a barn in December; normal, minimum 0.7-13.9°C, maximum 27.8-34.4°C, in a greenhouse over a complete season (September to March).

Results at High Temperatures

The nymphs were kept in glass tubes, covered at one end by butter muslin and stopped at the other with cotton wool plugs. A sprig of twin cress (Coronopus didymus (L.) Sm.) was replaced daily for food. Relative humidity was maintained by the presence of a bowl of water in the temperature cabinet. Five nymphs were placed in each tube, and generally two tubes at a time were tested. A total of eleven tubes of nymphs were subjected to varying temperatures, and the results are shown in Table 18.

TABLE 18

FORMS OF ADULTS PRODUCED WHEN NYMPHS SUBJECTED TO HIGH TEMPERATURES

Tube Number	Temperature, °C	Adults produced Males	Females	Wing Form	Stage of Nymphs when caught
1	34	2	1	sub-brachypterous	5th
2	34	4		" "	5th
3	34	2		" "	-
"		1		macropterous	-
4	34-35	4	3	sub-brachypterous	3rd
5	36.3		2	" "	4th
6	36.3	2	1	" "	4th
7	47	Died as nymphs			-
8	44	Nymphs lived 2 days			4th
9	44	Nymphs lived 4 days			4th
10	41.7		1	macropterous	4th
11	41.7	Died as nymphs			-

The stages of the nymphs when the experiment was set up (shown in the last column of Table 18), were confirmed by the number of exuviae left in the tubes. In the first two tubes together, the nymphs which were thought to be at the fourth stage, must have been at the fifth stage, for there were only seven exuviae (the remaining nymphs dies without moulting). The selection as fourth stage nymphs was made by naked eye on what seemed to be an obvious size difference, i.e. all the largest nymphs (fifth stage) were removed, and those next size down were taken as fourth stage. There are three possible explanations:

(1) that for M. huttoni a temperature of 34°C favoured adult characteristics to the extent that a premature moult to the adult occurred from the fourth nymphal stage.

(2) that fifth stage nymphs differ in size according to sex

(3) that two races were represented, each differing in size.

An explanation of type (1) has never been reported and seems doubtful, especially when later replications using genuine fourth stage nymphs moulted first to the fifth stage. The second explanation was disproved by the production of both sexes from these small fifth stage nymphs. The third explanation, therefore, seemed the most likely.

No brachypterous forms were produced. The majority of adults produced were sub-brachypterous. At 41.7°C/the one adult produced was macropterous, but there are no grounds for saying that at that temperature macroptery is favoured. On the contrary, from the evidence from all adults produced it was clear that high temperature did not favour macroptery.

In the case of tube 7, the temperature was 47°C, but this rose to 51°C on the second day, and was then reduced to 43°C. The nymphs died on the third day, before moulting. Thus the temperature range 47-51°C was definitely fatal, and from the results of tubes 8-10, the temperature of 43°C was probably also fatal. Tubes 8 and 9 were of especial interest. The nymphs in tube 8 survived only two days and did not moult. There was one sprig of twin cress placed in the tube. Tube 9 had two sprigs of twin cress. The nymphs died on the fourth day when the temperature

in the cabinet rose to 50°C (because of a sudden increase in outside day temperature). Further some moulted to the fifth stage before death occurred. Transpiration from a greater leaf surface in tube 9 raised the relative humidity sufficiently to permit longer survival. Therefore, the temperature of 44°C was very near the upper limit of temperature tolerance, which fell between 44°C and 50°C for survival of fourth and fifth stage nymphs. At high temperatures, relative humidity becomes a vital factor to survival, and as the nymphs died after moulting, it was probably in the critical period immediately following, and before the exoskeleton had hardened, that death occurred. Tubes 10 and 11 from which one adult was produced compared with tubes 6-9, indicated that a temperature of 41.7°C was probably the upper temperature limit allowing growth and moulting to the adult. Contrary to A. prolixus nymphs (Wigglesworth 1952), moulting at high temperatures (34-42°C) in H. huttoni was not retarded, but rather hastened.

Results at Normal Temperatures

Fourth stage nymphs from the field were reared in glass tubes in a greenhouse, and the form of the adults produced are shown in Table 19.

TABLE 19

FORM OF ADULTS PRODUCED AT NORMAL TEMPERATURES

Tube number	Adults produced Males	Females	Wing form	Stage of nymphs when caught
1	2		sub-brachypterous	5th
2	3	2	" "	5th
3	1	1	macropterous	5th
"	2		sub-brachypterous	5th
4	1	4	" "	4th
5	2	1	brachypterous	4th

From the number of exuviae, it was ascertained that in the first three tubes, the nymphs were at the fifth stage and not the fourth stage when caught. As the

same situation arose with the nymphs at high temperatures, the third explanation offered, i.e. that two races, differing in size were represented, is further supported. To the naked eye, both fourth and fifth stage nymphs appeared to be greyish-brown or reddish-brown on the abdomen, whilst earlier stages were orange. However, microscopic examination showed that the so called fourth stage nymphs were actually small fifth stage nymphs (because of wing pad development) and that fourth and earlier stages were orange-coloured on the abdomen.

In the normal temperature group, the forms of all adults reared from eggs in the greenhouse for fecundity and life cycle data and other information, have also been included, and are shown in Table 20. However, the experiment summarized in Table 19, for which the starting material was nymphs at (about) the fourth stage, was necessary for a comparison with the results from high and low temperature groups.

TABLE 20

FORMS OF ADULTS REARED AT NORMAL TEMPERATURES

	Number of insects	Macropterous males	Macropterous females	Sub-brachypterous Males	Sub-brachypterous females	Brachypterous Males	Brachypterous females
1st Generation	24	2	1	16	4		1
2nd "	26	3	1	10	5	1	6
3rd "	15	2	3	2	6	2	
4th "	2			2			
Progenies of cross series A	10	2		4	4		
Progenies of cross series B	13	2		4	4	1	2
Total	90	11	5	38	23	4	9

From the results shown in Tables 19 and 20 it is clear that the sub-brachypterous form was the most common form in both sexes, at normal temperatures. Of the macropterous form there were more males than females, but of the brachypterous form there were more females than males.

Results at Low Temperatures

Altogether seven adults were produced, two sub-brachypterous females, two brachypterous females and three brachypterous males. The mid-range temperatures were, maximum 10°C, and minimum 12.5°C. The range of times for development from fourth stage to the adult were 38-40 days. Later, two sub-brachypterous females were reared right through from eggs at this temperature range. No macropterous forms were produced. There was a slight tendency for the brachypterous form to increase in proportion (compared with the normal temperature result), but there were insufficient numbers to make any definite statement on this matter.

Conclusions

In conclusion, the evidence from the three temperature ranges indicated that in N. huttoni

(1) sub-brachyptery is normally the most common form of the species in both sexes

(2) subjection to high temperatures during the last two nymphal instars did not favour macroptery, but tended to suppress it, and also suppressed the brachypterous form

(3) subjection to low temperatures caused some increase in the brachypterous form, but suppressed the macropterous form.

As the number of insects studied at the two extremes of temperature were relatively small (especially in the low temperature group), this conclusion is presented tentatively, and further work should be undertaken.

Extremes of temperature during nymphal development appear to have a slight influence on wing form, mainly in suppressing the macropterous form; the sub-brachypterous form is probably the most common at all temperatures. Temperature probably is not a major factor in the determination of wing form in this species.

When it was discovered that there were three size groups in N. huttoni all the insects included in this experiment were examined and found to belong to the medium and small populations. Therefore, the above results and conclusions apply only to these two populations.

Crossing of Macropterous and Sub-brachypterous Forms

Crossing was necessary to determine whether or not the three forms were merely different forms of one and the same species. The insects used were called the Cross Series and are later referred to as such in the section on Bionomics.

As a preliminary, from field specimens, sub-brachypterous males were paired with macropterous females, and vice versa, to see if they would copulate. If they did not, then this simple test would have saved the time required to rear virgin adults from nymphs. All pairs copulated freely. Later, individuals of both forms were seen copulating in the field, and from examination of pairs preserved in copula it is clear that in the field all forms intercopulate in all combinations as follows:-

macropterous male with macropterous female
macropterous male with sub-brachypterous female
macropterous male with brachypterous female
sub-brachypterous male with macropterous female
sub-brachypterous male with sub-brachypterous female
sub-brachypterous male with brachypterous female
brachypterous male with macropterous female
brachypterous male with sub-brachypterous female
brachypterous male with brachypterous female

To simplify the experiment, only macropterous and sub-brachypterous forms were crossed. Virgin adults were obtained by keeping individual fifth stage nymphs separate. Two series were set up. Cross Series A, consisting of six pairs (A1 to A6), in which the females were sub-brachypterous (with the exception of female A6 which was brachypterous) and the males macropterous. Cross Series B, consisting of five pairs (B1 to B5), in which the females were macropterous and the males sub-brachypterous.

The eleven matings were all successful, for eggs were laid which later hatched, and the progeny also mated and bred. All three wing forms were produced, but

there was a majority of the sub-brachypterous form (see lower portion of Table 20). There was no noticeable reduction in fertility (hatchability) in either Cross Series A or Cross Series B, in comparison with that for the normal breeding experiments in which pairing was random.

When it was discovered that there were three size groups in N. huttoni (see part (b) of this Chapter), the insects used in the above experiment were examined and found to fall mainly within the medium sized population. However, two or three were of the small population, and male A6 was of the large population.

The experiment clearly demonstrated that the three forms are members of one and the same species. Woodward (1952) showed that in the British coreid Myrmus miriformis (Fallén), macropterous and brachypterous forms occur in both sexes, but the brachypterous form is by far the commoner (95% of those collected). The appearance of even two forms in the one species is very rare amongst the Orsillini, there being about two cases in the Hawaiian species (Nysius terrestris Usinger 1942 and Nysius longicollis Blackburn), but in both cases it is a sex difference, there being a somewhat shorter wing in the female. N. huttoni appears to be unique amongst the Orsillini, in occurring in three forms in both sexes.

VIEWS ON THE CAUSE OR CONTROL OF PTERYGO-POLYMORPHISM

Pterygo-polymorphism is common among Hemiptera (Butler 1923, Myers 1926, Woodward 1952, 1954 and 1957, and Kisimoto 1957). Although varying wing forms appear to be rare among the Orsillini, that this should apply to all such species does not necessarily follow. B. convexus is sub-brachypterous, and this is the only form of that species. Therefore N. huttoni seems to be unique among the Orsillini in existing in three forms. Further, there are varying degrees of wing reduction between each form. Butler (1923) in speaking about Stål's terms macropterous and brachypterous, says

> "... such a nomenclature, however, very inadequately expresses the true state of affairs; for the abbreviation of the organs of flight may and does exist in very various degrees in different species, and sometimes even in the same..."

Further, he mentions that in many species of Lygaeidae, both forms exist in each sex, though seldom equally commonly. In the N. huttoni population studied, the majority of males and females were sub-brachypterous. The three forms occurred in both sexes, but of the macropterous form there were more males than females, and of the brachypterous form more females than males. The effect of high temperature indicated by Wigglesworth (1952) did not apply in the case of N. huttoni, but the effect of low temperature was that brachypterous forms tended to increase. However, temperature is probably not a major factor in the determination of wing form in this species.

Kisimoto (1956b) showed with the brown plant hopper Nilaparvata lugens Stål, that the degree of crowding as nymphs influenced the wing form expressed in the adult. As the density (d) increased above 1 in the female and above 5 in the male, the proportion of macropterous forms increased reaching almost 100% when d = 20. No brachypterous males were produced when d = 1, but a maximum of 71.4% when d = 5, whereas in the female when d = 1, all adults produced were brachypterous. In the case of N. huttoni, usually 5 nymphs were reared per tube. As the sub-brachypterous form was produced in the greatest proportion, it is possible that a density of 5 was optimum for the production of that form. However, as no other densities were investigated this matter has still to be tested. The sub-brachypterous form was also the most common form collected in the field (medium and small populations). Kisimoto also showed that the ingestion of certain salt solutions inhibited the appearance of the brachypterous form in both sexes in N. lugens.

Diapause in the fourth larval instar has been shown to influence the form of the adult small brown planthopper, Delphacodes striatella Fallén, (Kisimoto 1956c). Diapaused larvae produced the brachypterous form in both sexes. From non-diapaused larvae, scarcely any brachypterous males were produced, but brachypterous females could still be obtained. Transfer of the larvae from diapause conditions to non-diapause conditions caused acceleration of nymphal development, but the percentage emergence of the brachypterous male was still low.

Two types of wing reduction, types (IV) and (V) mentioned by Butler (1923), seem to apply to N. huttoni, though not to the same degree. These are: "(IV) the whole hemielytron is much shortened, with the membrane either disproportionately reduced or absent altogether.... or (V) it is reduced to a strongly convex scale ... " He stated that there was some modification of the prothorax in brachypterous forms, because of the imperfect development of the muscles concerned in flight. He poses the question, as the abbreviated flight organs are of no use for flight, why is the abbreviation not carried further? Larsen (1955) reported for Nema cinerea L., a loss of the ability to fly in some insects and showed that this was due to a reduction of the flight muscles, but that the wings did not differ in size or shape from those of flight-capable insects. Butler suggests that reduction of the wings may result from living very close to the ground, and may limit distribution.

Thus several explanations of pterygo-polymorphism have been advanced, and usually a different one for each species studied. Therefore one may conclude that many factors are involved, and genetic factors should not be overlooked. In some species one form predominates, e.g. N. miriformis whereas in others, two forms alternate with season, so that both forms will always occur and predominate alternately, e.g. Notostira erratica L. (examples from Woodward, 1952).

There is some evidence that N. huttoni is gradually undergoing permanent reduction of flight organs and loss of the ability to fly. Thus the polymorphism exhibited may be transient (Ford 1955). The author has not seen the insects flying in the field, but has seen sub-brachypterous forms running quickly across the surface of the ground, flapping the wings to retain balance. Two macropterous insects were observed flying in the greenhouse. From the percentages of each form present in the population studied, it would appear that reduction from the macropterous form to the sub-brachypterous form has largely taken place. The next stage, i.e. reduction to the brachypterous form has already begun. If this is a move to permanent reduction of the wings, one would expect more and more

brachypterous forms in succeeding generations. There was a tendency in this direction (see Table 20).

However, it may be argued that all forms will always be present as they represent the variation in the species. This is also the case in a "balanced polymorphism" (Ford 1955). Richardson (1958) puts forward a four dimensional concept of a species, which would seem to support the above argument. Ford defined polymorphism as "the occurrence together in the same habitat of two or more discontinuous forms of a species in such proportions that the rarest of them cannot be maintained by recurrent mutation." In N. huttoni all forms were present in the localities studied, and there were intermediary grades, so that the forms are not discontinuous. Therefore, by the above definition, this variation in wing form is not polymorphism, but merely variation within the species. Thoday (1958) working with Drosophila melanogaster, showed that even the maximum amount of gene-flow (50%) cannot prevent two sub-populations diverging under divergent selection pressures. Thus with time, the variation in a species may be expected to increase.

Leaders in the field of polymorphism are Fisher and Ford (1947) and Wright (1948). They maintain that many factors are involved. Thus to explain the problem of wing variation in N. huttoni, its population genetics should be studied. This species would make very suitable material for genetical study, because of the variation present, not only in wing form, but also in colour and size.

(b) VARIATION IN SIZE

Body measurements were taken on 164 specimens, including both sexes, from 16 localities. To take a complete set of body measurements, as was done for the redescription of the imago (see Table 17 page 38) would have taken much time, and been unnecessary in this case. Six characteristics, which the author considered to be the most useful, were chosen. These were:-

head width (including eyes)

total wing length

body length (to wing tip in macropterous forms otherwise to posterior of abdomen)

body length (to posterior of abdomen)

width across hemelytra

length of head plus pronotum.

The two measurements of body length were taken to counteract the tendency for sub-brachypterous forms to fall into a smaller size group for this character.

The localities from which the specimens came are, in the North Island: Kaimai, Taumarunui, Horotiu, Westshore, Havelock North, Maraekakaho, Marton, Foxton, Waitarere, Hokowhitu and Massey Agricultural College; and in the South Island: Blenheim, Nelson, Tuamarino, Seddon and Leefield.

The results are shown graphically in Figs. 4-7 for females, and in Figs. 8-11 for males. All the measurements taken on individual insects, and also their locality and form are shown in Appendix IVa. Frequency distributions for each character are shown in Appendix IVb.

A trimodal graph was obtained for headwidth and wing length in both females and males, and for width across the hemelytra in males. Six of the remaining graphs showed bimodal distributions i.e. for body length and length of head plus pronotum in both sexes, and for width across hemelytra and body length (to posterior of abdomen) in females. The distribution of this latter measurement in males was monomodal.

On all characters, bar the one in males mentioned above, a small sizedpopulation was shown to be distinct. The fact that half of the graphs are merely bimodal may be interpreted as showing that there was no clear distinction between the medium, and large, size groups. However, closer study should be made of Figs. 5 and 6. In the graph of body length (to wing tip in macropterous forms) in females, the small population was shown to be distinct, but the second peak showed greater spread and an overlapping of the medium and large size groups. On

ADULT MALES

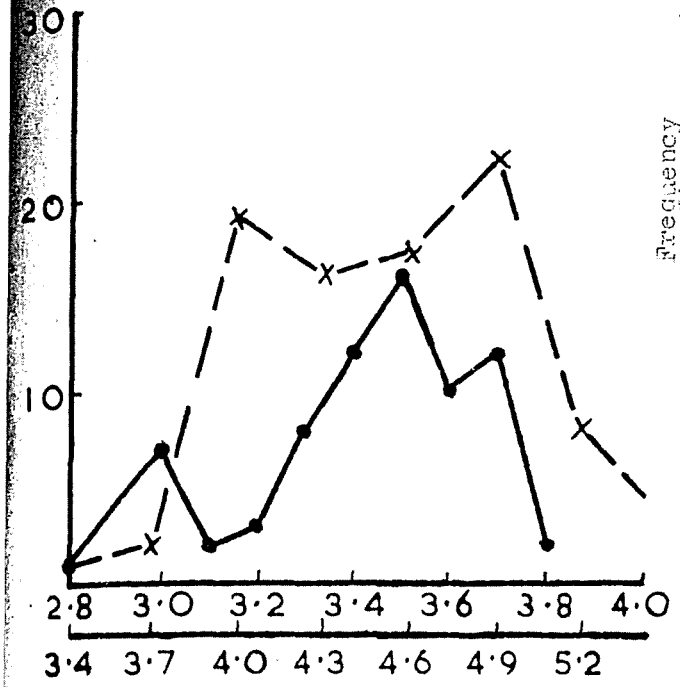


Fig. 8

Distribution of head width (solid line and upper scale) and length of head plus pronotum.

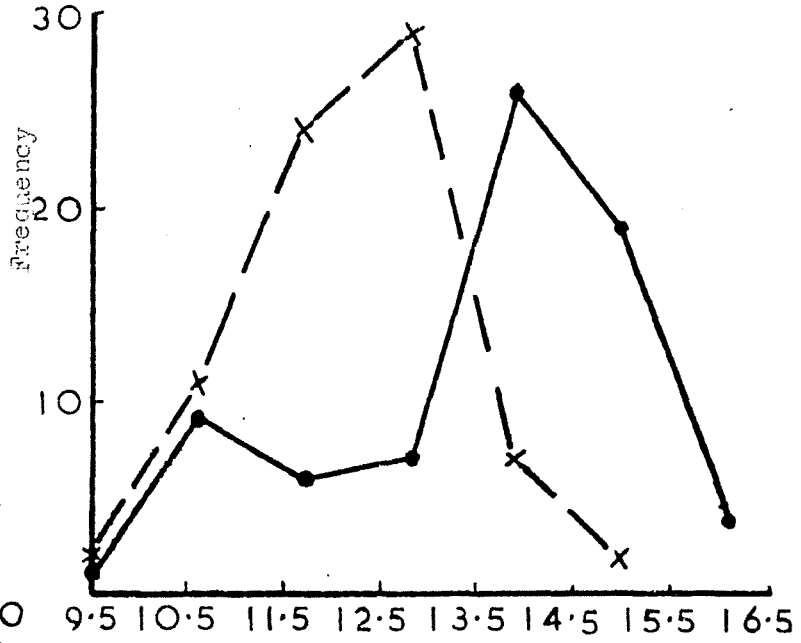


Fig. 9

Distribution of body length including wings (solid line) and body length to posterior of abdomen.

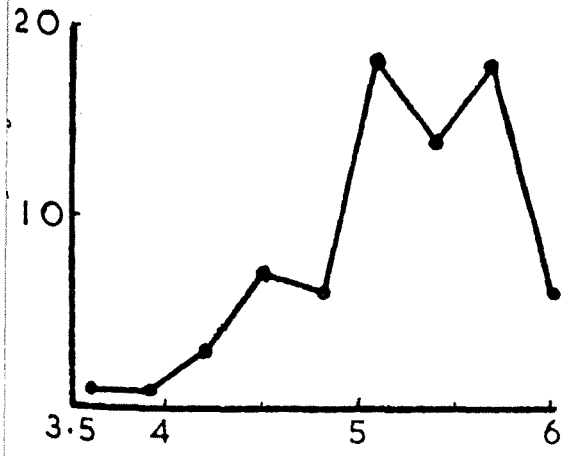


Fig. 10

Distribution of width across h.melytra.

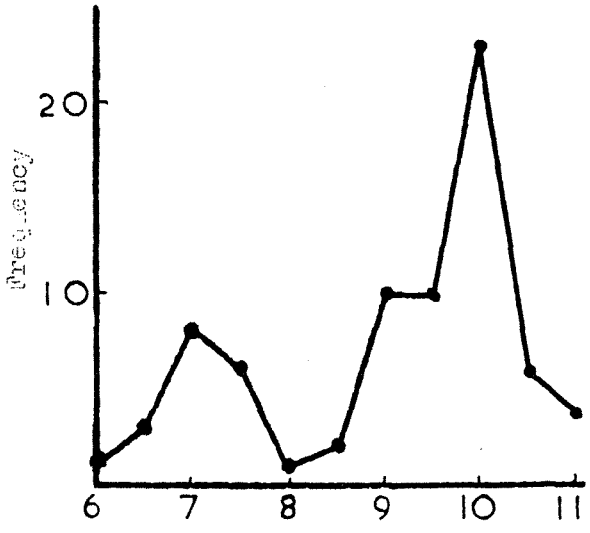


Fig. 11

Distribution of wing length.

All measurements in micrometer units.

ADULT FEMALES

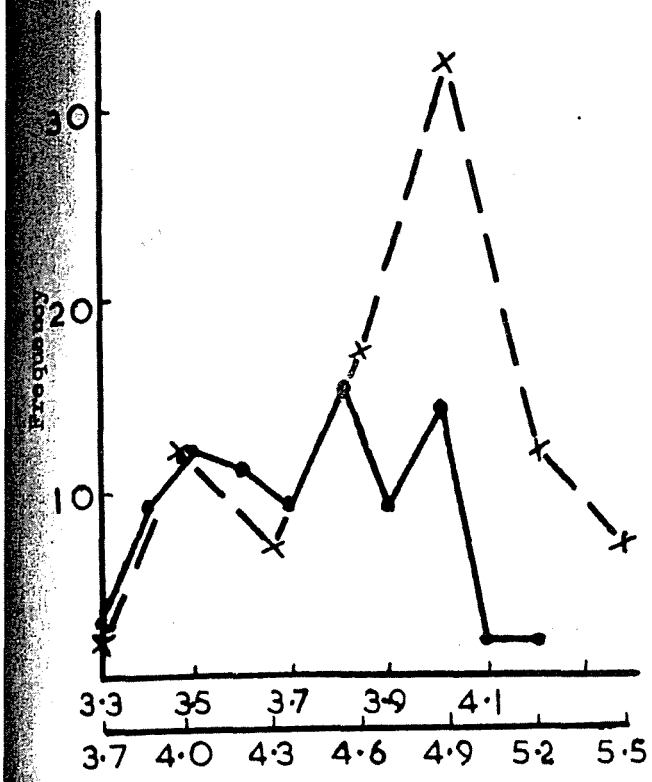


Fig. 4

Distribution of head width (solid line and upper scale) and length of head plus pronotum.

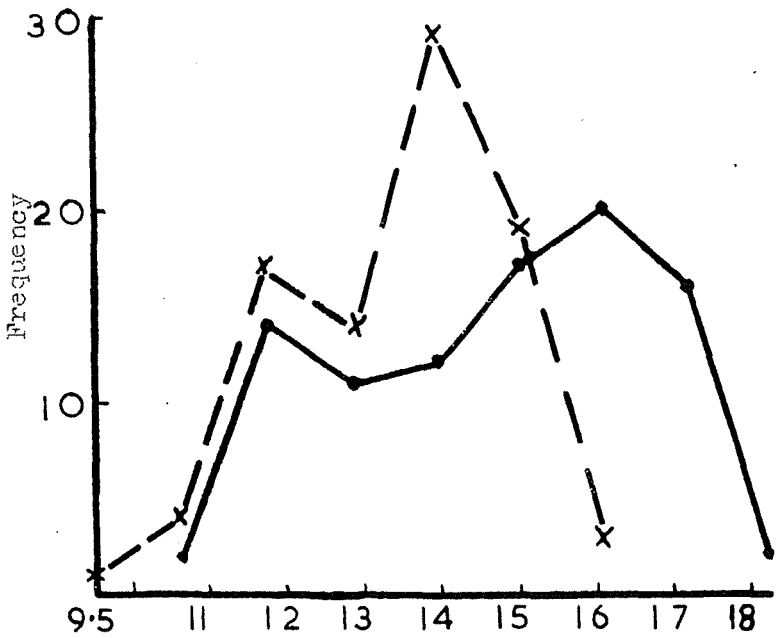


Fig. 5

Distribution of body length including wings (solid line) and body length to posterior of abdomen.

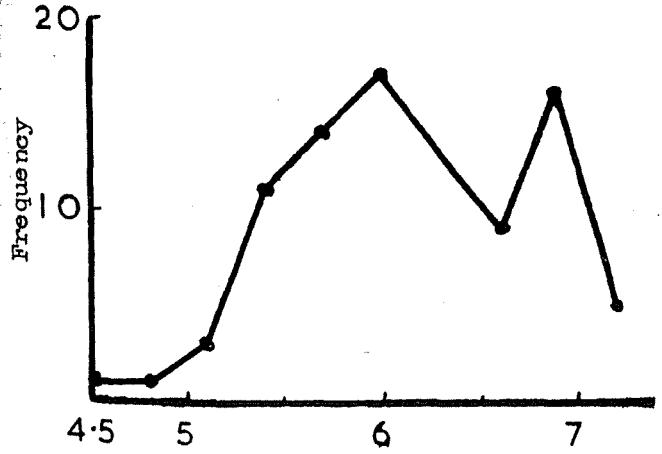


Fig. 6

Distribution of width across hemelytra.

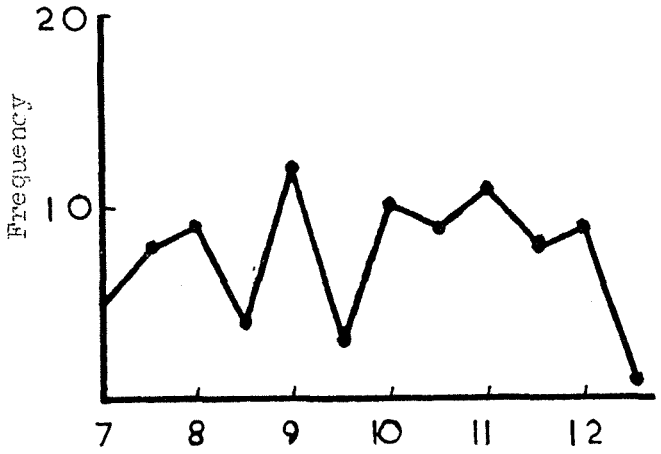


Fig. 7

Distribution of wing length.

All measurements in micrometer units

the other hand, in the graph of width across hemelytra in females, the large size group was shown to be distinct, but the first peak showed greater spread and an overlapping of the small and medium size gro ps. These two graphs combined, therefore, point to three size groups. This conclusion is supported by Fig. 10, a trimodal graph for width across the hemelytra in males. Therefore in the summation of all the graphs the balance was moved to over half, i.e. 7 out of 12 (4 characters out of 6) showed three distinct populations.

In further support of the above conclusion are the following:

(1) head width, which is the criterion of size in entomology, showed the three distinct size groups.

(2) the bimodal graph for the distribution of egg length (Fig. 1) for which the best explanation was a small sized, and a medium sized population. Further, from the body measurements of the females that laid the eggs (see Appendix IIb) it became clear that none of the large sized group were present, which explains the absence of the third peak in that case.

(3) The trimodal distribution which was obtained for headwidth measurements of 5th stage nymphs.

(4) The fact that 5th stage nymphs of the small population were mistaken for 4th stage nymphs of the medium population in experiments on effect of temperature on wing form.

The evidence of three populations, though conclusive enough in the adults alone, in several characteristics, was demonstrated not only in this instar, but accumulatively over several instars, including the egg.

It was further noted/that three forms occurred in the small and medium populations, but in the large population only macropterous forms have been observed. A possible explanation is that a reduction in wing length may be accompanied by a reduction in wing width, in which case the shorter winged individuals would be placed in the medium population. Representatives from each size population are illustrated in Plates 2 and 3, which also depict the three forms over the total

TABLE 21

Size of Small N. huttoni Population

Males		Females	
Length in mm.	Width across hemelytra in mm.	Length in mm.	Width across hemelytra in mm.
2.47	1.08	2.47	1.20
2.58	1.89	2.88	1.30
2.69	1.18	3.19	1.32
2.78	0.94	2.78	1.22
3.00	1.20	2.93	1.30

Clearly the small population is smaller than B. convexus, which therefore, on size, falls into the medium N. huttoni population and may be identical to sub-brachypterous forms.

As mentioned before (page 39), except for wing form, the proportions of the large N. huttoni population are very similar to those of B. convexus, though individual measurements are slightly larger. In all three N. huttoni populations the proportions are similar. Sub-brachypterous forms of the medium population were found to conform to the B. convexus description except for one ratio, that of length of pronotum to length of head. This may be due to the different method of measuring head length. Below, a comparison is made between the two species on this ratio, using Usinger's method of measuring head length. Usinger (1943) does not indicate the size of the scale used, but in all probability it was the same as that used by him in describing Hawaiian Orsillini (Usinger 1942).

B. convexus (one scale division = 0.055mm)
Length of pronotum to length of head -
in scale division, 10 : 12
in mm. 0.55 : 0.66

N. huttoni sub-brachypterous form, medium sized population
(one scale division = 0.063mm)
Length of pronotum to length of head -
in scale divisions, 9 : 11 in some specimens, and 11 : 11 in others
in mm 0.567 : 0.693 and 0.693 : 0.693

The comparison shows that there is no difference between the two species in this ratio, when the same method of measuring is followed.

Thus, from the description, B. convexus appears to be identical with sub-brachypterous forms of the medium N. huttoni population. Further, all forms of the medium population were proved, by interbreeding experiments to be members of one and the same species (see page 48). The author attempted to obtain the type specimens of B. convexus so that a final decision could be made, but these were not available. However, from the evidence to hand, there seems to be no justification for making B. convexus a separate species from N. huttoni.

Even if B. convexus does prove to be a distinct species, (i.e. after the comparison of the type specimens with N. huttoni, and after location of live material and trial interbreeding with N. huttoni), there can be no doubt that the erection of Brachynysius as a new genus is not justified. Usinger (1943), in a "key to the genera and species of Orsillini in New Zealand", gave the following condensed description of Brachynysius:

> "Hemelytra distinctly convex, costal margins strongly rounded beyond basal fourth. Membrane small, exceeding level of apices of coria by less than one-fourth the total length of membrane, without apparent veins
>
> Brachynysius convexus
> n. gen. and sp. "

The sub-brachypterous forms of N. huttoni conform to the Brachynysius genus description. Usinger had seen only 14 specimens of this complex; 11 N. huttoni specimens (which would have been macropterous), and 3 sub-brachypterous specimens which he described as B. convexus. It seems that he had in fact discovered two extremes of N. huttoni which were so different that he separated them. He examined dead material and did not carry out breeding experiments. The author examined about 2,000 specimens, and carried out breeding experiments. The extremes went from macroptery, beyond sub-brachyptery to brachyptery, and there were all grades in between. As all forms appear to occur in the localities sampled, this represents simply variation within the species, and thus is not even a cline.

It follows then, that Usinger's key to the genera and species of Orsillini in New Zealand should be amended so that Brachynysius is sunk, and Nysius is extended to include all forms (this would then include the brachypterous form here first recorded, and the sub-brachypterous form which was formerly designated as B. convexus).

SUMMARY OF SYSTEMATICS

1. The place of N. huttoni (together with the other New Zealand Orsillini) within the family Lygaeidae, is here reviewed.

2. The egg is described and compared with the eggs of allied Heteroptera.

3. Egg dimensions were studied in some detail and tended to fall into two distributions corresponding to two size groups, small and medium, of the female parents.

4. The five nymphal instars are described and illustrated. In addition to the obvious differences in size, it is shown that each nymphal instar is readily distinguished by head width, and by characteristic black pigmentation on the metanotum in the first three instars, and by wing pad development in the fourth and fifth instars.

5. The trimodal distribution for head width in the fifth nymphal instar is considered to indicate the presence of three populations, because a sex difference is apparently not involved.

6. The imago is redescribed and illustrated.

7. There was slight evidence that in the medium and small populations, subjection to high and low temperatures during nymphal development suppresses macroptery in the adult and that low temperatures may cause brachyptery to increase, but temperature is probably not a major factor in the determination of wing form in this species.

8. It is shown by interbreeding experiments in which sub-brachypterous forms were crossed with macropterous forms (both ways) that the three wing forms are members of one and the same species. N. huttoni is therefore unique amongst the Orsillini in occurring in three forms in both sexes.

9. What is at present designated as N. huttoni, is shown to comprise three populations differing in size. In the medium and small populations the sub-brachypterous form is the most common in both sexes, but in the large population, only the macropterous form has been observed.

10. As B. convexus by description appears to be identical with sub-brachypterous forms of the medium N. huttoni population, its status as a separate species is

considered invalid.

11. As sub-brachypterous forms of N. huttoni, which were reared from macropterous forms, conform to the Brachynysius genus description, there can be no doubt that Brachynysius should be sunk as synonymous with Nysius. This would also follow from 10.

SECTION B BIONOMICS

This section is presented in three main parts, fecundity (Chapter 4), life cycle (Chapters 5 and 6) and field ecology (Chapter 7). The insect material studied, except that dealt with under field ecology, was reared and kept in a greenhouse (unless otherwise stated), and the method employed is indicated below.

Materials and Methods

The aim was to maintain environmental conditions as near as possible to those existing in the field. An open insectary would have been ideal, but was not available. An unheated greenhouse was used. Its dimensions were - length 28 feet, width 9 feet, height at centre 8 feet, height at sides 5 feet 4 inches. The six vents, three in the roof and three in the sides, were kept wide open during spring, summer and early autumn, but were two thirds closed during winter. The aspect was almost due North and South (a bearing of 355°), so that the bench along the Western side received the morning sunshine (i.e. across the greenhouse, the bench along the Eastern side being shaded by that side), whilst the opposite occurred with the afternoon sunshine. Although the roof and sides were whitewashed, which reduced the maximum temperature by 20°F, temperatures within the greenhouse were expected to be higher than those occurring outside. Therefore, development of the insect in the greenhouse was expected to be a little faster than normal. However, the mean maximum temperature of 108°F recorded in the field at the surface of sand between 7th and 18th January 1956, was higher than that recorded in the greenhouse (89°F) during January. The mean minimum temperatures recorded over the same periods, were, for field and greenhouse respectively, 47°F and 57°F. The experimental insects were kept in glass tubes, were provided with a regular and no doubt excess food supply, were protected from natural enemies, and, except for changes in temperature and humidity, were subjected to a constant environment (e.g. absence of wind). Thus the insects developing in the greenhouse would have some advantages over insects developing in the field, but the temperature differences would tend to have

a counteracting effect. Probably, development under both conditions did not differ greatly.

The insects were kept in glass tubes 6 in. x 1 in., covered at one end by butter muslin cloth fixed by a rubber band, and stoppered at the other end by a cotton-wool plug. Food consisted of a sprig of twin cress which was renewed daily (except in the case of adults kept over winter, when it was renewed every three or four days). There was one pair of adults per tube. However, several nymphs, usually usually the whole of an egg batch, were placed in one tube. As some died in the early stages, there were generally three to six nymphs reared per tube.

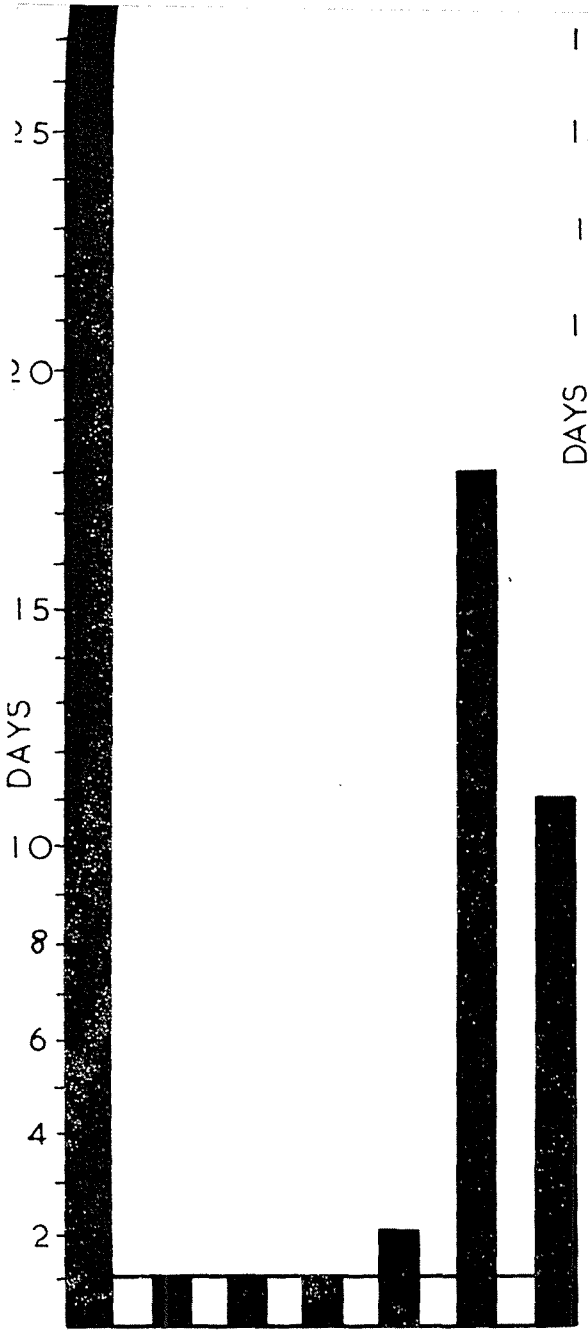


Fig. 29

Rhythm in egg laying for female H

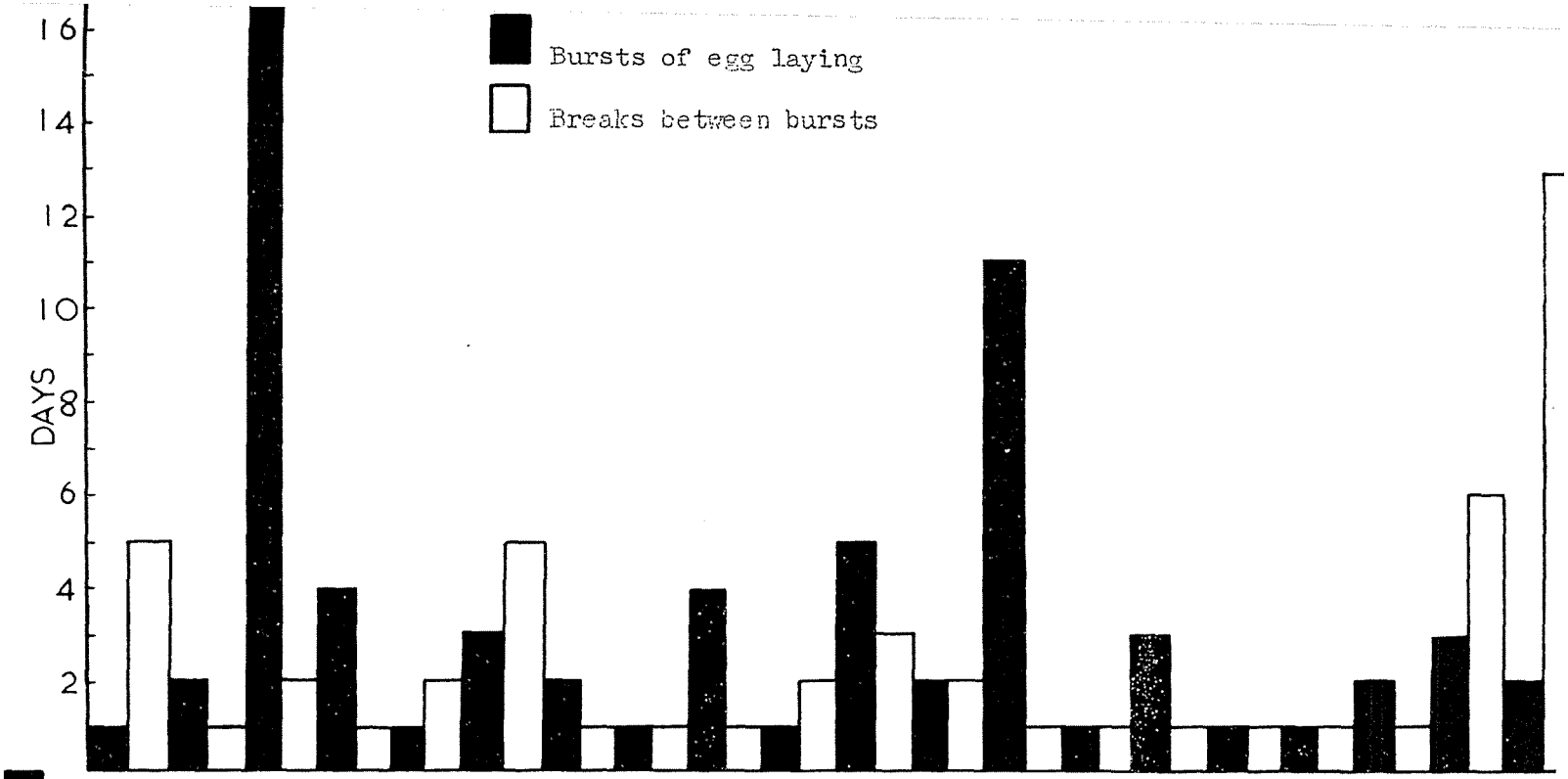


Fig. 30

Rhythm in egg laying for Control female

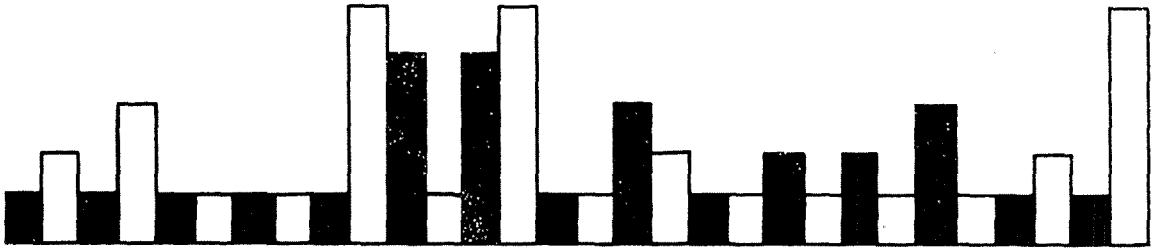


Fig. 31

Rhythm in egg laying for female 1 copa

CHAPTER 4

FECUNDITY

Definition of Fecundity

The definition of fecundity given by Lush (1945), was followed, "...fecundity is the potential capacity of the female to produce functional ova, regardless of what happens to them after they are produced ...". He also defines fertility as "... the ability to produce living young or, in the case of poultry, to produce eggs which will start to develop..." Further he said, "The distinction between fecundity and fertility is easily illustrated in poultry where a hen may have high fecundity, but her eggs may be low in fertility or hatchability..."

From the foregoing, it was clear that hatchability of the eggs should not be included in this Chapter, which is therefore restricted to egg production.

Oviposition and Ovipositon Stance

Oviposition was observed several times. The female would move over the cotton-wool selecting a site, or waiting until she was ready to lay. Concurrently the ovipositor was released and moved from side to side. When the site was selected, the typical oviposition stance was adopted. The terminal abdominal segments which have considerable latitude in movement, were flexed downwards on to the cotton-wool, and thus the ovipositor was inserted. Several times the abdomen was straightened and then flexed downwards again in a rythmic rocking motion, indicating that muscular exertion was required for passing the egg. Even in the cotton-wool the ovipositor was moved from side to side before the egg entered it. (Whether or not this signified that the egg was being rolled around in the genital chamber, as reported for Rhopalimorpha bugs by Fendergrast,(1952), is debatable). When the egg was actually being passed, the female took a more firm grip of the substrate with the tarsi, flexed the abdomen downwards so that the ovipositor was at its full depth, and even the posterior tip of the abdomen was slightly inserted. The

antennae were flexed backwards against the head, the hindlegs were placed behind the abdomen, and the mid- and forelegs supported the body in front in an almost upright position. The egg was held in the ovipositor for one or two seconds and could be seen through the thin membranes which assumed the shape of the egg. The egg was squeezed out slowly, and when three quarters free, the ovipositor was moved to one side, by which time the egg had been laid. The ovipositor was then withdrawn from the cotton-wool and moved from side to side two or three times after the egg was laid. Similar oviposition habits were reported for the Rutherglen bug by Smith (1927). After oviposition, the cephalic pole of the egg was uppermost. As N. huttoni lays eggs in the soil this orientation ensures that the nymph emerges upwards, head foremost, onto the soil surface. Eggs were laid either singly or in clusters, but in the latter case were not cemented together. The largest number laid by one female in one day was nineteen, but as a cluster seldom exceeded six eggs, these were laid in several clusters.

Aims and Set-up of the Fecundity Study

From the fecundity study it was hoped to determine

1. time elapsing between emergence and first copulation
2. time elapsing between emergence of female and laying of first eggs, length of oviposition period and post oviposition period
3. daily performance and the total number of eggs laid per female in a lifetime
4. rhythm if any, in egg laying
5. preferred time of day, if any, for oviposition
6. the effect of shading at certain times upon oviposition and any influence this may have on 5.
7. the effects of presence, and absence, of the male upon oviposition as under 2 - 4
8. adult longevity

Many of the eggs were incubated and the nymphs reared, to obtain information on life history, but this is outside the scope of this Chapter. The study was

carried out fully over two generations and partially over the third generation. Eggs were laid in the cotton-wool plugs. Observations were daily, and when eggs had been laid, the number were recorded and the cotton-wool plug replaced. However, to determine the time of day of oviposition, observations were at intervals of two hours (between 8am and 6.30pm) for a period of two months. The results are presented for each generation, firstly for aims 1 - 3 and 8, which are included under the heading "Total Egg Production", secondly for 4, rhythm, and finally for 5 and 6. Aim 7 is discussed throughout.

Parent Generation

The foundation generation (hereinafter known as the parent generation) were obtained from fifth stage nymphs caught in the field. The nymphs were kept separate, and after emergence as adults, 24 pairs were set-up, each pair in a glass tube. The adults emerged in the second week of March, 1957 and probably represent the last generation of adults to emerge before winter. Only three females laid before winter. Pairs A, B, C, D and E were caught in the field as adults in mid March 1957, and pairs X, Y and Z were caught late in May 1957. These have been included in the parent generation, but as they were not newly emerged for certain, their egg laying results were kept separate. The male of pair 23 died on 11th May 1957, and although mating had occurred, the oviposition of the female after winter was completely in the absence of a male. Therefore, the egg laying record of female 23 was also kept separate. Her eggs were fertile which showed that sperm can be stored over winter by the female.

First Generation

The adults used in this experiment were the offspring of the parent generation, and were reared in the greenhouse from the first egg batches laid after winter (in August) 1957. These emerged as adults during the latter half of October and the first week in November, and were the first generation of the new season. Until the treatments mentioned below were started, these adults were sexually

uncontaminated, because as fifth stage nymphs they had been kept separate. Seven pairs were set up. One female, known as the control female, was kept unmated to determine whether or not presence of the male was necessary for oviposition. Two females, known as 1 cop and 1 copa, were each given one copulation at the commencement of oviposition, and then the males were removed for good. This subsidiary experiment, from which it was hoped to determine how long the females could store sperm and continue to produce fertile eggs, was prompted by the results from female 23. Two more females known as Z' and Z" were each given one copulation per week; the males were removed from their presence between copulations. It was expected that some definite oviposition pattern, through stimulation by the male, would result. This particular subsidiary experiment was prompted by 1 copa which laid 16 eggs on the day of copulation, but thereafter her oviposition was at a steady, lower, rate.

Second Generation

These were offspring of the first generation and emerged as adults during January 1958. Individuals were kept separate from fifth stage nymphs until the experimental treatment was administered. Three pairs were set up, and two females, U' and U" remained unmated. Records were taken over part only of the second generation egg-laying. The reason was to check times of day of oviposition against those of the first generation which at the time of the investigation were ageing, were irregular in laying and were therefore probably unreliable. However, this partial record from 1st to 17th February 1958 was within the period of fastest lifecycle and highest temperatures, and was expected to show greatest egg production.

TOTAL EGG PRODUCTION

Table 22, reproduced from Gurr (1957), summarises all that is known about fecundity in this species. The last column has been added and was obtained by dividing column 3 by column 4.

TABLE 22

FECUNDITY OF NINE FEMALE N. huttoni

Serial No. of mated bugs	Days after final ecdysis that female oviposits for first time	No. of eggs laid	Oviposition period in days	Mean No. of eggs laid per day
A	8	137	38	3.6
B	8	36	17	2.1
C	4	76	43	1.8
D	8	20	9	2.2
E	3	134	30	4.5
F	8	1	1	1.0
G	11	174	24	7.2
H	6	25	5	5.0
I	11	77	10	7.7
Mean	7	76	20	3.9

The daily performance of seven pairs used in a preliminary investigation are shown in Appendix V.

Results for Parent Generation

The daily performance of each female, the mean number of eggs laid per day, and the date of emergence of each pair, are shown, for those which laid before winter, in Appendix VI, and for those which laid after winter, in Appendix VII. Totals, oviposition period, and other relevant data are summarised in Table 23.

Of the 24 females that emerged in the early autumn, only three (12.5%) laid before winter, and none of these three survived the winter.

Eighteen females (75%) did not survive the winter. This figure includes the three mentioned above. Six females (25%) survived the winter and laid in the spring, but none of these laid before winter. It is possible that the number surviving winter may have been greater had the bugs been accustomed to "tube conditions".

TABLE 23

FECUNDITY OF ADULT GENERATION FEMALES

e = escaped, a = accidentally killed. The mean for days to first copulation was taken over all observations. The last column was obtained by dividing the number of eggs laid by the oviposition period.

♀ Code No.	Days after final ecdysis: to first copulation	Days after final ecdysis: to first oviposition	No. of eggs laid	Longevity of ♀ adult in days	Oviposition period in days	No. of days on which each ♀ laid = No. of egg batches/♀	Mean No. of eggs laid per day
Those which laid before winter 1957							
8	15	18	7		5	3	1.4
18		13	66	60	28	18	2.4
24	11	11	72	50[e]	21	18	3.4
Mean		14	48	55	18	13	2.4
A			68		34	17	2.0
B			39		20	13	2.0
C			24		14	11	1.7
E			31		10	7	3.1
Mean			41		20	12	2.2
Those which laid after winter 1957							
5	9	146	82	201	44	27	1.9
7				163[e]			
9	7	154	114	297	143	42	0.8
13		159	43	186[e]	57	21	0.8
17		159	12	169[a]	10	5	1.2
Mean	11	155	63	203	64	24	1.2
D			82		68	34	1.4
Z			55		54	19	1.0
Mean			69		56	27	1.2
23		161	85	213	52	34	1.6

The mean number of days elapsing between the emergence of an adult female and her first oviposition was 14 for those which laid before winter. This was a longer time than that required by the spring and the summer generations, but was expected because the lower temperatures in March would slow down development. A mean of eleven days elapsed between emergence as adults and the first copulation. Thus males reached maturity three days earlier than females in this generation. Some females which did not lay before winter were seen in copulation with their mates.

Results for Females which laid before winter 1957

For the three females 8, 18 and 24 which laid before winter 1957, the mean number of eggs laid in a lifetime was 48 (range 7 to 72), and the mean oviposition period was 18 days (range 5 to 28 days). The mean length of female adult life was 50 days. The mean number of days on which females laid (or the mean number of egg batches per female) was 13. The mean number of eggs laid per female on any day was 2.4.

Females A, B, C and D which were not necessarily newly emerged, but could have been any ages, showed for that portion of their egg-laying recorded (which may or may not have been a complete record) a similarity to that of the three females described above.

Results for Females which laid after winter 1957

For females 5, 7, 9, 15 and 17 which survived the winter, the mean number of days elapsing between emergence of an adult female and first oviposition was 155 days, and there was a difference of only 9 days between the earliest and latest occurrence of first oviposition. The mean number of eggs laid per female in a lifetime was 68 (range 12 to 114), and the mean oviposition period was 64 days (range 10 to 143 days). The mean length of female adult life was 208 days. The mean number of egg batches laid per female was 34, and the mean number of eggs laid per female per day was 1.2. The post-oviposition period was very short, did

not exceed two days, and indicated that the females are capable of oviposition to the day of death. Females D and Z (which, according to the interpretation of the results must have been recently emerged when caught) were similar to the above females in all points of their egg-laying record. The same may be stated for the record of female 25, which shows that absence of the male during the oviposition period does not curtail fecundity in the female. Female Y which lived in captivity for five months did not lay a single egg.

Results for First Generation

The daily performance of each female, the mean number of eggs laid per day, and the date of emergence of each pair as adults, are shown in Appendix VIII. Total egg production, oviposition period, and other relevant data are summarised in Table 24.

The mean number of days elapsing between the emergence of an adult female and her first oviposition was 7, a figure which was considerably less than that for the parent generation laying before winter. The first copulation was observed in two cases

1. two days after the pair were put together - the female laid three days after that, and

2. five days after the male (the later of the pair) emerged, and this coincided with the day of first oviposition by the female.

As in the parent generation, these figures indicated that maturity in the male was attained (as would be expected) in a similar or slightly shorter time than maturity in the female.

TABLE 24

FECUNDITY OF FIRST GENERATION FEMALES

e = escaped, a = acidentally killed. The mean for days to first oviposition was taken over all observations.

♀ Code No.	Days after final ecdysis to first oviposition	No. of eggs laid	Longevity of ♀ adult in days	Oviposition period in days	No. of days on which each ♀ laid	Mean No. of eggs laid daily	Post-Oviposition period in days
D'	7	111	52	41	38	2.7	2
5'	6	387	185	137	104	2.8	42
8'	6	111	61	52	35	2.1	8
23'	5	123	94	86	46	1.4	
U	2	224	114	105	64	2.9	4
H	7	300	76	67	62	4.5	
O	8	102	30[e]	21	20	4.9	
Mean		204	87	72	52	3.0	13
Control	5	178	122	104	67	1.7	13
1 cop	9	277	116[a]	106	78	2.6	
1 copa	11	129	70	45	39	3.0	6
Mean	7	203	94	76	69	2.4	
2'		323	115	107	54	3.0	
2"		52	32[e]	17	12	3.1	
Mean		188	74	62	33	3.1	

The mean number of eggs laid in a lifetime was 204 (range 102 - 387), and the mean oviposition period was 72 days (range 21 - 137 days). The mean length of female adult life was 87 days. The mean number of days on which females laid, or the mean number of egg batches laid per female per lifetime was 58. The mean number of eggs laid per female on any day was 3.0. The mean post-oviposition period was 13 days, but the range was considerable (2 - 42 days).

The total egg productions for the control female and females 1 cop and 1 copa were within the range of those for the paired females, but their oviposition periods were longer than average. This indicates that the male does have a stimulatory effect on oviposition, and this is also evidenced in the figures for mean number of eggs laid per day.

All the figures shown for females Z' and Z" are similar to the corresponding figures for the seven paired females, which indicates that presence of the male for as short a time as one day per week was sufficient to maintain normal total egg production, although daily performance was stimulated at each visit by the male.

Results for Second Generation

For the seventeen-day period recorded, the daily performance of each female, the mean number of eggs laid per day, and the date of emergence of the females are shown in Appendix IX. The data is summarised in Table 25. The data is summarised in Table 25. The data for the unmated females is not kept separate in this case as their performance was similar to that for mated females.

The mean number of days elapsing between emergence of an adult female and first oviposition was 7 days. The mean number of eggs laid per female was 57 (range 10 - 114), and the mean oviposition period was 13 days. The mean number of egg batches laid per female was 11, and the mean number of eggs laid per female per day was 4.0.

TABLE 25

FECUNDITY OF SECOND GENERATION FEMALES

This was recorded over a 17 day period only, and not for the complete life of the generation. e = escaped.

Female Code No.	Days after final ecdysis to first oviposition	No. of eggs laid	Oviposition period in days (for the period of observation only)	No. of days on which each female laid	Mean No. of eggs laid/day
5"'		114	17	16	6.7
H"	10	76	17	16	4.5
5"		19	6[e]	5	3.9
U'	6	49	14	12	3.5
U"	4	27	13	7	2.1
Mean	7	57	13	11	4.0

Discussion of Total Egg Production Results

As the parent generation represented the last generation to emerge as adults at the close of the 1956-57 season, they provided information on the survival of the bug over winter. Further, a comparison of the egg production of the females surviving the winter with that of the first generation females of the new season, revealed the importance to the continuance of the species of the overwintering generation.

The females of the parent generation that laid before the winter had a shorter life, a shorter oviposition period and less egg production, than those of the other generations. None of them survived the winter. Apparently, of the females, only those emerging late in the season, and which do not lay before winter, have sufficient youth and vigour to survive the winter; they are the source of the population in the next season. The fact that the females A, B, C and [illegible] (caught as adults in the field) laid before winter, but did not survive the winter, and that females [illegible] and [illegible] (from the same source) did not lay before winter, but survived it and laid in the spring, supports this view. But the winter took much out of

these females because their oviposition period was shorter and their egg production was less than one third that of the first generation. On the other hand, in order to survive the winter, their length of life was more than double that of the first generation females. Another difference was in post-oviposition period which was 0 - 2 days in the parent generation, but 2 - 42 days (mean 15 days) in the first generation. A feasible explanation is that as the overwintering females are the major source of the population the following spring, there is a necessity for them to continue to oviposit until dead, whereas the necessity is not as great in the first generation. As the number of autumn-emerging females actually surviving winter is probably small, e.g. 25% in the parent generation, this necessity becomes more apparent.

Woodward (1952) proposed a classification of the main types of reproductive cycle in the Heteroptera. N. huttoni would be placed into class II (1) (b) which is as follows:

"II Species in which oviposition is restricted to the warmer parts of the year.

(1) Species with long-lived, overwintering adults (at least in one generation)."

(b) Bi- or multi-voltine species with the adults of the early generation or generations comparatively short-lived and those of the autumn, overwintering generation long-lived and ovipositing the following spring..."

He further stated that in this class either the production of egg rudiments is completely inhibited until spring, or their development is interrupted or considerably retarded during winter. He showed that in Scolopostethus decoratus (Lygaeidae), the formation of small egg rudiments begins in autumn but is arrested by the adverse conditions of winter. He sums up the situation with the sentence "In either case, formation and laying of ripe eggs is delayed until spring", and adds that, "... as far as is known, all Heteroptera which hibernate as adults do so before producing ripe eggs".

As some of the parent generation actually laid eggs in the autumn it was concluded that in N. huttoni development of egg rudiments begins in autumn, but is normally arrested during winter. Here was the possibility of autumn-emerging females ovipositing both before and after winter, but none of those which oviposited before winter survived the winter. The temperatures in the greenhouse for March 1957 were not recorded, but in March 1958 the maximum and minimum temperatures were respectively, 81° and 52°F. whereas the corresponding outside temperatures were 72° and 45°F. Probably the higher temperature in the greenhouse was the reason for the autumn oviposition recorded.

As the author caught a fifth stage nymph in the field in August, there can be no doubt that some fifth stage nymphs overwinter, emerge as adults in the spring, and aid in the build-up of the new season population.

The greater total egg production by each succeeding generation was also reflected in the mean number of eggs laid per female per day. These, for the parent generation laying before and after winter, the first, and the second generations, were respectively, 2.4 (range 1 - 9), 1.2 (range 1 - 6), 3.0 (range 1 - 16), and 4.0 (range 1 - 16). The comparable figure calculated from Gurr's data obtained at Nelson, was 3.9 (see Table 22) and the oviposition period was late December and January (personal communication). This agrees with the figure for the second generation which oviposited during February, the warmest month at Palmerston North. The figure was calculated by dividing the total number of eggs laid by the oviposition period, for each female, and obtaining the mean value: this is really the mean number of eggs laid per female on any day throughout the oviposition period, whether eggs were laid every day or not. It may also be calculated by using the ratio, total number of eggs laid, over number of egg batches. The figure thus obtained would then represent the mean number of eggs laid per day by any female (excluding days on which she did not lay). For the parent, first, and second generations it was respectively, 5.3 (before winter), 2.5 (after winter), 3.9 and 4.8, which is in each case higher than the corresponding figure given above. However,

as this refers to the days only on which eggs were laid, the author considers that it is of more value than the figure which was actually used (in order to draw a comparison with Gurr's data) because emphasis should be placed upon laying performance.

From the partial second generation record which was over 17 days, it seemed highly probable that their total egg production would have exceeded that of the first generation. A comparison was made between the three generations by determining production over the first 17 days and over two other 17 day periods. These are shown in Table 26. Of the second generation, except for female 5''', the period recorded was over the first 17 days (or less) of oviposition.

TABLE 26

NUMBERS OF EGGS LAID OVER 17-DAY PERIODS

Parent Generation

Code No. of female	No. of eggs laid in first 17 days	No. of eggs laid between 9.IX.57 and 25.IX.57
5	16	43
9	15	24
13	24	34 (29.VIII - 16. IX)
23	24	38

First Generation

		No. of eggs laid between 5.XII 57 and 21.XII 57	No. of eggs laid between 7.1.58 and 23.1.58
D'	55	-	-
5'	58	38	87
3'	61	13	-
23'	45	30	9
U	53	54	77
H	75	60	93
O	81	-	-
Control	26	22	39
1 cop	29	42	60
1 copa	-	25 (1st period)	73

Second Generation

5'''	114
H''	76
5''	19
U'	49
O''	27

In both the parent and first generations there was an increase in the number of eggs laid per 17-day period as oviposition progressed, which indicates a temperature response. An exception was the first generation during December, but this may be accounted for by the cooler temperature recorded during that month. The first generation produced more than the parent generation over all periods. The production by the first generation in January was similar to that of the second generation in February. Either the second generation was then already producing at its peak, or a greater peak was to be expected. Although February was the warmest month, the first generation by then were ageing, and laying irregularly, and so produced few eggs. The increase in production over succeeding generations may be attributed to increase in temperature, to acclimatisation, or both, but temperature was probably the major factor operative. The mean monthly maximum and minimum temperatures recorded in the greenhouse over the 1957-58 season are shown in Table 27.

TABLE 27

TEMPERATURES IN THE GREENHOUSE 1957-58 SEASON

Month of year	Mean maximum temperature in °F.		Mean minimum temperature in °F.	
July 1957	73		51	
August	85		41	
September	91		44	
October 1st-24th (roof white-washed 24th)	98	94	44	45
October 25th-31st	80		49	
November	85		50	
December (1st week)	82		50	
January 1958 (last week)	89		57	
February	89		57	
March	81		52	

Gurr (1957) did not find a correlation between air temperature and the number of eggs laid, but his study was not continued long enough to show seasonal trends. Smith (1927) working with the Rutherglen bug (a Nysius species) found a response, in oviposition, to temperature changes. He also showed that maturity in the female was reached in 4 - 9 days, that the oviposition period was 13 - 25 days, that the maximum number of eggs laid per day was 25 - 45 and the totals laid were 135 - 450 eggs.

Adult Longevity

The longevity of adult females of N. huttoni is shown in Tables 23 and 24. Woodward (1952) reported that in the Mirid Stenodema laevigatum (L.) the males die off earlier than the females, after the copulation period, and Pendergrast (1952) reported that in Rhopalimorpha bugs the males die soon after the copulation period. When males of the parent generation were still alive after two months, it was obvious that the above principle did not apply to N. huttoni males, and so the longevity of the parent and first generation males was determined. The results are presented in Table 28.

TABLE 28

LONGEVITY OF ADULT MALES

	Code No. of mated pair	Longevity of male adult in days
Parent generation	5	193
	9	293
	13	206
	14	204
	15	214
	17	207
	18	208
	23	65
	24	65
	Mean	184
First generation	5'	94
	23'	125
	U	74
	H	79
	O	87
	Mean	92

It is obvious that the males lived as long as the females. Consider first the parent generation. Male 24 died soon after his mate which laid eggs before winter, but male 18 lived far longer than his mate and survived well beyond the winter. Males 14 and 15 also well outlived their mates which did not survive the winter. Males 5, 9, 13 and 17 lived as long as their mates which did survive the winter. Both members of pair 9 exhibited extreme longevity. The first generation males also lived as long as the females. However, the maximum longevity of the first generation (4 - 6 months) and the mean longevity (3 months) were considerably shorter than those of the parent generation (10 months and 6 - 7 months). Copulation occurred throughout adult life (with the exception of winter time), and pair 9 were seen in copulation a few days before their death.

RHYTHM IN EGG-LAYING

Rhythm in Number of Eggs Laid per Day

In the numbers of eggs laid per day, Gurr (1957) found no apparent rhythm. From perusal of the individual daily performances shown in Appendices VI - VIII, this seemed also to be the case with the present study. However, when the mean number of eggs laid per day was graphed, a simple, general pattern, as shown in Figs. 12, 13 and 14 was revealed. There was a short period of low production, followed by a fairly steady peak level of production which tailed away to zero towards the end of the females' lives. Apart from this short rise and fall at each end of the oviposition period, the production was fairly steady and unrhythmical. Each generation, however, showed slight variations to this general pattern. Egg production by the parent generation females which laid before winter began to decline relatively early, indicating the curtailment of activity with the onset of winter. For the parent generation females which laid after winter, the peak level was interrupted by days on which no eggs were laid, and these were more frequent at both ends of the peak period.

In the first generation, egg production increased rapidly at first (probably

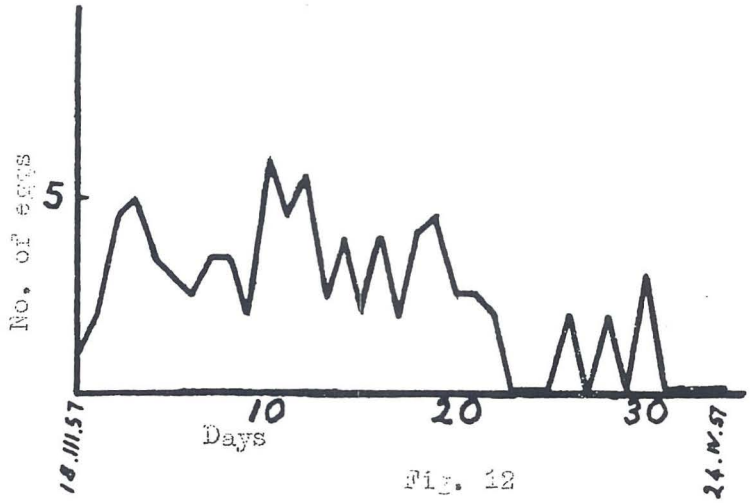


Fig. 12

Seasonal trend in mean number of eggs laid per day by parent generation before winter.

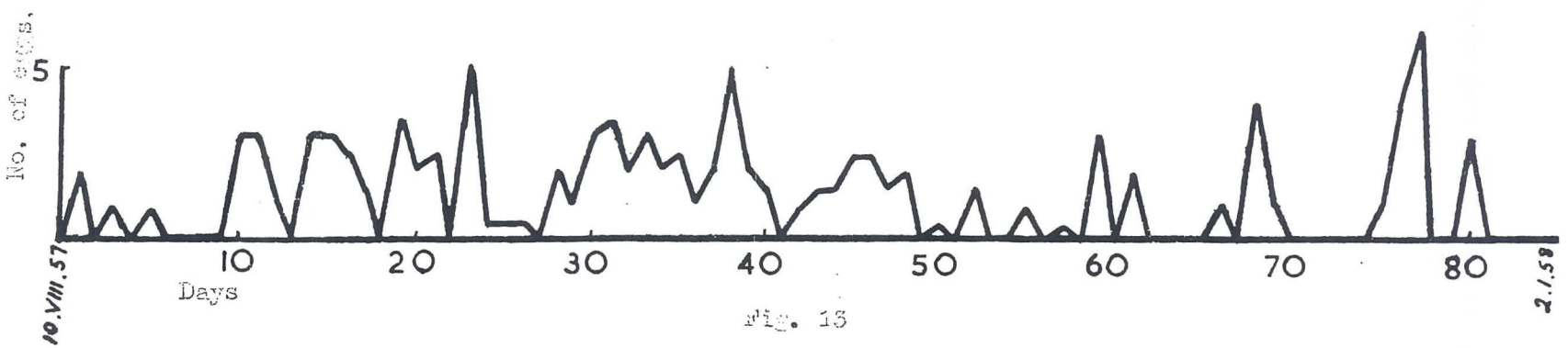


Fig. 13

Seasonal trend in mean number of eggs laid per day by parent generation after winter.

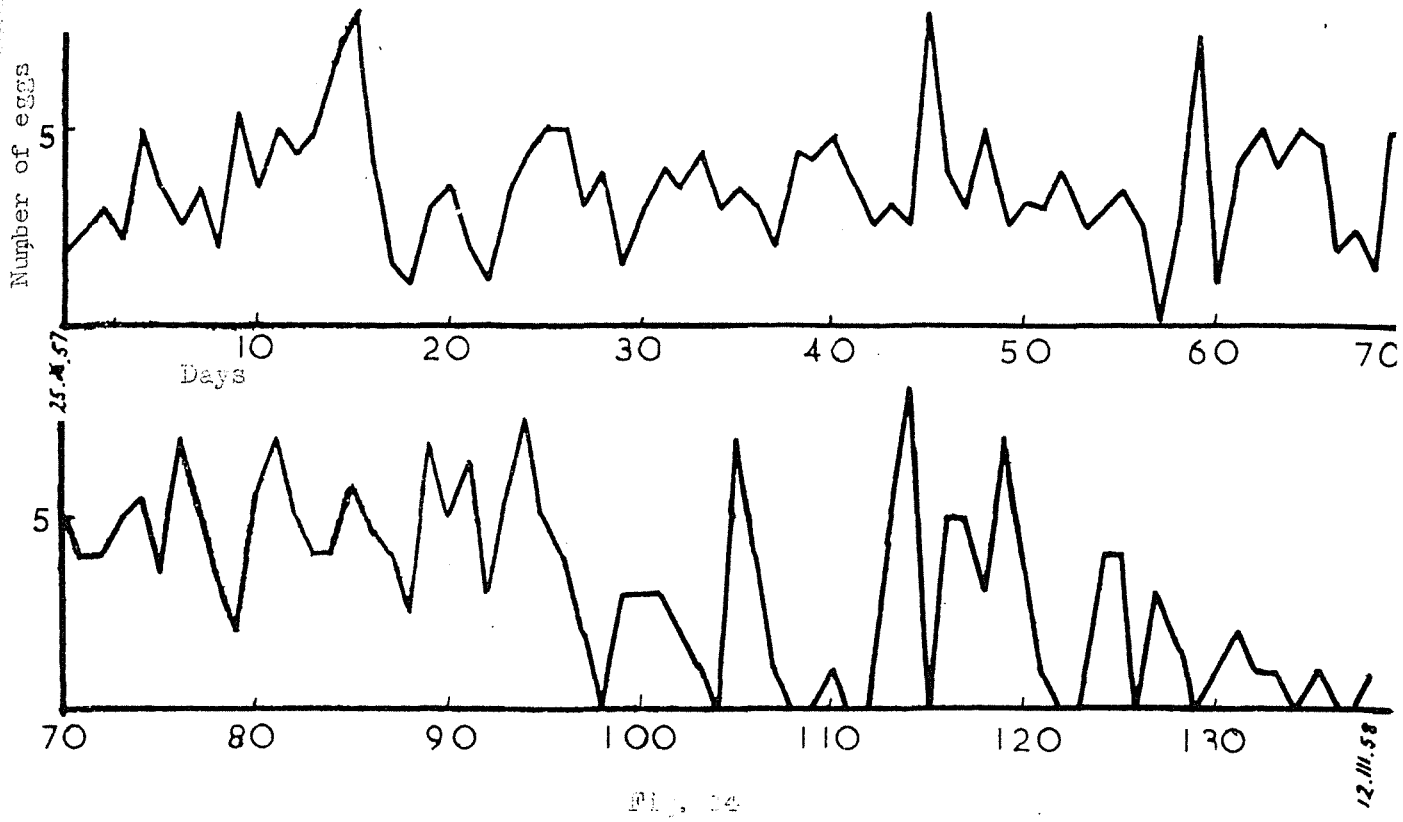


Fig. 14

Seasonal trend in mean number of eggs laid per day by first generation.

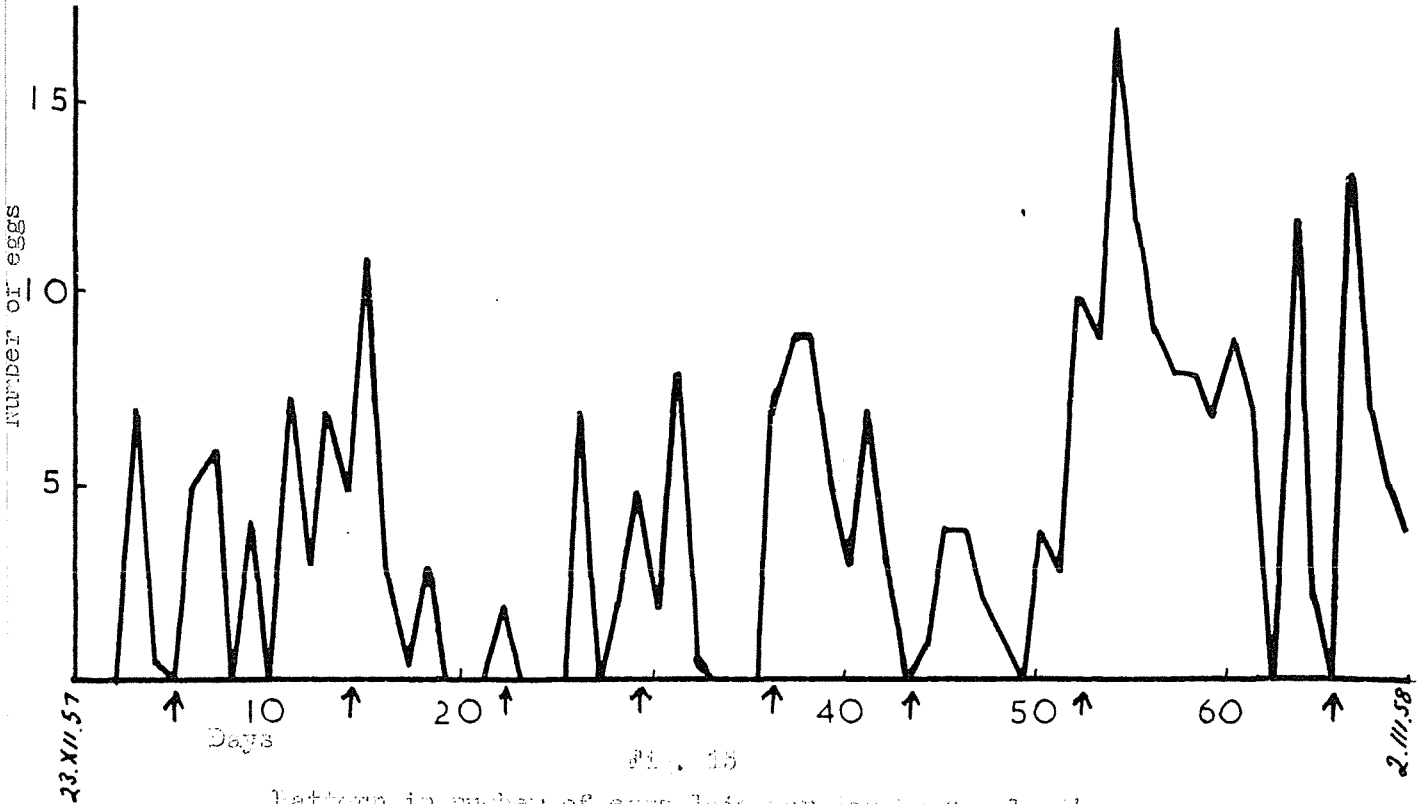


Fig. 15

Pattern in number of eggs laid per day by female 4' Arrows indicate days when copulation permitted

due to the warmer weather), and then settled on a steady level from mid-November to 23rd December. The increase at that time was maintained until mid January when a further increase in production was maintained until the end of January. A decline set in, but, probably in response to the warmer February weather, a short rise in production occurred. This was not maintained, mainly because of the age of the females; production then declined to zero.

Female 1 copa, which received only one copulation in her life, showed a distinct pattern. She laid sixteen eggs on the day of the copulation, but thereafter her production was at a steady, lower, rate of 1 - 8 eggs per day. Female 1 cop which recieved the same treatment, did not respond in the same way, but followed the general pattern of the mated females. The egg production of female 2' showed a distinct pattern (see Fig. 15) which demonstrated the stimulatory effect of presence of the male. In seven out of nine cases, the introduction of, and copulation by, a male, resulted in a marked increase in the number of eggs laid either on that day or the following day, or on both days.

Rhythm in Bursts of Egg Laying

Although there was no rhythm in the number of eggs laid per day, the author found that, for individual females, when the duration of bursts of egg laying were compared with the duration of the breaks between the bursts, a definite rhythm could be demonstrated. The following are definitions of terms used.

A burst refers to the number of successive days on which oviposition occurred, without interruption by a break.

A break refers to that period, between two successive bursts, during which the female did not lay.

Short, medium and long bursts are respectively, 1 - 4 days, 5 - 11 days and 12+ days.

Short, medium and long breaks are respectively, 1 - 2 days, 3 - 5 days and 6+ days.

Parent Generation

Of all the females in the three generations, female 23 had the most perfect rhythm (see Fig. 18) which the author regards as the basic or ideal rhythm. As her egg production was not checked daily until eleven days of oviposition had elapsed, the histogram begins at that point. As oviposition progressed, there was an increase in the duration of bursts to a peak, followed by a decline to short bursts at the close of the oviposition period. The reverse occurred with the breaks which were of two days duration at both ends of the oviposition period, but were reduced to one days duration over the central or peak production period. In detail, she did not lay in long bursts, for the longest was 8 days and the next longest 5 days. There was one burst of 4 days, three of 2 days and three of 1 day. She had nine breaks between bursts of egg laying, five of which were of two days duration and four of 1 days duration. Thus, generally she would lay on one or two days, miss two days or one day and then lay again on one or two days, etc. In fact of the parent generation she was the most regular layer, for there were no extensive breaks as in most of the others except females 7 and 13 which were in this way similar.

Most of the females varied somewhat from the above basic rhythm. Females 18 and 24 which laid before winter, differed in their rhythm (Figs. 16 and 17). The former laid her longest burst at the start of the oviposition period, and thereafter the duration of bursts declined, whilst for the latter the longest burst was in the middle of the oviposition period. The duration of the breaks also differed.

Of the parent generation which laid after winter, females 5, 9 and D showed similar rhythms (see Figs. 19, 20 and 21). There was a long break of about one week after the first burst of eggs were laid, and then medium to long breaks of 2 - 6 days between short bursts. From 9th - 27th September the duration of the bursts increased and that of the breaks decreased. Thereafter the reverse occurred and laying became very widely spread, especially in the case of female 9, for

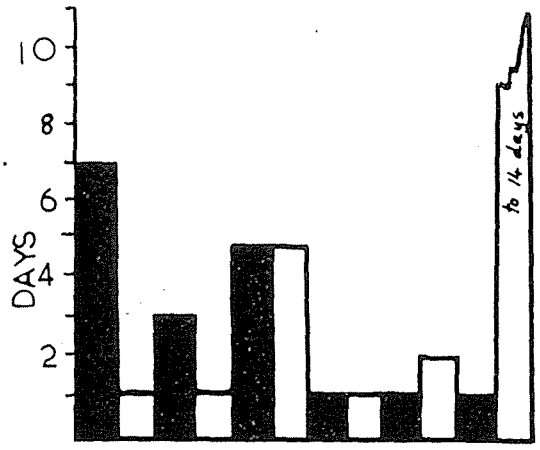


Fig. 16

Rhythm in egg laying for female 18.

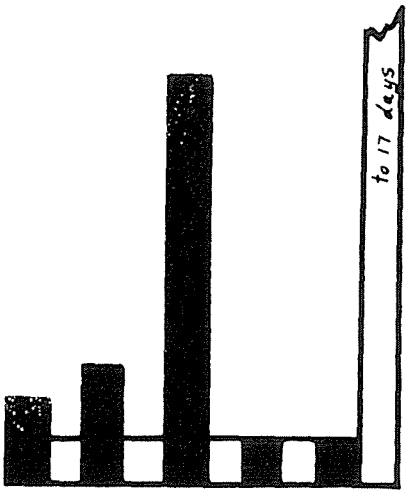


Fig. 17

Bursts of egg laying

Breaks between bursts

Rhythm in egg laying for female 24.

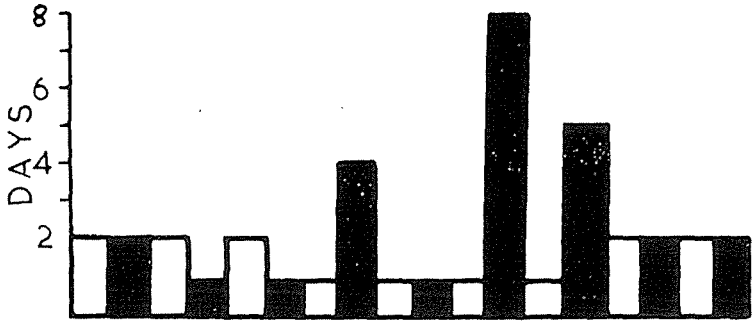


Fig. 18

Rhythm in egg laying for female 23

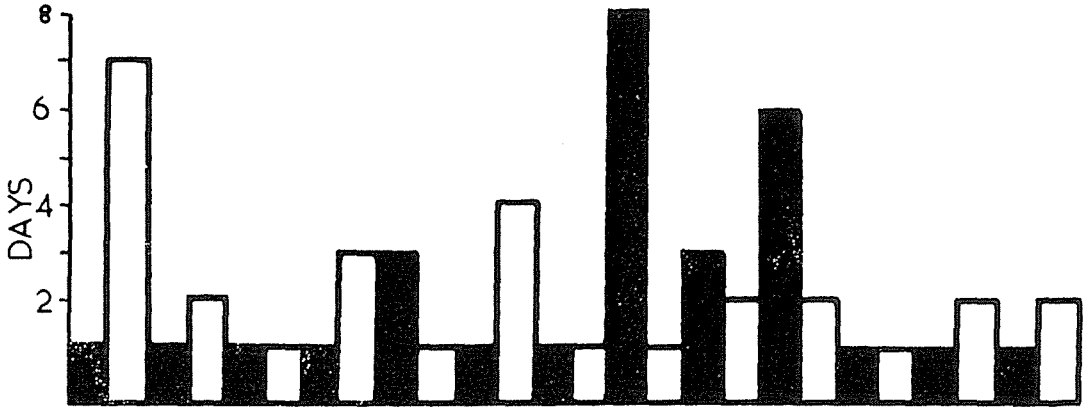


Fig. 19

Rhythm in egg laying for female 5

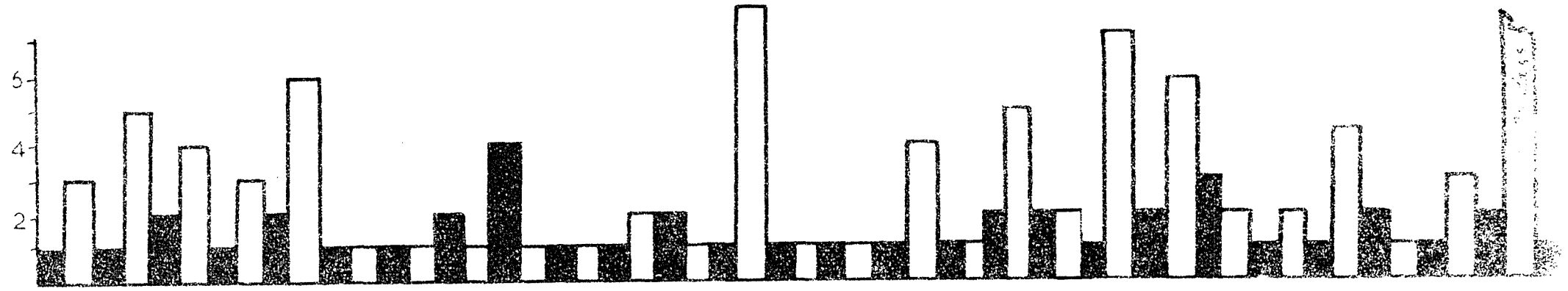


Fig. 20
Rhythm in egg laying for female 9

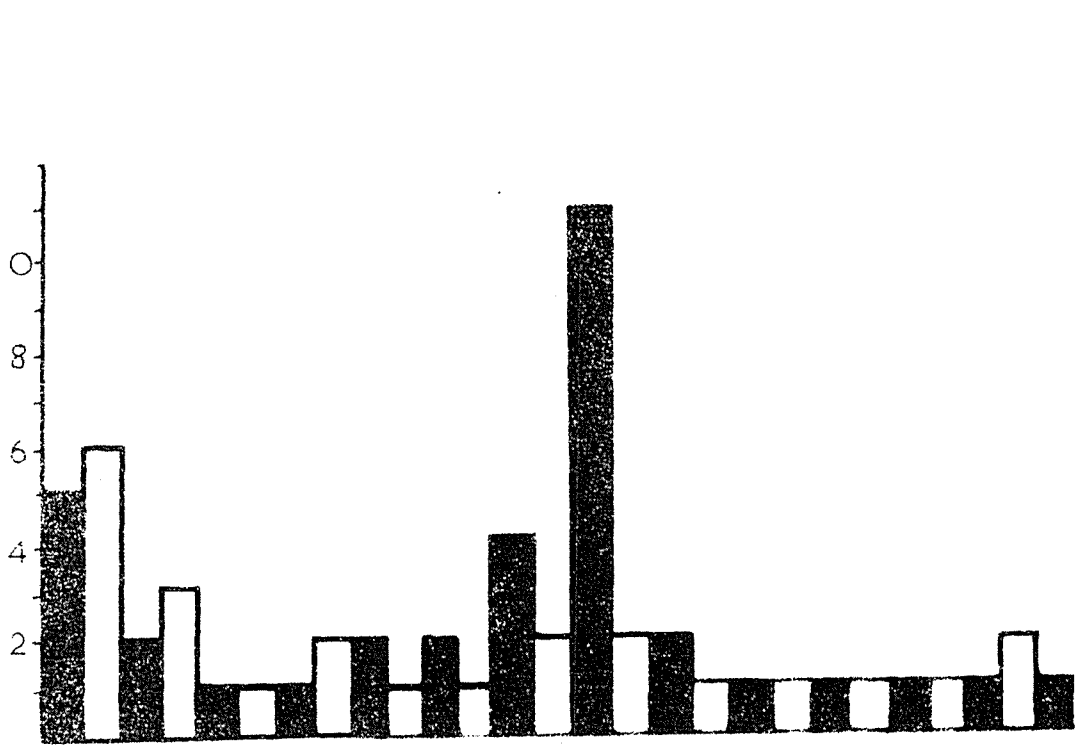


Fig. 21
Rhythm in egg laying for female D

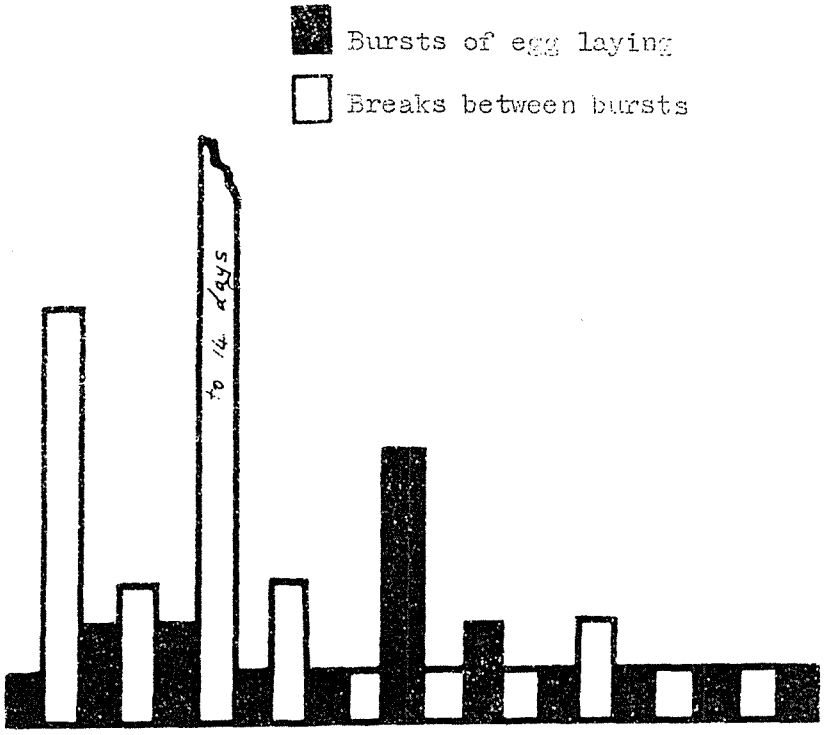


Fig. 23
Rhythm in egg laying for female Z

which long breaks of 7 - 9 days were recorded between short bursts of 1 - 3 days. These three conform to the basic rhythm.

For females 7 and 13 (Fig. 22) bursts at first were very short, but from the outset they laid more often, and their rhythm differed from that of females 5, 9 and D in the occurrence of very short breaks. From 27th August female 13 began to lay in successively longer bursts, 1, 3, 4 and 7 days in duration, but then escaped. All breaks were for one day only.

The rhythm for female E (Fig. 23) differed again. Early in the oviposition period she laid short bursts which were very widely spaced (breaks of 3 - 14 days). Next a break of one day was followed by the peak of her oviposition, a medium burst of 6 days from 16th - 21st September. From then until death, she laid in very short bursts, but the breaks did not increase in duration as in the basic rhythm.

Thus the rhythm for the majority of the parent generation females resembled the basic rhythm i.e. there was an increase in the duration of bursts and a corresponding decrease in the duration of breaks up to the middle of the oviposition period, after which the reverse set in.

First Generation

Four females showed a similar rhythm, three showed a distinct rhythm of their own, and the four females for which the male was present for varying times also showed different rhythms.

Females D', 5', 3' (Figs. 24, 25 and 26) and O first laid two medium bursts of from 5 - 11 days with a short break between. Next was a short burst of 2 - 3 days, a medium burst of 5 - 10 days and another short burst, all separated by short to medium breaks. From this point onwards the rhythms were different because of different longevity. Female O escaped before this point. Female D' laid three more short bursts and then died. The rhythm of her breaks was similar to the basic rhythm in that they were longer at both ends of the oviposition period.

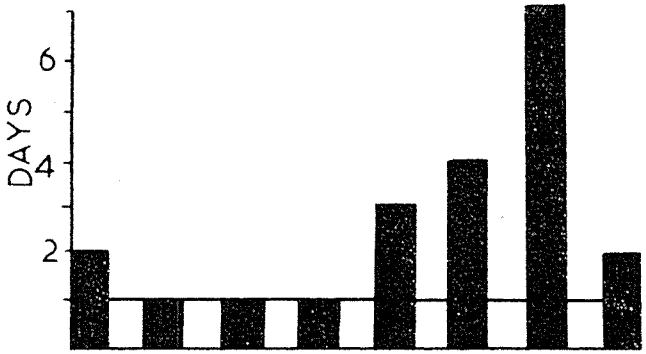


Fig. 22

Rhythm in egg laying for female 15

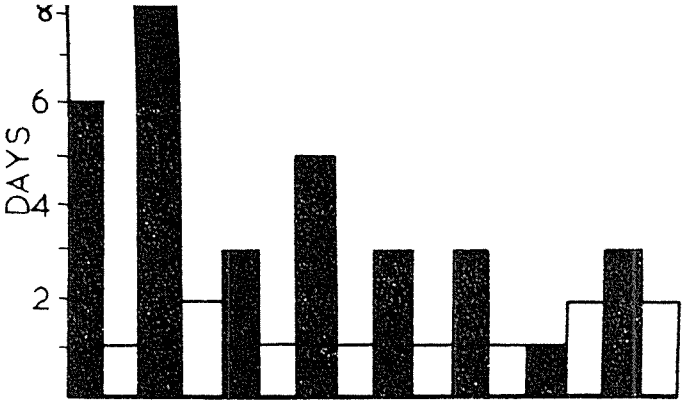


Fig. 24

Rhythm in egg laying for female D'

Fig. 25

Rhythm in egg laying for female 5'

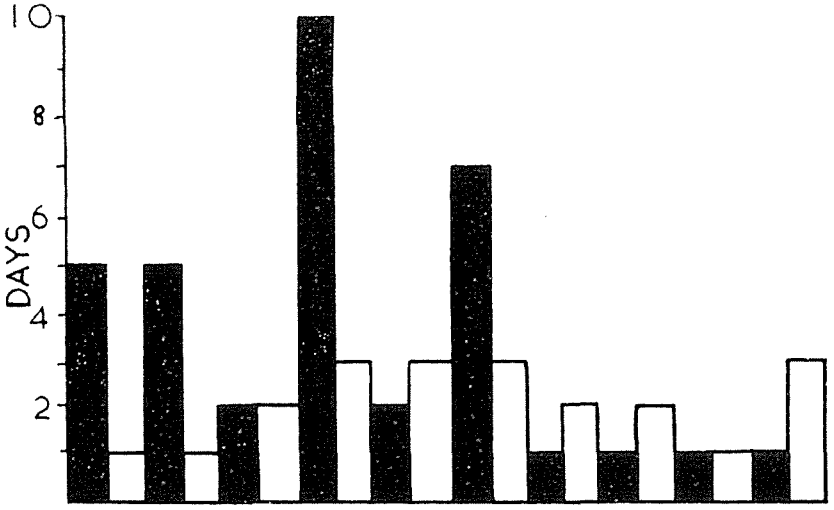


Fig. 26

Rhythm in egg laying for female 3'

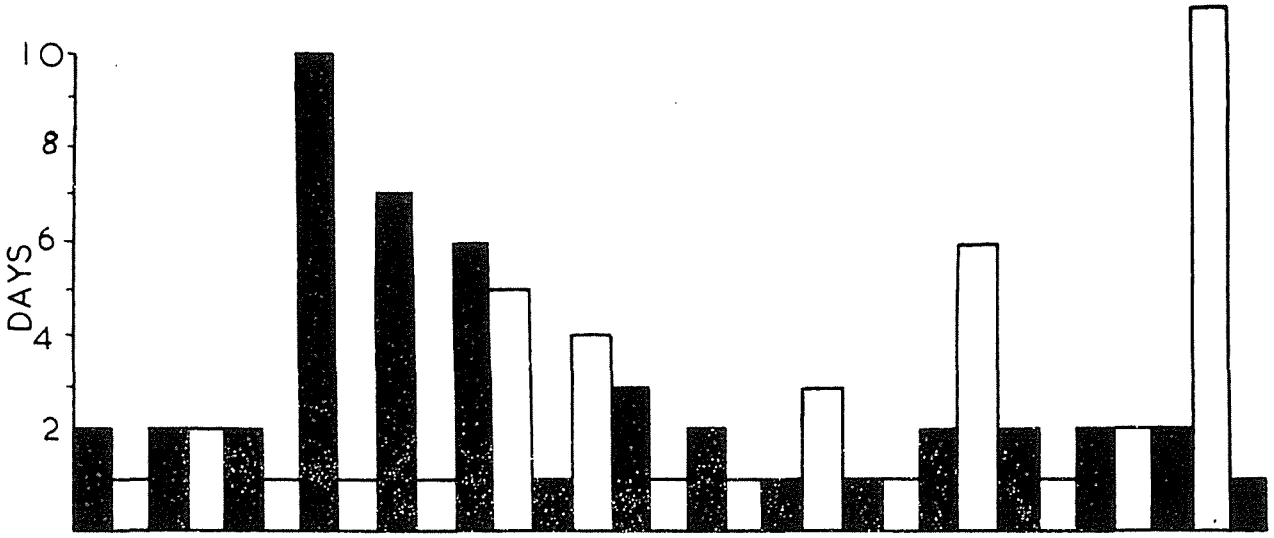


Fig. 27

Rhythm in egg laying for female 23'

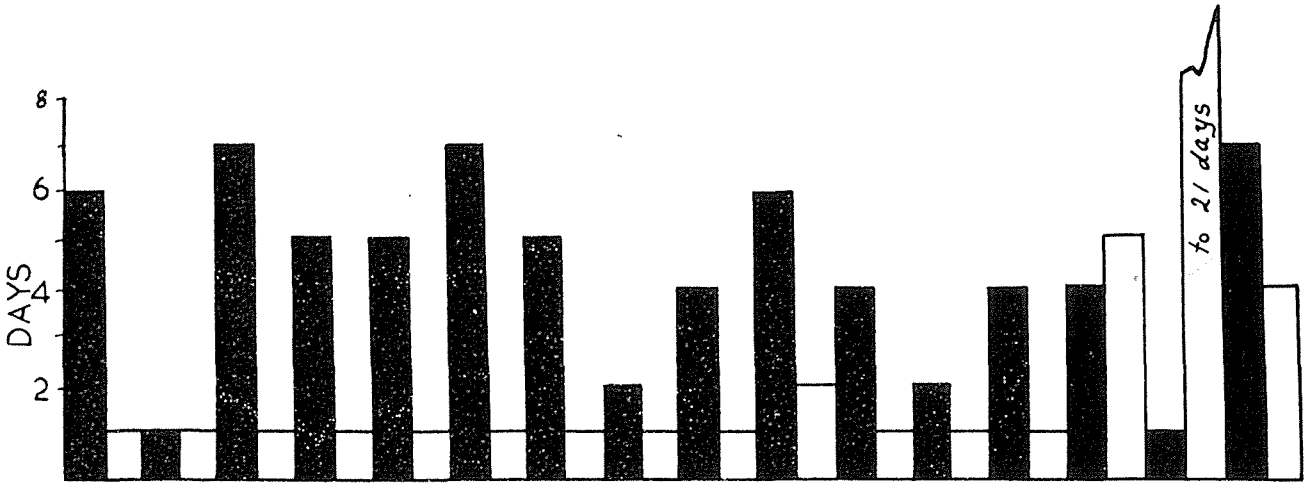


Fig. 28

Rhythm in egg laying for female U

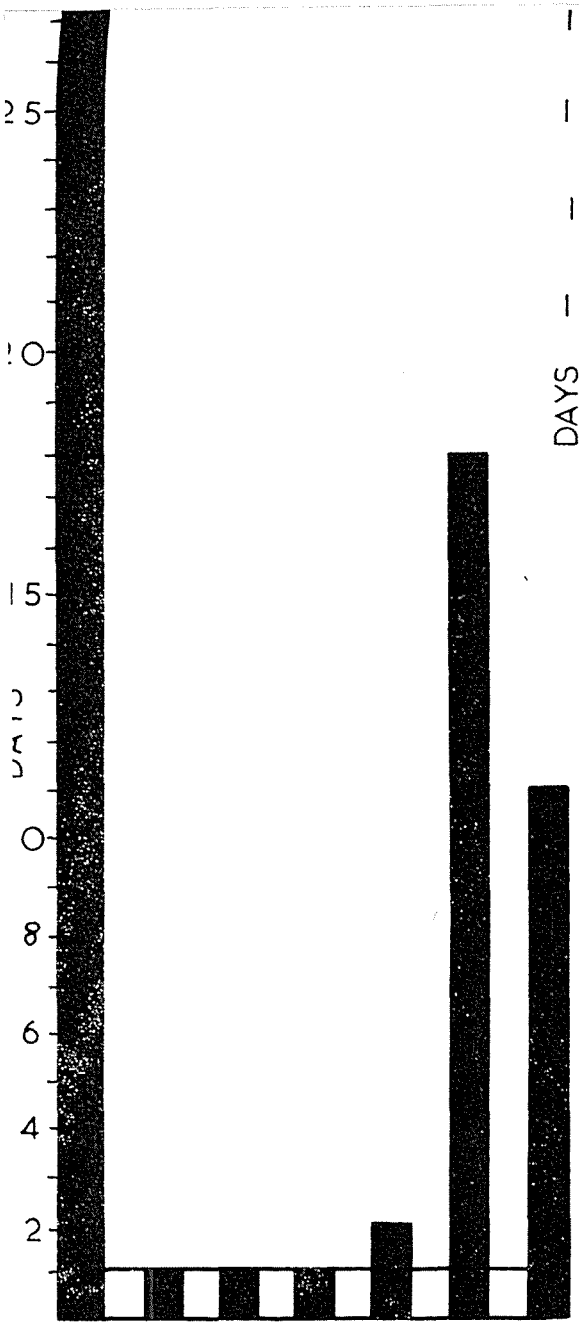


Fig. 29
Rhythm in egg laying for female H

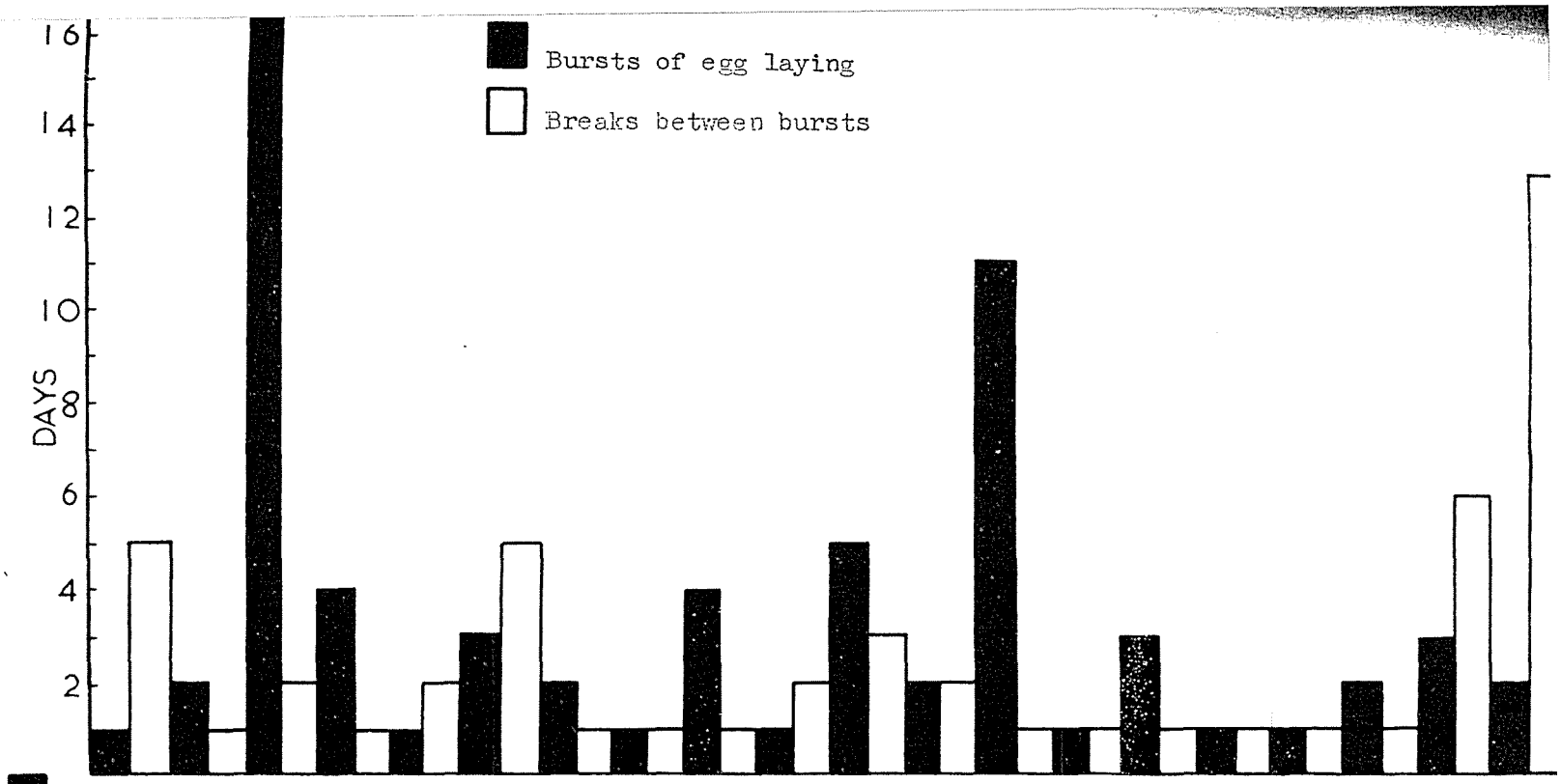


Fig. 30
Rhythm in egg laying for Control female

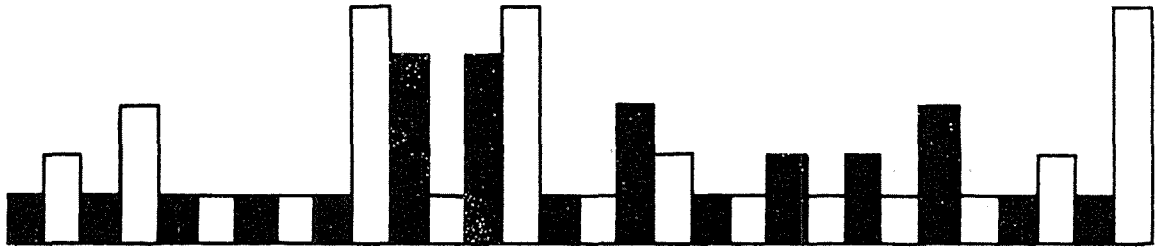


Fig. 31
Rhythm in egg laying for female 1 ...

Female 5' laid one more medium burst, and then four very short bursts which indicated a physiological decline before death. The longest breaks occurred in the centre of her oviposition period. Female 5' lived on for some time and laid in medium bursts of 5 - 6 days duration, but with two short bursts between longer bursts or groups of longer bursts. She laid one very long burst of 24 days and then a series of mainly short bursts. Death occurred after a long break of 42 days, but the breaks during the oviposition period were all short except the one before the longest burst.

Female 23' had a rhythm of her own which is shown in Fig. 27. First she laid three short bursts of 2 days duration, followed by three medium bursts and thereafter ten short bursts until death. The duration of the breaks between bursts were normally 1 - 3 days, but after the third medium burst the break was 5 days, after the following short burst the break was four days, and towards the end of the oviposition period there were long breaks. Of the first generation rhythms this was the closest to the basic rhythm. That is the duration of bursts increased and then decreased, and, apart from the first five short breaks, the opposite was true of the breaks. The fact that female 23' was a daughter of female 23, which produced the basic rhythm, may be of significance.

Female U laid very regularly (see Fig. 28). Breaks were very short, generally of one days duration except near the end of the oviposition period. The bursts were almost of uniform duration (which indicates steady production) except for four very short bursts which divide the oviposition period into sections.

The rhythm shown in Fig. 29 for female H was markedly different from any discussed thus far. First there was a very long burst of 28 days duration, followed by four very short bursts and then two long bursts of 18 and 11 days duration. The duration of breaks between bursts was always one day. As her oviposition period was relatively short, it would seem that she had "burnt" herself out by laying in such long bursts.

The rhythm for the control female (Fig. 30) was not unlike that for female

23' except that instead of tailing off in short bursts it showed one or two longer bursts towards the end of the oviposition period and then the usual short bursts before death. Thus it was something like double the rhythm for female 23'. The effect of complete absence of the male was reflected, not in long breaks, but in short bursts. This is in agreement with the earlier finding that a longer oviposition period was required by this female to produce a normal total number of eggs. Thus copulation is not a prerequisite for formation, and continued production of eggs, as is the case in Rhopalimorpha bugs (Pendergrast, 1952).

The rhythm for female 1 copa is shown in Fig. 31. It is similar to the basic rhythm. It is also similar to that for the control female in the occurrence of mainly very short bursts. Thus presence of the male for one copulation only, seemed insufficient for egg production in long bursts. It was also noted that this female remained fertile for life. In her second to last egg batch, fertility began to decline, for three eggs out of six failed to hatch, and the two eggs in her last batch did not hatch. This decline in fertility is not important because it occurs at the very end of her life; her third-last egg batch comprised nine eggs which all hatched. Thus from one copulation, sufficient sperm was stored by the female to fertilise more than 100 eggs. Female 23 of the parent generation also remained fertile for life. Her mate died before winter 1957, but she survived the winter, commenced oviposition in August, and on 5th October laid her last egg which hatched. Thus, should it occur that males fail to survive the winter, here would be a means of continuance of the species, for evidently females can store sperm overwinter in a viable state. Woodward (1952) showed that in the autumn generation of the Mirid N. erratica, fertilisation occurs in autumn, the males failing to survive winter. From the greenhouse experiment it could not be stated for certain that this did not normally happen in N. huttoni. However, as pairs in copula were seen in the field in early spring, there can be no doubt that males survive the winter. Maturity in the male therefore precedes maturity in the female (which fact was also found from the greenhouse experiment) and

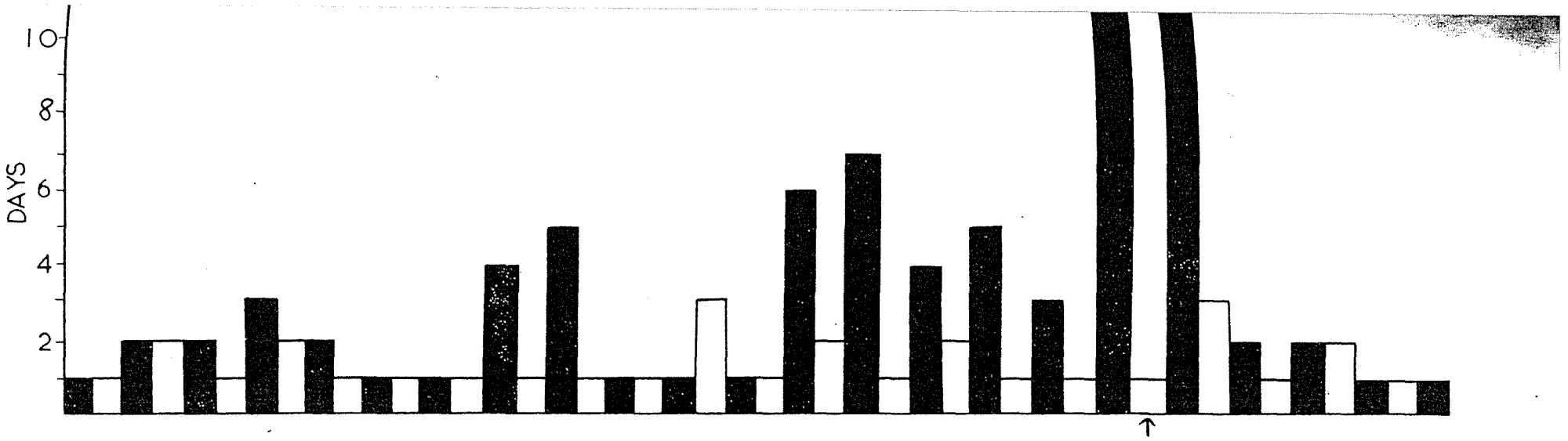


Fig. 32
Rhythm in egg laying for female 1 cop
Arrow denotes when male was discovered.

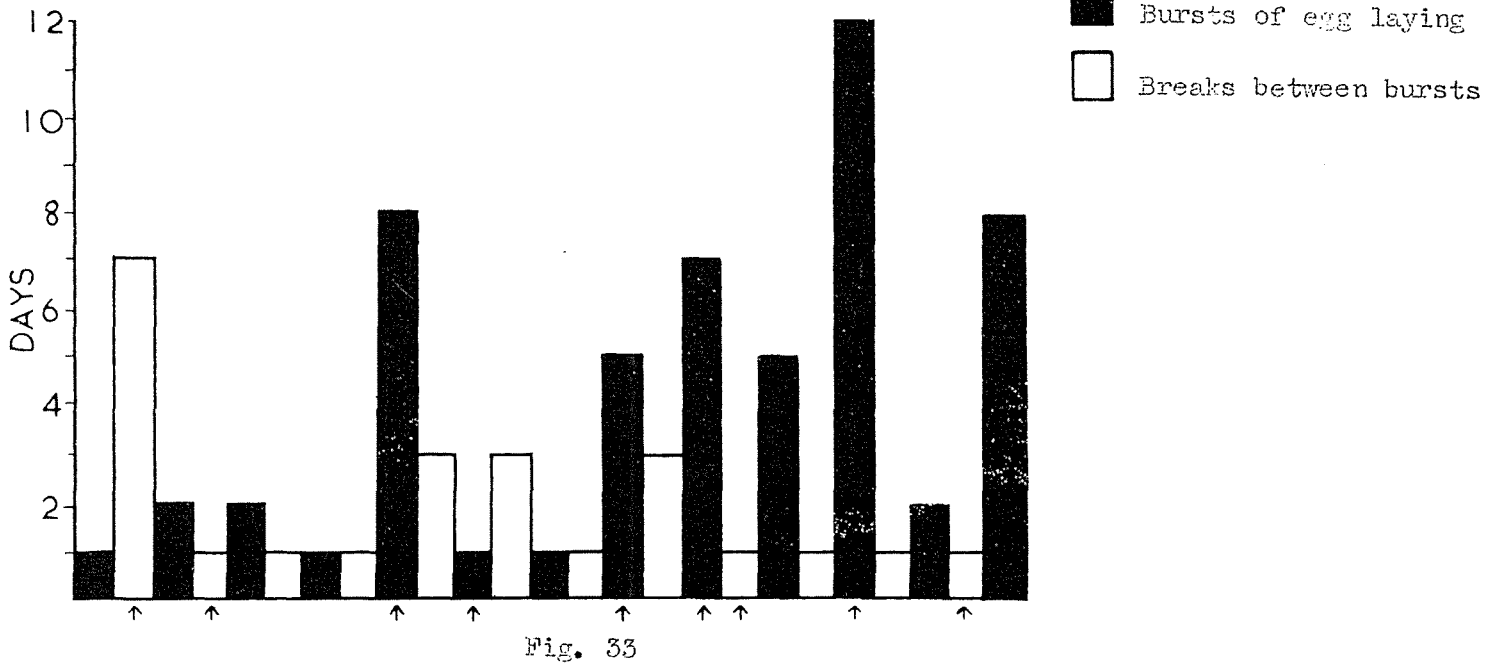


Fig. 33
Rhythm in egg laying for female Z'

copulation probably stimulates ovarian development.

The rhythm for female 1 cop is shown in Fig. 32. An incident (caused by an abnormality over which the author had no control) occurred, which caused a change in her rhythm; this actually enhanced the study by providing information which otherwise would not have come to light. On 9th February 1958, i.e. three quarters the way through her oviposition period, a male was noticed in the tube with her. A close examination of the tube revealed that occasionally she had oviposited on the paper name-tag instead of in the site almost invariably chosen by other females, the cotton-wool plug. The presence of nymphs in the tube indicated that the male was her own son, reared in the tube. The rhythm for the first half of her oviposition was similar to the rhythm for 1 copa, in that the bursts were short. The male may have been present unnoticed for several days, which would account for the sudden occurrence of medium bursts. Otherwise they would have to be attributed to the increase in temperature over late January and February. However, when the rhythm for female 2' is considered, it seems fairly certain that the longer bursts in the second half of female 1 cop's oviposition period can be attributed to the sudden appearance of the male. Thus Fig. 32 compared with Fig. 31 demonstrates the change in egg-laying rhythm caused by the sudden introduction of a male halfway through the oviposition period.

The check on fertility of the eggs laid by 1 cop had to be abandoned, but as her eggs laid prior to 9th February were fertile she must have utilised sperm stored from the first copulation, until the other male appeared. In the setting up of females 1 cop and 1 copa (and also of some of the pairs) the females laid one or two egg batches before the male was introduced. Yet some, if not most, of the eggs laid on the day of first copulation, were fertile.

The rhythm for female 2', which received one copulation per week, is shown in Fig. 33. Whenever a copulation occurred somewhere within a burst of egg-laying, the duration of that burst was prolonged. All other bursts were very short with the exception of one of 5 days duration. As a copulation occurred on the one day

break immediately preceding this burst, its duration may also be attributed to the stimulatory effect of copulation.

In conclusion, the basic rhythm was not common in the first generation. Most of the females began laying in fairly long bursts and the longest burst did not coincide with the middle of the oviposition period except for females 5' and 3'. The duration of bursts decreased towards the end of the oviposition period. There was generally no rhythm in the duration of breaks, which tended to remain constant. Possibly the females had a spell by laying one or two short bursts instead of having longer breaks. The more favourable climatic conditions existing at the time of the first generation oviposition probably obviated the short bursts and long breaks which were characteristic of the early oviposition period in the parent generation. Ageing would account for the decrease in duration of bursts towards the end of the oviposition period in both generations. In the number of eggs laid per day there was, within certain bursts, an increase to a central peak and then a decrease. However, this was not consistent, for often the peak number occurred at the beginning or end of a burst. No differences between females of different wing form could be detected in either rhythm or production.

Second Generation

In the partial fecundity record shown in Appendix IX, females 5''' and H" showed similar rhythms. Opposite ends of two long bursts are shown, separated by the minimum break of one day. As there was an increase in the duration of bursts from the parent generation to the first generation, it seemed likely that some of the bursts in the second generation would be at least of equal duration as the longest in the first generation (namely 28 and 24 days).

Females U' and U" which were unmated showed a different rhythm. The bursts were shorter, and for U" the breaks were longer. This indicates that absence of the male had a depressing effect upon oviposition. This was also evidenced in the control female and in females 1 cop and 1 copa.

Number of Ovarioles in N. huttoni

Pendergrast (1957) reported seven lobes per testis for three species of Lygaeidae examined. Woodward (mentioned by Pendergrast) showed that in most Heteropteran species, the number of ovarioles was generally the same as, or else within one of, the number of testis follicles. Therefore N. huttoni may be expected to have 6 - 8 ovarioles per ovary (i.e. assuming seven follicles per testis is general for this family). The N. huttoni females studied rarely produced the potential maximum, for batches of above 10 eggs per day were not common and did not occur at all in the parent generation. There were two batches of 16 eggs, one of 17 and one of 19. Highest daily production tended to occur in the centre of the oviposition period, whilst at both ends only one half to one quarter of the potential maximum production occurred.

TIME OF DAY OF OVIPOSITION AND THE EFFECT OF SHADING UPON THE SAME

For Nezara viridula L., Cumber (1951) showed that the main daily oviposition period was between noon and 4pm, and that shading of the bugs with a sheet of paper at mid-day seemed to stimulate oviposition. It was decided to determine for N. huttoni the preferred time of day (if any) for oviposition, and, by shading in the mornings (in an endeavour to cause maximum oviposition to occur in the morning) to determine whether or not shading stimulated oviposition.

Parent Generation

In the parent generation which laid before winter, the number of eggs laid over an 18 day period were checked at noon and 6 pm. Totals for that period laid in the morning and afternoon were, respectively, 61 eggs and 98 eggs. There was a definite preference for afternoon oviposition; 38% of the eggs were oviposited in the morning. There was no time before winter to determine the influence of shading upon oviposition.

With the parent generation which laid after winter, the effect of shading in

the mornings upon oviposition was tested over a 28-day period in September and October. The tubes were shaded by a sheet of newspaper on sunny mornings, but not on overcast mornings because then the tubes were already in the shade. Over the trial period, 11 mornings were sunny and 17 were overcast. The number of eggs laid in the morning and afternoon by each female are shown in Table 29.

TABLE 29

OVIPOSITION TIMES OF PARENT GENERATION WHEN SHADED IN THE MORNING

Code No. of Female	No. of egg clusters laid		No. of eggs laid	
	Morning	Afternoon	Morning	Afternoon
5	4	14	10	30
9	1	12	2	30
13	0	5	0	11
23	11	9	19	19
D	6	16	7	35
Z	4	11	7	38
Total	26	67	45	163

Female 23 laid a considerable number of eggs in the morning, but this did not exceed the number laid in the afternoon. In the first four days no eggs were laid in the morning, and some females did not lay in the morning until six days after the commencement of morning shading. This may be interpreted as indicating that morning shading did cause some eggs to be laid in the morning, but that at least four days were required for the treatment to take effect. However, when the percentage of eggs laid in the morning (22%) is compared with that for those which laid before winter, it is obvious that shading had no effect upon oviposition.

First Generation

On the first generation, a close check on oviposition extended over two months from 3rd December 1957 to 10th February 1958. Up to 30th January the bugs were not shaded. Shading in the morning was applied from 31st January to the end of

the period. During December, observations were at 8am, Noon, 4.30pm, and 6.30pm. However, in order to determine more accurately the preferred time of day of oviposition, observations over the remainder of the period were at 8am, 10am, Noon, 2.30pm, 4.30pm and 6.30pm. The number of eggs laid between each observation by each female are shown (for the whole period) in Appendix X. The totals laid by each female at each interval are shown, for the non-shaded period in Table 30, and for the morning shaded period in Table 31.

TABLE 30

OVIPOSITION TIMES OF FIRST GENERATION

The numbers in parentheses are the numbers of eggs laid in December in the morning and afternoon before these periods were each divided into two intervals.

Time Interval	6.30pm–8am	8am–10am	(8am–Noon) 10am–Noon	Noon–2.30pm	(Noon–4.30pm) 2.30pm–4.30pm	4.30pm–6.30pm
♀Code No.						
D'			(7)		(5)	
5'	16	10	(7) 12	19	(44) 23	10
3'	1	2	(4)		(6)	2
23'	1		(5) 1	2	(31) 1	5
U	12	6	(7) 8	37	(57) 9	20
H	11	1	(13) 7	27	(60) 23	2
O	2		(13)		(19)	
Control	2	2	(7) 10	20	(20) 16	7
1 cop	6		(9) 13	21	(23) 18	8
1 copa	2	1	(6) 11	22	(13) 13	19
2'	4		13	11	(1) 14	12
2"			6	10	4	2
Total	57	22	(76) 81	169	(277) 121	87

TABLE 31

OVIPOSITION TIMES OF FIRST GENERATION WHEN SHADED IN THE MORNING

Time Interval	6.30pm-8am	8am-10am	10am-Noon	Noon-2.30pm	2.30pm-4.30pm	4.30pm-6.30pm
Female Code No.						
5'	6	2	1	8	8	0
23'				1		
U				1	0	2
Control	2	4	3	1	5	0
1 cop	1	2	4	10	14	3
Z'	2	4	9	9	8	1
Total	11	12	17	30	35	6

From Table 30 it is seen that eggs may be laid at any time of day, but with an increase to a peak just after mid-day (Noon-2.30pm) and thereafter a very gradual decline. In fact oviposition was fairly steady from 10am through to early evening. These insects differ from higher animals in that greatest activity coincides with warmest day temperature. Only 30% of total eggs were laid in the morning.

A seemingly large number of eggs were laid overnight, mainly be females 5', U and H. Further investigation showed that no eggs were laid before 8am or after about 7.30pm. Hence those recorded as laid overnight would have been laid in the evening, soon after 6.30pm.

From Table 31 it is seen that shading in the morning did not induce oviposition in the morning. It is possible that morning shading may cause an increase in the number of eggs laid immediately after noon. There was actually a decrease in oviposition in this period, and an increase between 2.30pm and 4.30pm. Only 36% of the total number of eggs were laid in the morning. There can be no doubt that shading of the bugs did not stimulate oviposition.

Second Generation

As the first generation were ageing by February, a check was made on the second generation over a 14-day period from 1st - 14th February. For the first six days no shading was applied, on the next four days shading was applied between 11am and Noon, and on the last four days shading was applied between Noon and 2.30pm. The total number of eggs laid at the times indicated, over the whole period, were:-

6.30pm - 8am	31
8am -10am	21
10am - Noon	30
Noon - 2.30pm	61
2.30pm - 4.30pm	59
4.30pm - 6.30pm	41

A definite preference was shown for afternoon oviposition; only 31% of the eggs were laid in the morning. Shading did not stimulate oviposition, nor did it effect the number of eggs laid at any other time of day.

Both Cross Series A (sub-brachypterous females) and Cross Series B (macropterous females) also showed a preference for afternoon oviposition and a negative response to shading.

Effect of Changes in Weather upon Oviposition

Cooler weather tended to inhibit oviposition. With the parent generation there seemed to be a difference between an overcast day, and an overcast and cool or rainy day, for some eggs were laid on the former type of days but none on the latter. The maximum daily temperatures in the greenhouse from 14th January to 8th February are shown in Appendix X. The younger, first generation females still laid eggs on cold days, but the numbers were reduced. However, when these females aged, a cold day had more effect upon them.

SUMMARY OF FECUNDITY

1. The act of oviposition and the oviposition stance are described.

2. Results are presented for total egg production, rhythm in egg laying, time of day of oviposition and the effect of shading upon oviposition, as studied over three successive generations. Records of times for maturation, length of oviposition period, number of batches laid per female, number of eggs laid per day, post oviposition period and longevity were also kept.

3. It is shown that the last generation to emerge as adults in the autumn is the only generation with sufficient vigour to survive the winter. These oviposit for the first time after winter and are the major source of the new spring population. Egg rudiments begin to form in the autumn but their development is arrested by winter.

4. In order to survive winter, the autumn generation lived twice as long as, but had a shorter oviposition period than, the spring generation. The increased egg production by succeeding generations is accounted for by the more favourable climatic conditions as the season progresses from the end of winter to the height of summer.

5. It is shown that males do not die soon after copulation, but live as long as the females, and that copulation may occur at any time (excluding winter).

6. It is shown in all generations that maturity in the male is reached a little earlier than in the female. Observations show that this is also the case in the field. The time interval differed in each generation according to the environmental conditions.

7. It is shown that in the mean number of eggs laid per day, there was in all generations, a rise to a steady maximum level of production and then a decline before death. Environmental conditions prevailing affected the duration of the increasing, and the peak production period in each generation, but the decline phase was mainly a reflection of age.

8. It is shown that a definite rhythm can be demonstrated in the duration of

bursts of egg-laying and in the duration of breaks between bursts. In the parent generation the duration of bursts increased to a peak and them declined; the opposite was true of the breaks. In the first generation most of the females began laying in fairly long bursts, but towards the end of the oviposition period the duration of bursts decreased; breaks were generally short.

9. It is shown that presence of the male is not necessary for the formation of eggs or the continued supply of them. Complete absence of the male or his presence for only one copulation at the beginning of the oviposition period, had a slight depressing effect upon oviposition which was reflected in a different rhythm (short bursts), and a smaller number of eggs laid per day, from normal, and a longer oviposition period to produce normal total egg production.

10. Presence of the male for one copulation per week caused an increase in the number of eggs laid on the days of copulation or the day immediately following a copulation. The influence was also reflected in rhythm, in longer bursts.

11. One copulation is sufficient to fertilise a female for life. It is also shown that a female can carry viable sperm over winter and remain fertile for a complete oviposition period after winter without further contact with the male.

12. The number of ovarioles per ovary is estimated at 6 - 8. However, the females seldom oviposited at the potential maximum of 12 - 16 eggs per day, although in one case 19 eggs were oviposited in one day.

13. It is shown for all generations studied that there is a preference for afternoon oviposition. From the first and second generations and the Cross Series, it is shown that greatest oviposition occurs between Noon and 2.30pm. There was a gradual increase in oviposition from 8am - 10am, then a more rapid increase to a peak after mid-day, and thereafter a gradual decline. Although oviposition occurred at any time of day between 8am and 7.30pm, it did not occur outside those times.

14. It is shown for all generations studied that shading did not stimulate oviposition, nor did it alter the normal trend of daily oviposition as stated above (13).

15. No difference in preferred time of day of oviposition, or response to shading was shown in macropterous or sub-brachypterous females.

16. It is shown that cool days cause a decrease in, and that cold days may inhibit, oviposition.

CHAPTER 5

INCUBATION PERIOD

The eggs used in the preliminary incubation study, and those of some of the parent generation, were laid by females collected from the field. All other eggs (unless otherwise stated) were laid by females reared in the greenhouse. During incubation, the eggs, along with the cotton-wool in which they were laid, were placed into small jars 2" by 1" having screw-on lids. The lids were screwed on only lightly, so that some air would probably circulate.

Colour Changes of the Egg as Incubation Progresses

Freshly laid H. huttoni eggs are sometimes an almost colourless white, sometimes a very pale orange (see page 9). By the end of the day on which they were laid, the eggs are a pale orange. The eggs become progressively darker in intensity of colour as incubation proceeds.

A rapid determination of the colour changes was made by examining on the one day, eggs at different stages in incubation. A fresh egg, and eggs at 1, 5, 9 and 14 days were examined under a Zeiss lowpower stereoscopic microscope, using artificial lighting. Colours were compared with Ostwald's (1931) Colour Standards, and where applicable, the name alloted to a colour was obtained from the British Horticultural Colour Chart. The changes noted were as follows:

Egg fresh (6-8 hours): Amber yellow (Ostwald series VIII, 2 ia) throughout; small area at cephalic pole, deeper orange (O. XII, 5 na).

Eggs 1 day: Pale orange (O. VIII, 3 ia) throughout; cephalic pole as above.

5 days: Cadmium orange (O. XIV, 3 pa), colour deeper in cephalic half.

9 days: Saturn red (O. XIV, 5 pa) throughout; two red (O. XII, 7 pc) lateral spots, the eyes, one fourth of total length from cephalic pole; two red abdominal spots in similar positions near posterior pole.

14 days: Poppy red (O. XIV, 6 pa) throughout; eye spots deeper red (O.X, 7 pe);

two red abdominal spots as at 9 days.

In the detailed determination of colour changes, a batch of three eggs laid by a mated female were observed daily (as near as was possible) from oviposition to eclosion. Further, the colour changes occurring in two eggs laid by an unmated female were also determined. As both batches were laid on the same day, a day to day comparison of the colour changes occurring in both groups was drawn up. This is shown on page 96. The observations on the infertile eggs ceased when the fertile eggs hatched.

Discussion of Egg Colour Changes

The rapid determination is in agreement with the corresponding portion of the detailed determination on fertile eggs. From them both, the following brief, general pattern of colour changes during incubation, may be stated. On the third day, the developing eyes may be seen through the chorion as two deep orange spots, placed latero-ventrally one fourth of the total length from the cephalic pole. By the fifth day, the eyes are distinctly red. On the ninth day two dark orange spots show through the chorion, dorso-laterally in the region of the abdomen. On the tenth day their number is doubled and by the eleventh day both pairs of abdominal spots have fused. By the thirteenth day these become red abdominal streaks, and a third, abdominal blotch appears mid-dorsally. Prior to hatching, portions of the mature embryo can be seen through the chorion with the naked eye. The eyes are a deep red, and the antennae which are clearly segmented, are pressed against the ventral surface of the body. The abdomen is still rather a large orange blob at this stage.

The above general pattern is in accordance with that noted by Usinger (1942) for N. coenosulus eggs, and Pendergrast (1952) for Rhopalimorpha eggs.

Within a day the infertile eggs became darker than the fertile eggs, and by the fourth day they were a dull orange-brown. No eye spots developed, and by the

DAILY COLOUR CHANGES OCCURRING IN FERTILE EGGS

Date of oviposition 11th Dec. 1957

1st day, 7pm, 11th Dec. 1957: Straw yellow (Ostwald series X, 2 la) throughout; darker area at cephalic pole, marigold orange (O. XIV, 4 pa).

2nd day, 3pm: Lemon yellow (O. XIV, 2 pa) throughout; cephalic pole saturn red (O. XIV, 5 pa).

3rd day, 2pm: Mostly straw yellow (O. X, 2 la); darker area towards cephalic pole has reddish-orange spot showing through.

5th day, 9am: Definitely orange throughout, but still almost transparent; cephalic pole to one third of total length, cadmium orange (O. XIV, 3 pa), having a reddish spot showing through; remainder lighter, lemon yellow (O. XIV, 2 pa).

6th day, 4pm: As in fifth day.

8th day, 11am: Cephalic pole saturn red (O. XIV, 5 pa), grading through marigold orange (O. XIV, 4 pa) for one third total length, to cadmium orange (O. XIV, 3 pa), to lemon yellow (O. XIV, 2 pa) at the posterior pole; a reddish spot showing through marigold orange region.

9th day, 2pm: Cadmium orange (O. XIV, 3 pa); two lateral poppy red (O. XIV, 6 pa) spots, the eyes, towards cephalic pole; two poppy red blotches towards posterior pole. More uniform in colour throughout, but of slightly lighter intensity at posterior pole.

10th day, 3pm: A somewhat deeper orange (O. XII, 3 pc) throughout; eye spots red (O. XII, 7 na); four red blotches near posterior pole, two together on each side.

11th day, 3pm: Basically marigold orange (O. XIV, 4 pa); eye spots and abdominal blotches poppy red (O. XIV, 6 pa); lateral abdominal blotches have fused to one large blotch on each side.

13th day, 11am: Almost saturn red (O. XIV, 4 pa to 5 pa); two geranium lake red (O. XIV, 7 pa) streaks, one on each side, near posterior pole; a third orange-red blob between these two; eyes almost geranium lake red.

14th day, 9am: Saturn red (O. XIV, 5 pa) throughout; eyes and abdominal streaks geranium lake red (O. XIV, 7 pa); central abdominal blotch poppy red (O. XIV, 6 pa).

16th day, 10am: As in fourteenth day. Antennae also visible through shell.

DAILY COLOUR CHANGES OCCURRING IN INFERTILE EGGS

Date of oviposition 11th Dec. 1957

1st day, 7pm, 11th Dec. 1957: Already a darker orange (Ostwald series XII, 4 p than fertile eggs; darker area towards cephalic pole; cephalic pole p geranium lake red (O. XIV, 7 pa).

2nd day, 3pm: Basically as in 1st day; darker area towards cephalic pole mars orange (O. XII, 5 po); cephalic pole azalea pink (O. X, 6 la).

3rd day, 2pm: Deep orange (O. X, 4 nc) almost throughout, but more intense tow cephalic pole; cephalic pole now this colour; no spot showing through.

5th day, 9am: Darker than fertile eggs, mars orange (O. XII, 5 po) throughout, but darker for one third of total length from cephalic pole; no red sp showing through in this region; cephalic pole no longer red.

6th day, 4pm: Basically dark orange (O. XII, 4 pc), otherwise as in fifth day.

8th day, 11am: As in sixth day, uniform in colour throughout.

9th day, 2pm: Anterior half dark orange (O. XII, 4 pc); posterior half slightly lighter orange (O. XIII, 3 pc). Today, less uniform than fertile eggs No spots showing through because of no embryonic development.

10th day, 3pm: Also O. XII, 3 pc but darker at cephalic pole; a large marigold orange (O. XIV, 4 pa) spot showing through where an eye spot normally would be, but much larger.

11th day, 3pm: Still dark orange-brown (O. XII, 4 pc) large orange blotch near cephalic pole, as in tenth day.

13th day, 11am: As in eleventh day.

14th day, 9am: As in eleventh day.

16th day, 10am: No change.

tenth day a large orange spot, which was probably evidence of the rotting yolk, appeared. Curr (1957) noted that unfertilized eggs remain creamy-white in colour. However, in this batch, and in several other batches observed, the unfertilized eggs became a dull brown in one to two days, many of them having collapsed by this time.

Accuracy of the Method of Colour Description

Mayr et al (1953) stress the importance of using colour standards, especially in descriptions. As the use of such are as yet relatively new in this field, a note on the accuracy of the method as used here may be useful.

In some places there appear to be inconsistencies in the colours allotted on say three consecutive days, especially during the early stages of incubation. For instance in the detailed colour descriptions of the fertile eggs, the same colour was allotted on the first and third days, but a different colour was allotted on the second day. It is logical to conclude that the colour for the second day should probably have been the same i.e. straw yellow and not lemon yellow. In other words, on such a small object, the daily colour differences are too fine, at least over the first few days, to be exactly distinguished. However, over the whole incubation period, the general colour change is shown satisfactorily by this method. For example, the colours recorded on the 1st, 5th, 10th and 15th days are progressively darker. The appearance of eyes and abdominal blotches enable further distinction to be made between these days. Again, in the case of the unfertilized eggs, colours noted on different days are very similar and are approximately of the same intensity.

Duration of Incubation

Curr (1957), from thirty-seven eggs at Nelson, obtained a mean incubation period of 9.5 days, but ranging from eight to eleven days. In a preliminary study at Palmerston North during January 1957, normal duration of incubation over the first three weeks was eleven days, but over the final week was reduced to eight

days (see Table 32). Clearly the eggs of this insect show a marked response to normal temperature changes, and it was decided to follow the duration of incubation batch by batch and month by month over a complete breeding season, 1957-58.

Normal changes in Duration of Incubation throughout the Season

Incubation periods recorded for eggs laid by the parent generation before winter 1957 are shown in Table 33. The first eggs laid in the 1957-58 season hatched on 2nd September. From then onwards, egg batches were checked in succession until the 12th March 1958, when the last egg in the trial hatched. The results are shown in Tables 34 - 36. Table 34 shows the incubation history of eggs of the parent generation surviving winter; Table 35 gives the data for eggs of the first generation which succeeded the parent generation in late October and continued until the end of December; Table 36 includes data from the second generation and the Cross Series in January and February, and from the third generation in March.

TABLE 32

PRELIMINARY STUDY OF INCUBATION PERIOD

Date of Oviposition	No. of eggs laid	Number of eggs hatching in the number of days indicated							No. of eggs failing to hatch
		7	8	9	10	11	12	13	
23 Dec. 56	11							11	0
6 Jan. 57	-						3		-
7	-					4			-
7	10						9		1
8	5				2		2		1
9	18					7	11		0
10	12					5	6		1
11	7					7			0
12	6				2	2			2
13	13				7	5	1		0
14	13	3				9	1		0
19	2				2				0
20	4				2	1			1
21	6				6				0
22	4			2	1				1
23	6			4	2				0
		3	0	6	24	40	33		

Normal incubation period 11 days

25 Jan	4	4	0
26	3	3	0
27	14	14	0
28	5	4	1
	143	25	8

Normal incubation period 8 days

Fertility (hatchability) = 94%

TABLE 35

INCUBATION PERIOD OF EGGS LAID BY LAST GENERATION BEFORE WINTER

Date of Oviposition	No. of eggs laid	Number of eggs hatching in the number of days indicated									No. of eggs failing to hatch
		12	13	14	15	16	17	18	23	24	
21 Mar. 57	11		11								0
22	12		12								0
23	9			9							0
24	7			7							0
			23	16							
Normal incubation period 13 days											
25 Mar.	24		6		3	2	11	2			0
26	20				3	8	8	1			0
27	-			3	1	4	5				-
28	-				1	2	13				-
29	11					8	1	1			1
30	8					4	3				1
31	14				1	13					0
1 Apr.	8				5	5					0
2	6				3	1					2
6	-						3				-
7	7					2	4	1			0
14	6	1				4		1			0
16	3						1	2			0
		1	6	3	15	53	49	8			
Normal incubation period 16 - 17 days											
18 Apr.	6								4		2
22	2									1	1
	154								4	1	7

Normal incubation period 23 days

Fertility (hatchability) = 95%

TABLE 34

INCUBATION PERIOD OF EGGS LAID BY LARVAE GENERATION AFTER WINTER

Date of oviposition	No. of eggs laid	Number of eggs hatching in the number of days indicated											No. of eggs failing to hatch
		16	17	18	19	20	21	22	23	24	25	26	
9 Aug. 37	10									6	1		3
10	4								1	1		2	0
11	1											1	0
12	2											1	1
13	1										1		0
14	2										2		0
									1	7	4	4	
Normal incubation period 24 - 26 days													
19 Aug.	3								2				1
20	22					3	6	4	1				8
21	4						1	2					1
23	7					2	1						4
						5	8	6	3				
Normal incubation period 21 days													
25 Aug.	13				10								3
26	2					2							0
29	4			3									1
				3	10	2							
Normal incubation period 19 days													
30 Aug.	7		5										2
31	7	6	1										0
		6	6										
Normal incubation period 16 - 17 days													

Date of oviposition	No. of eggs laid	Number of eggs hatching in the number of days indicated										No. of eggs failing to hatch
		11	12	13	14	15	16	17	18	19	20	
2 Sep.	15				2	2	4					7
3	3					2	1					0
5	5			5								0
7	8			2	3	1						2
8	3			2	1							0
9	14		1	1	2	2	1					7
10	13	2		6	5							0
11	11			7	3							1
12	16			9	6							
		2	1	32	22	7	6					
Normal incubation period 13 days												

TABLE 34 (Cont.)

Date of oviposition	No. of eggs laid	Number of eggs hatching in the number of days indicated										No. of eggs failing to hatch
		11	12	13	14	15	16	17	18	19	20	
13 Sep. 57	4				3		1					0
14	18		2		3	7	5	1				0
15	10					3	5	2				0
16	11				2	4	3	1	1			0
17	20					4	3	13				0
18	10						5	4				1
19	7						2	5				0
20	9					2	3					4
21	5					2	3					0
22	3					2						1
23	13				7		4	1				1
24	15				1	5	2	1	3	1		3
25	10							5	5			0
26	5						2	2	1			0
27	6						2	2				2
29	10						9					1
30	3					1	2					0
		2	0	16	30	51	37	9	1			

Normal incubation period 16 days

1 Oct. 57	11					4	3	1				3
3	3				3							0
4	6				2		4					0
5	1					1						0
6	2											2
8	6				2	4						0
10	4				2	2						0
15	2					2						0
					9	13	7	1				

Normal incubation period 15 days

17	8								4	4		0
18	2										2	0
25	6						6					0
Grand total	387											60

Last 3 batches were by female 9 near the end of her life

Fertility (hatchability) = 84.5%

TABLE 35

INCUBATION PERIOD OF EGGS LAID BY FIRST GENERATION

Date of oviposition	No. of eggs laid	Number of eggs hatching in the number of days indicated										No. of eggs failing to hatch
		12	13	14	15	16	17	18	19	20	21	
25 Oct. 57	2						2					0
26								3				
27							1	2				
28	6						2	3				1
29	18						10	6	2			0
30	11							4	7			0
31	9						7					2
							22	18	9			
		Normal incubation period 17 days										
1 Nov. 57	4						3					1
2	2					1						1
3	17				13	4						0
4	7				7							0
5	16			8	8							0
6	13		6	4								3
7	18		7	10	1							0
8	26			24	2							0
9	26			14	9	2	1					0
10	13				11	2						0
11	3				3							0
12	1			1								0
13	11		8	2								1
14	14	2	7	2	3							0
18	-	4		2	4	10						2
19	8				8							0
21	4								1		1	2
22	33				20	9		4				0
23	6				3	2	1					0
24	20				1	15	1		3			0
25	16				8	4	1	1	1			1
26	26			8	9	6	3					0
27	12			1	4	2			2			3
28	21				7	7		2	3	2		0
29	2								2			0
		6	28	76	121	64	10	7	12	2	1	
		Normal incubation period 15 days										

TABLE 35 (Cont.)

Date of oviposition	Number of eggs laid	Number of eggs hatching in the number of days indicated									No. of eggs failing to hatch
		12	13	14	15	16	17	18	19	20	
2 Dec. 57	27		1	3	13	2	3	2			3
3	35			11	13	4	2				0
4	31		4		13	11					3
5	6						1		5		0
6	6					5					1
7							1				0
9	38			8	9	1	1	5	3	1	10
10	5			1	2		2				0
11	6			2		2		1			1
12	22				12	10					0
13	4						3				1
14	5							4	1		0
15	6				3	2		1			0
16	14			10		3	1				0
17	5					3		1			1
18	2					1	1				0
20	2				2						0
22	9			2		7					0
			5	37	72	51	15	14	9	1	

Normal incubation period 15 days

23				7	11		2				
24	2					2					0
25			13	22	1	2					
26	3			2	4						1
27			58								
28	80		65	5	2						8
29	8	1	4	2							1
30	6	4	1		1						0
31	4			1	2				1		0
Grand total	692	5	141	39	21	4	2		1		47

Normal incubation period 13 days

Hatchability for first generation = 93%

TABLE 36

INCUBATION PERIOD OF EGGS LAID BY SECOND AND THIRD GENERATIONS AND CROSS SERIES

Date of Oviposition	No. of eggs laid	Number of eggs hatching in the number of days indicated											No. of eggs failing to hatch
		8	9	10	11	12	13	14	15	16	17	18	
1 Jan. 58	11				1	4	6						0
2	8						1		4	2			1
3	5						1	2	2				0
4						5		2	1				
5						15	3	3					
6					5	5	1			2	1		
7	37				4	16	3	3					1
8						8	16	3	3				
9						3	25	5	6				
10							5	5	1				
11	3						3						0
					10	56	64	23	17	4	1		
Normal incubation period 15 days													
13	14					2	5	8	1				0
14	56			5	47	4							0
15	21			11	2	8							0
16	54		2	7	36	4	1						4
18	10				6	4							0
19	12			7	5								0
			2	30	98	23	9	1					
Normal incubation period 11 days													
20	2			2									0
21	62		53	3	2	5							1
22	46		24	14	5	3							0
23	93	15	14	49	11	3							1
24				16	20	1							
25	6					3							3
26	8			8									0
27	3			3									0
28	3					1							2
29	2			2									0
30	1			1									0
31	3		3										0
		15	94	98	38	14							
Normal incubation period 10 days													

TABLE 36 (Cont.)

Date of Oviposition	No. of eggs laid	Number of eggs hatching in the number of days indicated											No. of eggs failing to hatch
		8	9	10	11	12	13	14	15	16	17	18	
1 Feb. 58	4			4									0
2	6		6										0
3	3		1	1									1
4	9		6										3
5	1		1										0
7	6			6									0
9	19	2	6										11
11		5											
13	8		8										0
		7	23	11									
		Normal incubation period 9 days											
17	37			1			29						7
19	38					30							8
20	38				15	23	6						14
26			1										
27			4	1									
			5	2	15	53	35						
		Normal incubation period 12 days											
11 Mar. 58	3			1	1								1
12												1	
Grand total	642												58

Hatchability = 91%

TABLE 37

INCUBATION PERIOD OF EGGS LAID BY FEMALES FROM FIELD IN SEPTEMBER

Date of oviposition	No. of eggs laid	Number of eggs hatching in the number of days indicated						No. of eggs failing to hatch
		16	17	18	19	20	21	
26 Sept. 57					6			
29				1				
30				1				
9 Oct.					1			
10	5			5				0
11	3		3					0
12	6		3	3				0
14	5	2		1				2
15	3		2					1
16	4			3				1
17	4				2	2		0
18	6						1	5
19	3				1	1		1
21	6				2			4
22	10			7	3			0
23	3				3			0
24	15		15					0
25	3	2						1
3 Nov.	5	4						1
	79	8	21	21	18	3	1	16

Hatchability = 80%

Discussion of the Season's Incubation Data

The data falls into natural groups varying in time span from two-three days to about two months, but each such group has a definite incubation period. In the preliminary study (Table 32), for eggs laid between 23rd December 1956 and 23rd January 1957, the normal incubation period was 11 days, and for eggs laid during the rest of January it was 8 days. During March 1957 (Table 33) over a four day group it increased to 13 days, from 25th March to 10th April it was 16 to 17 days, and by the last week in April it was as much as 23 days. Clearly there was a change in incubation period over the season according to monthly temperature. In the 1957-58 season it was hoped to plot this trend accurately.

For eggs laid during the second week in August 1957 (see Table 34), the normal incubation period was 24-26 days. This decreased through 21 days, 19 days to 16-17 days for eggs laid at the end of August. Eggs laid in the first fortnight of September hatched normally in 13 days, but there was an increase to 16 days for eggs laid during the remainder of that month. October eggs however, showed a decrease to 15 days. Eggs of the first generation (Table 35) laid during the last week of October, showed a normal incubation period of 17 days. This increase was the result of whitewashing the greenhouse on 24th October. Eggs laid during November and the first three weeks in December had a normal incubation period of 15 days, but for the late December eggs it was reduced to 13 days.

In Table 36 the trend is adequately shown, over summer and into autumn, the end of the season. Eggs laid during the first eleven days of January 1958 still had a normal incubation period of 13 days. For mid-January (11th-19th) eggs, it had decreased to 11 days, and for the remainder of the January eggs, to 10 days. During the first half of February, the height of the summer, the minimum modal incubation period of 9 days was reached and thereafter an increase set in. Eight days was the shortest period recorded in Table 36, but in Table 32 a period as short as 7 days was recorded. For the remainder of February, normal incubation lasted 12 days, and in March about 18 days.

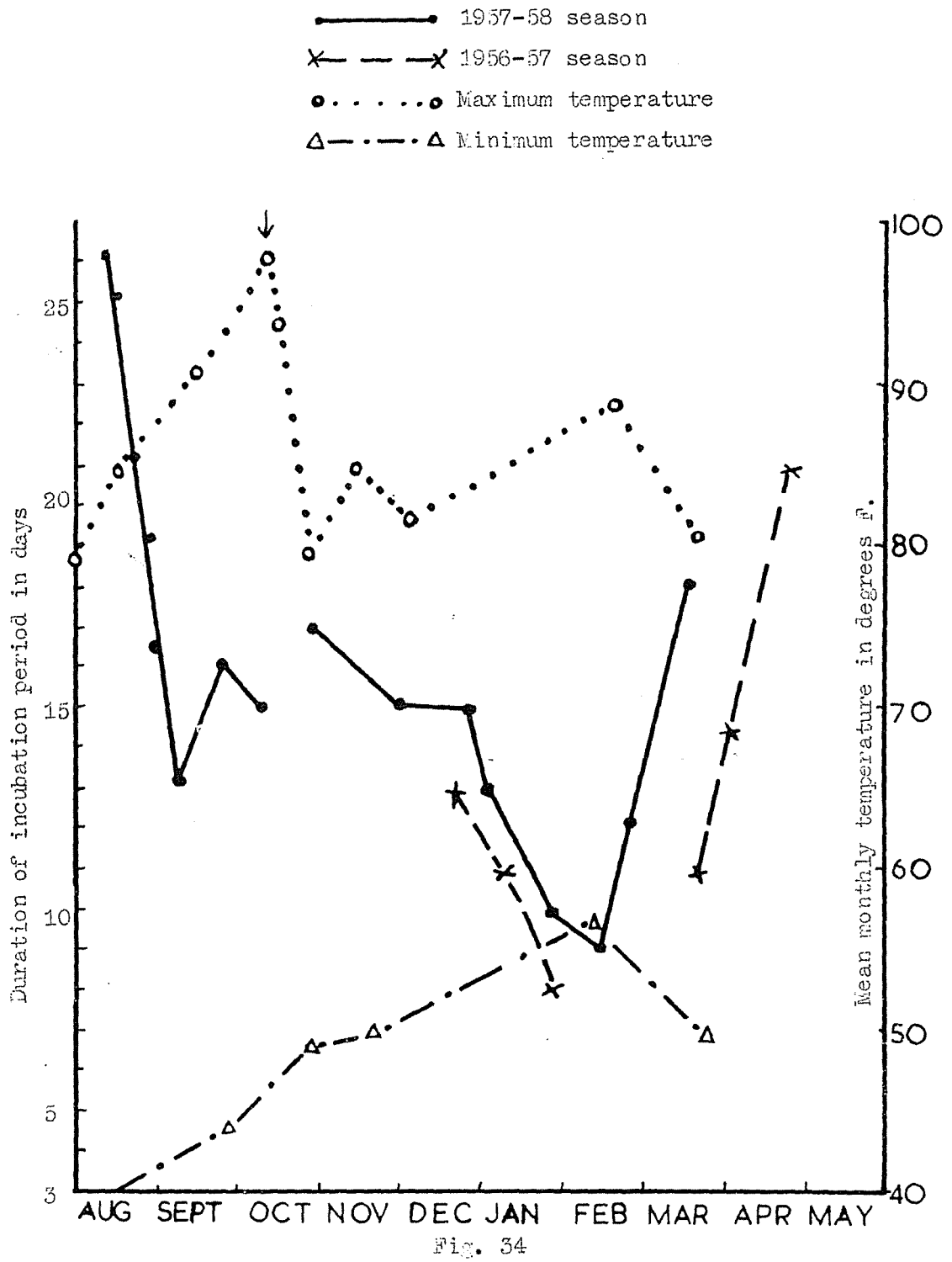


Fig. 34

Seasonal variation in duration of incubation of Nysius huttoni eggs.

Arrow indicates when greenhouse was whitewashed.

During the 1957-58 season, daily maximum and minimum temperatures in the greenhouse were recorded. The mean monthly temperatures were shown in Table 27 (page 76). The summation of the seasonal incubation data is shown graphically in Fig. 34.

The duration of incubation, or the changes in duration of incubation with changes in temperature, although not shown fully for the 1956-57 season, do show the decrease and increase before and after February, the warmest month. The end of this season is well shown and it is really only the spring and early summer portions which are missing from the graph. The graph for the 1957-58 season is complete and shows that incubation period normally varies from 26 days to 9 days. As temperature increases from spring to summer, so the duration of incubation decreases, the shortest period coinciding with the highest temperature in February. As expected, the reverse is true, incubation period increasing as the temperature decreases from summer to autumn.

The increase in incubation period, shown at the end of October - early November (over that earlier in October) coincides with the decrease in temperature caused by whitewashing the greenhouse. There was an immediate drop of about 20°F. However, this increase in incubation period also coincides with a slight flattening of the minimum temperature curve, so that reduction of maximum temperature, no doubt the most important factor, was not the only factor. Further, this late October - early November group of eggs are the first eggs laid by newly emerged females (the first generation females) and this may also be a factor concerning the longer incubation periods. The flattening of the incubation curve through to December is probably a reflection of a decrease in maximum temperature of 3°F early in December. The effect is slight, merely checking the downward trend of the incubation graph and not reversing it.

The reason for the sudden increase in incubation period in September is unknown, but it may be a reflection of the old age of the parent generation which were laying very irregularly at that stage. Probably also, the high mid-October

temperature would cause the reduction again to 15 days for the last eggs by the parent generation.

Environment of Parent and Incubation Period

To determine whether or not egg laying had commenced in the field, some adults were collected from the field on 24th September, and placed in the greenhouse. The answer was in the positive, as eggs were laid on 26th September. The incubaion period of some of these eggs was followed, and is of interest because it was longer than that for the parent generation eggs laid on the same day. Therefore the record of eggs laid by these females was kept separate and is shown in Table 37. Clearly the incubation period of these eggs follows the general trend already outlined. However, it started at 19 days at the end of September, and during October was still at a normal of 17-18 days which is, on average, 2 days longer than that for eggs laid by the parent generation.

This result is interpreted as indicating that incubation period may be influenced by the maternal parent, according to her environment. The females in the greenhouse were probably in a warmer environment than females in the field at that time of year. As the females from the field had recently been aroused from overwintering quarters, photoperiod may be a factor indirectly affecting incubation of the egg, but temperature was probably the major factor.

Duration of Incubation at Normal Low Temperatures

As the incubation period showed such a marked response to normal temperature changes, it was decided to determine the effect of lower temperatures. The commencement of oviposition in the greenhouse in the early spring (August) was about one month ahead of the field event (September). Therefore, by placing eggs outside in the shade of a barn (near the greenhouse) during October, a temperature range lower than that experienced by eggs in the field, and yet one that was certain to permit development, was obtained. The effect on the duration of incubation is shown in Table 38.

TABLE 38

INCUBATION PERIOD OF EGGS DEVELOPING IN SHADE OF BARN

Date of oviposition	No. of eggs laid	Incubation period of half of batch in greenhouse	Number of eggs hatching in number of days indicated										No. of eggs failing to hatch
			36	41	42	43	44	45	46	49	51	52	
29 Sep. 57	3	16	1*										2
9 Oct.	5	19									1	3	1
11	3	17								1			2
12	9	17								6	1		2
14	4	18								2		1	1
15	3	17							3				0
16	5	18						5					0
17	4	19					2	1					1
18	5	17					3	2					0
19	6	19			2		3	1					0
21	7	19			3	4							0
	54	Av. 18		1	5	4	8	4	5	3	9	2	4	9

Modal incubation period 40 days

Hatchability = 83%

Days -	20	21	25	26	27	29	32	33	35	
6 Dec. 57	6	16					2	1	2	1
22	3				2					1
23	3					3				0
26	5				3	2	1			0
27	6			1	3	2				0
			1	7	4	4	2	1	2	

Modal incubation period 26 days

9 Jan. 58	15	13	10	3	0
	36				2

Modal incubation period 20 days

Hatchability (Dec. & Jan) = 94.5%

*This batch was incubated for 10 days in the greenhouse before being placed in the barn on 9th October. All other batches were placed in the barn on the day of oviposition.

In most cases the egg batches were halved, one half remaining in the greenhouse for comparison (column 3). As the temperature in the shade increased from October to January so the incubation period decreased. For eggs laid in October, December and January, the modal incubation periods were, respectively, 49 days, 26 days and 20 days. This was longer than the normal period for eggs kept in the greenhouse by 31 days, 10 days and 7 days, respectively.

During October, the average maximum temperature in the greenhouse was 98°F, during December 82°F, and during January 89°F. During the period 13th December 1957 to 6th January 1958 the maximum temperature under the shade of the barn ranged from 61°F - 72°F; on only three days did it exceed 69°F (20.5°C) but this was for only a very short time of the day. The minimum temperature ranged from 45°F to 60°F, and on the same three days only, did it exceed 54°F (12°C).

The results indicate that the species is very adaptable to temperature changes. Further, the batch which was partially incubated before placing at the lower temperature is of special interest, because it shows that the species can survive a wide temperature change occurring during embryonic development. It hatched in a shorter time than those eggs incubated entirely outside. Thus development was merely slowed down from the moment of subjection to lower temperature.

Duration of Incubation at Extremely High Temperatures

The variation in incubation period at the temperatures so far discussed is great, and prompted this investigation into the upper temperature limit for incubation. A cabinet 2ft x 2ft x 2ft was used in which temperature, maintained by electric lights, was controlled by a Sunvic thermostat, type TS 2. Relative humidity, which was found to be a vital factor at high temperatures, was maintained by the method described on page 116. The experiment was repeated four times at different temperatures and the results are shown in Table 30. In column three a comparison with the normal incubation period in the greenhouse was made for each group.

TABLE 39

DURATION OF INCUBATION AT HIGH TEMPERATURES

Date of oviposition	No. of eggs	Normal incubation period in greenhouse	Number of eggs hatching in the number of days indicated				No. of eggs failing to hatch
			3.5	4	4.5	5	
Group 1 Mean temperature 34-35°C							
21 Jan 58	6	9-10 days				5	1
22	16			3		13	0
23	12			12			0
				15		18	1
		Modal incubation period 4-5 days Hatchability = 97%					
Group 2 Mean temperature 36.5°C							
27 Jan. 58	12	10 days	7	3			2
		Modal incubation period 3.5 days Hatchability = 83%					
Group 3 Mean temperature 44.3°C							
6 Feb. 58	10	10 days		4			6
		Incubation period 4 days Hatchability = 40%					
Group 4 Mean temperature 45.2°C							
12 Feb. 58	10	9 days		6	2	1	1
		Modal incubation period 4 days Hatchability = 90%					

Group 1 showed that at a temperature of 34-35°C. (93-95°F.), the incubation period was 4-5 days. For the second group, laid on 27th January, and kept at a mean temperature of 36.5°C.(97°F.), the modal incubation period was 8.5 days. Group three, incubated at a higher mean temperature (111°F, 44.3°C.) showed a high mortality (60%). The eggs were subjected to a very high temperature of 47°C.-51°C. over the first 15 hours, but this was reduced to approximately 43.5°C. over the remainder of the period. The eggs took four days to hatch. Relative humidity was slightly less in this case because the cotton-wool containing the eggs was not damp whereas in the other three groups it was. Whether or not the high mortality was caused by the very high early temperature or by the lower relative humidity, is a matter of surmise, and probably both were concerned. The implication is that the conditions prevailing for group three were near the upper limit of tolerance.

The eggs in group four incubated at a mean temperature of 115.4°F. (45.2°C.), hatched in four days. As the hatchability for group four was 90%, it follows that the temperature of 115°F. was not at the upper limit of tolerance. Compared with group three it seems that either the high temperature of 47°C.(116.6°F.) over the first few hours (in group three) was near the upper limit of tolerance, or that humidity is a vital factor at 43.5°C. Humidity was possibly a factor at 36.5°C causing a relatively low hatchability in group two.

Duration of Incubation at Extremely Low Temperatures

The eggs of this species have shown remarkable tolerance to temperature changes. The following experiment was designed to determine the lower limit of temperature tolerance. Freshly laid eggs were placed in refrigerators at 3°C. (37.4°F.) and 6°C.(43°F.) for periods of one month and two months. None of the eggs hatched. However, this did not necessarily mean that the eggs were dead and so they were shifted into the greenhouse. Some of the eggs hatched. The results are shown in Tables 40 and 41.

TABLE 40

EFFECT OF EXTREMELY LOW TEMPERATURE UPON INCUBATION PERIOD

No. of eggs	No. of days at 5°C	No. of days to hatch after shift to greenhouse	Total period from oviposition to hatching (days)	No. of eggs failing to hatch	Percentage hatch
6	32	16	48	0	100
6	32	16	48	5	17

Table 40 shows that embryonic development was merely suspended at 5°C, because when placed in the greenhouse in March, incubation was completed in 16 days which is near the normal incubation period for March. The total period from oviposition to hatching was 48 days.

Duration of the Cold Period as a Determining Factor

The eggs held at the low temperatures for longer than one month were also shifted into the greenhouse, but none of them hatched after a further 35 to 62 days. At this stage, being mid-May, the possibility arose that the normal greenhouse temperature was now too low for development to proceed, and that these eggs may not hatch until the following season. To test this hypothesis, some of the eggs were left in the greenhouse until the following spring, but none of them hatched. However, to hasten the process, some eggs were placed in a temperature cabinet controlled at 73°F, a mean daily summer temperature. The results are those shown in Table 41. None of the eggs hatched.

TABLE 41

FATE OF EGGS SUBJECTED TO EXTREMELY LOW TEMPERATURES FOR MORE THAN ONE MONTH

No. of eggs	No. of days at 5°C.	No. of days at 6°C.	No. of days in greenhouse	Date of shift to cabinet at 73°F	No. of days at 73°F	No. of eggs failing to hatch
5*	32		62	12th May 58	22	5
5	61		33	"	22	5
3	61		33	"	38	3
3	59		33	"	22	3
3		59	33	"	22	3

*The 5 failing to hatch from Table 40

From Table 40 and 41 it is clear that an exposure of eggs to 3°C. for longer than about 32 days (in this case 58-61 days) was fatal. The fact that not all eggs shown in Table 40 hatched indicates that 32 days at 3°C. is very near the lower limit of temperature tolerance. However, as the second batch of eggs were by a female known to have abnormally low fertility, the limit may not necessarily be at 33 or 34 days, but may be at any point between 33 and 59 days. Again, because an exposure to 6°C. for 59 days was fatal, it seems logical to conclude that an exposure to 3°C. would become fatal earlier. There is, therefore, a limit to the period of survival of eggs at temperatures of 6°C. and less. The hypothesis that normal temperatures in May are too low to permit embryonic development was not disproved, but the eggs were dead before removal from the refrigerators.

Fate of late Autumn Eggs in the Field

The question arises, would eggs hatch if laid in the field earlier in September, and later in April? The results from Table 40 suggests that they would, although the incubation period would be drawn out, and in the case of late autumn eggs development may be suspended until the following spring. Field temperature data for Palmerston North recorded at Grasslands Division of the Department of Scientific and Industrial Research over the period July 1957 to June 1958 are shown in Table 42.

TABLE 42

MEAN MONTHLY TEMPERATURES AT PALMERSTON NORTH 1957-58 SEASON

Month of year	AIR Max. °C.	AIR Max. °F.	AIR Min. °C.	AIR Min. °F.	Minimum on grass °C.	Minimum on grass °F.	Earth at 4" * °C.	Earth at 4" * °F.
July 1957	11.5	52.7	2.0	35.8	-1.0	30.4	5.7	42.3
August	14.0	57.4	6.2	43.1	3.0	37.5	8.0	46.9
September	15.5	59.9	6.7	44.0	3.2	37.7	9.9	49.8
October	16.0	60.9	7.0	44.8	2.8	37.1	12.0	53.4
November	19.0	66.3	9.8	49.6	6.3	43.3	15.0	59.1
December	19.3	66.7	10.5	50.8	6.5	43.7	16.2	61.2
January 1958	21.0	70.9	12.4	54.3	9.6	49.5	18.5	65.3
February	24.3	75.8	14.3	57.8	10.6	51.2	20.0	68.0
March	22.4	72.3	12.5	54.5	7.2	45.0	15.3	59.6
April	17.0	62.8	7.0	44.7	1.5	34.7	12.5	54.5
May	15.0	59.2	7.5	45.5	4.6	40.3	10.3	50.5
June	13.4	56.1	4.0	39.3	0.4	32.7	7.7	45.8

*Recorded at 9 am

Geiger (1950) stated "... the highest temperature at about noon is the boundary between ground and air; starting from here the temperature decreases upwards and downwards." The opposite is true at night. H. huttoni oviposits in the soil, and as the earth temperature in Table 42 was recorded at 9 am, the minimum temperature on grass is more useful in this problem.

Eggs would not survive June and July, but eggs (if any) laid in August would hatch because the duration of the minimum temperature is for a portion of the day only. Eggs laid in April may hatch, but the nymphs may find it hard to survive. Any eggs laid in May would probably be too late and would therefore not survive the two coldest months, June and July.

However, the original question is hardly justified, because evidence from the fecundity study indicates that some mechanism operates in the female to prevent oviposition too early or too late in the season. Photoperiod and temperature are probably the controlling factors. In the 1956-57 season an egg was laid in the greenhouse as late as 23rd April. This hatched on 11th May, but the nymph did not survive the winter. The last egg was laid on 1st May and this did not hatch.

Effect of Humidity on Incubation

At Extremely High Temperatures

Early attempts to hatch eggs at 34°C.(93°F.) were unsuccessful. The eggs literally cooked and shrivelled. Obviously relative humidity is a vital factor at high temperatures. Relative humidity within the cabinet was raised considerably by two simple methods recommended by Peterson (1949). A sheet of blotting paper 12" x 4" pinned to one wall, and with the lower portion placed into a flask of water, increased the evaporative surface of that water. Subsequent egg batches were placed into smaller jars (1" x ½") which were inverted and stood on a cloth stretched over a tray containing water. In the case of groups one, two and four (Table 39) the level of water in the tray was of sufficient height to cause the cotton-wool to become moistened. On the other hand, in the case of group three the level was lower so that the cotton-wool did not take up moisture. The effect

was marked, and compared with group two would seem to indicate that the mean temperature, 44.3°C, is near the upper limit of temperature tolerance. However, the success of group four at 45.2°C. contradicts this view and emphasises the vital role of humidity.

At Normal Temperatures

No humidity data were recorded in the main incubation experiment at normal temperatures because no suitable equipment was available. However, the relative humidities recorded in the field at Grasslands Division of the Department of Scientific and Industrial Research, Palmerston North over the 1956-57 and 1957-58 seasons are shown graphically in Fig. 35. (A similar result would be expected in the greenhouse). It should be considered in conjunction with the incubation-temperature graph, Fig. 34. From early spring to summer, duration of incubation decreases as temperature rises and as relative humidity decreases; the reverse takes place from summer to autumn. Under natural conditions, the decrease in relative humidity is not great, and at all times relative humidity was adequate; therefore temperature is the major factor operative.

Later in the 1957-58 season, some eggs incubating at normal temperatures within the greenhouse were tested for survival under low relative humidity. The actual humidity attained was not determined, but the method used is known to produce dry air. A liberal amount of anhydrous calcium chloride was placed in a desiccator which was then left for one day before the experiment began. This experiment had some slight variations as follows: some egg batches were partially incubated at normal humidity before being placed in the desiccator; some batches were halved, one half being placed in the desiccator on the day of oviposition, the other half acting as a control; some batches were divided into three, one third being a control, the other two thirds going into the desiccator on the day of oviposition but one third having the jar lids removed; one complete batch was placed into the desiccator on the day of oviposition. The results are shown in Table 45.

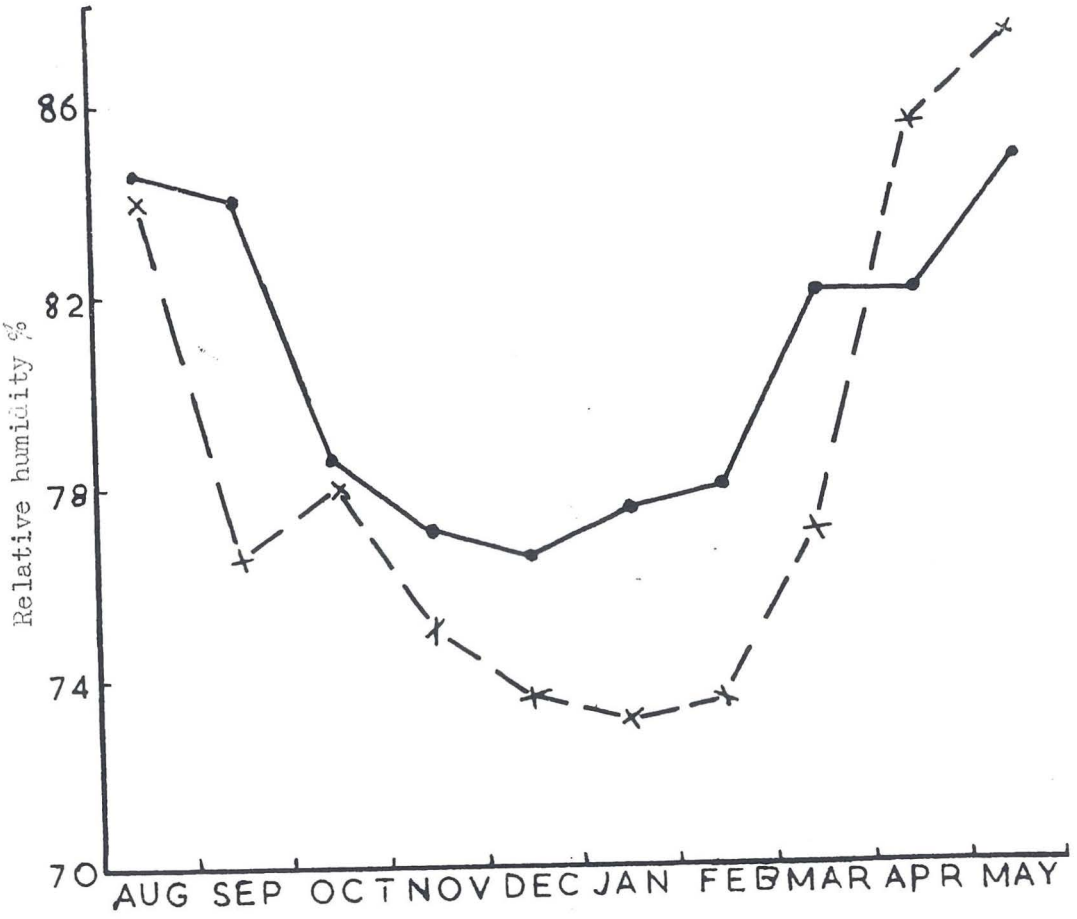


Fig. 35

Variation in relative humidity at Palmerston North for the 1957-58 season (solid line) and the 1956-57 season.

TABLE 45

EFFECT OF DRY AIR ON INCUBATION

No. of eggs	No. of days at normal humidity	No. of days in desiccator	No. failing to hatch	Remarks	Control portion of same batch at normal humidity	
					No. of eggs	No. failing to hatch
5	7	4	1			
2	7	4	0			
2	8	4	0			
9			1			
	11% not hatching					
4	0	13	1	lid on jar	3	1
5	0	13	3	no lid		
5	0	13	0		4	0
5	0	13	1	lid on jar	2	0
3	0	13	1	no lid		
3	0	11	1	no lid		
23			7		9	1
	30.4% not hatching				11% not hatching	

Assuming that humidity is a necessary factor for development of these eggs, it was a surprise to find that some hatched. In explanation, it was possible that although the jar lids were loosely screwed on, the normal air they contained was trapped in, and therefore not dried. Hence the removal of jar lids.

The group that was partially incubated at normal humidity (shown in the first three lines of the Table) all hatched bar one. Compared with eggs under normal conditions, shown in the right hand side of the Table, there is no difference. The percentage hatch is also in agreement with the results from the main incubation experiment (Tables 32-36). It would seem that the eggs can imbibe sufficient moisture early in incubation to last them through the period in the desiccator.

On the other hand, when eggs were completely incubated in the desiccator

(see lower left of table) the mortality was considerably higher, namely 30.4%. In one case of two comparable batches, there is evidence of higher mortality when the lids were left off the jars, but the numbers are too small to place any value on this fact. What is more important, considering the lower left portion of the Table as a whole, is that at a very low relative humidity, 69.6 of the eggs were still able to hatch at normal temperatures. Apparently there is sufficient moisture in the egg at oviposition to enable complete embryonic development and hatching. This water may become "bound" to prevent loss through desiccation.

At Extremely Low Temperatures

Some of the eggs subjected to long periods in the refrigerator at 6°C. and 3°C. were shrivelled. Thus cold, in addition to suspending development and eventually killing, also desiccated the eggs. The author is not suggesting, however, that had the air been kept humid, these eggs would have survived the cold.

Comparison of Percentage Hatch over all Incubation Experiments

The percentage hatchability (fertility) of the eggs has been indicated in the Tables throughout this section.

At Normal Temperatures

Normally, hatchability (fertility) was very high ranging from 91-95% as shown by the preliminary experiment eggs laid in January 1957, 94%; by the parent generation eggs laid before winter 1957, 91%; by the first generation eggs laid in October, November and December 1957, 93%; by the second generation and cross series eggs laid in January, February and March 1958, 91%. The parent generation eggs laid after winter in August, September and October 1957 had a slightly reduced hatchability, 84.5%. Eggs laid in October 1957 by females caught in the field at that time were found to have a similar reduction in hatchability to 80%. Here again is evidence of the ageing or detrimental effect of winter on the overwintering female and there is agreement between the reared females and the females from the field. This may be a reflection of the age of the overwintered males.

Beament (1947) showed that in A. prolixus eggs there is a decrease in the number of micropyles with the age of the female and that this accounted for the decrease in fertility of the eggs; eggs laid by an old female were sterile. This situation did not occur in N. huttoni because in the spring and summer generations, fertility remained high even up to the last egg batches by old females.

Eggs incubated at normal temperatures, but at a very low level of relative humidity (dry air) were found to have a lower hatchability than both summer generations and early spring laid eggs, namely 69.6%. Clearly humidity is necessary at normal temperatures, but because the reduction in hatchability was not excessive, the minimum relative humidity requirement must be low.

At Low Temperatures

For eggs laid during October and incubated in the shade of the barn, hatchability was 83%, but for the December and January eggs it was 94.5%. Clearly a reduction of temperature (from December to October) retarded hatchability in addition to increasing the incubation period. However, by December and January, the general increase in temperature even in the shade permitted normal hatchability. Thus an estimate of the lowest temperature permitting the normal 91-99% hatchability was obtained and was 15.6°C.(i.e. the average of the mean maximum, 19.4°C and the mean minimum, 11°C recorded in the barn in December).

At Extremely Low Temperatures

As indicated earlier, development was very slow, but more probably suspended by the temperatures 6°C.and 3°C. When returned to normal conditions, some of the eggs developed, but hatchability was reduced to 58.4%. This demonstrates the tremendous adaptability of the eggs of this species.

At Extremely High Temperatures

At high temperatures the percentage hatch depends on humidity. Provided that relative humidity is not a limiting factor, eggs may be incubated at a temperature as high as 45.2°C.(113°F) without reduction in hatchability. When relative humidity was not adequate, hatchability at 44°C.was as low as 40%, and when no attempt was made to maintain humidity, hatchability at 34°C.was 0%.

Soil versus Cotton-wool as a Substratum for Incubation

Using a small batch of five eggs in soil, it was found that they hatched one day earlier than the majority of eggs laid in cotton-wool over the same period. Therefore incubation periods in the field may be a little shorter than those recorded in the greenhouse.

Eclosion from the Egg

At the completion of embryonic development the mature embryo lies motionless within the chorion until the commencement of hatching. However, heat from a bright light a day before hatching is due will induce the embryo to wriggle violently.

The first movement was a wave of muscular contraction from posterior to anterior. Shifting of the red eye spots was readily noticed as the head was thrown backwards and the body arched. These slow and comparatively weak muscular waves continued for about three minutes. During this period blood pressure was built up in the head to facilitate bursting of the chorion. At the termination of a body wave, a split was made in the chorion at the cephalic pole and a portion of the head momentarily appeared. On the next body wave the head began to emerge and the following wave forced the head and part of the thorax free. There was a conical projection on the head mid-way between the eyes. With the next forward surge the anterior half of the body emerged and began to wave from side to side, almost freeing the embryo from the shell. However, the embryonic cuticle still covered the posterior half of the nymph and remained attached (by the posterior) to the "mouth" of the shell.

The time elapsing from the first splitting of the chorion until this stage ranged from 2-5 minutes. The swelling on the head was then withdrawn flush with the surrounding head cuticle. Its nature suggests that this was the eggburster which swells up with blood pressure to split the chorion, and having accomplished its task, was withdrawn. The chorionic split was ventral and extended from the

cephalic pole down the midline, a distance approximating the body width of the nymph. A somewhat similar process is described by Pendergrast (1952) in eggs of Rhopalimorpha bugs (Pentatomidae) but in those eggs the split was continued to the posterior pole. It is possible that the first segment of the rostrum, being forced against the chorion when the head is thrown back, aids in splitting the chorion. Since the split was ventral, the movement of the body at hatching, was forwards and downwards.

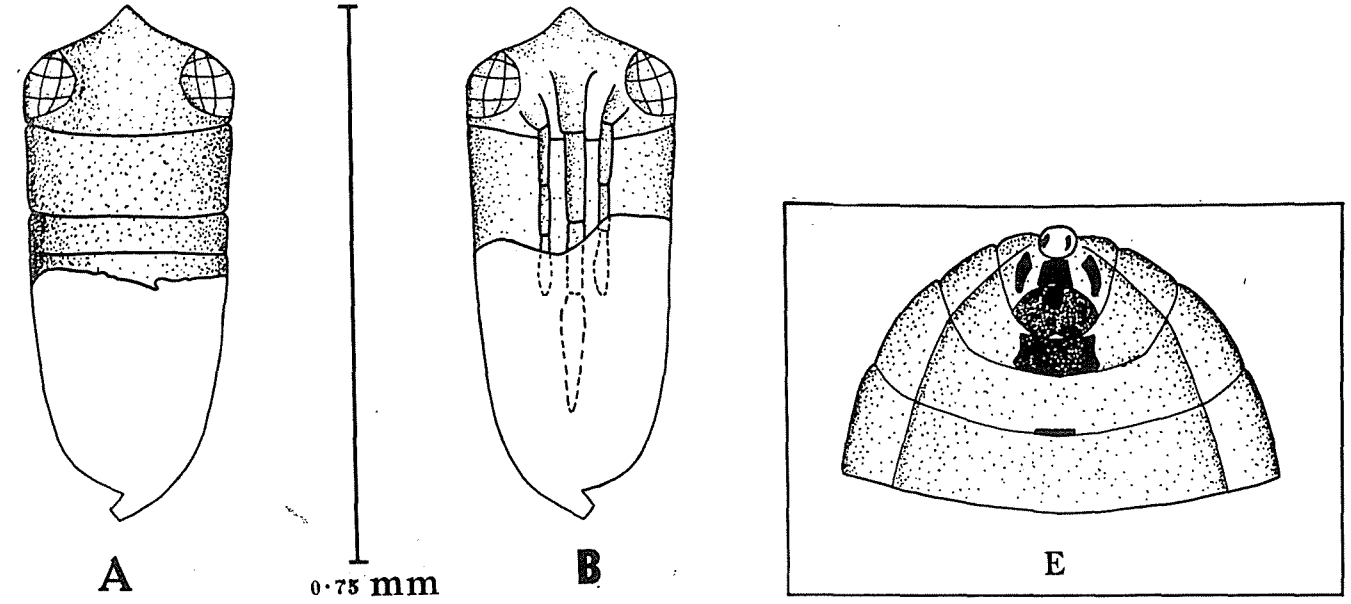
The nymph lies motionless at the mouth of the shell for 2-3.5 minutes. The posterior half of the body was enclosed in a membrane - the embryonic cuticle (Wigglesworth,1939) of the "inactive pronymph" (Tillyard,1926). It enclosed only the abdomen on the dorsal side but extended further forward on the ventral side to enclose the legs and the distal half of the rostrum and antennae, producing a mummified appearance or the "legless larva" (Usinger, 1942). The antennae lie folded under the body, one on each side of the rostrum and parallel to it (see Plate 4 A and B).

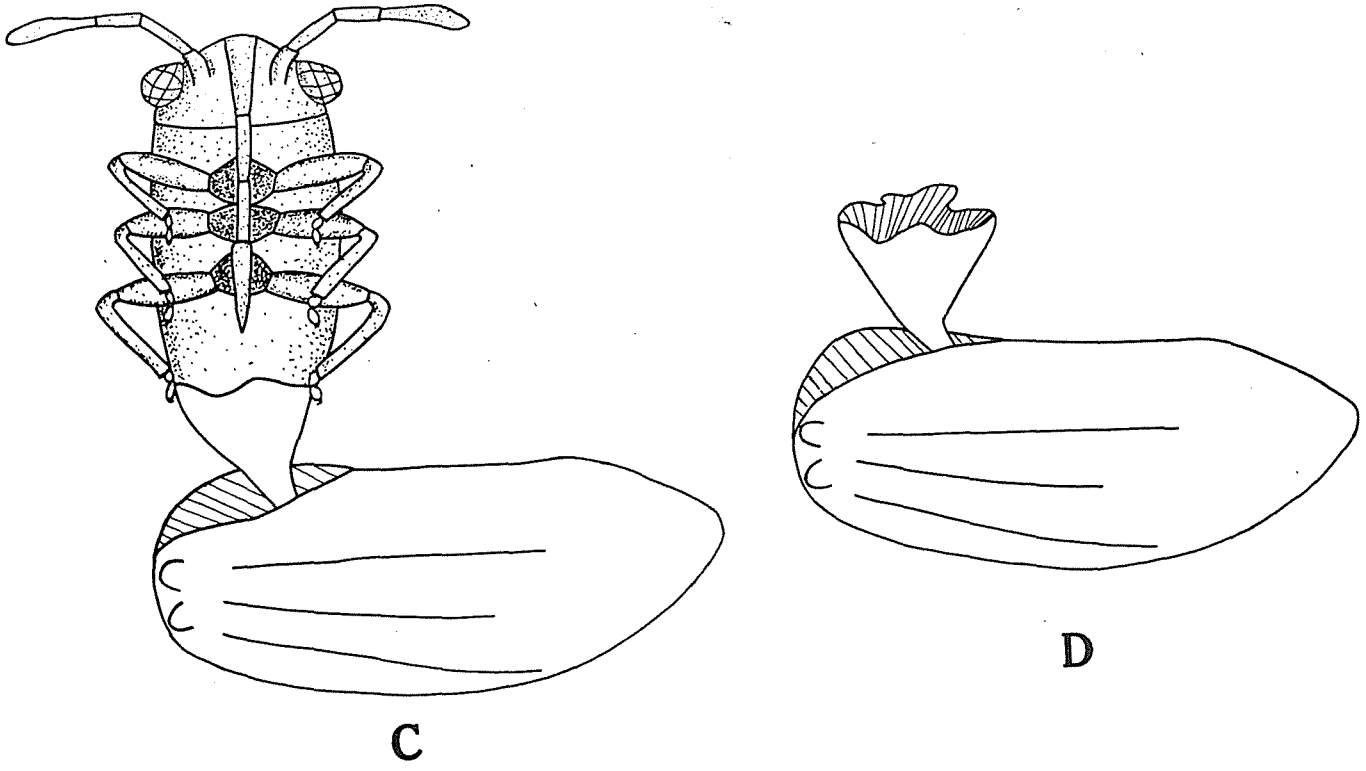
After this first period of inactivity, waves of muscular contraction began again, commencing at the anus and ending at the head. The most noticeable part of the movement was the throwing back of the head, arching of the body, and a simultaneous movement of the rostrum and antennae away from the body. There was also slight swaying of the body from side to side. On one "beat"/as the back was arched, the antennae and forelegs were freed, on the fifth beat the mid-legs were freed, and on the seventh beat the hind-legs were freed. The range of times taken to free the appendages were 1-5 minutes.

The nymph, still attached by the posterior abdominal segment to the embryonic cuticle (Plate 4, C) entered a second motionless period for 2-3 minutes (except for the occasional flick of an appendage). The nymph attempted to walk away, but the cuticle still being pliable, this portion merely stretched. Eventually the nymph broke free, the posterior abdominal segment being drawn out to the extreme like a "tail". This contracted to the normal abdominal shape in a matter

PLATE 4

A - D, hatching. E rudimentary external genitalia of female fifth stage nymph - ventral, slightly posterior view (not to same scale).





of seconds. When completely free the nymph stood motionless on the empty egg shell for 4 to 5 minutes before moving away.

The total hatching time, taken from first splitting of the chorion until when the nymph was completely free was 9-11 minutes. To this could be added about 3 minutes of preliminary"beats" inside the shell. Usinger (1942) reported a hatching time of ten minutes followed by a motionless period of ten minutes in N. coenosulus.

In summarising, the times and ranges (from seven observations) were made up as follows:

(a) From first splitting of chorion until nymph motionless in shell mouth	2 - 3 minutes
(b) First motionless period	2 - 5.5 minutes
(c) "Egg burster" is present for	4 - 5 minutes
(d) Time to free appendages	1 - 5 minutes
(e) Second motionless period	2 - 5 minutes
(f) Time to free posterior abdominal segment	up to 1 minute

Sometimes before the first inactive period, the nymph comes away completely from the chorion but takes the lower portion of the embryonic cuticle with it. It still observes the same periods of activity and inactivity. However, when freeing its appendages from this sheath, the mid-legs assist (when freed) by pushing outwards and downwards on the embryonic cuticle.

Discussion on Eclosion and the Embryonic Cuticle

Southwood (1956) stated that where an operculum or true egg cap is present (Cimicomorpha - see page 9) the larva escapes through it at eclosion and does not split the chorion, but in the Pentatomomorpha where there may or may not be a pseudoperculum, the chorion in both cases is split irregularly at eclosion. Andre (1934) as mentioned by Southwood says that in the egg of Oncopeltus fasciatus Dallas, a representative Lygaeid egg, the chorion is split irregularly at ecdysis.

Usinger (1942) describes the hatching of eggs of N. coenosulus, "Eclosion is accomplished by a splitting of the chorion somewhat irregularly near the anterior end of the egg, forming a flap or lid which is forced open as the embryo expands". He considers this the general pattern in Orsillini.

In N. huttoni eggs, the split was neat and not irregular, the two sides merely being forced apart as the nymph emerged. (see Plate 4, D). The embryonic cuticle normally remained attached to the shell mouth, and this, splayed out, presented an irregular surface.

Southwood also stated that "The embryonic cuticle develops over the whole surface of the embryo and envelops each appendage separately; it is shed immediately after eclosion. Strictly it should be considered as the cuticle (and subsequently, exuvium) of the first larval instar, thus giving a total of six larval instars in most Heteroptera". Tillyard (1917) (cited by Southwood, 1956) discussing Odonata, refers to the cuticle as the pronymphal sheath and states that the pronymph really represents the first larval instar. Usinger (1942) states that in Orsillini an embryonic membrane is cast when the embryo quits the chorion.

In the case of N. huttoni only the lower portion of the embryonic cuticle has been noted - the legs, antennae and rostrum are not each enclosed separately but are merely pinned down under it. It could not, therefore, be termed an extra instar. Although searched for, the anterior portion was not found. Sikes and Wigglesworth (1931) observed N. prolixus eggs during embryonic pulsations and stated that the membranes are ruptured at the same time as the cap is displaced. An explanation of the fate of the embryonic cuticle in N. huttoni now becomes apparent. It must have been split when the chorion was split, and it probably slipped backwards as the nymph moved forwards, so that the anterior portion was at the mid-body level and the posterior portion collapsed. The process by which the nymph freed itself from this stage (Plate 4, A, B and C) has already been described above. Here then, is another fact showing that in N. huttoni the embryonic cuticle cannot be regarded as an additional instar - namely, that before the nymph completely emerges

from the egg it has moved part of its way out of the embryonic cuticle. Therefore no part of its nymphal life is spent entirely within the embryonic cuticle.

Time of Day of Hatching

The first eggs laid by the parent generation after winter hatched on 2nd September 1957. During September, the majority of hatchings occurred between 9am and noon, but none outside the times 8am and 4pm. As air temperature increased from September to October, more hatchings began to occur earlier than 9am, but no more in the afternoons.

During a 10-day period from 15th to 24th December 1957 and from 7th to 11th January 1958, observations were at 8am, 10am, noon and 4pm, and the number of eggs which hatched between those times were as follows:-

4pm - 8am	73
8am - 10am	153
10am - Noon	46
Noon - 4pm	28

Of the total hatchings 51% occurred between 8am and 10am. As a large number of hatchings were recorded between 4pm and 8am observations were extended later in the evening and earlier in the morning, and proved that the hatchings occurred earlier than 8am, but not in the evening. Therefore 91% of the hatchings over the period occurred in the morning.

It was decided to divide the 8am - 10am interval into two, and so over a 21 day period from 14th January 1958 to 4th February, observations were at 8am, 9am, 10am, Noon and 4pm. The number of eggs that hatched between these times was as follows:-

4pm - 8am	142
8am - 9am	176
9am - 10am	74
10am - Noon	71
Noon - 4pm	22

It is seen that the number of hatchings increased rapidly to a peak between 8am and 9am (when 36% of the hatchings occurred) then declined gradually to mid-day,

after which it suddenly declined. In the morning 99% of the hatchings occurred. Often many eggs hatched between 8am and 8.15am, and this, together with the fact that a large number hatched shortly before 8am, indicates that at the height of summer the preferred time for eclosion was about 8am.

SUMMARY OF INCUBATION PERIOD

1. Daily colour changes in fertile eggs are described and compared with those in infertile eggs. The former became progressively darker as incubation progressed and eventually the mature embryo became visible through the chorion, but the latter soon turned a dark brown and eventually collapsed. The employment of colour standards was found to be satisfactory.

2. It is shown that the duration of incubation over the season varies inversely with normal temperature changes, e.g. 26 days in August, 9 days in February and 23 days in May. As it is also shown (by using dry air) that the relative humidity requirement for incubation at normal temperatures is very low, and therefore not a limiting factor, temperature is the major factor operative.

3. It is shown that the eggs of this species are very resistant to adverse conditions because:-

(a) incubation period at normal low temperatures (in the shade) was 40 days in October-November, 26 days in December at 15.6°C, and 20 days in January.

(b) in a controlled temperature cabinet at 45.2°C it was as short as 3.5-4 days

(c) exposure to 6° and 3°C for 32 days merely suspended development; when removed to normal temperatures the eggs hatched in the normal number of days.

4. It is shown that the upper limit of temperature tolerance depends on relative humidity because when this was limiting the value was below 34°C, when it was not quite adequate hatchability was only 40% at 44.3°C, but when it was adequate a normal hatchability of 90+ was obtained at 45.2°C.

5. It is shown that the lower limit of temperature tolerance depends on the duration of the cold period. At temperatures of 6°C - 3°C the maximum period of survival is between 35 and 58 days.

6. From a comparison of temperatures in the field with the results of (5) above, it follows that should any eggs be laid in the field late in autumn they would not

survive winter. However, from the fecundity study it is clear that some mechanism (in all probability stimulated by photoperiod and temperature) operates in the female to prevent oviposition either too late or too early in the season for eggs to develop.

7. It is shown that hatchability was normally 91-98%, but in the overwintering generation it was reduced to 80%. In contradistinction to *N. prolixus* eggs which decrease in fertility with age of the maternal parent, *N. huttoni* eggs were highly fertile up to the last batch laid by the female.

8. It is shown that eggs incubated in soil tend to hatch in a shorter time than eggs incubated in cotton-wool. Therefore incubation periods in the field over the height of summer are likely to be slightly less than those demonstrated in the greenhouse.

9. Eclosion from the egg is described.

In contradistinction to the normal procedure in eggs of the Pentatomomorpha, it is shown that in *N. huttoni* eggs the chorion does not split irregularly at eclosion.

Contrary to the generally held belief that the embryonic cuticle represents the first larval instar, it is shown that this cannot be so in *N. huttoni*.

10. It is shown that hatching, unlike oviposition, occurred almost entirely in the morning, with a peak period between 8am and 9am.

CHAPTER 6

IMAGINAL DEVELOPMENT

As the preliminary incubation study had indicated a marked response to monthly temperature changes, it seemed likely that each instar would show a similar response. Accordingly, the duration of each instar was recorded for all individuals reared over the 1957-58 season. The naming of the generations was the same as that used in the chapter on Fecundity. Four generations were reared through to the adult from eggs, in the 1957-58 season.

Colour Changes Occurring after Eclosion

Hourly observations were made under a microscope using a low power objective, the source of illumination being daylight only. Colours were compared with Ostwald's (1931) Colour Standards.

Eclosion occurred between 8.15am and 8.45am 9th December 1957.

9.10am: Pale orange throughout; head and thorax slightly paler, (Ostwald series X 31a), but more shiny than abdomen (O. X, 41a). Legs and antennae tinged with orange, but transparent. Eyes bright red (O. XIV, 7pa).

10.10am: Colouration as above except for legs and antennae taking on a greyish tinge (O. II, 1ec), though still somewhat transparent, and the appearance of a mid-dorsal abdominal orange spot of slightly deeper intensity, anterior to the anus.

11.10am: Grey tinge on head and thorax (except metathorax); legs and antennae have lost their transparency. Head and thorax orange-grey (O. IV, 3ie). A V-shaped portion on midline of pro- and mesonota (which portion does not darken), and the head stripes, orange as the abdomen. Legs and antennae light grey (O. Plate 2 series O. e). Abdomen now a deeper orange (O. X 41a); the dorsal spot now red (O.X,6 1a).

12.10pm: To the naked eye, head and thorax appear brown. Head, thorax (except metathorax) legs and antennae grey-brown (C. IV, 21g), but the mid-dorsal "V" and head markings, orange. Eyes remaining red. Abdomen a bright orange (C. X, 5ia). Two further dorsal spots present near the metathorax, one on each side. All three spots now red (C. X, 7a.c.).

2.10pm: To the naked eye, black just appearing on head and thorax. Head and thorax (except metathorax) brown (C. II, 5 li); mid-dorsal strip and head stripes not darkening. Legs, antennae, and rostrum grey-black (C. series C, i). Fourth segment of rostrum a darker black. Two black, lateral oblique, stripes present on the metathorax. The underside of the thorax remains orange except the coxae and sub-coxal plates - brown. The rostrum, though, darkens like the legs and antennae.

Abdomen: a deeper orange (C. XII, 5 na). Only the posterior red spot on the abdomen now visible (C. XII, 6 pe).

Openings of two dorsal abdominal scent glands become visible for the first time at centre of edges of fourth and fifth, and fifth and sixth segments. The edges of all segments clearly discernible.

5.20pm: Head, pro- and meso-thorax, and lateral metanotal markings blackish (C. IV, 4 pl). Mid-thoracic "V" and head markings still orange. Eyes red. Legs, antennae and rostrum grey-black, (C. II, 1 li). Distal rostral segment black (C. series C n). Abdomen and metathorax - same general colour (C. XII, 5 na). Two lateral red spots appear, possibly parts of the viscera showing through. One of the head markings proves to be the ecdysial suture.

This is considered full colour, the nymph appearing half black-half orange to the naked eye, the time taken for darkening being about seven hours. Next morning colours were again checked but no further changes had occurred. Over several observations the following have been recorded for time taken to darken to full colour 6, 8, 7 and 6.5 hours; mean 7 hours.

Colour of other stages following moults

After all moults the insect was pale in colour, but darkening and hardening of the exocuticle was completed in several hours. For example, the newly emerged second stage nymph was (like the first stage) pale orange in colour, but later, black pigmentation appeared on the head and thorax. The newly emerged fifth stage nymph was cream in colour, then gradually darkened through green to greyish-brown, and finally to black on the head and thorax. The adult turned through the colours cream, to green on the head, buff on the wings and pink on the appendages, to full colour.

First Feeding of Nymphs

On hatching, a nymph was placed on a sprig of twin cress. It walked actively over the plant but did not attempt to feed in the first 15 minutes after hatching (when the observation ceased). When nymphs three hours old were given food they immediately began to feed, some on the tips of fresh young leaves, others on green seed-cases. When food was offered two hours from hatching, feeding occurred. Thus the nymphs were able to feed well before full colouration was assumed. The tapered tip of the rostrum was partially inserted into the plant tissue, and on the leaves, the veins seemed to be the site of insertion.

The duration of the first feeding period ranged from 14 - 18 minutes; mean 16 minutes. After about five minutes of feeding, the abdomen seemed to have distended, and so some measurements were taken on nymphs which had not fed and on the same nymphs immediately after the first feed. The mean measurements over three nymphs were:

unfed: body length 0.36mm, length of abdomen 0.28mm

after first feed: body length 0.76mm, length of abdomen 0.40mm.

Wigglesworth (1934) showed that R. prolixus nymphs can ingest six to twelve times their own weight of blood at a single meal, and that the abdomen is capable of enormous distension. One N. huttoni nymph examined four hours after hatching had

not fed, but the abdomen had shortened indicating partial desiccation. Later in the day it had fed, because the abdomen was distended. This indicates that consumption of a meal within a few hours of hatching is essential.

Normal Changes in Duration of Nymphal Development Throughout the Season

The life-cycle of H. huttoni was studied by Gurr (1957) at Nelson and Table 44 summarising his results is reproduced from his paper.

TABLE 44

DURATION IN DAYS OF INCUBATION PERIOD AND NYMPHAL INSTARS OF H. huttoni

	No. of eggs	Incubation period in days	
		Mean	Range
	37	9.5	8-11

Instar	No. of nymphs	Duration of nymphal instars (days)	
		Mean	Range
1st	24	6	5-7
2nd	17	5	4-7
3rd	3	17	14-18
4th	2	15	13-17
5th	2	14	13-15

The present study was continuous over the 1957-58 season and included the first generation, the progeny of adults caught from the field in October, the second to fourth generations, and the progenies of the cross series. Each batch, or part thereof, hatching on the same day was reared separately. The month indicated refers in all cases to the month in which the eggs hatched, and therefore the same batches can be traced from stage to stage through the Tables 45 - 49 to give the duration of total nymphal development. The results for the full season, for each instar are presented separately, but the changes in duration of total nymphal development of the season are presented later.

Duration of First Nymphal Instar

The normal changes in duration of the first nymphal instar are shown in

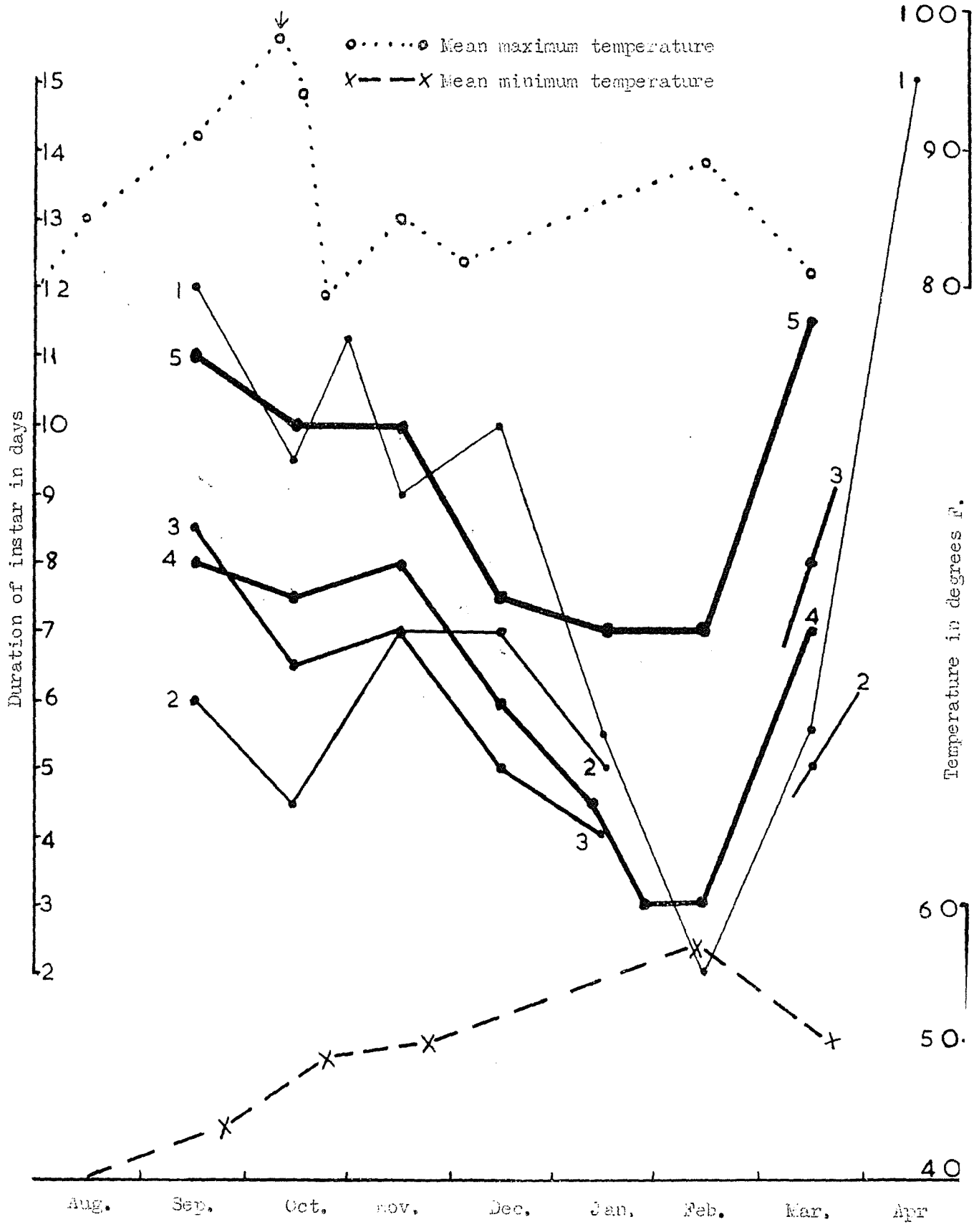


Fig. 38

Seasonal variation in the duration of each nymphal instar. Numbers 1 - 5 indicate nymphal instars and arrow indicates when greenhouse whitewashed.

Table 45, and graphically in Fig. 36. During September, the normal duration of the instar was 12 days. In October, before the 24th (when the greenhouse roof was whitewashed) the mean life of the instar was 8.5 days, and after the 24th 11.3 days. In November, the modal duration of the instar was 9 days, in December 10 days, in January 5-6 days, in February 2 days, in March 5 days, and in April 15 days. The range in duration of the instar was 1 - 15 days.

Duration of Second Nymphal Instar

The normal changes in duration of the second nymphal instar over the season are shown in Table 46 and graphically in Fig. 36. As expected, a similar trend was shown, as the normal or modal duration of the instar was 5-7 days in September, 4-5 days in October, 7 days in November, 7 days in December, 5 days in January, and 6 days in March. No figures are available for February, but that month would normally show the shortest period. The range in duration of the instar was 3-15 days. Between October and November, the general increase from 4 or 5 days to 7 days was accounted for as the effect of whitewashing the greenhouse.

Duration of Third Nymphal Instar

The normal changes in duration of the third nymphal instar over the season are shown in Table 47 and in Fig. 36. The normal or modal duration of the instar, for nymphs which hatched in the month indicated, was 8 or 9 days in September, 6 or 7 days in October, 7 days in November, 5 days in December, 4 days in January, and 8 days in March. Again the response was a shortening of the instar length as the temperature increased from early spring to summer, and the reverse from summer to autumn. The duration of the instar ranged from 3 - 11 days.

TABLE 45

DURATION OF FIRST NYMPHAL INSTAR

Month of hatching		No. of nymphs	Number of nymphs moulting to 2nd stage in the number of days indicated 1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17
Sep. 57	1st generation	16	1 1 2 2 4 2 2 1 1
			Normal duration 12 days
Oct.	1st generation) (before 24th))	13	1 3 2 3 3 1
	after 24th	4	1 1 1 1
			Mean duration before 24th 9.5 days, after 24th 11.3 days
Nov.	1st generation	5	3 1 1
	(a)	4	1 2 1
	2nd generation	11	1 2 1 1 2 3 1
	Total	20	2 7 1 2 2 0 3 0 2 1
			Normal duration 9 days
Dec.	2nd generation	18	1 8 3 1 3 1 1
			Normal duration 10 days
Jan. 58	2nd generation	5	3 1 1
Progeny of Cross Series B		18	3 7 3 1 2 1 1
Progeny of Cross Series A		7	1 1 3 1 1
	3rd generation	11	1 6 1 2 1
	Total	41	2 10 11 7 3 3 2 1
			Normal duration 5 or 6 days
Feb.	3rd generation	3	1 1 1
			Normal duration 1 or 2 days
Mar.	4th generation	1	1
Progeny of Cross Series B		2	1 1
Progeny of Cross Series A		1	1
	Total	4	1 2 1
			Normal duration 5 days
Apl.	4th generation	1	1
			Duration 15 days

(a) = progeny of females caught in field September 1957

TABLE 46

DURATION OF RECORD NORMAL INSTAR

Month of hatching		No. of nymphs	Number of nymphs moulting to third stage in the number of days indicated										
			3	4	5	6	7	8	9	10	11	12	13
Sep. 57	1st generation	5	1		1	1	1		1				
		Normal duration 5-7 days											
Oct.	1st generation	10	1	3	3	1	1		1				
		Normal duration 4 or 5 days											
Nov.	(a)	2					1						1
	2nd generation	11		1	2	1	3	3		1			
		13		1	2	1	4	3		1			1
		Normal duration 7 days											
Dec.	2nd generation	15	1	2	1	2	4	1	1	2			1
		Normal duration 7 days											
Jan. 58	2nd generation	2				1	1						
	progeny of Cross Series B	9		2	3	1	3						
	progeny of Cross Series A	6	1	2	3								
	3rd generation	8		3	5								
	Total	25	1	7	11	2	4						
		Normal duration 5 days											
Mar.	4th generation					1							
		Duration 6 days											

(a) = progeny of females caught in field September 1957

TABLE 47

DURATION OF THIRD INSTAR NYMPHS

Month of hatching		No. of nymphs	Number of nymphs moulting to fourth stage in the number of days indicated								
			3	4	5	6	7	8	9	10	11
Sep. 57	1st generation	5			1			2	2		
		Normal duration 8 or 9 days									
Oct.	1st generation	11	1	2		3	2	1	1		1
	(a)	3				1	2				
	Total	14	1	2		4	4	1	1		1
		Normal duration 6 or 7 days									
Nov.	1st generation	2	1				1				
	(a)	1					1				
	2nd generation	13	1		1	2	8	1			
	Total	16	2		1	2	10	1			
		Normal duration 7 days									
Dec.	2nd generation	17		2	7	4	2	1	1		
		Normal duration 5 days									
Jan. 58	2nd generation	2		1	1						
progeny of Cross Series B		10		3	5	2					
progeny of Cross Series A		5	1	2	1	1					
	3rd generation	14	7	6	1						
	Total	31	8	12	8	3					
		Normal duration 4 days									
Mar.	Cross Series progeny							2	1	1	
		Normal duration 8 days									

(a) = progeny of females caught in field September 1957

TABLE 48

DURATION OF FOURTH NYMPHAL INSTAR

Month of hatching		No. of Nymphs	Number of nymphs moulting to fifth stage in the number of days indicated								
			3	4	5	6	7	8	9	10	11
Sep. 57	1st generation	7		1	1	1	1	2			1
Oct.	1st generation	11			2	3	2	3	2		1
	(a)	3			2		1				
	Total	21		1	5	3	4	4	2	0	2
		Normal duration in September and October 7-8 days									
Nov.	1st generation	4		1			1	2			
	(a)	2						2			
	2nd generation	11		1	1	2	1	1	2		3
	Total	17		2	1	2	2	5	2		3
		Normal duration 8 days									
Dec.	2nd generation	16	1	1	4	6		3	1		
		Normal duration 6 days									
Jan. 58	2nd generation	3	2		1						
progeny of Cross Series B		9	2	4	2		1				
progeny of Cross Series A		7	1	2	2	1	1				
	3rd generation	13	5	2	3	3					
	Total	32	10	8	8	4	2				
		Normal duration 3-5 days									
Feb.	3rd generation		1								
		Duration 3 days									
Mar.	Cross Series progeny					1	2	1			
		Normal duration 7 days									

(a) = progeny of females caught in field September 1957

TABLE 49

DURATION OF FIFTH INSTAR

Month of hatching		No. of nymphs	Number of nymphs moulting to adult in the number of days indicated											
			4	5	6	7	8	9	10	11	12	13	14	15
Sep. 57	1st generation	13					3	1	2	3	1		1	1
		Normal duration 8-11 days												
Oct.	1st generation	11				2	2	1	6					
	(a)	2				1				1				
	Total	13				3	2	1	6	1				
		Normal duration 10 days												
Nov.	1st generation	2							1	1				
	(a)	3						1	1	1				
	2nd generation	9					1	2	4	2				
	Total	14					1	3	6	4				
		Normal duration 10 days												
Dec.	2nd generation	16		1	1	4	5	3	1	5				
		Normal duration 7 or 8 days												
Jan. 58	2nd generation	3				3								
progeny of Cross Series B		12		2	1	4	3	1	1					
progeny of Cross Series A		7	3		2	2								
	3rd generation	13	1	1	4	5	1	2	1					
	Total	35	4	3	7	12	4	3	2					
		Normal duration 7 days												
Feb.	3rd generation					1								
		Duration 7 days												
Mar.									1			1		
		Duration 10-15 days												

(a) = progeny of females caught in field September 1957

Duration of Fourth Nymphal Instar

The normal changes in duration of the fourth nymphal instar over the season are shown in Table 48 and Fig. 36. The modal duration of the instar (for nymphs which hatched in the month indicated) was 7-8 days in September and October, 8 days in November, 6 days in December, 4 or 5 days in the first three weeks of January, 5 days in the last week of January, 3 days in February, and 7 days in March. The duration of the instar ranged from 3-11 days.

Duration of Fifth Nymphal Instar

The normal changes in duration of the fifth nymphal instar over the season are shown in Table 49 and Fig. 36. The modal duration of the instar (for nymphs which hatched in the month indicated) was 8-11 days in September, 10 days in October, 10 days in November, 7 or 8 days in December, 7 days in January, 7 days in February, and 10-13 days in March. The duration of the instar ranged from 7-15 days.

Discussion on Nymphal Development

The nymphal development is summarized in Fig. 36 in which the duration of each instar is plotted month by month against mean monthly maximum and minimum temperatures recorded in the greenhouse. As expected, the duration of each instar decreased as the temperature increased from September to February, and then increased as the temperature decreased from February to April. The relative humidity data for Palmerston North, shown graphically in Fig. 35 should be considered in conjunction with this figure. However, as relative humidity at normal temperatures was shown (in Chapter 5) to be adequate for incubation, it is considered also to be adequate for nymphal development. Thus the changes noted, were due primarily to changes in temperature.

With the exception of the fifth instar, the effect of whitewashing the roof of the greenhouse on the 24th October, showed as a peak in the graphs in November, marked in the first and second instars. The fifth instar graph did not continue

downwards but flattened out temporarily at that point. The maximum temperature decreased by 20°F. The graph for the first instar showed a second peak in December. This was the effect of the slight decrease (of 5°F) in maximum temperature early in December. There is also evidence that the second instar was affected, for there was a flattening-out of the graph before the normal downward trend continued. There was no evidence of a response in the other instars. The foregoing indicates that the first two instars (especially the first) are far more sensitive to temperature changes than are later instars. A change of the order of 5°F (1.7°C) affected the first instar and also the second instar slightly, but not later instars, whereas a change of 20°F (11°C) affected all instars, but the fifth instar (which was the most resistant) only slightly. The incubation period was also affected by the drop of 5°F as shown by a flattening of the graph in December (Fig. 34).

Table 50 which tabulates the duration of each instar month by month enables the comparison of nymphal development at Palmerston North with that at Nelson shown in Table 44 page 132) which refers to development in mid-December 1950 (Gurr, personal communication).

TABLE 50

DURATION OF SUCCESSIVE INSTARS AT PALMERSTON NORTH OVER THE 1957-58 SEASON

Instar	No. of nymphs	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	Season mean
		Modal duration of instar in days								
1st	119	12	10	9	10	5.5	2	5	15	7.6
2nd	82	6	5	7	7	5	-	6		6.0
3rd	83	8.5	6.5	7	5	4	-	8		6.5
4th	91	7	7	8	6	4	3	7		6.0
5th	93	11	10	10	8	7	7	12		7.7
Total		44.5	38.5	41	36	26.5	33	38		36

The total developmental period at Nelson was 57 days. Considering first the month of December, obviously the two Tables are not in agreement, and only in the case of the second instar is there anything like agreement. The total of 33 days in February was recorded for nymphs which hatched late in February and which therefore developed mainly in March; hence the discrepancy between total and individual instar values in February. In no month does the Palmerston North data, which covers a wide range of temperature changes, agree with the Nelson data. Therefore, some factor other than environmental differences was operating.

However, several factors must be considered: at Nelson there were insufficient numbers in the last three instars which are most strongly different; at Nelson the nymphs were in an open insectary whereas at Palmerston North they were in a greenhouse; the environmental conditions of the two experiments may have differed; this may be purely a food effect, as the Nelson nymphs were fed on shepherds purse, and the Palmerston North nymphs on twin cress; the two populations may be exhibiting a geographical difference. As the insects marked "Nelson" in Gurr's collection are of the large population, it is highly probable that his results shown in Table 44 are for the large population. The results shown in Table 50 are for the medium and small populations.

Of all instars, the second, third and fourth seemed consistently to be shortes in duration. The first instar was considerably longer in duration, except for the very warmest months, and it was only in January, February and March that it was shorter in duration than the fourth instar. The fifth instar was generally the longest in duration but on two occasions the duration of the first instar was longer. Here, again, is evidence that the first instar is the most sensitive to changes in temperature. The mean duration over all months (excluding April) showed that the third instar slightly exceeded the second and fourth instars in duration. The descending order of instars for greatest duration was fifth, first, third, and second and fourth. The incubation period was, in all cases, longer than the duration of any single nymphal instar. In the Nelson population the incubation

period was shorter in duration than the last three instars, and the descending order of instars (for greatest duration) was third, fourth, fifth, first, and second. The variation (in duration) between instars, is greater in N. huttoni than that shown by Smith (1927) for the Rutherglen bug.

Duration of Total Nymphal Development

The duration of total nymphal development from hatching until emergence as adults is shown in Table 51 and graphically in Fig. 37. For comparison, the mean incubation periods are shown in column 5 and the summation, that is the duration of total development from oviposition until emergence as adults is shown in column 6, and also in Fig. 37. Total nymphal development and the summation of embryonic and nymphal development both show (as expected) a similar response to normal temperature changes over the season, as each stage separately. For nymphs hatching in September, the mean duration of nymphal life was 42 days, and when a mean incubation period of 19 days (for August and September) is added, the total developmental period becomes 61 days. The longest nymphal developmental period (in September) was 46 days, and the longest incubation period (August-September) was 26 days - totalling 72 days. The shortest nymphal developmental period, 25 days was recorded for those hatching in the last week of January and which therefore developed almost entirely in February, the warmest month. When incubation period is included, the figure becomes 35 days, i.e. half of the longest time recorded. By March, the periods had increased to 41 days for nymphal, and 54 days for total, development.

These two graphs should be compared with those for each nymphal instar (Fig. 36) and for incubation period (Fig. 34) because they all follow the same trend very neatly even to the two reversed temperature changes occurring during the experiment. The decrease in maximum temperature of 20°F caused by whitewashing the greenhouse was shown as an increase in the total developmental period, and the effect of the decrease in temperature of 3°F in December was shown by a temporary check in the downward trend. Although not observed in individual instars after the second,

TABLE 51

DURATION OF TOTAL NYMPHAL PLUS EMBRYONIC DEVELOPMENT

Month of hatching	Nymphal Development * No. of observations	Mean total No. of days from hatching to emergence as adults	Embryonic Development Normal incubation period in days	TOTAL Total No. of days from oviposition to emergence as adults
Sep. 57 1st generation	12	42	19+	61
Oct. 1st generation	11	39	15	54
Oct. last week (a)	3	56		
Nov. 1st generation	2	40		
(a)	4	41 (41)	15	56
2nd generation	10	42		
Dec. 1st-12th 2nd generation	11	41	15	56
20th-31st 2nd generation	7	32	13	45
Jan. 58 2nd generation	3	28		
progeny of Cross Series B	14	28 (27)	12	39
progeny of Cross Series A	7	25		
Jan. last week 3rd generation	13	25	10	35
Feb. 3rd generation	3	33	9	42
Mar. 4th generation	2	43	13	54
progeny of Cross Series B	3	40 (41)		
Apl. 4th generation	1	33 days for 3 instars		
	1	36 days for 3 instars		

* The figures recorded here are only for nymphs which developed right through to the adult, and hence differ slightly from the totals shown in Table 50.

+ Mean of all "normal incubation period" figures for August and September.

(a) Progeny of females caught in field September 1957.

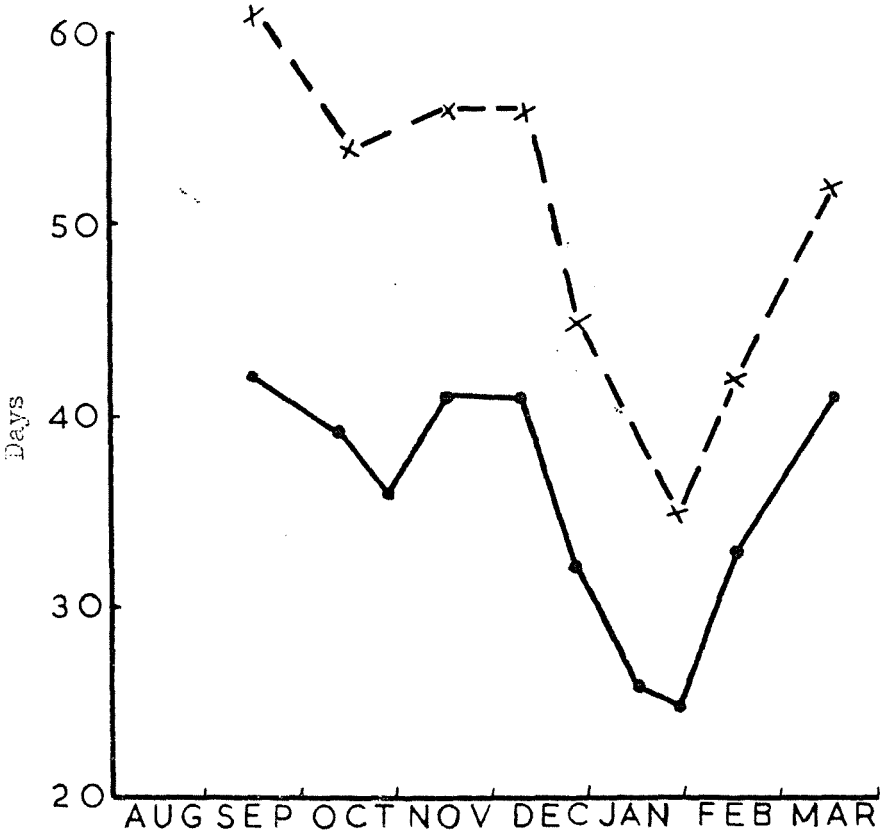


Fig. 37

Seasonal variation in duration of total nymphal development (solid line) and in embryonic plus nymphal development.

its effect on the first two was sufficient to show in the total.

The duration of total nymphal development in males and females was checked and found to be the same.

Duration of Nymphal Development at Normal Low Temperatures

The nymphs used in this experiment hatched from the eggs incubated in the open barn at low temperatures. As in the case of embryonic development, nymphal development was slower under those conditions. The results are shown in Table 52. Unfortunately the number used was small, and therefore consistency could not be confirmed. However, those surviving gave an indication of the adaptability of the nymphs. The month indicated is the month in which the eggs hatched. Thus the two adults which emerged in mid-March had hatched on 27th January and so their nymphal development was mainly in February and partly in March. In comparison with February nymphs in the greenhouse the total period was about 20 days longer (53:33), and in comparison with March nymphs, about 15 days longer, 53:38. Compared instar by instar with nymphs developing in the greenhouse in March, it was found that the first instar was prolonged, and the fourth instar slightly, whilst instars 2, 3, and 5 were of similar duration. Compared with February nymphs in the greenhouse, the duration of each instar was longer.

The development of the first and third instars in the barn in November took much longer than the same development in any month in the greenhouse, and in January in the barn. The same general trend shown by the greenhouse nymphs, that is a decrease in the developmental period from early spring to the height of summer was indicated by these nymphs reared at the lower level of the normal temperature range.

The fact that two nymphs completed their development in the January-February period and that one survived as far as the fifth stage in the November-December period (at a mean temperature of 16.6°C) indicates that this was near the lower level of adaptability (or tolerance) of the species for complete development. The addition of the incubation period for those hatching in January (36 days) showed that the total developmental period from oviposition to emergence as adults was

TABLE 52

DURATION OF NYMPHAL DEVELOPMENT AT LOW-NORMAL TEMPERATURES

Instar	No. of nymphs	Duration of instar in days November	January	Normal duration in March	Incubation period in days
1st	3	22	14, 19	5	Oct. 29
2nd	1		7	6	Dec. 26
3rd	2	24	7	8	
4th	1		12	7	
5th	1		11	12	
Total	2 adults		59, 48	38	
			plus 26		
Duration of first 3 instars	49,57		74 - 85 days total development		
Duration of first 4 instars	79		37		

74-85 days. This was longer than the longest period (72 days) recorded for the earliest (August) batch in the greenhouse. The nymph which hatched in November but died in the fifth stage took longer to complete four instars (79 days) than the earliest batch in the greenhouse to complete total embryonic plus nymphal development (72 days). The addition of the incubation period of 49 days to the former, showed that the fifth instar was reached after 128 days, that is over four months in development, and the duration of the final instar was still to come.

Duration of Nymphal Development at Extremely High Temperatures

The nymphs used were those hatching from the eggs incubated at high temperature In most cases the nymphs were dead by the next day. In the case of nymphs from group one eggs (see Table 39 page 112) four lived for four days, and two of them moulted on the fourth day.

Although the duration of the first instar (4 days) was shorter than that in the greenhouse for January (5 days), it was not shorter than that in the greenhouse for February (3 days). It seems that the temperature 34-35°C either slows

down development, or retards moulting. Wigglesworth (1952) reported that above 30°C moulting was slightly retarded in fourth stage R. prolixus nymphs. Since first stage H. huttoni nymphs soon died at temperatures of 36.5°C and above, it is considered that 34-35°C is the upper limit of tolerance. The experiment showed that first stage nymphs are less tolerant of high temperature than are the eggs. The fact that death coincided with the day of moulting in two cases indicates that the nymphs, which were showing reasonable tolerance to desiccation, became very susceptible at that time. Either relative humidity, which was sufficient for incubation and eclosion, or temperature, or both were unsuitable for nymphal development.

No nymphs were reared from eggs at high temperatures. However, for those fourth and fifth stage nymphs used in determining the effect of high temperature on wing form in the adult (Section A), development was hastened considerably. The upper limit of temperature tolerance for fourth and fifth stage nymphs was 41-43°F, but humidity, although maintained, may not have been adequate.

Tolerance of Fourth and Fifth Stage Nymphs to Extremely Low Temperatures

As the nymphs were able to adapt themselves to a considerable range of temperatures, an attempt was made to determine the lower level of temperature tolerance on fourth stage nymphs. Eggs when exposed to temperatures of 3°C and 6°C underwent suspension of development. It was considered that early nymphal stages would not survive long under such conditions. Accordingly, some fourth stage nymphs were placed in glass tubes in a refrigerator at 6°C. A sprig of wireweed, (Polygonum aviculare) was replaced every three days. Survival was prolonged, and some of the nymphs moulted to the fifth stage. None survived to the adult stage, so that the wing form expressed under such conditions remains unknown. Survival periods are shown in Table 53.

That the nymphs survived more than a few days at 6°C indicates the extreme tolerance of this species. The temperature of 6°C proved to be below the lower limit of temperature tolerance, but from the survival periods, apparently not very

TABLE 53

SURVIVAL OF 4th AND 5th STAGE NYMPHS AT 6°C

Instar	Number of nymphs	Number of nymphs surviving the number of days indicated				
		Less than 36	36	40	42	48
4th	16	5	3	2		
5th			2		2	2

far below that value. Usinger (1942) stated "Some members of the tribe Orsillini can flourish under almost any natural conditions." This section on bionomics has certainly shown that this is true of N. huttoni, which explains its wide distribution in New Zealand and outlying islands.

One of the fourth stage nymphs which survived 40 days was large. Some of its body measurements in scale divisions, are: head width 12; body length 32; abdominal width 24; length of mesonotum to tip of wing pad, 7. However, there were some nymphs reaching these dimensions (except for head width) amongst those measured in Section A (see Table 8 page 23). As it was larger than the other nymphs in this experiment, there is the possibility that 6°C may prevent moulting; hence attainment of this maximum size. However this isolated case is insufficient evidence to make any decision. From wing pad development there is no doubt that this was a fourth stage nymph.

As well as eventually killing the nymphs, the low temperature had desiccated them. One of the fifth stage nymphs had been stuck to the inside of the glass tube. The region of contact, the left dorsal abdominal surface, appeared as if rusted from "frost burn".

General Colouration of Fifth Stage Nymphs Kept at 6°C.

Although dark, the dorsal abdominal surface particularly laterally, and the pleura, had a distinct reddish or pinkish tinge. The thorax, basically black, had considerable lighter areas of red and white blotches. The head stripes, orange in younger nymphs, were white, but the rest of the head was black.

Moulting

The insect emerged from the old cuticle through the undarkened, mid-dorsal thoracic strip and the ecdysial suture of the head. The ecdysial suture (a term introduced by Du Porte, 1957), extends, on the dorsal surface, from the centre of the posterior of the head, forwards and sideways to immediately anterior to the eyes (see Plate 1). In the exuvium, the dorsal portion of the head cuticle anterior to this suture, was pushed forwards so that it was inside out. The mid-thoracic split was in the pro- and mesonota only. Emergence from the old cuticle was mainly forwards. It seemed that the thorax was burst open first, but emergence was not through this as the split was too narrow, but rather the insect moved forwards and slightly upwards, through the larger opening contributed to by both the thorax and the head. Sometimes there was a short lateral split posterior to each eye, and sometimes the head on the exuvium was normal, i.e. the dorsal surface was not turned inside out, and the ecdysial suture was not split fully forwards. These two facts further support the above view on the method of emergence. The antennae were flexed backwards under the body before the commencement of moulting.

A newly emerged adult remained motionless for five minutes and then began slow movements, such as twitching the antennae and altering its position, but with frequent rests. Nine minutes after emergence it became fully active. Two fifth stage nymphs fed for two minutes on the inner surface of the exuvium, no doubt for liquid end products of histolysis.

Many exuviae were measured, and it was found that in the measurements taken, namely length, breadth, headwidth, and lengths of antennae and rostrums, there was an increase in size at each instar, and a size-range characteristic of each instar. Headwidth of the exuvium was slightly greater than head width of the nymph.

Time of day of Moulting

The times at which moults occurred over a 24-day period during January and February were recorded, and the totals were:

6.30pm	-	8am	5
8am	-	10am	25
10am	-	Noon	8
Noon	-	2.30pm	20
2.30pm	-	4.30pm	19
4.30pm	-	6.30pm	7

Moulting occurred at any time during daylight hours, and apart from the unaccountable decline between 10am and Noon, occurred at a steady maximum rate from 8am-4.30pm

Sex Ratio

The sex of all insects reared was recorded on emergence as adults. Monthly totals for each sex are shown in Table 54.

TABLE 54

SEX RATIO IN THE ADULT

Month of final ecdysis	No. of males emerging	No. of females emerging
October	5	2
November	12	6
December	7	7
January	11	11
February	11	20
March	0	2
April	4	1
	50	49

Over the season, the ratio of males to females was 1:1. However, at the extreme ends of the season, i.e. October, November, March and April the ratio was 2:1, whilst over December, January and February the proportions of the sexes emerging were almost equal, but the females were in the majority (1:1.3).

Sexing as Nymphs

It was discovered that the nymphs could be sexed in the fifth stage for, as mentioned in the description, rudiments of the external genitalia were apparent in

the female (see Plate 4, E) but not in the male. Microscopic examination was necessary. In the adult female (Plate 3, B and C) the four posterior abdominal segments do not lie straight across on the ventral surface, but slant forwards into the ovipositor. In the female fifth stage nymph these abdominal segments show a tendency to this "slanting", and densely darkened areas occur on the mid-ventral line of segment eight. In the male nymph as in the adult male (Plate 3, A and D) the abdominal segments lie straight across on the ventral surface.

This sexing method was tested at the end of the 1957-58 season. Fifteen fifth stage nymphs were caught in the field late in May. Seven were identified as females and put in a separate tube, and eight as males. As development is slow at this time of year, the experiment was hastened by placing the nymphs in a constant temperature cabinet at 73°F. Of the seven nymphs identified as females, one died and six became adult females. Of the eight nymphs identified as males, two died and six produced adult males. The results showed that the method was very accurate and 100% accuracy may be expected.

The nymphs could also be sexed by naked eye with 80-90% accuracy, the distinction being a dark streak on the female abdomen.

SUMMARY OF NYMPHAL DEVELOPMENT

1. It is shown that full colouration is attained by the first stage nymph seven hours after eclosion. Following all moults, the insect is pale, but assumes full colouration in several hours.

2. It is shown that first stage nymphs are capable of feeding within two hours of hatching: measureable distension of the abdomen occurs.

3. It is shown that the duration of each nymphal instar, of total nymphal development, and of total embryonic plus nymphal development, varies inversely with normal temperature changes over the season. The nymphal instars in descending order of greatest duration, are fifth, first, third, and second and fourth.

4. It is shown that the first and second nymphal instars are far more sensitive to changes in temperature than are later instars. The development of the former was affected by a change in temperature of 3°F (1.7°C), whereas a change in temperature of 20°F (11°C) affected the duration of all instars, but the fifth slightly.

5. It is shown that the lower limit of temperature tolerance for complete development is near 60°F (15.6°C).

6. The nymphs of this species show remarkable tolerance to adverse conditions:

   (a) the fastest total developmental period (including incubation) during January-February at normal temperatures was 35 days. At lower temperatures obtained by shading (in a barn) development up to the end of the fourth nymphal instar took 128 days during September-December.

   (b) first stage nymphs survived for four days at 34-35°C and some of them moulted. Fourth and fifth stage nymphs survived to adults at 41.7°C but not at 44°C.

   (c) fourth stage nymphs survived up to 40 days at 6°C, and some of them moulted to the fifth stage, to survive another 8 days. This result indicates that fifth stage nymphs would be capable of surviving winter. The egg is more resistant to extremes of temperature and humidity than are the nymphs, with the exception that fourth and fifth stage nymphs may be more tolerant to low temperatures.

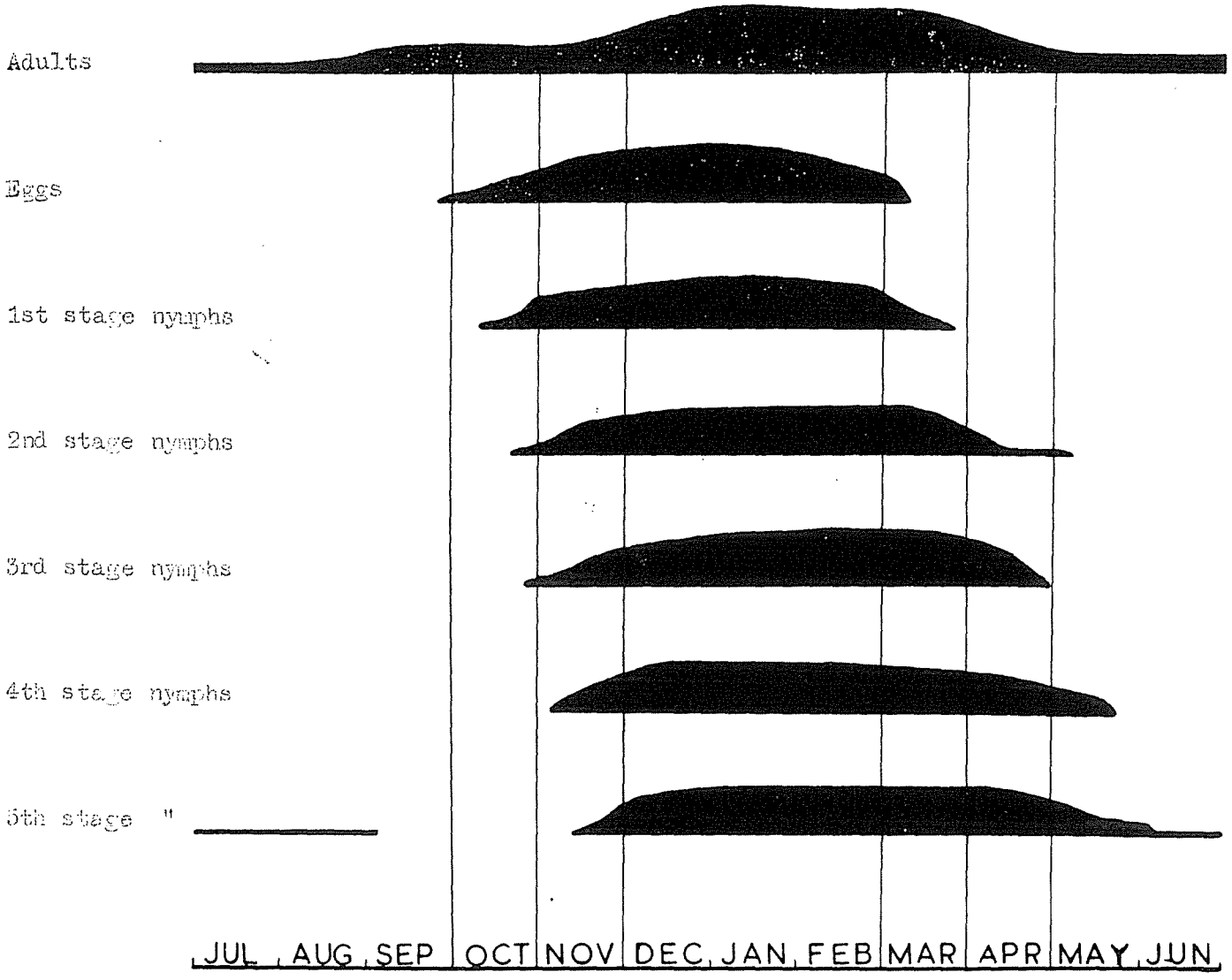


Fig. 38

Seasonal occurrence of Nysius huttoni at Palmerston North, 1957-58

With the onset of autumn and the approach of winter, the last appearance of each instar was noted. Myers (1926) recorded that all stages were present in March, but that in April only the three older nymphal stages were present. The seasonal occurrence of the H. huttoni population in the field at Palmerston North over the 1957-58 season is summarised in Fig. 38. First stage nymphs were last seen in March, so that the last eggs of the season were probably laid early in March. The last egg was laid in the greenhouse on 1st May 1957, and adults caught in the field at the end of April had ceased laying. Very few second stage nymphs were present by 11th April, but one was seen as late as 7th May. Third stage nymphs were last seen on 27th April, and fourth stage on 20th May. The fifth stage seemed more hardy, and two were caught as late as 3rd June were placed in the greenhouse. Both had moulted to adults by 19th, which indicated that fifth stage nymphs would become adults by early winter. However, on 14th August 1958 a fifth stage nymph was caught in the field, thus establishing that some fifth stage nymphs overwinter.

The adults seemed to decrease in activity by the end of April, no copulating pairs were found on 8th May, and thereafter hibernation seemed to set in. Fewer adults were active on the area, and their movement was very sluggish.

In the 1958-59 season activity was resumed early, for eggs were laid early in September, and by 2nd October the first three nymphal instars were present. The dates of first appearance of the second and third nymphal instars shown in Fig. 38 were calculated by allowing the same developmental period as in the greenhouse. As expected, the season began earlier in the greenhouse, but it was significant that in both greenhouse and field populations approximately one month elapsed between first copulation and first oviposition. The dates of hatching and emergence as adults of the first individuals in each generation (in the greenhouse) were:

1st generation	2nd September 1957,	16th October 1957
2nd generation	22nd November 1957,	2nd January 1958
3rd generation	25th January 1958,	17th February 1958
4th generation	8th March 1958,	20th April 1958

It seems certain that in the field there are four broods or possibly four and a half broods per season.

Habitat and Host Plants

"The species of Nysius are noteworthy sunlovers" - Myers (1926). Gurr (1957) stated that N. huttoni prefers situations where vegetation is sparse and the direct sunlight strikes through to the ground. Although Gurr stated that the greatest activity of the bug occurred around mid-day, it was noted that both nymphs and adults seek the shade of plants during the warmest part of the day. Further, when sheltering, they move into the edge of thicker vegetation. The insect lives on, or very close to, the ground, and has often been observed under one-eight of an inch of leaf litter and under small stones. To avoid being caught, they either crouch close to the ground or move into a crack in the soil. At night the insects shelter under leaf debris. Fourth and fifth stage nymphs when molested exuded a transparent malodorous fluid from the scent glands and anus. The above is a description of the spring and summer habitat.

In autumn, although bugs were still present in the same area, they were more sluggish and tended to shelter more under grass straw, leaf litter, and at the base of Brown Top (Agrostis tenuis Sibth) plants. Often during the warmer part of the day they would move to the surface of the soil or plant to bask in the sun.

The winter habitat on the study area was restricted almost entirely to the bases of Yorkshire Fog (Holcus lanatus L.) and Brown Top plants. The former plant is tufty, has hairy sheaths, and dead leaf litter at the bases of the stems, and thus offers reasonable protection to the insect.

The host plants at Palmerston North together with an indication of their importance to the insect are shown in Table 55. Twin cress, lucerne and red clover have been recorded before, but the others are here recorded as hosts for the first time. Myers (1921, 1926) reported lucerne, red clover and Cassinia leptophylla R. Br. as hosts; Morrison (1939) reported wheat; Woodward (1954) reported this insect from the Three Kings Islands on prostrate ngaio (Myoporum laetum Forst. f.).

Chenopodium triandrum Forst., Disphyma australe (A. Cunn.) Black, puka (Meryta sinclairii (Hook.) Sam.), and on flowering kanuka (Leptospermum ericoides); Gurr (1967) reported shepherds purse (Capsella bursa-pastoris (L.) Medik.), Curnow's curse (Calandrinia caulescens H.B.K.), twin cress, and cruciferous plants.

TABLE 55

HOST PLANTS OF Nysius huttoni

Botanical name	Common name	Importance of Host
Coronopus didymus	Twin cress	Major spring and summer host
Rumex acetosella	Sheep sorrel	Major spring and summer host
Polygonum aviculare	Wireweed	Major spring and summer host
Trifolium dubium	Suckling clover	Major spring host
Spergularia campestris	Sand spurrey	Major summer host
Silene gallica	Catch fly	Medium spring and summer host
Triquetrella papillata	a moss	Medium host
Trifolium repens	White clover	Minor summer host
Trifolium pratense	Red clover	Minor summer host
Medicago sativa	Lucerne	Minor summer host
Anagallis arvensis	Scarlet pimpernel	Minor summer host
Salvia sessilis	Onehunga weed	Medium summer and shelter host
lawn grasses and yarrow		Medium hosts
Hypochaeris radicata	Cats ear	Summer shelter host
Juncus bufonius	Toad rush	Shelter host
Holcus lanatus	Yorkshire fog	Major winter host
Agrostis tenuis	Brown top	Major autumn and winter host
Lolium perenne	Perennial ryegrass	Minor winter host
Paspalum dilatatum	Paspalum	Minor autumn host

Quiescence in N. huttoni

In the few detailed studies on the ecology of Heteroptera, the winter condition assumed by the insects have been passed off by such statements as "adults overwinter at the bases of rushes","hibernating adults", or "only the adults survive the winter" (Butter 1923, Myers 1926).

It is generally understood that these insects become inactive during winter but no attempts to determine the intensity of the "hibernation" have been made. The word hibernate, defined in the Shorter Oxford English Dictionary "to spend the winter in some special state suited to resist it", is a very general term giving no indication of the nature of that state. The term diapause was introduced by Wheeler in 1893 to mean a resting stage (Lees, 1955). Lees further clarifies the definition by distinguishing between diapause and quiescence. "One insect will develop without delay when temperature (and other conditions) are 'favourable', whereas a second fails to develop or grows slowly and irregularly. These states are respectively quiescence and diapause". Therefore, from evidence interpreted according to this definition, the overwintering state in N. huttoni is quiescence.

Seasonal onset, duration and awakening from quiescence

In the height of quiescence, the adult insects were motionless, not moving so much as an antenna unless disturbed. However, this intense quiescence was not continuous over a full day, but tended to be broken over the warmer part of the day. The most intense period was over June and July. Woodward (1952) stated:

> "In hibernation a distinction is to be drawn between physiological activity of the insect and suppression of mitotic activity and growth generally, as involved, for example, in gonad development. Neither Notostira nor Stenodema are completely inactive except at very low temperatures, and both can be induced to walk, although rather sluggishly, when disturbed during cold weather in their winter quarters."

This seemed also to be the case in N. huttoni. The last brood of nymphs showed remarkable hardiness, and the fourth and fifth stage nymphs exhibited inactivity, which would have led on to quiescence in the overwintering fifth stage nymphs.

There was a gradual change from summer activity, through reduced autumn

activity, to restricted winter activity, followed by the reverse through late winter to spring. When the dates for the last appearance of each instar (see Fig. 38) are compared with the mean monthly field temperatures (Table 42 page 115) it is seen that there was increasing ability to withstand low temperatures, in each succeeding instar. These dates are set, with slight variations from season to season, either by the effect of temperature or photoperiod on the female, or by the direct effect of environment upon eggs and nymphs, or most probably, by a combination of both factors. The Fecundity study indicated that the females cease oviposition in the autumn before temperature becomes too low for the eggs to develop. This means that the full cycle to the adult would be completed before winter. If this mechanism in the female does not exist, or if for any reason it was slightly inaccurate, then nature would set the dates, because only those eggs that are permitted to by the environment, would develop.

The first instar would persist until the minimum temperature it can tolerate was reached, its development would be slowed down (see Chapter 6), and it may show partial quiescence. If it did become quiescent it would not moult to the second stage, but field observations indicated that this did not occur. Therefore, before quiescence set in, the nymph would moult to the second stage which has a greater tolerance to low temperature. The second stage nymph would develop but would eventually become sluggish as its lower limit of temperature tolerance approached. Quiescence would again be forestalled by moulting to the third stage. Similarly, the fourth and fifth instars were expressed. When the imago was reached, there being no further moult or "by pass" move, the insect responded to the further decrease in temperature by entering quiescence. One case was noted where the fifth instar was "beaten" by the environment, and overwintered as such.

The appearance of sluggishness on very cold days, and a general shortening of the period of activity on normal days, was noticeable in the adults by mid-April when second stage nymphs and above were still present.

Quiescence stance and intensity of quiescence

The legs were tightly drawn in under the body and the antennae were flexed backwards along the sides of the head. This crouching stance, by reducing the area of body surface exposed, and by minimising circulation of air under the body, is probably a heat conserving reaction. Adults were often found in groups in the crowns of Yorkshire fog and Brown top, and this would tend to raise the temperature within the grass tuft. Woodward (1952) stated that humidity seemed important for hibernation, and showed that the relative humidity within a tuft of grass was greater than in the air outside of it.

The insect did not take up a position and literally not move until the winter was over, yet it probably remained within the one grass tuft. During the less intense quiescent period (i.e. before and after June and July) the insects often moved to the top of the grasses to bask in the sunshine, and may have consumed some food. However, during the coldest four weeks (mid June - mid July) the majority of the time was passed in a motionless condition.

During May, the insects overwintering in the greenhouse would move when disturbed. During early June some would be walking about on a warm day. During late June and July, the bugs became completely inactivated at the lower temperatures, for example even at 10am, when disturbed they would merely twitch legs and antennae for the briefest possible time, but would not move in relation to the substrate. Yet by 3pm, the temperature in the greenhouse was raised sufficiently (on sunny days) for the bugs to walk around. Copulation in the greenhouse began in the second half of July, in the afternoons. In the autumn, copulation occurred after the cessation of oviposition, for the last copulation noted in the greenhouse was on 6th May, 5 days after the last egg was laid.

Copulation

The male approaches the female from behind, or from the side. Mounting is sudden, the male clinging to the side of the female, in a head to head position, so that his ventral surface is against her lateral surface. He holds himself in

this position, until the genitalia are linked, by clamping the mid- and hind legs round her body, the forelegs gripping near the head. Meanwhile the female releases the ovipositor from its groove. The mobile terminal segments of both sexes are turned upwards to facilitate linkage. In the male, they are turned through almost ninety degrees and flexed forward, whilst in the female they are turned only slightly towards the male so that the ventral surfaces contact. The claspers of the male clamp firmly round the ovipositor to give strength to the linkage, and the aedeagus is inserted in the ovipositor and can be seen pulsating within the ovipositor. During this period the male antennae are flexed down onto the female head and antennae; the female, by a side to side jerking motion may attempt to dislodge the male; the male may use a similar side to side shaking to induce an unwilling female to permit union.

When linkage of the genitalia is established, the male releases his leg grip and places the tarsi on the ground. As the female walks forwards, the male swings through 180 degrees, his hind legs placed momentarily along the pleurites of the female abdomen, probably to lessen the strain involved in such a move. Thus the normal position for copulation is assumed, the partners facing in opposite directions. A variation has been noted: the male had not turned round so that he was facing away from the female, but the two were standing side by side, motionless, yet definitely in copula.

Copulation does not appear to interfere with locomotory activity in the female which often drags the male along backwards. The male may actively walk backwards, or passively allow itself to be dragged along, the forelegs serving merely to keep the head off the ground. In one exceptional case where the female had died whilst the pair were in copula, the male was walking forwards dragging the dead female backwards.

Copulation normally continues for several hours. The following times noted were short of the total duration because often the beginning was unknown, and when the separation was between observations, the last time they were seen in copula

was taken as the time of separation: 6.5 hours, 5.5 hours, 5 hours and 4 hours. However, copulation may occupy a much shorter time as indicated by the following observations: eight minutes (twice), three minutes (twice), and two minutes. Copulation is repeated many times during the season, and in the case of macropterous males the tips of the hemelytra often become permanently turned up from pressing against the female abdomen. This has also been reported in Oxycarenus vittatus (Fabr.) by Myers (1926) and in Rhopalimorpha bugs by Pendergrast (1952).

Courtship

There appeared to be no prolonged period of courtship, as is understood for the higher vertebrates. Neither is it known whether the partners have ever seen one another before, nor will ever pair again other than by chance.

In the field, copulation seemed very sudden, and from reared specimens this was also the case with males and females which had copulated before. But young individuals, about to copulate for the first time showed preliminary movements of excitement, which indicates an attraction between the sexes, and such may be termed courtship. N. huttoni may therefore be contrasted with Rhopalimorpha species in which there is no courtship (Pendergrast, 1952). However, experience seemed to affect courtship, for "experienced" males would mount almost immediately, and courtship would be brief or non-existant. Rosenblatt and Aronson (1958) showed that in male cats, previous sexual experience before castration enabled normal sexual behaviour up to three and a half years after the operation.

Further, a bond appeared to be maintained between copulations by the pairs, for during winter or in the cool of the evening, they would often remain side by side or facing one another, antennae touching. At the extremes of the breeding season, (August, and April and May) there seemed to be a reluctance to copulate and the "courtship" period was prolonged. Courtship behaviour is discussed under the following headings:

(i) Courtship between a newly emerged male and a newly emerged female.

(ii) Courtship between a male which had mated before and a newly emerged female.

(iii) Courtship between a male and a female which had both mated before.

(i) Courtship between a newly emerged male and a newly emerged female

When first put together (in February) both adults had emerged three or four days. On sight of the male, the female stood still and the anus began to pulsate. She rushed over to the male, touched him, and then withdrew a short distance. The male began fidgeting, rubbing the fore- and mid tarsi together, on one side. The female stood still, but the anus was pulsating approximately 160 times a minute. Next the male turned to face the female, rubbing his front tarsi together. The female (which was much larger than the male) ran up to the male, touching of the antennae followed, and then the male walked right over the top of the female, turned round so that he approached from behind, and mounted. The pulsation in the female continued when the union was established. Thus copulation began five to seven minutes after both were aware of the other's presence.

In another case, where the male emerged only the day before putting together, and the female three days before (also in February), the male did not mount. Although the female did all she could to attract him by touching him and finally by walking right over him, she only succeeded in stimulating fidgeting in the male which walked past her and away. This would indicate that the male was not yet mature.

(ii) Courtship between a male which had been mated before and a newly emerged female

The male seemed to know that she was not his previous mate, for he did not go straight up to her, but walked quite close to her several times. At times pulsations at the tip of the ovipositor and anus could be seen from the dorsal surface of the brachypterous female. The male attempted to mount, but the female would not release her ovipositor. Next he set his hooked claspers to work and tried to dig the ovipositor out of its groove. Several times he managed to pull it down from its groove but the female would as vigorously pull it away again. The male moved forwards up the side of the female shaking her violently, and ran

his antennae over her head, but with no effect. She shook him off. He made three more brief attempts, even tried gently caressing her with his antennae, and then violent action again, but was unsuccessful. All of this took about ten minutes and is the most vigorous male display observed in this species.

Although no mating was made in which the experience of the individuals was the reverse, the result would probably be similar to that in the second case of (i) and eventually, the first case of (i).

(iii) Courtship between a male and a female which had both mated before

In most cases the male rushed straight up to the female (when they were aware of each other's presence) and mounted straight away. In one case a male was observed attempting to mount a female that was already in copula, but he moved away on discovering the situation. This further demonstrated the absence of courtship by experienced males.

SUMMARY OF FIELD ECOLOGY

1. It is shown that the breeding season at Palmerston North extends from September to March inclusive, that copulation may occur at any time during the season, and that four to four and a half broods may be produced per season.

2. The first and last appearance of each instar are here recorded, and it is shown that fifth stage nymphs as well as adults overwinter. This confirms the statement made in the summary of Chapter 6, that fifth stage nymphs seemed capable of surviving winter.

3. The summer, autumn, and winter habitat of the bug are described.

4. Fifteen host plants are here first recorded for N. huttoni, and the importance of each to the bug is indicated.

5. Quiescence in N. huttoni is described. It is shown that the insect does not remain motionless overwinter, but may move to the surface of the grass tuft during the warmest part of sunny days.

6. It is shown that the last brood, with the exception of some fifth stage nymphs,

complete their development to the adult before winter. Each instar seems to persist until its lower limit of temperature tolerance is almost reached, when it moults to the next stage which is more hardy.

7. Copulation is described. With inexperienced or immature adults there is a short courtship period of from 5 minutes to 3 days. When the males are mature and experienced, they become very vigorous to copulate and the courtship period is brief or non-existant.

SECTION C - DISTRIBUTION

CHAPTER 8

DISTRIBUTION OF NYSIUS IN NEW ZEALAND

From the literature and available collections it was apparent that N. huttoni is widely distributed in this country.

Distribution in the South Island

Hutton (1897) reported the localities, Canterbury and Otago. Myers (1926) mentioned Blenheim and Central Otago, whilst Usinger (1943) added Ashburton. Gurr (1957) added Nelson and North Canterbury to the list of South Island localities.

In addition, from a collection by Mr. L. Gurr, the author notes the following localities marked on the specimens: Ruby Bay, Nelson, Tuamarino, Seddon, Leefield, Waihopai River, the delta of the Wairau River, and Rangiora. Also in this collection is one specimen from Tadmor, collected by J. Timlin. These were all collected in 1950. Further, two specimens marked "Blenheim, lucerne, 1921", which are probably Myers' specimens, are in this collection. By mapping all the localities now recorded, a distribution map of N. huttoni in the South Island (Fig. 59) was drawn up.

Distribution in the North Island

Myers (1926) listed the following North Island localities: Te Paki, Kaitaia, Whangarei, Auckland, Ohakune, Hastings, Levin, Wellington, and on the Tararua Range plentiful up to an altitude of 5000 ft.

The author has collected N. huttoni specimens at Westshore, Havelock North, Takapau, Marton, Hokowhitu, and Massey Agricultural College.

Dr. Cumber (personal communication) of Entomology Division, D.S.I.R., in a survey of the North Island grasslands insects, found N. huttoni in the following additional areas: Greytown, Taueru, Masterton, Dannevirke, Norsewood, Porangahau, Hunterville, Maraekakaho, Rangipo, Taumarunui, Tolaga Bay, Opotiki, Whakatane, Kaimai, Horotiu, Morrinsville, Paeroa, Whananaki.

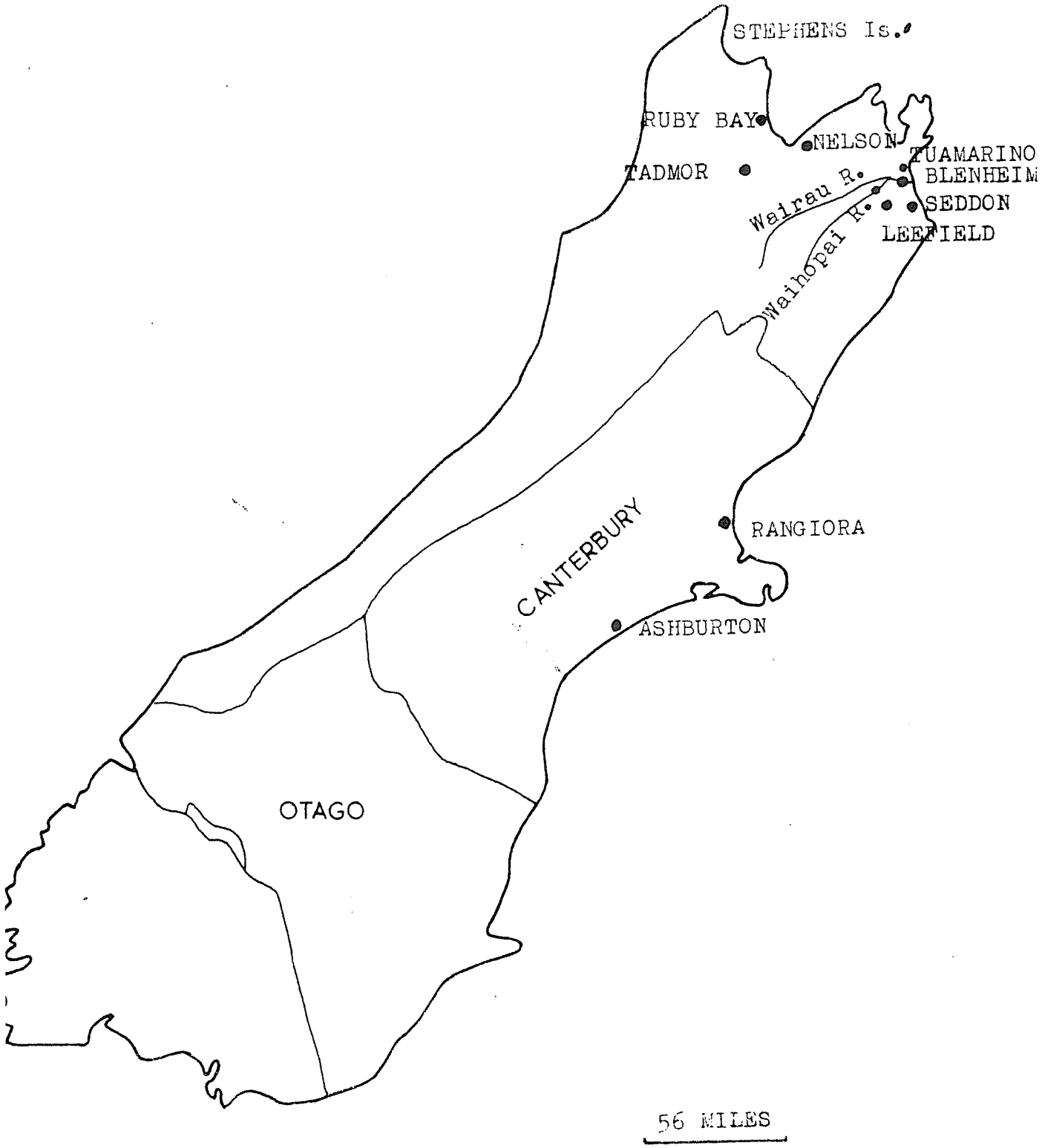
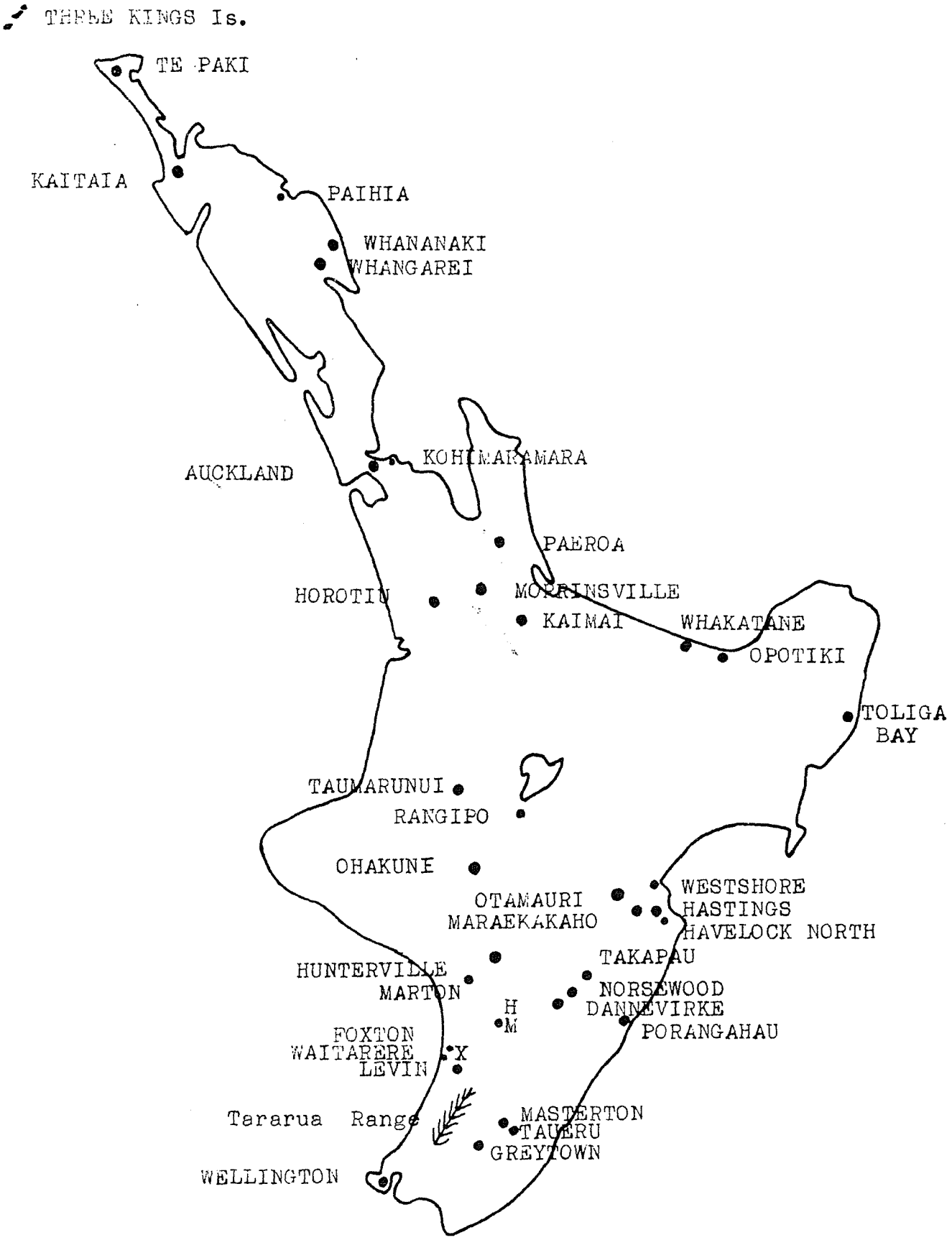


Fig. 39

Distribution of Nysius huttoni in the South Island.



M=Massey Agricultural College
H=Hokowhitu
X=Paiaka

Fig. 40

Distribution of Lysias huttoni in the North Island.

From an earlier collection by Dr. Cumber, the author notes the following localities marked on the specimens: Waitarere, Foxton, Paiaka, Kohi-arumara, and Paihia. In Mr. Curr's collection is one specimen from Otamauri.

A map showing the distribution of N. huttoni in the North Island (see Fig. 40) has been drawn up from the above data.

Distribution in Outlying Islands

Myers further reported this insect from Stephen Island, Woodward (1954) recorded it from the Three Kings Islands, whilst Alfken (1905) and Kirkaldy (1908) have both recorded it from the Chatham Islands.

Distribution of Short Wing Forms

Sub-brachypterous forms have been collected from Kaimai, Taumarunui, Horotiu, Havelock North, Marton, Foxton, Waitarere, Paihia, Hokowhitu, Massey Agricultural College and Seddon.

Brachypterous forms have been collected from Maraekakaho, Havelock North, Marton, Foxton, Hokowhitu and Massey Agricultural College.

Distribution of the Size Populations

The three populations occur at Palmerston North, but the large population seems rare. Accurate distribution of these populations has yet to be determined. However, in collections from the Northern part of the North Island the large population seemed to predominate, and in the collection from the South Island the large population predominated at Nelson and Leefield, whilst the medium population predominated at Seddon.

Distribution of Four Un-named Nysius Species mentioned by Myers

Myers (1926) mentioned four Nysius species, which are apparently still un-named. One species he reported was very common in the Wellington district, and was confined to tauhinu (Cassinia leptophylla). The second species was specially attached to Raoulia tenuicaulis Hook. f., and was collected on the Tararua and Rimutaka

Ranges from sea-level up to 4000 ft. and at Arthur's Pass up to 3800 ft. He noted that adults occurred also on the flowers of Angelica montana (Forst) Cockayne. He further reported that a third species of Nysius appeared to be purely sub-alpine in distribution, and noted Arthur's Pass from 2600 ft. to 3500 ft., Lake Wakatipu and Gouland Downs (2500 ft.), as localities. He noted that it was very abundant on the flowers of Celmisia coriacea (Forst. f.). The fourth species, "One undescribed species, much smaller than the other described New Zealand species, has been found on Juncus at Ashburton (South Island) by Mr. W.W. Smith."

This fourth species may correspond to the small population.

It is clear that N. huttoni has established itself successfully throughout New Zealand. The fact that the remarkable variation in size, shape, and wing length (or form) is not confined to Palmerston North, but is general, indicates that this species is still adapting itself along lines different from those reported elsewhere in the World for this genus.

SUMMARY OF DISTRIBUTION

1. It is shown that N. huttoni occurs throughout New Zealand. The list of localities recorded for the insect is reviewed, and further additions are here made.
2. It is shown that all three forms, macropterous, sub-brachypterous, and brachypterous are widely distributed.
3. An indication of the distribution of the three size populations is given tentatively.
4. The distribution of the four un-named Nysius species mentioned by Myers is here reviewed.

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APPENDIX I

ECONOMIC IMPORTANCE

Cruciferous Crops

An attempt was made to determine the damage caused by N. huttoni to cruciferous seedlings. Five crop plants were tested, namely chou moellier, rape, swede, soft turnip and hard turnip. Plants were grown singly in pots, and a nylon gauze was used to cage in the insects. The insects were admitted at varying stages of plant growth, from appearance of the first two true leaves to appearance of five or six leaves. As a control, some plants were kept free of the insect.

Damage occurred on the five crop plants and even on well established plants (4-5 ins. high). The effect was similar in each case. The bugs showed a preference for the leaves and leaf petioles. The veins of the leaves were tapped, and concentrated feeding in the one area caused distortion of the leaves. In one case where a vein was attacked at about the centre of a leaf, the upper portion of the leaf withered and died, but the lower portion continued to grow. Thus the feeding punctures prevented the flow of sap to the leaf, and probably most of the sap from the upper portion of the leaf was tapped by the bug.

The petiole, when attacked, would often become twisted, and the leaf and petiole would wither and die. On the petioles, the inner surface (facing the stem) seemed to be preferred. On a hard turnip control plant, this surface was white with more or less parallel stripes, but on plants attacked by the bug, repeated insertion of the rostrum upset this pattern into bumps and hollows, producing a lacerated effect. Where feeding punctures occurred on the outer surface of the petiole, the epidermis was pushed in at the puncture mouth. This roughening effect also occurred on attacked stems, but in the control plants the epidermis was smooth.

In rape and soft turnip seedlings, continued feeding by the bugs on the young meristem sometimes resulted in the sprouting of four or five secondary meristems. On chou moellier the damage seemed to be restricted mainly to the leaves.

None of the above effects occurred on the control plants. These results were produced by 10-20 adult insects per plant, but the larger nymphs also seemed capable of causing such damage. Therefore it is shown that should this insect build up in large numbers it could become a serious pest on cruciferous crops. In the Manawatu, the insect did not occur in large numbers on these field crops, and was often not present at all. This is no doubt due to the fact that the vigorous growth of grass and weeds at the edge of the crop is unsuitable bug habitat, and that the paddock was probably previously in pasture.

However, in the South Island, Mr. A. Lowe (personal communication) noted that N. huttoni occurred in large numbers and was damaging swede plants one foot in height, at Ashburton in 1958. Many of the plants were actually broken off at the stems as a result of weakening through feeding punctures.

Wheat

N. huttoni is not a pest of wheat or cereal crops in the Manawatu, because the crops visited had a vigorous growth of grass and weeds at the edge. This being unsuitable bug habitat would be unlikely to harbour bugs until the crop appeared. This insect was not found in or around the cereal crops visited.

Lucerne

In the Manawatu, lucerne was found to be only a minor host for this species. Although Myers (1921) reported considerable damage by the insect to lucerne in Wellington, that year must have been favourable to an unusually large build up of the N. huttoni population.

APPENDIX II(a)

ALL MEASUREMENTS TAKEN ON INDIVIDUAL EGGS

Measurements are in eye-piece scale divisions; one scale division = 0.063mm. 1, 2 and 3 are the three measurements taken on each egg and m is the mean.

M = macropterous. Sb = Sub-brachypterous. B = Brachypterous

Code No. size and form of female	Egg Length				Egg Width			
	1	2	3	m	1	2	3	m
♀	11.4	11.5	11.2	11.3	4.0	4.0	4.0	4.0
	11.5	12.0	11.4	11.6	4.5	4.5	4.5	4.5
small	11.0	11.0	11.0	11.0	4.1	4.3	4.3	4.2
	11.0	11.0	11.0	11.0	4.2	4.0	4.0	4.1
Sb	11.5	11.0	11.0	11.2	4.3	4.2	4.2	4.2
	11.0	11.5	11.5	11.3	4.5	4.5	4.5	4.5
	11.9	11.2	11.5	11.5	4.2	4.2	4.5	4.3
	12.0	11.8	11.9	11.9	4.5	4.0	4.5	4.3
	11.8	11.5	11.2	11.5	4.5	4.5	4.0	4.3
	11.5	11.5	11.5	11.5	4.0	4.2	4.1	4.1
	12.7	12.6	12.6	12.6	4.5	4.5	4.5	4.5
	11.6	11.5	11.5	11.5	4.0	4.1	4.0	4.0
	12.0	12.0	12.0	12.0	4.5	4.5	4.5	4.5
	11.5	12.0	11.5	11.7	4.5	4.5	4.0	4.3
	12.0	11.0	11.0	11.3	4.0	4.0	4.0	4.0
	12.0	12.0	12.0	12.0	4.0	4.0	4.2	4.0
	11.9	11.5	12.0	11.8	4.0	3.6	4.0	3.9
	11.1	11.0	11.0	11.0	4.0	4.0	4.5	4.2
	11.0	11.0	11.0	11.0	4.5	4.6	4.5	4.5
	11.5	11.5	11.5	11.5	4.0	4.0	4.5	4.2
	11.5	11.6	11.5	11.5	4.5	4.5	4.5	4.5
	11.7	11.5	11.5	11.5	4.0	4.1	4.0	4.0
	12.0	11.9	11.8	11.9	4.5	4.2	4.5	4.5
	12.0	12.0	12.0	12.0	4.5	4.0	4.5	4.5
	12.0	12.0	12.0	12.0	4.5	4.5	4.0	4.5
	12.0	12.2	12.0	12.1	4.5	4.5	4.5	4.5
	11.5	11.5	11.5	11.5	4.2	4.1	4.0	4.1
	12.0	11.9	12.0	12.0	4.0	4.0	4.0	4.0
	11.0	11.0	11.0	11.0	4.7	4.7	4.7	4.7
	11.8	12.0	12.0	12.0	4.0	4.2	4.0	4.0
	11.0	11.0	11.0	11.0	4.5	4.1	4.6	4.4
	11.5	11.5	11.0	11.3	4.1	4.1	4.5	4.2
	11.5	11.5	11.5	11.4	4.1	4.1	4.0	4.1
♀	11.0	11.0	11.3	11.1	4.5	4.0	4.4	4.3
	11.0	11.2	11.5	11.2	3.9	4.0	4.5	4.1
small	11.2	11.2	11.7	11.4	4.5	3.5	4.2	4.1
	11.0	11.0	11.0	11.0	4.5	4.5	4.0	4.3
M	11.0	11.0	11.0	11.0	4.8	4.2	4.2	4.4
	12.0	12.2	12.5	12.2	4.2	4.2	4.1	4.2
	12.5	12.8	12.5	12.6	4.0	4.0	4.0	4.0
	11.0	11.5	11.1	11.2	4.1	4.0	4.0	4.0
	11.9	12.0	12.0	12.0	4.0	4.0	4.0	4.0
	11.5	11.1	11.5	11.4	4.5	4.5	4.0	4.3
	12.0	11.5	11.5	11.7	4.0	4.0	4.0	4.0
	11.8	12.0	12.0	12.0	4.0	4.0	4.0	4.0

APPENDIX II(a) (Cont.)

Code No. size and form of female	Egg Length				Egg Width			
	1	2	3	m	1	2	3	m
5	11.9	12.0	12.0	12.0	4.8	4.6	4.5	4.6
	11.0	11.0	11.0	11.0	4.5	4.0	4.0	4.2
small	10.0	10.0	10.0	10.0	4.0	4.0	4.0	4.0
	11.0	11.0	11.0	11.0	4.0	4.0	4.0	4.0
	11.4	11.2	11.0	11.2	4.5	4.5	4.5	4.5
Sb	9.5	9.6	9.5	9.5	4.5	4.7	4.2	4.5
	11.0	11.2	11.5	11.2	4.0	4.0	4.5	4.2
	11.0	11.0	11.0	11.0	4.0	4.0	4.0	4.0
18	13.1	13.0	13.1	13.1	4.5	4.5	4.7	4.6
	13.1	13.1	13.1	13.1	4.5	4.5	4.7	4.6
small	13.1	13.1	13.5	13.2	4.5	4.5	4.5	4.5
	13.1	13.0	13.0	13.0	5.0	4.5	4.5	4.7
	13.1	13.5	13.4	13.5	4.5	4.5	4.6	4.5
M	13.2	13.0	13.1	13.1	4.7	4.4	4.5	4.5
	13.1	13.0	13.1	13.1	4.8	5.0	4.7	4.8
	13.1	13.0	13.0	13.0	4.9	4.9	4.9	4.9
	12.5	12.5	12.5	12.5	4.5	4.5	4.5	4.5
	13.0	13.0	13.0	13.0	4.5	4.5	4.3	4.4
	13.5	13.2	13.2	13.3	4.8	4.8	4.6	4.7
	13.0	13.0	13.0	13.0	4.5	4.5	4.7	4.6
D'	11.0	11.2	11.2	11.1	4.5	4.2	4.5	4.4
small	11.5	11.5	11.8	11.6	4.2	4.5	4.5	4.4
Sb	12.0	12.0	12.0	12.0	4.0	4.1	4.5	4.2
5'	11.0	11.0	11.1	11.0	4.5	4.4	4.1	4.3
small	11.0	10.9	11.0	11.0	4.9	5.0	4.5	4.8
Sb	11.0	11.0	10.9	11.0	4.2	4.5	4.2	4.3
23	13.0	13.0	13.1	13.0	5.0	5.0	4.5	4.8
	13.1	13.0	13.2	13.1	4.2	4.7	4.1	4.3
Medium	13.0	13.0	13.0	13.0	5.0	4.3	4.2	4.5
	13.1	13.2	13.1	13.1	5.0	5.3	4.1	4.8
M	13.0	13.0	13.0	13.0	4.9	4.9	4.9	4.9
	13.5	13.6	13.5	13.5	4.5	5.0	4.5	4.7
	14.0	14.0	14.0	14.0	4.5	4.5	4.5	4.5
	14.1	14.0	14.0	14.0	4.3	4.5	4.5	4.5
	13.0	13.0	13.0	13.0	4.8	4.5	5.0	4.8
	13.0	13.0	13.0	13.0	5.0	5.0	5.0	5.0
	12.7	12.9	12.5	12.7	5.0	5.1	4.0	4.7
	13.1	13.5	13.6	13.4	4.9	4.8	4.5	4.7
	12.9	12.9	12.8	12.9	5.0	4.6	4.9	4.8
	13.0	12.0	13.0	12.6	4.5	4.7	4.8	4.7
	13.0	13.0	14.0	13.3	4.5	4.5	4.8	4.6
	13.9	13.8	13.5	13.7	4.0	5.0	4.5	4.5
	13.0	14.0	13.5	13.5	4.8	5.0	4.5	4.8
23'	11.5	12.0	12.0	11.8	4.7	4.8	4.7	4.7
small	12.5	12.5	12.5	12.5	4.1	4.2	4.2	4.2
Sb	12.5	12.7	12.8	12.7	4.2	4.1	4.2	4.2
A2	12.7	12.6	12.9	12.7	4.2	4.9	4.5	4.5
small	12.0	12.1	12.5	12.2	4.5	4.4	4.5	4.5
Sb	12.8	12.8	13.0	12.9	5.0	5.0	4.5	4.8

APPENDIX IV (a)

BODY MEASUREMENTS OF ADULTS (FOR SIZE DISTRIBUTION) *

Head Width	Length Head plus Pronotum	Body Length To Wing tip	Body Length To end abdomen	Width of Hemelytra	Wing Length	Wing Form +	Location
Females							
3.7	5.0	15.0	15.0	6.5	10.0	M	Hokowhitu
3.7	5.6	17.2	14.3	6.9	11.6	M	"
3.6	5.2	15.4	13.1	6.4	10.2	M	"
3.5	4.5	14.5	12.9	6.0	10.0	M	"
3.8	5.3	17.3	14.3	7.0	12.0	M	"
3.4	4.5	13.5	11.8	5.7	9.0	M	"
3.5	5.0	15.0	15.0	6.0	10.0	M	"
3.7	4.9	13.9	13.4	5.7	9.0	M	"
3.2	3.7	11.7	11.7	5.3	8.0	Sb	"
3.2	4.0	11.8	10.8	5.5	7.8	Sb	"
3.3	4.7	12.0	12.0	5.4	7.5	Sb	"
3.5	3.8	11.8	11.8	5.3	8.0	Sb	"
3.4	4.5	12.2	11.2	5.4	7.7	Sb	"
3.2	4.1	12.0	11.0	5.3	7.9	Sb	"
3.3	3.9	11.9	11.3	5.7	8.0	Sb	"
3.5	5.2	13.4	12.7	5.8	8.2	Sb	"
3.5	4.6	12.0	12.0	5.0	7.6	Sb	"
3.2	3.3	10.3	9.7	5.0	7.0	Sb	"
3.4	4.0	11.0	10.7	5.6	7.0	Sb	"
3.4	5.0	12.0	12.0	5.3	7.0	Sb	"
3.6	4.3	15.2	12.5	6.0	10.0	M	"
3.4	4.0	13.5	12.3	5.6	9.3	M	"
3.9	5.0	15.8	14.3	6.8	10.8	M	"
3.3	4.3	12.3	12.3	5.4	7.7	B	"
4.0	4.6	14.8	14.3	6.4	10.2	Sb	"
3.8	5.0	14.0	14.0	7.0	9.0	Sb	"
3.7	5.0	12.4	13.3	5.9	7.4	B	"
3.7	5.0	14.2	13.4	6.4	9.2	M	"
3.8	4.9	15.1	13.9	6.4	10.2	M	"
3.4	4.3	13.3	12.0	5.5	9.0	M	"
3.5	4.3	12.5	12.5	5.9	8.0	Sb	"
3.4	4.6	13.4	12.1	5.6	8.8	M	"
3.6	4.0	13.0	14.0	6.2	9.0	B	Massey Agric. College
3.6	5.0	14.3	12.3	5.8	9.0	M	"
3.3	4.0	11.6	10.9	5.1	7.6	Sb	"
3.4	4.0	11.7	11.7	5.3	7.7	Sb	"
3.9	5.0	15.0	13.8	6.3	10.0	M	"
3.2	4.2	11.4	11.4	4.6	7.2	Sb	Taumarunui
3.3	4.3	12.3	11.5	5.8	8.0	Sb	"
3.4	4.0	12.9	11.5	6.0	8.9	Sb	"
3.3	5.0	14.3	13.2	5.4	9.3	M	"
3.3	4.3	12.6	11.8	6.0	8.1	Sb	"
3.6	4.0	12.7	12.7	5.8	8.7	Sb	"
3.3	4.7	11.7	11.7	5.7	7.0	Sb	Kaimai
3.9	5.0	14.0	14.7	6.2	9.0	B	Foxton
3.8	4.6	13.6	13.6	6.1	9.0	Sb	"

*All measurements are in micrometer units; one unit = 0.24mm

+ M = Macropterous. Sb = Sub-brachypterous. B = Brachypterous.

APPENDIX IV (a) (Cont.)

Head Width	Length Head plus Pronotum	Body Length To Wing tip	Body Length To end abdomen	Width of Hemelytra	Wing length	Wing Form	Location
3.8	4.8	13.3	13.3	6.0	8.5	Sb	Waitarere
3.2	4.2	11.6	11.6	4.8	7.4	Sb	"
3.8	5.0	13.4	14.0	5.7	8.4	B	Waraekakaho
4.0	5.4	17.2	15.5	7.0	11.8	M	Massey Agric. College
3.9	4.5	16.3	13.5	6.9	11.8	M	Hokowhitu
3.9	5.0	16.9	13.9	7.0	11.9	M	"
4.0	5.5	17.0	15.0	7.0	11.5	M	Massey Agric. College
4.0	5.2	16.2	15.2	6.8	11.0	M	"
3.9	5.0	16.8	14.8	6.9	11.8	M	South Island
4.0	5.0	17.0	15.4	7.3	12.0	M	Tuamarino
4.0	4.7	16.7	14.7	7.0	12.0	M	"
4.0	5.0	16.5	15.2	7.2	11.5	M	"
4.1	5.5	16.5	15.0	7.0	11.0	M	Leefield
4.0	5.3	16.8	14.8	7.0	11.5	M	"
4.0	5.0	16.7	15.2	7.3	11.7	M	Tuamarino
3.8	5.0	16.0	14.2	6.6	11.0	M	Blenheim
4.2	5.2	17.9	16.0	7.3	12.7	M	Nelson
4.0	5.0	16.0	14.8	6.7	11.0	M	"
3.6	5.0	16.0	14.2	6.0	11.0	M	Seddon
3.9	4.7	15.7	14.0	6.6	11.0	M	"
3.6	4.0	14.4	12.7	6.0	10.4	M	"
3.8	5.0	15.9	14.9	6.6	10.9	M	"
3.9	5.0	15.9	13.9	6.6	10.9	M	"
3.8	4.9	15.4	14.1	6.2	10.5	M	Westshore
3.6	5.4	15.9	13.5	6.0	10.5	M	"
3.8	5.2	15.2	13.9	6.2	10.0	M	"
3.7	4.7	15.2	13.5	6.1	10.5	M	"
3.8	5.0	15.7	14.3	6.5	10.7	M	"
3.8	5.2	16.1	14.4	6.3	10.9	M	Massey Agric. College
3.8	5.1	14.3	13.6	5.9	9.2	M	"
3.7	4.8	15.8	13.6	6.4	10.8	M	"
3.7	4.4	14.7	13.7	6.2	10.3	M	"
4.0	5.0	16.6	14.9	6.6	11.6	M	"
3.6	4.7	15.3	13.6	6.0	10.6	M	Havelock North
3.8	5.0	14.5	13.1	6.0	9.5	M	"
3.7	4.6	16.6	14.6	6.6	12.0	M	"
3.6	4.0	14.5	12.7	5.8	10.5	M	"
3.8	4.8	13.3	13.3	6.0	10.5	M	"
3.5	4.8	13.1	12.4	5.7	8.6	Sb	Hokowhitu
Males							
3.2	5.1	13.1	12.3	4.7	7.0	B	"
3.5	4.8	13.0	13.8	5.0	8.2	B	"
3.0	4.5	12.0	12.2	4.5	7.5	B	"
3.4	4.7	12.7	-	5.1	10.0	B	"
3.2	4.3	11.2	11.2	4.9	6.9	Sb	"
3.1	3.6	10.6	10.6	4.5	7.0	Sb	"
3.2	3.5	11.0	11.0	4.7	7.5	Sb	"
3.5	4.3	14.1	12.6	5.3	9.8	M	"
3.3	4.8	11.8	12.8	5.8	7.0	B	"
3.0	4.0	12.7	10.8	5.0	8.7	M	"
3.4	4.8	14.0	12.4	5.7	9.2	M	"
3.5	5.0	14.8	12.8	5.9	9.8	M	"
3.0	3.9	10.3	10.3	4.5	6.4	Sb	"
3.0	4.0	11.0	11.0	4.5	7.0	Sb	"
3.0	4.0	10.3	9.9	4.3	6.3	Sb	"

APPENDIX IV (a) (Cont.)

Head Width	Length Head plus Pronotum	Body Length To Wing tip	Body Length To end abdomen	Width of Hemelytra	Wing Length	Wing Form	Location
2.8	4.0	9.9	9.5	3.7	8.0	Sb	Hokowhitu
3.3	3.8	11.2	10.6	4.7	7.4	Sb	"
3.1	4.0	10.3	10.3	4.5	8.3	Sb	"
3.3	4.0	11.6	11.6	3.9	7.6	Sb	"
3.0	4.0	11.0	11.0	4.6	7.0	Sb	"
3.3	4.0	12.5	12.5	5.0	8.5	Sb	"
3.5	4.7	12.0	12.0	4.2	7.3	Sb	"
3.6	5.0	14.2	12.4	5.3	10.0	M	"
3.3	4.0	11.0	10.5	4.0	7.5	Sb	Horotiu
3.5	4.0	13.2	12.0	4.9	9.2	M	Massey Agric. College
3.0	4.2	11.2	11.5	4.2	7.0	B	"
3.6	5.0	15.0	15.0	6.0	10.0	M	"
3.4	3.9	11.1	10.6	4.7	7.5	M	"
3.3	4.7	14.7	12.3	5.0	10.0	M	"
3.5	4.4	14.4	11.8	5.6	10.0	M	"
3.5	4.3	14.3	12.2	5.0	10.0	M	Hokowhitu
3.4	4.2	13.0	11.0	5.0	8.8	M	"
3.4	5.3	14.5	12.0	5.5	9.0	M	Marton
3.4	4.4	14.0	11.8	5.0	9.6	M	Havelock North
3.5	5.0	15.0	15.0	5.0	10.0	M	"
3.4	4.8	13.8	11.8	5.2	9.0	M	"
3.5	4.5	14.0	12.0	5.0	9.7	M	"
3.5	4.1	13.9	11.9	5.5	9.5	M	"
3.5	4.6	14.6	11.8	5.7	10.0	M	"
3.5	4.1	13.1	11.4	5.0	9.0	M	Westshore
3.5	4.2	13.2	11.2	5.0	9.0	M	"
3.6	4.1	14.3	11.7	5.7	10.2	M	"
3.6	5.0	14.8	12.4	5.3	9.8	M	"
3.4	4.6	14.2	12.3	5.4	9.6	M	"
3.5	4.5	14.2	12.6	5.6	9.7	M	Massey Agric. College
3.2	4.5	14.5	12.0	5.2	10.0	M	"
3.7	4.5	14.5	12.5	6.0	10.0	M	"
3.3	4.8	13.6	12.2	5.4	8.8	M	"
3.3	4.7	14.2	12.6	5.3	9.5	M	"
3.4	4.4	13.7	11.8	5.0	9.5	M	Seddon
3.3	4.6	13.8	12.1	5.3	9.4	M	"
3.7	4.4	14.1	12.7	5.5	9.7	M	"
3.6	5.0	15.0	13.0	5.5	10.0	M	"
3.6	4.7	14.4	12.9	5.5	9.7	M	"
3.7	4.3	14.6	13.2	5.6	10.3	M	Leefield
3.7	4.3	13.1	13.1	5.6	10.8	M	"
3.7	4.5	14.3	12.7	5.6	9.8	M	"
3.4	4.3	13.3	11.3	5.4	9.0	M	Nelson
3.7	4.0	14.0	12.3	5.7	10.0	M	"
3.8	4.3	14.9	13.5	5.7	10.5	M	"
3.5	4.7	13.7	12.1	5.2	9.9	M	Massey Agric. College
3.7	5.0	15.0	13.3	5.0	10.0	M	"
3.7	5.0	15.4	13.2	5.9	10.4	M	Leefield
3.4	4.4	14.3	12.5	5.5	9.3	M	"
3.7	4.4	15.2	13.2	5.9	10.3	M	"
3.7	4.2	14.5	12.3	5.7	10.1	M	"
3.7	4.9	15.4	13.0	5.9	10.5	M	"
3.4	4.1	13.8	12.3	5.2	9.7	M	"
3.6	4.0	14.2	12.5	5.6	10.2	M	"

APPENDIX IV(b)

FREQUENCY DISTRIBUTIONS FOR SEX CHARACTERISTICS

All measurements are in micrometer units; one unit = 0.24mm. Measurements from the ten adults used in the species redescription are included here.

Frequency distribution for Head Width

Class	Females	Males
3.8		1
3.0		7
3.1		2
3.2	6	3
3.3	3	8
3.4	9	12
3.5	12	16
3.6	11	10
3.7	9	12
3.8	15	2
3.9	9	
4.0	14	
4.1	1	
4.2	2	

Frequency distribution for Wing Length

Class Interval	Class	Frequencies Females	Frequencies Males
6.0	5.8-6.2		1
6.5	6.3-6.7		3
7.0	6.8-7.2	5	8
7.5	7.3-7.7	8	6
8.0	7.8-8.2	9	1
8.5	8.3-8.7	4	2
9.0	8.8-9.2	12	10
9.5	9.3-9.7	3	10
10.0	9.8-10.2	10	23
10.5	10.3-10.7	9	6
11.0	10.8-11.2	11	4
11.5	11.3-11.7	8	
12.0	11.8-12.2	9	
12.5	12.3-12.7	1	
13.0	12.8-13.2	1	

FREQUENCY DISTRIBUTIONS FOR BODY LENGTH

Class interval	Class	Including Wings Females	Including Wings Males	To posterior of abdomen Females	To posterior of abdomen Males
9.5	9.0-10.0	0	1	1	2
10.6	10.1-11.1	2	9	4	11
11.7	11.2-12.2	14	6	17	24
12.8	12.3-13.3	11	7	14	29
13.9	13.4-14.4	12	26	29	6
15.0	14.5-15.5	17	19	19	2
16.1	15.6-16.6	20	4	3	0
17.2	16.7-17.7	16	0		
18.3	17.8-18.8	2	0		

APPENDIX IV (b) (Cont.)

FREQUENCY DISTRIBUTION FOR LENGTH OF HEAD PLUS THORAX

Class Interval	Class	Frequencies	
		Females	Males
3.4	3.3–3.5	1	1
3.7	3.6–3.8	2	2
4.0	3.9–4.1	12	19
4.3	4.2–4.4	7	16
4.6	4.5–4.7	17	17
4.9	4.8–5.0	32	22
5.2	5.1–5.3	12	8
5.5	5.4–5.6	7	3

FREQUENCY DISTRIBUTION FOR WIDTH ACROSS HEMELYTRA

Class Interval	Class	Frequencies	
		Females	Males
3.6	3.5–3.7		1
3.9	3.8–4.0		1
4.2	4.1–4.3		3
4.5	4.4–4.6	1	7
4.8	4.7–4.9	1	6
5.1	5.0–5.2	3	18
5.4	5.3–5.5	11	14
5.7	5.6–5.8	14	18
6.0	5.9–6.1	17	6
6.3	6.2–6.4	15	
6.6	6.5–6.7	9	
6.9	6.8–7.0	16	
7.2	7.1–7.3	5	

APPENDIX VI

DAILY EGG LAYING PERFORMANCE OF PARENT GENERATION BEFORE WINTER

air code number	Date of emergence as adults	Number of eggs laid 18 III 57	19	20	21	22	25	24	25	26	27	28	29	30	31	1 IV 57	2	3	4	5	6	7	8	9	10	14	15	16	17	18	21	22	23
8	2.III.57				2	-	4	-	1																							
18	12.III.57								5	2	9	4	6	1	9	-	3	1	2	-	5	3	1	4	3	-	-	3	-	4	2
24	7.III.57	1	2	-	8	3	2	-	6	5	6	2	5	7	3	4	3	3	4	-	4	-	4									
Mean		1	2		5	3	3		4	3.3	7.5	3	5.5	4	3	4	3	2	3		4.5	3	2.5	4	3			3		4	2
A	(caught			3	-	4	3	-	4	-	7	11	7	4	-	3	3	-	-	-	3	-	3	3	-	3	-	1	-	2	-	-	2
B	from field			6	-	2	-	4	1	1	7	3	-	3	-	3	3	3	-	-	-	2	-	3	-	-							
C	early			3	-	4	-	3	-	1	1	3	1	2	3	1	-	1														
E	March)														8	1	7	3	-	3	-	9	-	3	-	-							
Mean				4.6		3.3	3	3.5	2.5	1	3	6.3	4	3	3	2.2	4.6	1.6		2	3	5.5	3	3		2		1		2		2

APPENDIX VII

DAILY EGG LAYING PERFORMANCE OF PARENT GENERATION AFTER WINTER

air code number	Date of emergence as adults	Number of eggs laid 9 VIII 57	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	1 IX 57	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
5	19.III.57				2	-	-	-	-	-	-	-	4	-	-	3	-	3	-	-	-	3	2	2	-	4	-	-	-	-	2	-	3	6	1	3	3	3	2	-	7
9	0.III.57		2	-	-	-	1	-	-	-	-	-	3	2	-	-	-	-	3	-	-	-	1	4	-	-	-	-	-	-	2	-	2	-	3	2	-	2	1	2	3
13	14.III.57												2	2	-	2	-	2	-	1	-	1	2	2	-	6	1	2	1	-	2	2	3	1	2	3	1	-	1	2	escaped
17	13.III.57											3	2	-	-	2	-	3	-	2	-	died																			
Mean			2		2		1					3	3.3	2		3		3.3	3	1.5		3		1.6	2.7	3	1	2	1		2	2	3.3	3.0	2	3	2	2.3	1.5	2	3
23	7.III.57											2 (between 16. VIII and 28. VIII 10-20 eggs)				-	-	4	3	-	-	3	-	-	3	-	4	2	4	3	-	3	-	4	4	1	4				
D	(From field early	10	1	1	2	1	-	-	-	-	-	-	6	2	-	-	-	3	-	1	-	-	2	1	-	2	2	-	1	1	3	1	-	-	3	4	1	3	1	2	3
Z	March)		1	-	-	-	-	-	-	-	-	-	3	2	-	-	-	1	2	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	3	-	3	3		
Mean		10	1	1	2	1							4.5	3				2	2	1			2	1		2	2		1	1	3	1		2	2	4	1	3	1	2.5	3

	18 IX	19	20	21	22	23	24	25	26	27	28	29	30	1 X	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27
5	2	1	-	-	3	3	2	3	2	-	-	-	1	-	3	-	-	2	-	died																					
9	-	2	-	2	-	-	3	2	-	3	-	-	-	-	-	-	-	-	-	1	-	0	-	4	-	-	-	-	2	-	8	3	-	-	-	-	-	1	6	-	-
Mean	2	1.5		2	3	3	2.5	2.5	2	3			1		3			2		1																					
23	1	1	3	3	-	4	2	1	1	2	-	-	3	4	-	-	4	1																						
D	2	2	3	1	-	-	3	4	-	2	-	3	-	2	-	2	-	-	1 died																					
Z	3	1	3	2	-	6	3	-	2	-	-	3	-	2	-	3	died																							
Mean	3.3	1.5	3	1.5		3	4	4	2	2		3		2		2.3		1																						

	26 X	29	30	31	1 XI	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	1 XII	2	10	11	31
9	3	-	-	-	-	-	-	-	-	-	-	3	2	-	-	-	-	-	-	-	-	3	3	2	-	-	1	-	-	2	-	-	-	-	2	3	-	3	3	2	3

APPENDIX VIII (a) TABLE 16 LAYING PERFORMANCE OF FIRST GENERATION

Pair code number	Date of emergence as adults	Number of eggs laid daily: 25 X 57	26	27	28	29	30	30	1 XI	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	1 XII 57	2	3
D'	♀ 16.X.57 ♂ 16	2	3	4	1	3	4	-	3	2	3	2	6	5	5	6	8	-	-	1	4	3	-	3	4	3	3	2	-	2	1	2	-	5	2	1	-	4	-	-	6
5'	♀ 20 ♂ 21		2	2	1	6	2	3	-	-	3	2	6	2	5	8	9	5	2	-	5	3	1	-	7	3	3	4	4	3	1	1	-	-	6	-	3	1	-	-	2
3'	♀ 22 ♂ 20				4	5	4	2	4	-	11	5	4	6	7	-	8	2	-	-	1	1	1	2	3	2	0	4	2	1	-	-	-	3	3	-	-	-	1	3	1
23'	♀ 5.XI ♂ 29.X																	5	1	-	3	3	-	-	6	2	-	5	1	4	1	3	3	4	4	2	2	-	1	3	4
C	♀ 8.XI ♂ 10																						3	3	2	4	3	3	-	4	-	4	3	3	6	3	3	3	-	3	3
H	♀ 10 ♂ 7																								1	2	0	6	3	3	3	5	6	2	4	4	4	4	4	3	7
U	♀ 10 ♂ 29.X																									11	9	8	3	4	2	3	3	3	5	5	4	-	4	1	C	3
Mean		2	2.5	3	2	3	3.3	2.6	3.5	2	3.7	2.3	3.3	4.3	5	7	8.3	4	1.5	1	3.3	3.6	2	1.3	3.6	4.7	5.7	5	3	4	1.0	3	4	4.0	4.3	2.0	3.3	3.3	1.8	4.4	4.3
Control 1 cop	5.XI.57 ♀																	1	-	-	-	-	-	-	1	1	-	1	3	2	3	4	3	3	4	1	3	2	-	2	3
																										1	-	2	4	-	-	3	2	-	3	4	2	-	-	3	4

		4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	1.I.58	2	3	4	5	6	7	8	9	10	11
D'		3	1	-	died																																			
5'		4	1	1	3	-	-	3	3	6	4	3	-	4	3	3	2	3	-	-	7	-	3	3	7	2	4	-	3	-	4	4	-	-	-	11	0	3	5	2
3'		2	1	1	1	-	-	-	3	-	-	2	-	-	2	-	3	-	-	died																					
23'		6	3	4	2	-	3	3	2	3	1	2	-	-	-	-	-	2	-	-	-	-	3	2	3	-	2	1	-	1	-	-	-	2	-	1	1	-	-	-
C		6	7	2	-	3	7	2	4	3	-	4	3	3	2	4	5	2	-	2	7	1	1	10	-	10	4	-	3	1	6	6	-	4	5	7	3	0	6	-
H		4	4	5	6	2	3	7	3	3	5	3	-	3	-	3	-	2	-	6	6	-	5	3	3	3	9	3	1	2	5	3	4	6	3	3	4	6	5	5
U		3	6	2	4	-	9	escaped																																	
Mean		4.7	3.5	3.3	3.2	2.5	3	3.3	3.3	3.3	3.3	2.3	3.3	3.3	3.3	3.3	3.5	2.3	3.5	3.0	4	3	6.6	4.0	4	3	4.0	3	4.3	2.0	2	4.3	4	5.0	5.6	3.6	6.7	5	3.5
Control		3	2	-	-	1	2	3	2	-	2	-	-	1	0	2	-	-	-	-	-	-	2	3	-	0	-	1	1	1	1	-	3	-	-	1	1	4	1	3	-
1 cop		-	6	-	1	-	2	2	1	3	-	3	3	3	3	3	3	-	3	-	7	-	-	-	3	-	2	4	3	1	11	2	-	-	2	3	3	4	3	3	3
1 copa	25.XI.57			3	-	-	16	-	-	-	4	-	1	-	1	-	-	-	-	-	-	2	3	3	4	-	2	3	1	4	-	-	-	-	-	4	-	3	3	3	-
2'																2	*	-	-	-	-	-	-	-	7	1	*	3	6	-	4	-	7	3	7	3*	11	3	1	3	-
2"	15.XII.57																												3*	1	1	6	2	-	-	-	-	3	4	4	4

		12.I 58	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	1.II.58	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
D'		2	7	1	4	6	4	7	5	3	4	6	6	6	3	4	8	4	5	2	-	3	3	3	2	1	-	7	4	2	-	-	1	-	-	4	6	-	5	5	3
23'		-	-	-	1	1	-	1	1	-	-	1	2	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-													
U		-	4	8	7	5	-	9	6	-	1	7	8	7	-	7	7	5	3	-	-	-	-	-	3	-	-	-													
H		-	3	11	8	4	4	7	7	5	3	15	3																													
Mean		2	4.0	6.3	5	4	4	6.0	4.7	4.0	3.3	6.7	4.7	6.3	3	5	7.5	4.5	4	2	0	3	3	3	2	1	0	7	4	2	0	0	1	0	0	4	6	0	6	5	3
Control		-	-	5	6	-	-	7	1	3	1	4	3	3	5	6	3	5	-	2	-	3	3	1	-	1	-	2	-	3	1	-	3	3	1	-	-	-	-	-	-
1 cop			3	3	6	7	-	-	7	2	5	7	3	-	2	0	3	-	3	1	4	0	0	1	4	1	2	6	2	disc?	2	9	2	9	1	4	6	3	3	2	4
1 copa		-	12	-	5	7	-	8	5	-	6	7	9	-	6	-	-	3	-	-	-	-	died																			
2'		-	-	2*	-	-	-	7	-	2	5*	3	8	1	-	-	-	7*	9	0	5	3	7	3	*	1	4	4	2	1	-	4	3	10*	9	17	12	9	0	8	7
2"		-	10	2*	7	escaped																																			

* Denotes when females 2' and 2" received a copulation.

Continued

APPENDIX V

PRELIMINARY - DAILY EGG LAYING PERFORMANCE

Pair number	Number of eggs laid 21 XII 56	22	23	24	27	28	29	30	31	4 I 57	7	8	9	10	11	12	13
1	-	-	-	-	-	died	-	-	-	2	5	-	5	4	2	7	7
2	-	1	-	-	8	-	-	-	-	8	-	6	5	3	1	-	-
3	3	6	5	-	-	-	4	4	-	18	3	5	5	3	2	2	3
4	-	-	1	8	10	7	-	-	15	14	6	3	6	4	3	3	6
5	-	3	13	5	10	5	-	escaped									
6	-	10	-	7	died												
7	-	8	-	5	2	-	-	-	-	-	-	-	-	-	-	-	-
Mean	3	5.6	6.3	6.3	7.5	6	4	4	15		5	4.6	5.3	3.5	2	4	5.3

Pair number	Number of eggs laid 14 I 57	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	
1	6	1	-	-	2	2	4	-	1	3	-	4	3	5	3	escaped	
2		1	-	-	-	-	-	1	1	-	-	-	-	3	4	2	died
3		-	died														
4	6	2	died														
5																	
6																	
7	3	-	2	-	-	-	3	4	2	-	-	4	4	6	6	5	
Mean	5	1.3	2	-	2	2	3.5	2.5	1.3	3	-	4	3.5	4.5	4.3	5	

APPENDIX VIII (Cont.)

Pair code number	Number of eggs laid dialy																		
	21 II 58	22	23	24	25	26	27	28	1 III 58	2	3	4	5	6	7	8	9	10	11	12
5'	7	4	1	-	-	4	4	-	3	2	-	1	2	1	1	-	1	-	-	1 died 23.IV.58
U		-	-	-		4	-	-	-	died										
Control	3	2	-	-	-	-	-	-	-	-	-	-	-	-	died					
1 cop	4	-	-	-	1	1	-	1	1	-	-	2	-	3						
♀'	9	7	-	12	2	*	13	7	5	4	5	10	5	6						

ANNEXE IX

DAILY EGG-LAYING PERFORMANCE OF SECOND GENERATION

Female Code. No.	Date of emergence as adults	Number of eggs laid 1 II 58	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
5'''	2.I.58	1	7	3	3	6	6	9	-	8	8	13	5	3	16	6	6	12
5''	23.I.58	3	1	3	5	7	3	5	1	3	-	6	7	2	14	7	2	7
5'					1	5	1	10	-	2	escaped							
0'	29.I.58				3	3	4	-	4	5	3	8	5	-	3	1	5	5
0''	31.I.58				5	7	3	2	-	-	-	2	7	-	-	-	2	-
Mean		2	4	3	3.4	6.4	3.2	6.5	2.5	4	5.5	7.3	6	2.5	11	4.7	3.7	8

Female Code No.	3rd Dec. 57				4th Dec.				5th Dec.				6th Dec.				7th Dec.				8th Dec.				9th Dec.			
	1	2+3	4+5	6	1	2+3	4+5	6	1	2+3	4+5	6	1	2+3	4+5	6	1	2+3	4+5	6	1	2+3	4+5	6	1	2+3	4+5	6
D'		5	1			2	1				1																	
5'		1	1		1	1	2		1	2				1				3										
3'		1					2				1			1				1										
23'			4		1		5				3				4			3									7	1
U		1	4				0		1		6				2						5						6	1
H		1	0			1	3		2		2			3	2		5	3				2					8	
0		3	3			5	3				6				2		2	2							5	4		
Control			3				3				2												1		2			
1cop		3	1							1	5						1											2
1 copa															3													16
Total		15	22	0	2	9	35	0	4	3	36	0	0	5	18	0	6	0	11	0	3	0	3	0	0	7	25	20

	10th Dec.				11th Dec.				12th Dec.				13th Dec.				14th Dec.				15th Dec.				16th Dec.			
	1	2+3	4+5	6	1	2+3	4+5	6	1	2+5	4+5	6	1	2+3	4+5	6	1	2+3	4+5	6	1	2	3	4+5	6	1	2	3	4+5	6
5'		1	2				3				6			1	5				3		2	1	1			2		1		
3'								2										2								1	1			
23'		1	2				2			2	1				1				2										
U		1	1	1			4				5							4					0					2	
H	2	4	3				3				8				5			4	1		2								
Control		1	3				2							2									1			1	2	3	
1 cop			2							5					1				3		2		2			1	3	1	
1 copa														4								1				1			
Total	2	8	12	1	0	0	14	2	0	7	18	0	0	7	10	0	0	10	11	0	6	1	2	1	0	4	3	5	7	0

	17th Dec.				18th Dec.				19th Dec.				20th Dec.				21st Dec.				22nd Jan.							
	1	2	3	4+5	6	1	2	3	4+5	6	1	2	3	4+5	6	1	2	3	4	5	6	1	2	3	4	5	6		
5'		2		1		1			1					1	2														
3'		1	1					1		2																			
23'														1	1														
U				2		2				5					2				1	Not									
H						2								2															
Control						1				2									2	check									
1 cop										2				2	1														
1 copa																			2										
Z'		2																											
Z"																													
Total	8	0	0	7	0	0	1	0	9	0	0	0	0	6	6	0	0	0	22	0	0	5							

	9th Jan. 58					10th Jan.						14th Jan. (70°F)					15th Jan. (70°F)					16th Jan. (74°F)					17th Jan. (68°F)					20th Jan. (64°F)				
	1	2	3	4+5	6	1	2	3	4	5	6	1	2	3	4	5	6	1	2	3	4	5	6	1	2	3	4	5	6	1	2	3	4	5	6
5'	2			6		1	1		1	2					1				1	5					5	1			4			1	1	1	
23'																1					1				1										
U	2		1	3					3		3		1			2	5	3		4				5										
H				6					4	1					5	4	2			6	2			1		3			4			3			
Control				1					1		2		1	1	3					6													3		
1 cop			1	2					2	1					3					4	2				5	2							2		
1 copa				8			3													5				2		5								
Z'				1		1			2								2																	2	
Z"			3	1					4						1	2				5	2													
Total	4	0	5	28	0	2	1	3	15	6	5	0	1	1	7	15	11	3	0	0	20	30	1	2	1	6	10	15	1	0	0	0	0	8	0	0	0	0	6	6	3

	21st Jan. (88°F)						22nd Jan. (95°F)						23rd Jan. (95°F)						24th Jan. (93°F)						25th Jan. (84°F)						26th Jan. (80°F)						27th Jan. (90°F)					
	1	2	3	4	5	6	1	2	3	4	5	6	1	2	3	4	5	6	1	2	3	4	5	6	1	2	3	4	5	6	1	2	3	4	5	6	1	2	3	4	5	6
5'					3	1			3	3	2					4				5			1		1	1		1			3		1					1	5		2		
23'										1	1					1																												
U		1							7					5	3		2			4	1	2					2		1	2	1		3				1	3	1	2			
H					3				7	4	2				3																											
Control				1					3		1				2		1	1		2						3		2					4	1	1			3				
1 cop				3	2				3	4	1				5										2						1		3	4				3				
1 copa				6					7					5	4												6															
Z'						5			2					3	5					1																						
Total	0	1	0	10	8	6	0	0	16	28	5	4	0	0	11	20	5	3	1	0	5	7	1	3	5	1	0	4	6	4	4	2	2	5	7	5	0	0	2	14	1	4

	28th Jan. (92°F)						29th Jan. (87°F)						30th Jan. (83°F)						31st Jan. - shaded am.						1st Feb. (80°F) shaded am.						2nd Feb. (90°F) shaded am.						3rd Feb. (95°F) shaded am.					
	1	2	3	4	5	6	1	2	3	4	5	6	1	2	3	4	5	6	1	2	3	4	5	6	1	2	3	4	5	6	1	2	3	4	5	6	1	2	3	4	5	6
5'		2		2			2	2		1				2													2	1			1			1	1			1		2		
U			2	2	1					2	1																															
Control		1	1	2	1									2													3		2					1						1		
1 cop																1				4								2	4					3	5			1				
1 copa						2			2																																	
Z'					6	1			5	2		2			5		4				5						2		1				2	3	1	1			2			1
Total	0	3	3	6	8	3	2	2	7	5	1	2	0	0	9	0	3	0	0	0	0	9	0	0	0	0	5	4	8	0	2	3	3	6	5	0	1	0	3	0	3	1

	4th Feb. (98°F) Shaded am.						5th Feb. (98°F) shaded am.						6th Feb. (93°F) shaded am.						7th Feb. (93°F) shaded am.						8th Feb. (75°F) shaded am.						9th Feb. - shaded am.						10th Feb. - shaded am.					
	1	2	3	4	5	6	1	2	3	4	5	6	1	2	3	4	5	6	1	2	5	4	5	6	1	2	3	4	5	6	1	2	3	4	5	6	1	2	3	4	5	6
5'		2					1														3		4																				
23'			1																																							
U			1		2																																					
Control							1														2																		1			
1 cop		1	3							1						1					6					1	1														2
Z'										1			2		2					2	1	1	3				2					1									
Total	0	3	5	2	0	2	2	0	0	0	2	0	2	0	0	3	0	1	3	2	1	5	11	0	1	1	0	0	6	0	0	2	2	1	0	0	0	1	0	0	0	2