

Life cycle of the wood-borer *Aenetus virescens* (Lepidoptera: Hepialidae)

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Abstract Results of a 4 year survey on the larval and pupal stages of *Aenetus virescens* are presented and supplemented by observations on the duration and seasonal abundance of the egg, larva, pupa, and adult. The length of the life cycle varied from about 1-4 years. Adults emerge mainly in spring and early summer (September-December). Eggs mature within 1 month and young larvae feed on dead wood and fungi for about 2 months. New tunnels were constructed in trees throughout the year but the numbers peaked in January-March. New pupae were observed from March-November. The pupal stages that began after June lasted for a progressively shorter time.

Keywords life history; life cycle; seasonality; larva; Lepidoptera; Hepialidae, *Aenetus virescens*

INTRODUCTION

Aenetus virescens (Doubleday) is the only true wood (timber) boring species of Lepidoptera in New Zealand. Its large size and taxonomic isolation (it is the only member of its genus in New Zealand) was possibly responsible for the considerable interest it received from some early New Zealand entomologists (Gosset 1878; Hudson 1885, 1892, 1894, 1898; Illidge 1899; Quail 1899, 1902; Illidge & Quail 1901). Even though the life-history was of recognised interest for New Zealand entomology (Quail 1900a; Hudson 1900) the details remained largely unknown. This situation may be seen partly because larval feeding was not easily observed or duplicated in the laboratory (Hudson 1885). *A. virescens* is principally a forest insect. The larva bores a tunnel into the stems and branches of trees and shrubs. The tunnel entrance is open to the surface of the host but is covered by a silk web. The

larva feeds at night on callus tissue which grows around the tunnel entrance where the larva has removed surface tissue (Dugdale 1975; Grehan & Winstanley 1980).

In several recent accounts I demonstrated that the life history of larval stages is more complex than previously recognised. The well known tree dwelling habit ("tree-phase") is preceded by a "litter-phase"; i.e., larvae live in litter for the first few instars and feed on fungi and dead wood (Grehan 1979, 1981, 1983a, 1984, 1987a; Grehan & Winstanley 1980). The two stages are linked by a "transfer-phase" which exhibits a different pinacula arrangement and coloration. The transfer morph appears by a single moult and, after establishing itself in a tree or shrub, the larva moults and reverts to the "normal" appearance (Grehan 1981). This paper provides an outline of the entire life cycle, based on a survey of a larval population, over a 4 year period, supplemented by other individual observations.

STUDY AREA

A population survey was carried out from March 1979 to January 1983 at Lake Pounui Reserve in the southern Wairarapa (41°S, 175°E, 20 m a.s.l.). The study area consisted of two gullies on each side of an intervening ridge on the northern shore of Lake Pounui (Fig. 1). Improved pasture was immediately adjacent to both sites on the west facing slopes of each gully.

The sites were chosen for accessibility and the presence of *Carpodetus serratus*, which is a major host of *A. virescens* (Grehan 1984). Other hosts present in each study area were *Nothofagus solandri*, *N. truncata*, *Leptospermum scoparium*, *L. ericoides*, and *Cyathodes fasciculata*. *C. serratus* was chosen for survey because it was a common plant and its smooth, pale coloured bark did not obscure presence of newly established tunnels. Although *Nothofagus* is a major host, trees in the study area were too large for larvae to occupy the lower trunk. The other hosts were not considered to be practical for survey because they were infrequently used by *A. virescens* (c.f. Grehan 1984), and the rough flaky bark of *L. ericoides* and *L. scoparium* also obscured the presence of tunnels.

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The survey of *C. serratus* was along two broad transects where many of the trees were relatively close to each other. The survey was confined to the lower 2 m height of each tree because tunnels located higher up were not accessible to regular survey without the use of specialised or elaborate equipment such as ladders, platforms, and climbing gear. Therefore, it was not possible to estimate population density of *A. virescens* in the study area. At the beginning of the survey 219 larvae were present in the lower 2 m of 133 *C. serratus* trees in an area of about 0.5 ha.

METHODS

(1) Eggs. Eggfall from the canopy was surveyed in a forest gully (41°S, 174°E) in the Wellington Regional Water catchment at Wainuiomata. Four 4 × 2 m plastic sheets were suspended under the forest canopy and examined daily for eggs over 26 days. To collect virgin females, emergence traps were placed over the tunnel entrance. The trap consisted of a container of Galt's solution (Moeed & Meads 1983) placed below the tunnel entrance with a nylon mesh enclosure.

(2) Larvae. Trees were labelled with Allflex® ear tags and the tunnels by coloured drawing pins. In later surveys each new (i.e., unmarked) tunnel was labelled with a colour coded drawing pin. Each tree and its complement of larvae or pupae was examined at monthly intervals. New larvae were located visually by the presence of freshly exposed wood fragments incorporated into the web during tunnel construction (c.f. Grehan 1983a).

Duration of the litter-phase was investigated by preparing three cages, each containing dead wood and a seedling of *Nothofagus solandri* as a tree-phase host. Initial attempts to rear larvae in these cages were unsuccessful but results were obtained from one sample of 40 first instar larvae of unknown age collected from the field.

(3) Pupae. At the onset of pupation the larva deposits a small amount of dust sized particles at the tunnel entrance (produced while the larva smooths the tunnel sides) (Fig. 2a) and dismantles the cover of the tunnel entrance. Often the larva only removes fragments of the cover (Fig. 2b), leaving it weakened but intact. To determine if a larva had pupated it was necessary to check all tunnels by pressing a finger onto the cover to confirm its condition.

(4) Emergence. At emergence the pupa makes its way to the tunnel entrance and protrudes for part of the way out from the tree (Hudson 1885). The adult sex was determined by removal of the pupal

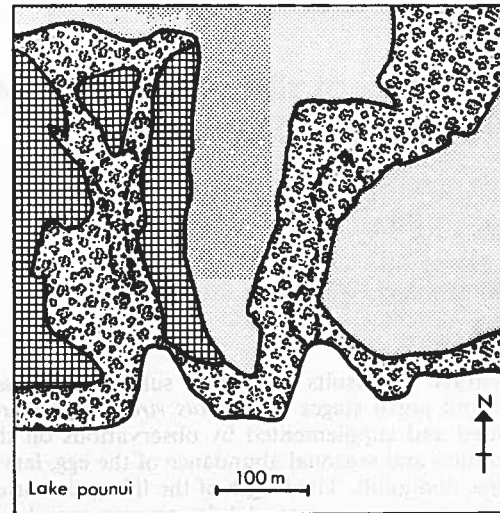


Fig. 1 Study sites (dashed lines) for *Aenetus virescens* larvae on north shore of Lake Pounui. Stippled texture — pasture, curled texture — broadleaf/*Leptospermum* dominated forest, cross-hatched — *Nothofagus* dominated forest.

Table 1 Correlation of *Aenetus virescens* tree-phase larval establishment with adult emergence where establishment is lagged behind emergence from 0 to 12 months. (*; lag significantly correlated.)

Lag	Correlation
0	-0.111
1	0.286
2	0.587 *
3	0.680 *
4	0.620 *
5	0.311
6	0.350
7	0.191
8	-0.336
9	-0.457
10	-0.420
11	-0.317
12	-0.082

exuvium and noting the genital primordia as described by Waller (1966) for *Wiseana*. During the main emergence period, pupal tunnels were checked at weekly or bi-weekly intervals to decrease the time over which a pupal exuvium could dry out and become brittle. A slow, steady removal is often necessary to remove the entire exuvium successfully. If a pupal exuvium dries out it becomes difficult or impossible to remove intact. If the genital region becomes lodged in the sharp bend of the

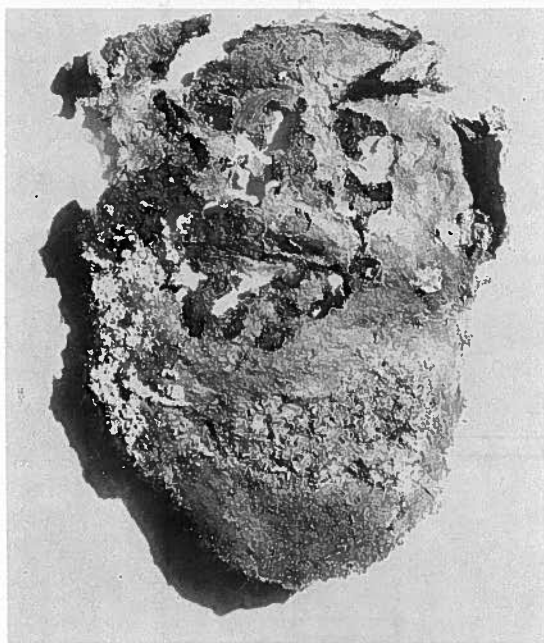
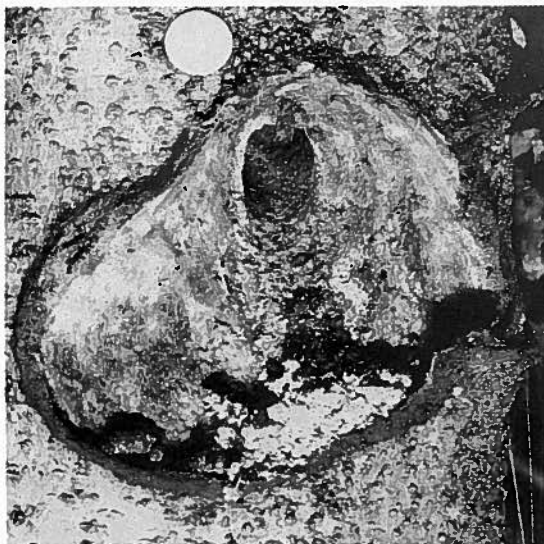


Fig. 2. Evidence of pupation by *Aenetus virescens* (a) deposition of wood frass at the tunnel entrance (b) perforation of cover.

"7" shaped tunnel (see Grehan 1987b for tunnel description), a torch and pair of forceps may be required to pull out the pupal fragments. Later in the study, a mesh bag was placed below the tunnel entrance because the pupa exuvium was some-

times dislodged by tree wetas (*Hemideina* sp., Orthoptera: Stenopelmatidae) entering the vacant tunnel.

Growth and development of the tree-phase were estimated by the tunnel diameter at the entrance. A horizontal measurement was taken because the lateral sides of the tunnel were most nearly parallel. The tunnel diameter was recorded at establishment and upon removal of the pupal exuvium. The mean tunnel size and development time of males and females were compared by a one way non-parametric analysis of variance.

LIFE CYCLE

Adult

In the population survey, adults emerged from August until February, most commonly from October to December (Fig. 3). The adult does not eat. All the moths collected at light traps were in pristine condition as if they had emerged the same evening. I have recorded two females resting among tree foliage during the daytime but no males have been seen in this situation. Adults emerge from mid-afternoon until dusk (Hudson 1884; Quail 1902; Grehan & Winstanley 1980). The pupa protrudes from the tunnel entrance and the emergent moth is usually found at rest on the branch or stem, a short distance above the tunnel site.

Males appear to fly at or very soon after dark, but, for five newly emerged females placed under observation, the onset of the first flight varied from just after dark to as much as 2 h later. The male is a swift and erratic flier whereas the female is comparatively slow and steady with the abdomen held in nearly vertical position. I attempted to induce copulation by the moths using the hand pairing method (Ueda 1981), but was unsuccessful.

Egg

Oviposition behaviour has not been recorded in detail. Eggs may be deposited by virgin females before flight and specimens collected at lights will continue to oviposit at rest. Adult females have been recorded depositing eggs during flight in the forest (M. J. Meads pers. comm.), but the relative importance of this mode compared to oviposition at rest is unknown. The use of egg traps in Wainuiomata did not provide any conclusive evidence on oviposition behaviour. Only 78 eggs were collected, including 42 from one sample. This survey did, however, show that there is an eggfall from the forest canopy. It is possible that the large sample of 42 eggs was from a single female at rest in the forest canopy. A more extensive sampling regime may determine if the eggs have a clustered

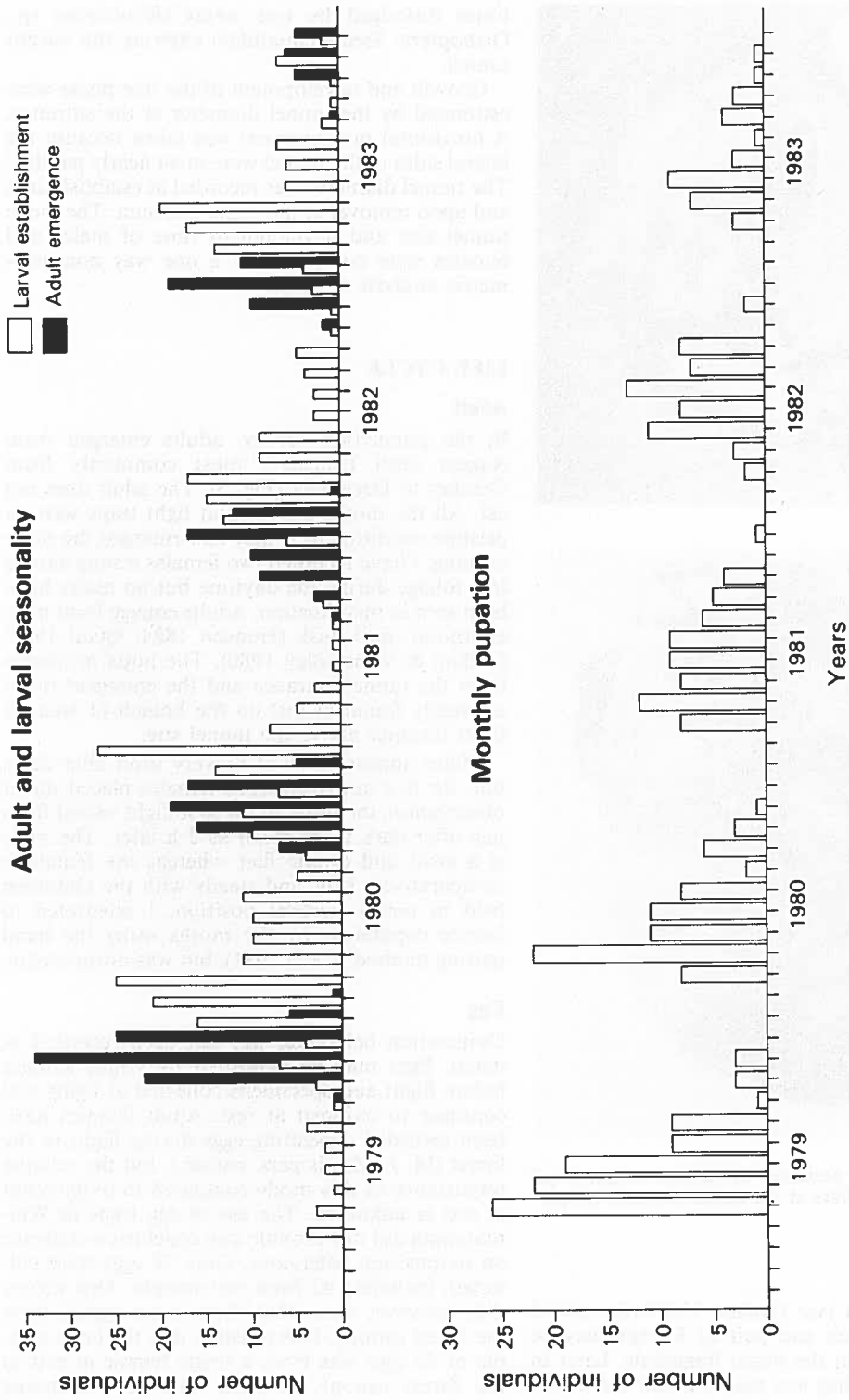
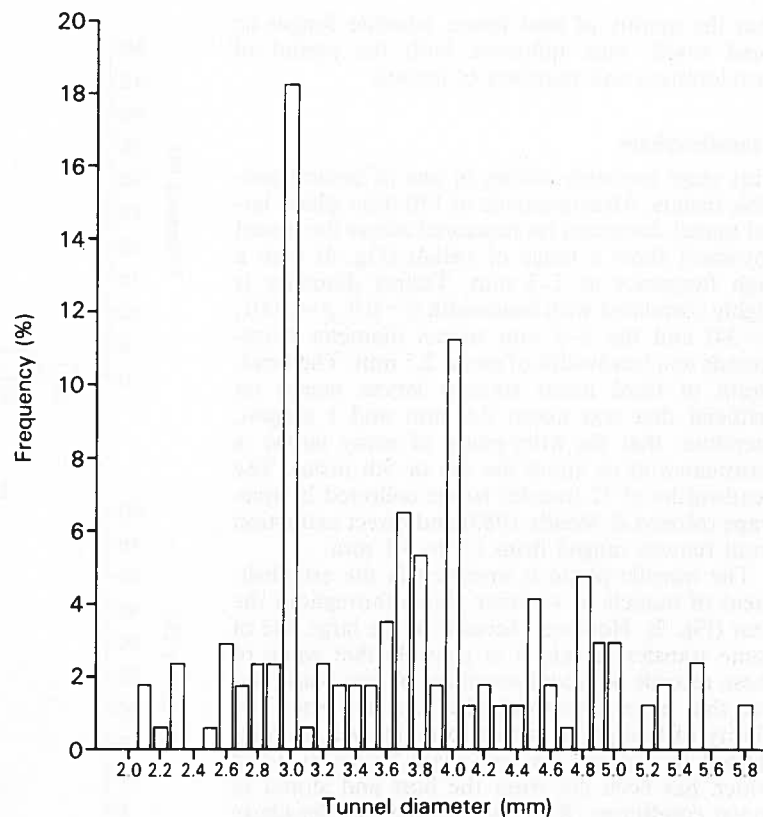


Fig. 3 Seasonality of *Aenetus virescens* adults, pupae and tree-phase larvae at Lake Pounui Reserve, southern Wairarapa.

Fig. 4 Diameter range and frequency of tunnels for newly established tree-phase tunnels of *Aenetus virescens*.



distribution. An average of 1700 eggs were dissected from each of 12 females. Because fertile females are infrequently attracted to lights it was not possible to undertake extensive studies of egg development. Eggs reared in saturated humidity at 15°C hatched after 19 days.

Litter-phase

In a preliminary note (Grehan 1979), I suggested that the litter-phase was completed within 1 year. This appears to have been incorrectly cited by Miller (1984) and Fleet (1986), who state that the litter-phase lasts a full year. Duration and growth of individual litter-phase larvae in the field has not been determined by direct observation. Of the 40 first instar larvae reared in cages, second instar larvae were observed in one cage after 7 days and third or older instar larvae were observed after 16 days. Further observations did not reveal the presence of any larvae; presumably, all died.

Duration of egg and litter-phase can be estimated by comparison of time separation between the peaks in adult emergence and larval establishment. Fig. 3 shows that an increased frequency of adult emergence is followed by an increase in larval

establishments. To determine the significant time separation between the frequency distributions of the two life history stages, I applied a time-series analysis. This analysis showed that adult and larval frequencies were highly correlated with a time separation of 2–4 months, peaking at 3 months (Table 1). On a monthly scale I suggest, therefore, that for most larvae, development occupies about 3 months before establishment.

The number of litter-phase instars could not be determined from field samples. Multivariate analysis of larval head width, length, and setal distance (F1-F1, F2-F2. c.f. Grehan 1981) did not suggest any discrete groups. When larvae were reared on artificial diet, the transfer morph appeared at the third or fourth instar after 30 days. Unlike the normal situation, however, larvae on artificial diet retained the transfer morph in later moults (up to 10 before end of experiment). Two transfer larvae reared on artificial diet were caged onto the surface of a host and left to tunnel into the stem. After the first moult they were extracted and found to have reverted to normal tree-phase appearance. The largest litter-phase larvae have been recorded feeding directly on fungi and it is therefore possible

that the quality of host tissue, whether fungus or dead wood, may influence both the period of development and numbers of instars.

Transfer-phase

This stage probably occurs in one of several possible instars. Measurements of 170 litter-phase larval tunnel diameters (as measured across the tunnel entrance) show a range of values (Fig. 4) with a high frequency at 2–3 mm. Tunnel diameter is highly correlated with headwidth ($r=0.9$, $p=0.001$, $n=34$) and the 2–3 mm tunnel diameter corresponds to a headwidth of about 2.7 mm. The headwidth of third instar transfer larvae reared on artificial diet was about 2.0 mm and I suggest, therefore, that the litter-phase of many larvae is terminated at or about the 4th or 5th instar. The headwidths of 72 transfer larvae collected by tree-traps (Moeed & Meads 1983) and direct extraction from tunnels ranged from 1.9 to 5.1 mm.

The transfer-phase is involved in the establishment of tunnels in vascular plants throughout the year (Fig. 3). However, because of the large size of some transfer larvae, it is possible that some of these records represent reversion of tree-phase larvae that have re-established into a new site. The ability of tree-phase larvae to revert was demonstrated by keeping six tree-phase larvae in wood which has been cut from the host and stored in moist conditions. Reversion to the transfer-phase was directly observed when a young (about litter-phase size) tree-phase larva was collected from a small (5 mm diameter) stem. The larva moulted within 2 h of collecting and had reverted to the transfer morph.

Tree-phase

At Lake Pounui the duration of the tree-phase (larva + pupa) varied from 8 months to 3 years 10 months (Fig. 5). The mean development time of female larvae (Table 2) is significantly longer than in the male ($P=0.001$). Tunnel diameters of transfer larvae were recorded to determine if larger transfer larvae resulted in shorter development times; however, no significant correlation was found. A significant difference ($P=0.03$) was found between male and female larval size as estimated by the final diameter of the tunnel (Table 2).

Pupa

New pupae were found in every month from March to October with one record in November (Fig. 3). Mean duration of the pupal stage (Table 2) is not significantly different between males and females. Individuals with an earlier pupation tend to have a longer pupal period, the shortest duration occur-

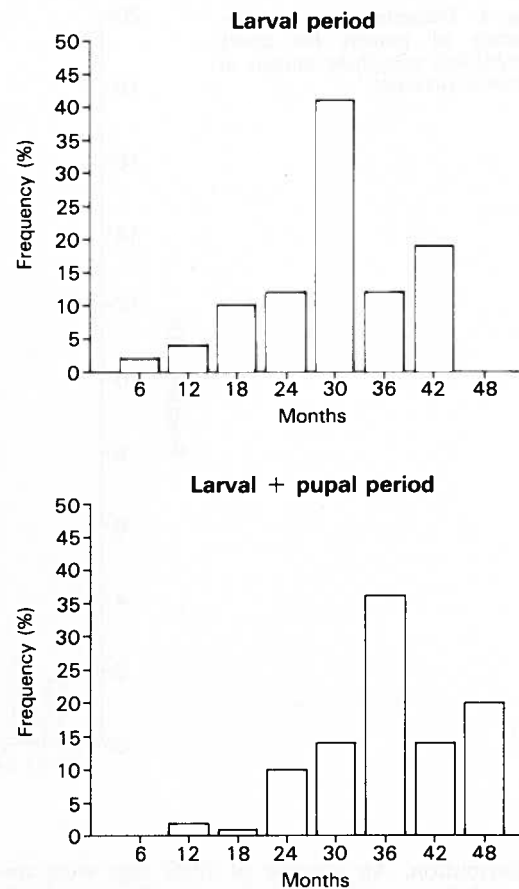


Fig. 5 Duration of tree-phase of *Aenetus virescens*. Class sizes divided into 6 monthly intervals for a sample of 49 individuals.

Table 2 Mean values for development stages of *Aenetus virescens* tree-phase and larval size (measured as tunnel diameter D). IND = tunnel diameter at establishment; OD = tunnel diameter at pupation; \pm standard deviation.

Mean	Male	Female
Larval (days)	665 \pm 217	935 \pm 188
Pupal (days)	151 \pm 43	173 \pm 41
Total (days)	813 \pm 233	1108 \pm 196
IND (mm)	4.1 \pm 0.9	11.5 \pm 1.7
OD (mm)	10.3 \pm 1.6	11.5 \pm 1.7

ring in individuals pupating in September and October (Fig. 6). The probability that this pattern was caused by chance alone was calculated by a "runs test" and found to be 0.0286 (1980), 0.0551 (1981), and 0.00794 (1982).

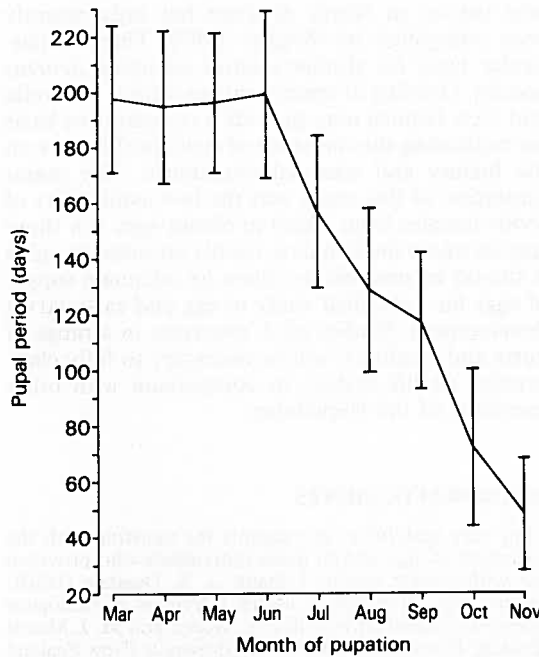


Fig. 6 Duration of pupal stage of *Aenetus virescens* in relation to month of pupation. Vertical bars indicate range for termination of pupal period.

Table 3 Flight records of *Aenetus* in Australia, New Guinea (NG), and New Caledonia (NC). Flight records from CSIRO collection unless otherwise indicated by reference.

Species	Record
<i>A. astathes</i>	February
<i>A. blackburnii</i>	March–April
<i>A. cohici</i>	November–January (Grehan 1983b) (NC)
<i>A. crameri</i>	January (Viette 1956) (NG)
<i>A. cyanochlorus</i>	November, January–February
<i>A. dulcis</i>	April–May
<i>A. eximius</i>	September–January
<i>A. hamptoni</i>	February (Joicey & Noakes 1914) (NG)
<i>A. lewinii</i>	August, January–March
<i>A. lignivorus</i>	September–January, April
<i>A. mirabilis</i>	September
<i>A. paradiseus</i>	September–October
<i>A. paradiseus montanus</i>	October–December
<i>A. ramsayi</i>	February–April
<i>A. scotti</i>	October–March
<i>A. scriptus</i>	March–April
<i>A. splendens</i>	December–February
<i>A. tephroptilus</i>	April
<i>A. toxopeusi</i>	November (Viette 1956)

DISCUSSION

Duration of the tree-phase has been widely commented on in the literature, and estimates have ranged from 2 to 7 years (Gosset 1878; Quail 1899, 1900b; Illidge & Quail 1901; Hudson 1900, 1928; Dumbleton 1937; Miller 1971; Sharell 1971; Dugdale 1974; Fox 1974; Grehan & Winstanley 1980). Results of this study demonstrate that there can be considerable variation within a single population. It is not known how the life-history stages vary in other habitats, hosts, or even in relation to tunnel height above the ground.

Differences in flight period with altitude were recorded by Fox (1971) who observed that onset of the flight period was later at higher altitudes. This may suggest that larval and pupal development is environmentally influenced, possibly by temperature. The main altitudinal range of *A. virescens* is below about 600 m in: the Akatarawa Saddle (40°56'40"S, 175°06'50"E); the Orongorongs (40°21'10"S, 174°59'E) (above the DSIR Ecology Division field station); and Mount Egmont and Mount Holdsworth (the tree-line, in, or near these localities, extends to about 1000 m). On Mount Ruapehu, *A. virescens* is common up to 900 m then sparse up to 975 m (R. M. J. McKenzie pers. comm.). Duration of the pupal stage may reflect the colder conditions faced by those larvae which pupate earlier; however, it is also possible that termination is dependant on photoperiod. The behaviour of the pupa before emergence shows that it is not insulated from external conditions. Up to 3 months before emergence pupae may push through the pupal operculum and "rest" at the top of the longitudinal tunnel (in which they pupated). In this position pupae are visible from the tunnel entrance.

The emergence period in the study area, and flight records taken at Wainuiomata (near Wellington) (41°16'S, 174°57'E, 100 m a.s.l.), indicate a major period of emergence from spring to early summer. Records in the literature have stressed a spring emergence or 1 or 2 months within this period (Gossett 1878; Hudson 1898, 1928; Dumbleton 1966; Miller 1971; Sharell 1971; Alma 1977). However, adults are occasionally collected at other times of the year (J. S. Dugdale pers. comm.; Gaskin 1970; Miller 1971) and a second, minor flight period also occurs in March in the northern North Island (J. S. Dugdale pers. comm.).

The life cycles of other *Aenetus* species are very poorly known apart from recent studies on the larval stages of some species (Grehan 1987b). Collecting records (Table 3) suggest that the flight period of some species is limited to 1 or 2 months in the spring or autumn whereas others fly over a relatively long period. These records do not, how-

ever, indicate the frequency of adult emergence during the flight period. Adult emergence of *A. virescens*, for example, ranges from winter to autumn but the main period is from spring to early summer. From my own observations of *A. cohici* (Grehan 1983b) I suggest it may have a similar flight period to *A. virescens*.

The afternoon emergence of the adult appears to occur widely in *Aenetus*. King (1962) records adult emergence between 4.00–5.00 P.M. for *A. scotti* (Scott), *A. ramsayi* (Scott), *A. splendens* (Scott), *A. lewinii* (Walker), and *A. ligniveren* (*lignivorus*) (Lewin). The related wood-borer *Zelotypia staceyi* (Scott), endemic to the Sydney region of Australia, has been observed to emerge about 3.00 P.M. in the afternoon by Froggatt (1907). In contrast, the wood-borer *Leto venus* (Stoll) of South Africa emerges after dark about 8.00–9.00 P.M. (Scoble 1981)

The courtship behaviour of *A. virescens* and other *Aenetus* species has not been recorded. The hind tibia of *A. virescens* males have brush organs which are also strongly developed in some other species of the genus (Grehan 1983b). In other hepialids where male brush organs are present and the courtship is known, the males fly in groups at dusk and the females fly to them before copulation. In these species, the brush organs are believed to emit pheromones which attract females (Mallet 1984). The presence of brush organs in the males of *Aenetus* led Mallet (1984: 79) to predict a similar courtship pattern. My observations suggest that if females are attracted to flying males, courtship does not take place until after dark. Observations by King (1962) of copulating pairs of Australian *Aenetus* species flying above the forest after dark also suggest that courtship is nocturnal.

The only detailed record of courtship behaviour of live-stem boring Hepialidae is for *Hepialus* spp. (*sensu latissimo*) in North America where a lekking pattern has been observed with the males flying in groups and attracting females (Wagner 1985). A mating pair of the wood-boring species *Endoclita purpurascens* (Moore), was observed at rest in the early morning by Phillips (1938). The female was hanging from a leaf, head uppermost; the male was hanging from the female with his head facing downwards. This position also occurs in the wood-borer *Endoclita excrescens* (Butler) after being hand paired (Ueda 1981).

This life cycle survey of a wood-boring hepialid is incomplete, but it has provided a preliminary understanding between the developmental and seasonal relationship of the litter- and tree-phase stages. There is, however, a lack of comparable information on other arboreal Hepialidae (an account of immature stages of stem boring *Hepi-*

alus species in North America has only recently been completed by Wagner 1985). There is particular need for similar studies on other *Aenetus* species. Overlap of species ranges within Australia and New Guinea may provide a comparative basis for evaluating the influence of ecological factors on life history and seasonal abundance. The major limitation of this study was the low availability of fertile females from which to obtain eggs. For those species where the female is readily attracted to lights it should be possible to obtain an adequate supply of eggs for a detailed study of egg and early larval development. Studies of *A. virescens*, in a range of hosts and localities, will be necessary to fully characterise its life history in comparison with other members of the Hepialidae.

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REFERENCES

- Alma, P. J. 1977: *Aenetus virescens* (Doubleday) (Lepidoptera: Hepialidae). *Forest and timber insects of New Zealand*, no. 16. Forest Research Institute.
- Dugdale, J. S. 1974: Pasture and forest moths. *New Zealand's nature heritage* 4: 1564–1567.
- 1975: The insect in relation to plants. In: G. Kushel ed., *Biogeography and ecology in New Zealand*. The Hague, Junk. (Monographiae Biologicae 27).
- Dumbleton, L. J. 1937: Borers in fruit trees. *New Zealand journal of agriculture* 1937: 295–298.
- 1966: Genitalia, classification and zoogeography of the New Zealand Hepialidae (Lepidoptera). *New Zealand journal of science* 9(4): 920–981.
- Fox, K. 1971: The Lepidoptera of the Egmont National Park. *New Zealand entomologist* 5: 56–58.
- 1974: Egmont National Park. *New Zealand's nature heritage* 1: 136–141.
- Fleet, H. 1986: The concise natural history of New Zealand. Auckland, Heinmann.
- Froggatt, W. W. 1907: *Australian Insects*. London, William Brooks & Co. Ltd.
- Gaskin, D. E. 1970: Analysis of light trap catches of Lepidoptera from Palmerston North, New Zealand in 1966–68. *New Zealand journal of science* 13: 482–499.

- Gosset, C. H. 1878: Notes on the life history of *Charagia virescens*. *Transactions and proceedings of the New Zealand Institute* 11 : 345–346.
- Grehan, J. R. 1979: Larvae of *Aenetus virescens* (Lepidoptera: Hepialidae) in decaying wood. *New Zealand journal of zoology* 6 : 583–586.
- 1981: Morphological changes in the three-phase development of *Aenetus virescens* larvae (Lepidoptera: Hepialidae). *New Zealand journal of zoology* 8 : 505–514.
- 1983a: Larval establishment behaviour of the borer *Aenetus virescens* (Lepidoptera: Hepialidae) in live trees. *New Zealand entomologist* 7 : 413–417.
- 1983b: Description of the male of the endemic New Caledonian species *Aenetus cohici* (Lepidoptera: Hepialidae). *New Zealand journal of zoology* 10 : 285–288.
- 1984: The host range of *Aenetus virescens* (Lepidoptera: Hepialidae) and its evolution. *New Zealand entomologist* 8 : 51–64.
- 1987: Fungal and vascular plant polysaccharide digestion by larvae of *Aenetus virescens* (Lepidoptera: Hepialidae). *New Zealand journal of entomology* 10 : (in press).
- 1987a: Evolution of arboreal tunnelling by larvae of *Aenetus* (Lepidoptera: Hepialidae). *New Zealand journal of zoology* : (in press).
- Grehan, J. R.; Winstanley, W. J. 1980: The puriri moth: a colourful insect. *Forest and bird* 13 : 28–32.
- Hudson, G. V. 1885: Life history of *Charagia virescens*. *Entomologist* 18 : 30–36.
- 1892: An elementary manual of New Zealand entomology. London, West, Newman & Co.
- 1894: Notes on *Hepialus virescens* and other early insects in New Zealand. *Entomologists' monthly magazine* 30 : 11.
- 1898: New Zealand moths and butterflies. London, West, Newman & Co. 144 p.
- 1900: Entomology in New Zealand. *The entomologist* 33 : 186–189.
- 1928: The butterflies and moths of New Zealand. Wellington, Ferguson & Osborn. 386 p.
- Illidge, R. 1899: Life history of timber moths. *Proceedings of the Royal Society of Queensland* 14 : 21–27.
- Illidge, R.; Quail, A. 1901: Australasian wood boring Hepialidae. *Proceedings of the Royal Society of Queensland* 16 : 65–72.
- King, C. 1962: Life history notes of the genus *Aenetus* (Lepidoptera, Hepialidae). *Queensland naturalist* 16 : 102–103.
- Joicey, J. J.; Noakes, A. 1914: A new *Oenetus* from New Guinea. *Annals and magazine of natural history* 8 : 282–283.
- Mallet, J. 1984: Sex roles in the ghost moth *Hepialus humuli* (L.) and a review of mating in the Hepialidae (Lepidoptera). *Zoological journal of the Linnean Society* 79 : 67–82.
- Miller, D. 1971: Common Insects in New Zealand. Wellington, Auckland, Sydney, and Melbourne. Reed.
- 1984: Common Insects in New Zealand. Revised by A. K. Walker. Wellington, Auckland, Sydney, and Melbourne. Reed.
- Moeed, A.; Meads, M. J. 1983: Invertebrate fauna of four tree species in Orongorongo Valley, New Zealand, as revealed by trunk traps. *New Zealand journal of ecology* 6 : 39–53.
- Phillips, W. W. A. 1938: The mating of the moth *Phassus purpurascens*. *Ceylon journal of science* 21 : 63–64.
- Quail, A. 1899: A fragmentary paper on the larval structure etc of *Hepialus ? virescens* (D'bl'd) of New Zealand. *Proceedings of the Royal Society of Queensland* 15 : 89–93.
- 1900a: Entomology in New Zealand. *The entomologist* : 335–339.
- 1900b: Life histories in the hepialid group of Lepidoptera with descriptions of one new species and notes on imaginal structures. *Transactions of the Entomological Society of London* 1900 : 411–432.
- 1902: On *Charagia virescens* Dbl'd. *Transactions and proceedings of the New Zealand Institute* 35 : 249–255.
- Scoble, M. J. 1981: Collecting in a national park. *Custos* 9 : 28–30.
- Sharell, R. 1971: New Zealand Insects and their Story. Auckland and London, Collins.
- Ueda, K. 1981: On the mechanism of copulation in hepialid moths, *Endoclita excrescens* (Butler) and *Hepialus fusconebulosa* (De Geer) (Lepidoptera: Hepialidae). *Bulletin of the Kitakyushu Museum of Natural History* 3 : 27–39.
- Viette, P. E. L. 1956: Contribution a l'etude des Hepialidae (Lepidoptera). (32^{eme} note). Hepialidae de Nouvelle-Guinee. *Nova Guinea, new ser.*, 7 : 41–58.
- Wagner, D. L. 1985: The biosystematics of *Hepialus* F. s. lato with special emphasis on the *californicus-hectoides* species group. Ph.D thesis, University of California, Berkeley, U.S.A.
- Waller, J. B. 1966: Sexing of pupae of *Wiseana cervinata* (Walker) Hepialidae. *New Zealand entomologist* 3 : 5.