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THE BIOLOGY OF THE THREE SPECIES OF PHASMATIDS (PHASMATODEA) WHICH OCCUR IN PLAGUE NUMBERS IN FORESTS OF SOUTHEASTERN AUSTRALIA

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The Hon. J. G. Beale, M.E., M.L.A.,
Minister for Conservation, New South Wales

THE BIOLOGY OF THE THREE SPECIES OF PHASMATIDS (PHASMATODEA) WHICH OCCUR IN PLAGUE NUMBERS IN FORESTS OF SOUTHEASTERN AUSTRALIA

K. G. CAMPBELL AND P. HADLINGTON
FORESTRY COMMISSION OF N.S.W.

INTRODUCTION

Most species of the Phasmatodea usually occur in low numbers, but some species have occurred in plagues and in such instances serious defoliation of trees has resulted. Plagues have been recorded from the U.S.A. by Craighead (1950), from Fiji by O'Connor (1949) and from the highland areas of southeastern Australia by various workers.

The species involved in the defoliation of the eucalypt forests of southeastern Australia are *Podacanthus wilkinsoni* Macl., *Didymuria violescens* (Leach) and *Ctenomorphodes tessulatus* (Gray). In north-eastern New South Wales on Mount Warning, *P. wilkinsoni*, *P. viridoroseus* (Gray), and *D. violescens* have occurred in high numbers. *P. wilkinsoni* and *D. violescens* occurring on Mount Warning, while apparently the same species as those in the highland forests, differ in the duration of their life cycle, which is related to their diapause behaviour in the egg stage so that their specific status may yet require some clarification.

Repeated infestations have resulted in heavy mortality of trees over some areas and the loss of annual wood increment has occurred whenever dense populations of insects have been recorded. This, particularly in the southern highlands of New South Wales, has caused forest-management problems involving the salvage of marketable logs and the re-calculation of yield. These silvicultural problems have been accentuated on Bago State Forest, near Batlow, when the defoliation of the forest has affected regeneration of the economically favoured timber species. In highland areas where defoliation has occurred on steep slopes, e.g., near Jenolan, N.S.W., erosion has apparently been due to the reduction, and in some cases elimination, of the tree cover.

Early observations on the plague phasmatids were made by Froggatt, but these only involved the feeding habits and some cursory data on the life cycle of the two highland species. The records are rather scant, but they do indicate that plagues of phasmatids occurred in the Walcha and Jenolan areas of N.S.W. from 1880–1925 either continuously or intermittently. No further work was done, nor are data available, for the period from 1925 to 1948. In 1948 high numbers of phasmatids were again recorded from Jenolan and Nundle areas in the central highlands of New South Wales, and in 1949–50 plagues were present over wide areas in this region. Preliminary observations were made by officers of the Forestry Commission of New South Wales. A taxonomic study of the Cleptid egg parasites was made by Riek (1955) and this was followed by a study by Key (1957) of the kentromorphic phases of the three phasmatid species.

Campbell (1960) studied the methods of population estimation in the field, particularly in relation to aerial applications of pesticides. Campbell (1961) later studied the effect of forest fires on the egg stage of the three phasmatid species.

The phasmatid *D. violescens*, which had been recorded in high populations from Bago State Forest in the southern highlands of New South Wales in 1953, was in 1958 found to be present also in plague numbers over large areas of northeastern Victoria with the characteristic defoliation of forest areas. At the request of the two State Forestry Authorities the Commonwealth Scientific and Industrial Research Organization considered the problem and appointed a research team in 1960 to work on the ecology of the phasmatids. At present this ecological team is working on the various aspects associated with phasmatid ecology while entomologists of the Forestry Commission of New South Wales are studying the egg parasite-host relationship of *P. wilkinsoni* and the diapause in the eggs of the same species. Egg diapause in *D. violescens* is also being studied by a member of the staff of the University of New South Wales.

The detection of large and suspected incipient populations of *D. violescens* is being carried out in the Victorian forests by officers of the Forests Commission of Victoria. The State Electricity Commission of Victoria has carried out aerial spraying of phasmatids at Bogong using a helicopter in a successful attempt to reduce the phasmatid population and to prevent defoliation and possible death of trees in the upper catchment area of the Kiewa river.

HISTORICAL

Phasmatid outbreaks have been recorded in newspapers from time to time and notations made on maps during survey operations by officers of the Forestry Commission of New South Wales. These have been summarized as follows:

P. wilkinsoni and *D. violescens*—

1880 —Fish River Caves.
1897 —Jenolan and Oberon Areas.
1900 —Nowendoc.
1905 —Nowendoc.
1906 —Glen Innes.
1910–13—Yarrowitch.
1919 —Yarrowitch.
1928 —Walcha.
1930 —Nowendoc.
1932 —Walcha.
1947–63—Recent series of plagues.

The years given represent observations and it is not known whether observers saw damage or high numbers of insects. It has therefore not been possible to determine whether the years listed represent a "plague" or a "non-plague" year or whether, in fact, plagues did occur at two-year intervals or were an annual event.

From past records it may only be concluded that populations of the stick insects *P. wilkinsoni* and *D. violescens* have been recorded as reaching plague proportions at intervals since 1880 in the highland forests of southeastern Australia (Macleay 1881, Olliff, 1891). Outbreaks have occurred intermittently since then and Froggatt (1905) records an outbreak in the Nowendoc district in 1905.

No records of occurrences of plagues are available from 1932 to 1948. However, in 1948 the two plague species again appeared in large populations in the northern and central highland areas of New South Wales and continued until 1957 when wild fires burnt, during the early summer, extensive forested areas near Jenolan and Nundle. Although large populations have been present in the Nundle area from 1957 to 1962 these have not been as destructive and as widespread as the early infestations, particularly those during 1949–50 and 1951–52. In the Jenolan area populations of phasmatids have been negligible since 1957 and very little defoliation due to these insects has occurred.

An area, near Wombeyan Caves that may be regarded as an extension of the Jenolan infestation, was defoliated during 1959–60 and undoubtedly several seasons before this, but no reliable records are available prior to the observations made in 1959.

In the southern highlands of N.S.W., *D. violescens*, which is the only species present in plague numbers in this area, was first recorded in high numbers in the 1952–53 season and since then high numbers have occurred every second year up to 1962–63.

Small populations of *D. violescens* were detected in northeastern Victoria in 1956–57 and since that time, as the result of intensive searching this species has been found to occur in large populations over much of the highland forests of that State.

C. tessulatus was first noticed in plague numbers during January, 1956, on Ingalba, Collombatti, Tanban, Wedding Bells, and Toonumbar State Forests in New South Wales. Incipient populations probably went unnoticed during 1954 and 1955. The occurrence of these plagues has been recorded by Hadlington & Hoschke (1959).

HOSTS

The three phasmatid species vary in their food acceptability. The host trees of *P. wilkinsoni* and *D. violescens* are the same where these species occur in association with one another; in New South Wales south of Wombeyan, and in Victoria *D. violescens* occurs alone.

P. wilkinsoni and D. violescens

Most of the *Eucalyptus* species are acceptable as food, though there are preferences within the genus. While no quantitative tests have been done on food preferences it has been noted in nature that the narrow-leaved "peppermints" *E. radiata* Sieb. and *E. robertsoni* Blakely, the broad-leaved "peppermint" *E. dives* Schauer and the "gums" *E. viminalis* Labill., *E. huberiana* Naud., *E. dalrympleana* Maiden, *E. mannifera* (A. Cunn. Herb.) Mudie, *E. stellulata* Sieb., *E. pauciflora* Sieb., and *E. bicostata* Maiden, Blakely and Simmonds appear to be favoured species, and are the first to be defoliated. Other species which are known to have

been severely defoliated are *E. laevopinea* R. T. Baker, *E. obliqua* L'Hérit., *E. delegatensis*, R. T. Baker, and *E. fastigata* Deane and Maiden, though these appear to be less favoured than the former groups. *E. andreana* Naud. is an acceptable species and has been used for most laboratory rearings. Some *Eucalyptus* species are avoided and these will only be eaten when there is no choice of food.

In the Mount Warning area *E. grandis* (Hill) Maiden (rose gum), *E. saligna* Sm. (Sydney blue gum) and *E. major* (Maiden) Blakely (grey gum) are also hosts.

The only field record of a tree species other than those of the genus *Eucalyptus* being eaten by these two species of phasmatid appears to be *Tristania conferta* R. Br. (brush box). Adult phasmatids will eat sparingly *Angophora* species when no choice exists, but will die if forced to eat this host solely.

C. tessulatus

The host range for *C. tessulatus* is much wider than that for *P. wilkinsoni* and *D. violescens* for it not only eats *Eucalyptus* species, but attacks tree species belonging to unrelated genera and different families. Food preferences were not studied, although in the field *Eucalyptus maculata* Hook., *E. paniculata* Sm., *E. propinqua* Deane and Maiden, *E. gummifera* (Gaertn.) Hochr., *E. resinifera* Sm., *E. punctata* D.C., *E. triantha* Link, *E. pilularis* Sm., and *Casuarina torulosa* Ait. were severely defoliated. *Syncarpia laurifolia* Ten., and *Acacia floribunda* (Vent.) Willd. were also eaten.

In the laboratory this species has been fed successfully on *Acacia mollissima* Willd., *Angophora costata* Domin., *E. dives*, *E. radiata* and *E. andreana*.

GENERAL SEASONAL CYCLE

1. *P. wilkinsoni*

This phasmatid species generally has a two-year life cycle, though one-year life cycle forms do occur. During plagues the adults are usually present in high numbers in the summer of the even-numbered years, and in low numbers in intervening years. The adults copulate often and remain together for long periods. The adult stage is present during the period between early summer and late autumn; egg laying does not commence until about one week after the final nymphal ecdysis or moult.

Eggs are dropped singly on to the forest floor beneath the crown of the tree on which the female is feeding. Most of the eggs hatching in the field are from fertilized females, but a small percentage may develop parthenogenetically. The eggs lie amongst the forest litter for up to eighteen months and sometimes longer before hatching. Generally no development of the embryo is perceptible until the first summer following oviposition, when development takes place though hatching is usually delayed by a diapause until the next spring. In a small number of cases the eggs develop and hatch within one year but some do not hatch until the third season after oviposition.

Nymphs eclode during the spring and rarely early summer; eclosion takes place during periods of high humidity, usually during the early hours of the morning. There are seven or eight nymphal instars, growth being complete by about mid-summer.

2. *D. violescens*

The mature female oviposits during late summer and autumn and development of the egg follows a similar course to that of *P. wilkinsoni*. The nymphs eclode in late spring and early summer, their development generally corresponding to that of *P. wilkinsoni*.

During plagues, adults of *D. violescens* are present in high numbers during the late summer, autumn and sometimes early winter of the odd-numbered years, though small numbers are present in the intervening years. The males are capable of limited flight but the females, although they have small wings, cannot fly but glide clumsily down from elevated positions.

Dense populations of both these species of phasmatids have been recorded only from highland (above 2,000 ft) forest areas of southeastern Australia, though occasional insects are found at low altitudes and near the coast. Exceptions to this are small areas on the side of Mount Warning near Uki in N.S.W., and near Powelltown in Victoria; both species are present in the former locality but only *D. violescens* in the latter.

3. *C. tessulatus*

This species has occurred in high numbers in coastal forests from 200–2,000 ft altitude, occasional specimens being found near the coast at lower altitudes.

The eggs of this phasmatid are dropped on to the forest floor by the female during summer and normally hatch in the spring of the same year.

There are six or seven nymphal instars, depending on the sex, the nymphs reaching maturity in early summer. The sex ratio is usually about 1 : 1 and copulation occurs soon after the adult stage is reached though oviposition does not occur until about two weeks later. The males are smaller and can fly readily, the females cannot fly because of their relatively small wings, but may glide from elevated positions. Both nymphs and adults feed at night and day, but no overt gregariousness has been observed.

THE EGG STAGE

(a) Embryogenesis and Diapause

The development and the movements of the embryos during embryogenesis appear to be similar in all three species so that in describing the relevant aspects of embryogenesis the species are considered together.

The embryo is first visible as a small plate-like structure in the region of the micropyle. The developing embryo, with its dorsal surface directed inwards towards the yolk, then moves posteriorly among the

micropylar area towards the operculum during anatrepsis and in the opposite direction around the posterior pole during the early stages of catatrepsis. Throughout this development, the embryo is slightly folded. Towards the completion of catatrepsis it almost entirely occupies the chorion, the head being located at and facing the operculum, while the dorsal surface of the embryo lies along the micropylar area. When in an advanced stage of catatrepsis the embryo is pigmented, and the mandibles are strongly chitinised. Once embryogenesis is initiated it is continuous for 12–16 weeks, depending on the climatic conditions until late catatrepsis when diapause supervenes.

PLATE I. Eggs of several species of Phasmatids

Top row, left to right—

Ctenomorphodes tessulatus (Gray), *Ctenomorpha chronus* (Gray), *Podacanthus wilkinsoni* (Macleay), *P. viridiroseus* (Gray), *P. typhon* (Gray).

Bottom row, left to right—

Didymuria violescens (Leach), *Acrophylla titan* (Macleay), *Extatosoma tiaratum* (Macleay), *Tropidoderus childreni* (Gray).

The stages prior to the formation of the platelet cannot be observed without staining and the use of high magnifications, and as this work has not yet been done, the precise stage at which the first diapause stage occurs has not been determined. From investigation it appears that the diapause occurs after the fusion of the male and female nuclei and this diapause is referred to as "pre-embryonic". In those eggs having two diapauses the first diapause supervenes at the "pre-embryonic" stage. The occurrence of a diapause at this stage is somewhat unusual in insects as it generally supervenes some time after the formation of the blastoderm.

In those eggs which hatched during the first year, the first diapause occurred when the embryo was fully formed, so that this stage has been referred to as "post-embryonic". In eggs which had two diapauses, the second was a post-embryonic diapause.

These periods of suspended development (diapauses) coincide with the winter months when low temperatures prevail, while morphological development in the egg occurs during the summer and autumn months, usually during January–April, when higher temperatures occur. The variability which occurred in the duration of the pre-embryonic diapause determines the length of life cycle. The second or post-embryonic diapause does not show the same variability in time, since the developed embryo, which for some reason does not emerge during the spring-summer period, degenerates.

The eggs of *P. wilkinsoni* and *D. violescens* having a one-year life cycle showed no indication of a pre-embryonic diapause, as the embryo commenced to develop soon after oviposition and progressed to a stage of advanced development when the post-embryonic diapause supervened. Hatching occurred from these eggs during the following spring. Two diapauses, namely pre-embryonic and post-embryonic, occurred in eggs which produced two-year and three-year insects.

The diapauses in relation to the life cycles of the phasmatids are briefly summarized in Table I.

TABLE I

Diapause in relation to one, two and three-year life cycles

Species	One-year	Two-year	Three-year
P. wilkinsoni			
First diapause ..	Post-embryonic	Pre-embryonic	Pre-embryonic.
Second diapause ..		Post-embryonic	Post-embryonic.
D. violescens			
First diapause ..	Post-embryonic	Pre-embryonic	Pre-embryonic.
Second diapause ..		Post-embryonic	Post-embryonic.
C. tessulatus			
First diapause ..	Pre-embryonic or Post-embryonic	Pre-embryonic	Pre-embryonic.
Second diapause ..		Post-embryonic	Post-embryonic.

The one-year insects of *C. tessulatus* may have either a pre-embryonic or post-embryonic diapause.

(b) Parthenogenesis

In the Phasmatodea parthenogenesis occurs frequently, and in some species whose reproduction is entirely parthenogenetic the male is unknown. Parthenogenesis occurs in the three plague species. Eggs from unmated females of *P. wilkinsoni* and *D. violescens* yielded female individuals only, and thus the parthenogenesis appears to be thelytokous. Unfertilized eggs of *C. tessulatus* produced both males and females, establishing deuterotokous parthenogenesis for this species.

The incidence of parthenogenesis in all three species was low and reproduction by this method is considered of minor occurrence only (Hadlington 1962). However, reproduction by parthenogenesis is likely to be more frequent at low population densities than during plagues.

The females of *C. tessulatus* are able to store sperms for lengthy periods often in excess of ten weeks, while the other two species appear to store them for at least one week.

(c) Hatching

The eggs of the three species hatch when the average temperature rises, which is usually from August to November depending on the species, region of occurrence and the seasonal conditions which prevail. Hatching of *D. violescens* in the southern highlands of New South Wales is normally somewhat later than that in the central highlands and this appears to be related to temperature and diapause.

The young phasmatid is able to emerge from eggs more satisfactorily in the presence of moisture and *C. tessulatus* eggs will not hatch in dry conditions. The presence of sand or litter helps the young phasmatid to completely free its metathoracic legs—if the eggs are placed loosely on the surface the nymph frequently cannot accomplish this and usually dies still attached to the shell.

NYMPHAL STAGE

P. wilkinsoni

The nymphs of this species eclode in late October and November, usually during the early hours of the morning. The nymphs emerge head first after pushing off the operculum and become active almost immediately. If conditions at the time of eclosion are very dry or the egg is free to move, the nymph may be unable to free its third pair of legs (or one of these) from the amniotic sac. This is not uncommon in laboratory cultures, but rare in the field where the egg is usually buried or held fast in the forest litter in relatively most conditions. Nymphs usually eclose when the humidity is high and moisture conditions are most favourable for survival. After emergence, the nymph climbs any vertical object, and if this is a suitable host, i.e., a *Eucalyptus* sp., it starts to feed, but if not, the insect drops off and seeks another vertical object. Most of this behaviour appears to be the result of the negative-geotaxis exhibited by the nymph, but it appears also to have some visual response to objects in the locality and it usually seeks to ascend the tallest rather than the nearest vertical object. If it ascends and the host is not acceptable, searching continues until one is found or the phasmatid dies. Nymphs have been observed to live for several days without food, although they will imbibe free water if it is available. The longer a nymph is without food after eclosion, the less is its chance of survival in the early instars. Young tender leaves appear to be essential as food for the first instar nymphs and if these are not available the proportion of deaths will be high.

There are seven or eight nymphal instars, growth usually being complete by mid-January. After a period of growth, at the end of each instar, a nymph undergoes ecdysis, the nymphal skin splits dorsally along a median line and the nymph emerges head first, thorax and legs next

and abdomen last. If a nymph is dislodged from its moulting position and falls to the ground before its legs are free, death frequently ensues as the nymph is then seldom able to free itself from its exuviae. In the newly-moulted condition the nymph is soft and very vulnerable to predators, but hardening of the cuticle usually takes place within a few hours. During the warm daylight hours, nymphs exhibit little activity, movement in the foliage being limited unless disturbed by predators. If the population is very dense and jostling through competition for feeding locations occurs, some insects are inevitably dislodged and there is a continuous vertical movement of insects. There does appear to be some activity during the hours of darkness, even when numbers are not very high.

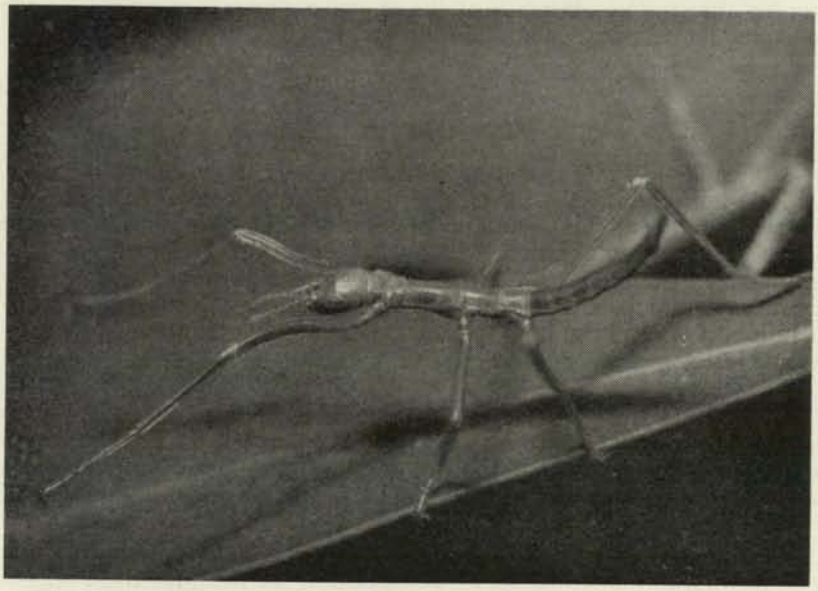


PLATE II. Young nymph of *P. wilkinsoni*

D. violescens

Most nymphs of this species eclode in late November and December, though some emergences take place from the end of September to the end of October, their general behaviour differing little from that of *P. wilkinsoni* nymphs. Where this species occurs in the same locality as *P. wilkinsoni* (northern and central highland forests of N.S.W.) it usually

is less important economically as a defoliator, becoming a more serious pest the further south it occurs. Nymphal development is usually complete by the end of March, five or six nymphal instars, depending on the sex, being completed before maturity.

C. tessulatus

Eclosion of the nymphs of this insect occurs in late August and September. Males pass through six and females seven instars before maturity. As with the two previously discussed species, no overt gregariousness has been observed in this species, though crowding together in feeding on terminal branchlets is common. *C. tessulatus* has been observed to feed more frequently during the day than at night, and also on their exuviae, sometimes devouring them completely. Development is usually complete by mid-January.

Except when in extremely high numbers, the amount of damage to foliage caused by the feeding of nymphal stages of all these species is not readily discernible. Because of the negative geotaxis exhibited by the nymphs, the terminal shoots are the first to be defoliated.

KENTROMORPHIC PHASES

Nymphs of all three species when reared from early instars in crowds or isolation exhibit typical kentromorphic phase differences in the colour pattern quite analogous to those of locusts. The "low-density" phase exhibits normal colouration, whereas the "high-density" phase is conspicuously patterned with black, yellow and sometimes white. The extreme conditions are connected by all intergrades and for *P. wilkinsoni* a rating scale has been used to measure the phase level attained by individual insects.

All three species showed morphometric phase differences also analogous to those of locusts: the length of femur III, the rates of length of femur III/width of head, and of sexual dimorphism with respect to width of head all tended to lower values in the "high-density" phase.

For practical purposes, the estimation of population density from examination of individual nymphs collected in the field, the most appropriate phase character—the colour pattern—is probably the most useful. Individual *P. wilkinsoni* with a pattern rating $< 1{\cdot}5$ are regarded as in the low-density phase and $> 3{\cdot}0$ in the high-density phase; at 3·0 the black areas are extensive. Since females exhibit greater development of the pattern than males, it may be advisable to base determinations of the phase status of populations on females only.

Key (1957), who described the kentromorphic phases in these insects, has discussed the possible causes of such pattern transformations and favours the explanation of a direct link through the central nervous system between sensory stimulation and an endocrine organ in which neither gregariousness nor increased muscular activity plays a significant part.

On the question of the biological function of this pattern change, there is no doubt of the relative conspicuousness of the high-density nymphal pattern compared to the strongly pro-cryptic colouration of the low-density phase and Key suggests an aposematic (warning colours) function. However, in the field the high-density nymphs are well camouflaged by their resemblance to the midribs of leaves and small shoots. Adult females are quite acceptable as food to birds, and a considerable degree of mortality of nymphs is caused by these also.

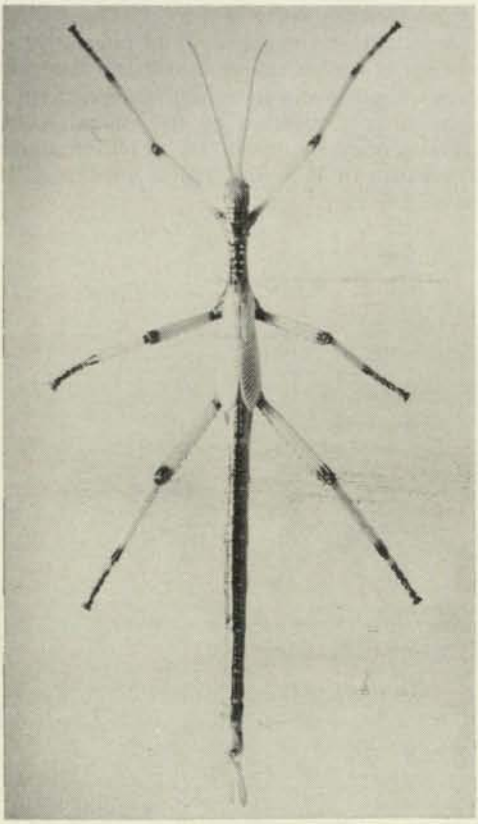


PLATE III. Last instar male nymph of *P. wilkinsoni* showing "high density" kentromorphic phase colouration

ADULT STAGE

P. wilkinsoni

During plagues adults of this insect are usually present in high numbers in the even-numbered years (though low numbers are usually present in the intervening years) during the period January to April and even early May.

Pairing and copulation take place soon after maturity, though oviposition does not commence until about twelve days after maturity. Pairing is continuous and copulation frequent, feeding and oviposition occurring over long periods in pairs, with the male clinging to the back of the female. Disturbance by predators or accident may separate a pair, but females usually do not remain alone for very long. Both males and females of *P. wilkinsoni* can fly, but unless take-off is from an elevated position, the flight is short. If the insect launches itself from an elevated position, flights of up to a third of a mile across open ground have been observed (in no-wind conditions or downwind). When the female becomes gravid, however, its flight is merely a controlled glide of short duration. Movement within the forest stand in relatively flat (tableland) country by this means is not extensive, but down the slope of a ridge or across a valley considerable distances are traversed (a mile or more). Repopulation of an area devastated by fire or exhaustion of the food supply may be accomplished by this means. Differential dispersal of the sexes may occur because of their differences in flying ability, especially along the margins of a forested area.

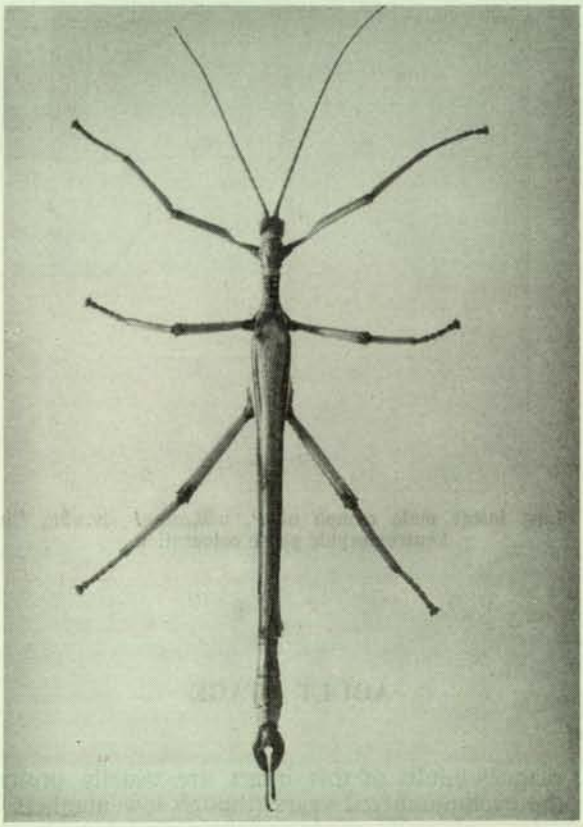


PLATE IV. *P. wilkinsoni* **male**

The adults are voracious feeders, but much of a leaf is often wasted by the insect as it chews through the leaf blade, the excised portion falling to the ground uneaten (sometimes the insect falls with this portion but does not attempt to eat the leaf when on the ground). Movement of the adult phasmatids in areas with dense populations and consequent severe defoliation and possible exhaustion of the food supply affects the distribution of the eggs on the forest floor and hence that of the next generation. If the food supply is not exhausted, eggs may be distributed throughout the affected area, usually in a non-random manner because of preferences for certain *Eucalyptus* hosts and limitation of movement. If the food supply is depleted, movement will be toward the periphery of the defoliated area and beyond, and eggs will be more numerous in these localities. Although most *Eucalyptus* spp. are eaten, there is a definite preference shown for "gum" and "peppermint" types and these are usually most heavily defoliated.

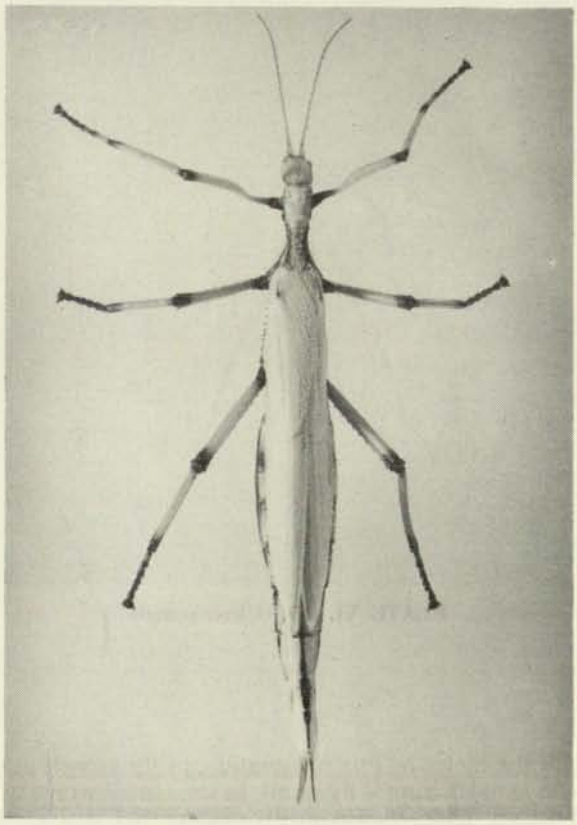


PLATE V. *P. wilkinsoni* **female**

D. violescens

Adults of this stick insect occur in high numbers usually during the odd-numbered years with low numbers in the intervening years in the central and southern highland forests. As with *P. wilkinsoni*, a population with a one-year life cycle at Mount Warning may be in high numbers every year. The adults are present usually from late February to May, oviposition taking place about one week after maturity.

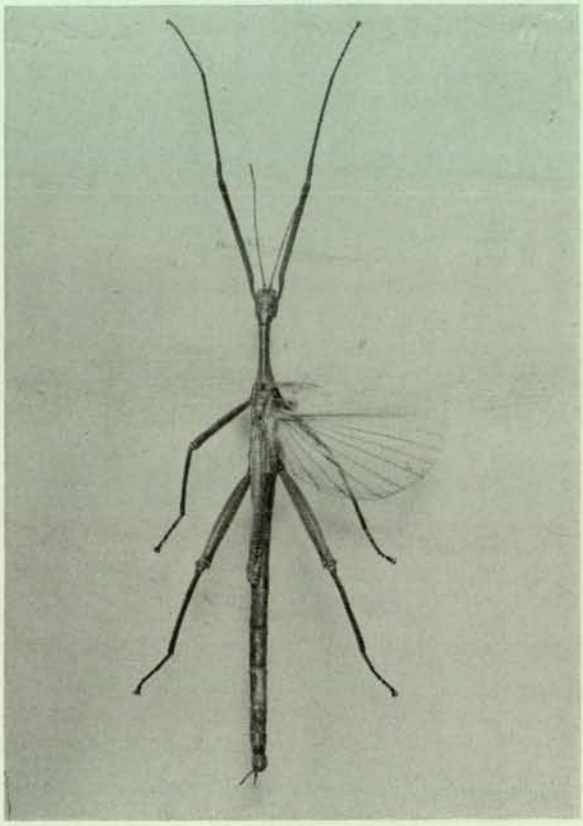


PLATE VI. ***D. violescens*** **male**

Although the males of this phasmatid can fly as well as those of *P. wilkinsoni*, the females cannot fly at all, having small wings which permit only a controlled glide, consequently differential distribution of the sexes may be even more marked in *D. violescens*, concentrations of males

often being found along margins of open spaces in a forested area. Spread of a population on a relatively flat area thus is therefore not extensive, usually downwind; some spread downhill has been frequently observed.

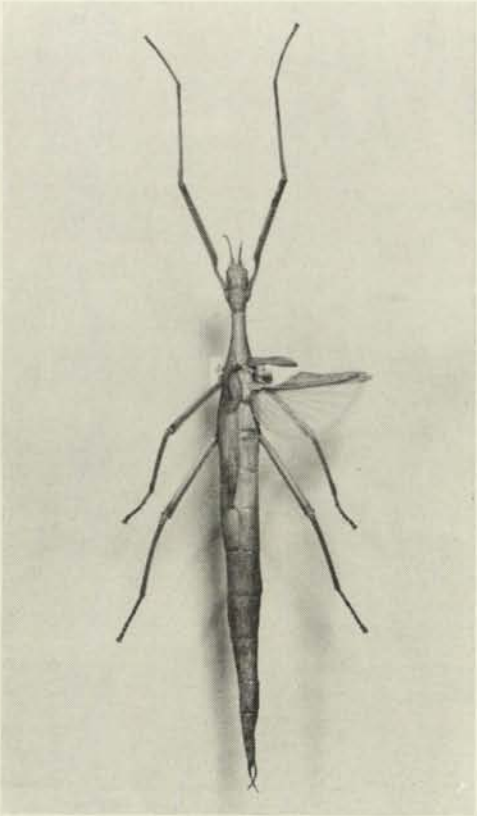


PLATE VII. *D. violescens* **female**

C. tessulatis

The adults of this species are present from mid-December until February and sometimes March. Although copulation occurs soon after the adult stage is reached, about two weeks elapse before the female commences to lay. As is the case with the other species, the males and females remain coupled for long periods, moving about to feed in this position; copulation occurs at irregular intervals, oviposition taking place between these acts. The sex ratio is 1 : 1 but the males are usually less long-lived than the females, and in some sites females predominate.

The males are able to fly readily, but the females have relatively small wings and like those of *D. violescens* are capable only of a controlled glide.

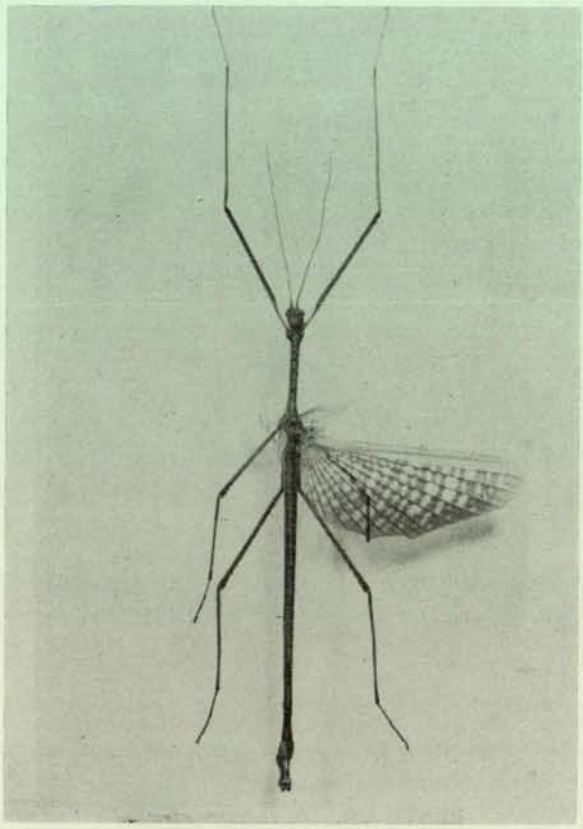


PLATE VIII. *C. tessulatus* **male**

Although individually capable of consuming as much foliage as either of the other two plague phasmatids, large areas of forest have not been defoliated by *C. tessulatus*, and high numbers have been present only for limited periods; small localities have been severely affected and there appears to be a definite avoidance of *E. microcorys* F. v. M. (tallowwood); *Casuarina torulosa* (forest oak) is always present as an understorey tree in outbreak localities.

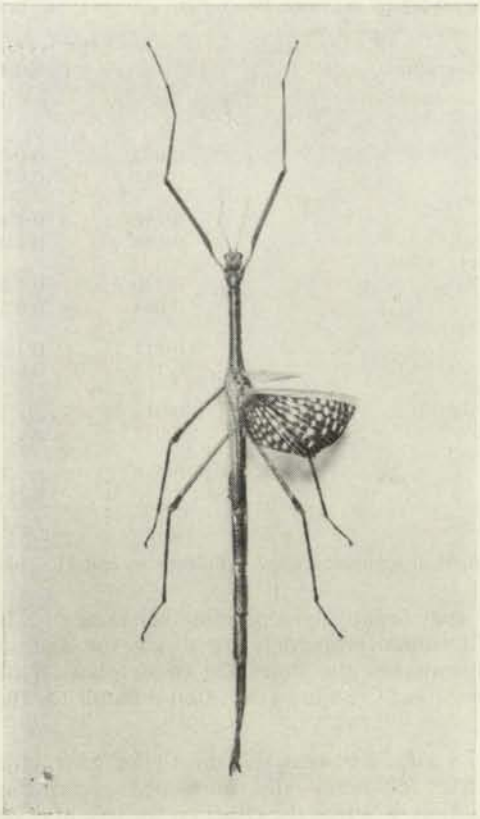


PLATE IX. *C. tessulatus* **female**

DESTRUCTIVE POTENTIAL

The damage caused to leaves by the feeding of nymphs is usually small until the ultimate instar, but even this is negligible compared to that caused by the adults, particularly the females during the period of oviposition.

The destructive potential of the three plague phasmatids has been compared by Hadlington, the results being shown in the following table:

TABLE II

Comparison of Destructive Potential of Three Plague Phasmatids
(results shown as grammes of oven-dry weight of material per insect per day)

Phasmatid	Faeces	Foliage	Total
P. wilkinsoni (male)			
Maximum	0·092	0·092	0·184
Average	0·054	0·044	0·098
P. wilkinsoni (female)			
Maximum	0·296	0·131	0·427
Average	0·188	0·066	0·254
D. violescens (male)			
Maximum	0·140	0·140	0·280
Average	0·084	0·023	0·107
D. violescens (female)			
Maximum	0·211	0·196	0·407
Average	0·156	0·062	0·218
C. tessulatus (male)			
Maximum (1 day)	0·012	....	0·012
Average (1 day)	0·012	....	0·012
C. tessulatus (female)			
Maximum	0·278	0·337	0·615
Average	0.176	0.111	0.287

Insects held in separate cages. Hadlington and Hoschke, 1959

Because of the negatively-geotactic behaviour exhibited by the phasmatids, the terminal branchlets are always the first and most heavily attacked and this makes the detection of defoliation of less favoured hosts, e.g. *E. delegatensis* (alpine ash) often difficult for the inexperienced observer.

In this species all the newest and most effective foliage may be eaten and the older leaves left practically untouched, giving the appearance of only slight defoliation, whereas the effect on the tree may be severe because the energy normally available for wood production is diverted to the growing of new effective foliage. In the case of more favoured hosts, e.g. *E. radiata* (peppermint) and *E. viminalis* (ribbon gum) all the foliage may be eaten, but again the terminal growth is first to be destroyed.

Some of the foliage is wasted because of the insect's habit of biting through the leaf blade. Even in cages, foliage dropped in this way is not eaten by the phasmatids, which will starve rather than descend to feed.

Repeated defoliation by either *P. wilkinsoni* and *D. violescens* results in the death of trees. In areas where *D. violescens* has occurred in high numbers only *E. delegatensis* has been affected in this way, due probably to its relatively poor re-crowning capabilities. This has occurred mainly at Bago S.F. near Batlow, N.S.W., following severe defoliation by this insect in 1955. In Victoria, *E. regnans* F. v. M. (mountain ash) has also been killed (personal communication C. J. Irvine F.C.V.).

On the central highlands and New England Tableland, N.S.W., however, large areas of Eucalypts have been killed, particularly in the Jenolan area, all species, even peppermints, being affected. *P. wilkinsoni* is the insect mainly responsible for the defoliation in these areas, and its larger size and longer active life are no doubt contributory factors.

EGG PRODUCTION

The number of eggs laid per female per day is variable, and depends largely on the conditions of crowding and availability of food.

Final instar nymphs of *P. wilkinsoni* and *D. violescens* were collected in the field at Jenolan, N.S.W., December, 1957, and held in cages at Hurstville. *C. tessulatus* nymphs were collected from Tanban S.F. (near Kempsey) and held similarly.

The following graph shows the daily oviposition rate throughout the oviposition period.

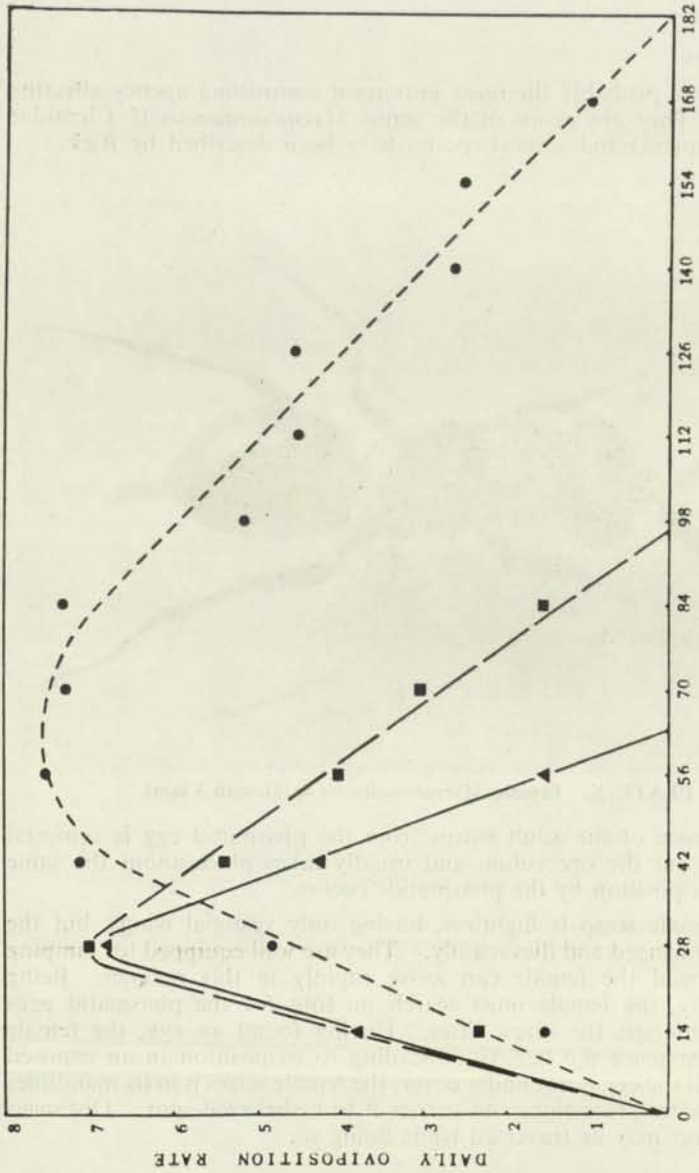


FIGURE I. Average daily oviposition rate per female phasmatid

With respect to *D. violescens* it will be seen that a maximum of seven eggs per day were laid twenty-eight days after the commencement of oviposition with seventeen females present, whereas a maximum of just under three eggs per day were laid with about forty females present (the same sized cages 18 in x 18 in x 24 in were used to confine the insects in each case).

MORTALITY FACTORS

Some of the significant mortality factors observed with respect to these insects appear to be those affecting the eggs. This stage occupies, in most instances, the greater part of the life cycle and is the most accessible for study.

Egg parasites

These are probably the most important controlling agency affecting this stage. They are wasps of the genus *Myrmecomimesis* (f. Cleptidae O. Hymenoptera) and several species have been described by Riek.

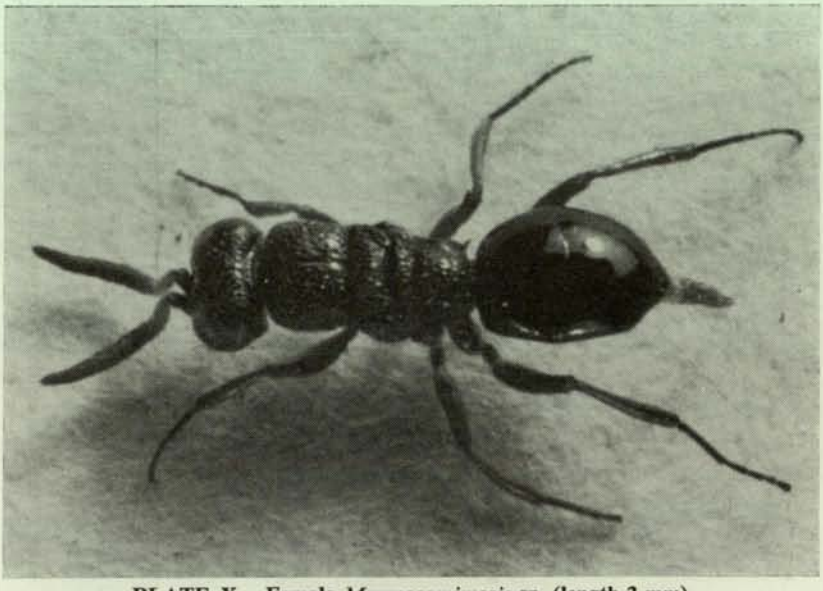


PLATE X. Female *Myrmecomimesis* sp. (length 3 mm)

Emergence of the adult wasps from the phasmatid egg is achieved by pushing out the operculum and usually takes place about the same time that oviposition by the phasmatids occurs.

The female wasp is flightless, having only vestigial wings, but the male is fully winged and flies readily. They are well equipped for jumping and if alarmed the female can move rapidly in this manner. Being unable to fly, the female must search on foot for the phasmatid eggs which lie amongst the forest litter. Having found an egg, the female will not commence the behaviour leading to oviposition in an exposed position. If the egg is not under cover, the female seizes it in its mandibles by a convenient projection, and carries it to a sheltered spot. Distances of several feet may be traversed while doing so.

The female then mounts the egg and chews a hole through the shell, and it may feed on the yolk. It then reverses its position and the ovipositor is then inserted, oscillated and then withdrawn. The ovipositor may then be inserted a second time, the egg being laid at either insertion. The punctures so made can be seen externally quite plainly in the shell of a *D. violescens* or a *C. tessulatus* egg, but not in that of a *P. wilkinsoni* because of its ornamentation; occasionally several punctures may be made in an egg.

Although possibly more than one egg may be laid in a phasmatid egg, only one wasp larva will develop. Larval development is rapid, the larva being fully grown in about three weeks, a diapause then supervenes and pupation does not occur until the following summer. In some cases emergence takes place later during the same summer. This one-year life cycle is not general and in many instances these wasps have a two-year life cycle in phase with their hosts. Research is currently taking place into the biology of these egg parasites.

Several species of these wasp parasites have been determined, and the following table summarizes the data concerning their respective hosts and localities.

TABLE III

Phasmatid Egg Parasites—Hosts and Localities

Host egg	Locality	Parasite
C. tessulatus ..	Toonumbar S.F. (near Kyogle, N.S.W.)	*M. rubrifemur.*
	Wedding Bells S.F. (near Woolgoolga, N.S.W.)	*M. rubrifemur.*
	Tanban S.F. (near Kempsey, N.S.W. ..	*M. rubrifemur.*
	Ingalba S.F. (near Kempsey, N.S.W.)..	*M. rubrifemur.*
	Ingalba S.F. (near Kempsey, N.S.W.)..	*M. nigripedicel.*
	Ingalba S.F. (near Kempsey, N.S.W.)..	*M. bispinosa.*
P. wilkinsoni ..	Nundle/Hanging Rock S.F., N.S.W. ..	*M. coeruleus.*
	Nundle/Hanging Rock S.F., N.S.W. ..	*M. bispinosa.*
	Nundle/Hanging Rock S.F., N.S.W. ..	*M. semiglabra.*
	Nundle/Hanging Rock S.F., N.S.W. ..	*M. rubrifemur.*
	Hassan's Walls, N.S.W.	*M. nigripedicel.*
	Hassan's Walls, N.S.W.	*M. bispinosa.*
	Hassan's Walls, N.S.W.	*M. rubrifemur.*
	Hassan's Walls, N.S.W.	*M. semiglabra.*
	Jenolan, N.S.W.	*M. coeruleus.*
	Jenolan, N.S.W.	*M. semiglabra.*
	Bowenfels, N.S.W.	*M. nigripedicel.*
	Wombeyan, N.S.W.	*M. semiglabra.*
	Wombeyan, N.S.W.	*M. bispinosa.*
	Konangaroo S.F. (near Jenolan, N.S.W.).	*M. bispinosa.*
D. violescens ..	Jenolan	*M. bispinosa.*
	Bowenfels	*M. bispinosa.*
	Konangaroo S.F.	*M. bispinosa.*
	Island Bend, N.S.W.	*M. bispinosa.*
	Bago S.F. (near Batlow, N.S.W.) ..	*M. bispinosa.*
	Bago S.F. (near Batlow, N.S.W.) ..	*M. semiglabra.*
	West Kiewa, Victoria.	*M. semiglabra.*
	West Kiewa, Victoria	*M. rubrifemur.*
	Bogong, Victoria	*M. rubrifemur.*

In most cases the proportion of eggs parasitized is relatively low, but in several instances where the population of phasmatides has become less dense, the percentage of eggs parasitized has increased greatly, whereas where the numbers have remained high, little or no increase in the percentage of parasitism has resulted.

In the case of *C. tessulatus* most of the decline in population density may be attributed to egg parasitism and deterioration. A population of *P. wilkinsoni* in the Wombeyan area which has been studied gives an example of increasing egg parasitism with diminution of numbers of phasmatids. Here the number of parasites was high, in the site studied about as high as the number of phasmatids which eclosed, but mortality amongst the latter was high and very few eggs were laid. Parasitism was expected to be high in these eggs with a consequent decline in population, and this did occur.

Some of the information obtained from dissection of field collected eggs is shown in the following table.

TABLE IV

Field-collected Eggs—total number and numbers affected by parasites or diseased and deteriorating

Area	Date	No. of sites	Total No. eggs with contents	Population density	No. Parasitized	Parasitized %	No. diseased or deteriorating	D. or D. per cent
P. wilkinsoni								
Tuggolo S.F.	3–6–57	9	754	H	91	12	346	45
Tomalla S.F.	3–6–57	4	134	M	25	19	60	45
Nundle S.F.	3–6–57	7	428	M	61	14	227	53
Konangaroo S.F. ..	11–6–57	14	52	L	22	42	22	42
Wombeyan	17–5–61	5	489	M-H	230	47	50	10
Nundle	19–6–61	7	733	M	40	18	10	76
D. violescens								
Island Bend	0–6–57	5	479	M-H	33	7	237	48
Konangaroo S.F. ..	11–6–57	14	102	L	27	27	59	58
Bogong (Vic.) ..	31–10–57	12	186	M-H	24	13	27	14
Bogong (Vic.) ..	5–3–58	12	172	M-H	30	17	57	31
Bago S.F.	19–3–58	7	1,011	H	17	2	443	44
Bago S.F.	30–9–58	5	427	H	7	2	231	54
C. tessulatus								
Toonumbar S.F. ..	0–4–56	5	2,122	H	587	27	608	29
Wedding Bells S.F. ...	0–4–56	5	656	M	217	33	372	56
Tanban S.F.	0–4–56	10	3,506	M-H	1,059	30	1,536	44
Ingalba S.F.	0–4–56	5	2,681	H	704	26	843	31
Collombatti S.F. ..	0–4–56	2	111	L-M	12	11	77	48
Wedding Bells S.F. ..	21–5–57	20	1,007	L-M	225	22	759	75

H = High M = Medium L = Low.

The number of eggs affected adversely by parasites is probably higher than the figures shown, which represent actual establishment of wasp larvae in the eggs. No doubt many other eggs are damaged by the female wasps during oviposition and these may not develop into phasmatid nymphs but deteriorate, thus reducing the expected phasmatid population.

A large number of eggs do not develop because of factors not well understood at present. Some appear diseased and may be infected by various bacterial and/or fungal organisms, but whether these were the initial cause of deterioration is not known. Some degeneration may be due to the attempts at oviposition by the parasitic wasps from which no larvae develop, although in the case of eggs laid by caged phasmatids not exposed at all to parasites the percentage deteriorated is quite high.

Although parthenogenesis is present in all three species, its occurrence is rare (*P. wilkinsoni* 1·4 per cent; *D. violescens* 0·6 per cent) except in the case of *C. tessulatus*.

The following table shows the greater proportion of deteriorated eggs which have been laid by unmated females compared to those laid by mated females.

TABLE V

Emergences and Embryonic Conditions of Eggs—Coastal Environment (expressed as percentages of total eggs)

Species	From mated females				From unmated females			
	Emergences	Dead embryos	Undeveloped eggs	Deteriorated	Emergences	Dead embryos	Undeveloped eggs	Deteriorated
P. wilkinsoni ..	44·0	2·8	44·7	8·5	1·4	1·7	77·7	19·2
D. violescens ..	32·8	0·6	54·0	12·6	1·2	0·2	50·4	48·2
C. tessulatus ..	77·5	2·4	12·7	7·4	10·4	3·0	74·1	12·5

Although sperms may be stored by the females (two weeks in the case of *P. wilkinsoni* and *D. violescens* and up to ten weeks in the case of *C. tessulatus*) if the population density is low or there is a preponderance of females in certain localities, non-fertilization of the eggs may result in a high percentage of deterioration.

Eggs are undoubtedly damaged by mandibulate predators, possibly ants, lizards or birds, and the number so affected may be considerable. Eggs placed in exposed positions for study have all been removed, some no doubt merely carried away by wasp parasites or ants but others eaten as evinced by the broken empty shells. Many eggs, however, fall into the litter on the forest floor and may not be so subject to these hazards.

NYMPHAL AND ADULT STAGES

Predators

Several birds have been observed to be predatory on phasmatids, a lizard (water dragon) has also been observed eating live insects which have fallen from trees, and ants have also been seen carrying off dead phasmatids killed by insecticide in control operations.

Birds are undoubtedly important predators of phasmatids. Pied Currawongs, Wattle birds, Ravens, and rarely Magpies have been observed eating them, most commonly the female phasmatids, though males are often seized and damaged, but less seldom eaten. The gravid females are favoured because of the large abdomen which is usually bitten off leaving the remainder uneaten.

Where the phasmatids are numerous, flocks of birds will onggregate to feed but seldom do they have any marked effect in reducing the numbers of insects except in small localities. At least two instances have been observed where they have contributed to such a reduction, one near Jenolan where an isolated small area of bushland was heavily infested mainly by *P. wilkinsoni.* Here Crows concentrated on this population and practically eliminated it in 1957, very small numbers being present there since. At Nundle S.F. following the application of insecticide to an area experimentally, the numbers of *P. wilkinsoni* were reduced to a low level. A flock of Currawongs which had been present prior to spraying, concentrated on the residual population and here again almost eliminated it.

Birds often eat large numbers of phasmatids in outbreak areas, but the proportion of the population killed by them is usually small except in the circumstances already discussed.

The scorpion fly, *Harpobittacus* sp., has been seen rarely carrying off nymphs in the Jenolan and Nundle areas and a small proportion of phasmatids are no doubt accounted for in this way.

Ants have been seen carrying off insects (both nymphs and adults) which have been killed or damaged. They have also been observed attacking active insects and probably act as scavengers as well as predators.

PARASITES

Few parasites of the active feeding stages of insects have been recorded and their significance as controlling agencies is little known. A tachinid fly (*O. Diptera*) has been found endoparasitic on *D. violescens*, but this is in turn hyperparasitized by chalcid wasps.

Gordion worms (*Nematoda*) have been recorded as endoparasites of late instar nymphs and adult *D. violescens* and *P. wilkinsoni.* In 1962, when a high-density population of *P. wilkinsoni* occurred in the late nymphal stage at Wombeyan, N.S.W., a large number were found to be infested by gordion worms. Heavy mortality of the phasmatids occurred in the field and it is interesting to note that very few eggs were laid in an area where the insects had been numerous near maturity.

FIRE

Forest fires may affect phasmatids in several ways, depending on the stage of the insect present, the time of the year when the fire occurs and the nature and intensity of the fire.

When the eggs are present n the forest litter on the ground a fire capable of destroying this litter is usually necessary to have any effect on the contents, whether these be phasmatid embryos or parasite larvae. Fires which burn slowly over the ground or occur during the hotter periods of the year, may accomplish this, otherwise the effects are not severe.

Although nymphs and adults may be killed by high air temperatures, these conditions are rarely experienced in their natural environment. Fires, however, may provide these and may kill the insects in this way without actual contact. In a wild fire, however, most are killed by actual burning either on the foliage or after having been dislodged by heat or smoke.

Thus fire may act as a mortality factor in the several ways outlined, or may prove beneficial by killing numbers of egg parasites. Fire can, however, modify the habitat by killing trees or by favouring unsuitable hosts (wattles, etc.) to the detriment of the phasmatids and if this occurs repeatedly, conversion of the forest to a woodland or a savannah in which the species cannot persist.

The severe fires of 1957 at Jenolan and the Nundle-Tuggolo areas caused extremely high mortalities in the phasmatid populations. High numbers are present now only in areas not burnt over by these fires.

In the Duncan's Creek section of Nundle S.F. a fire in 1951 reduced the *P. wilkinsoni* population to a very low level. In 1961–62 this population has again reached plague numbers, partially by a slow build-up of the residual population and by dispersal from nearby dense populations unaffected by fire.

FOREST STAND FACTORS

The effects of the forest stand conditions on the phasmatid population are at present not fully understood, but it is considered that some of these are favourable and others unfavourable to increase in numbers. High numbers of both *D. violescens* and *P. wilkinsoni* occur almost entirely in highland forests above 2,000 ft (and mainly above 3,000 ft) in altitude with the exceptions already mentioned.

In the case of *D. violescens* some of these forests are characterized by the occurrence of stands of trees relatively even aged which have grown up as a result of past catastrophes, mainly fire. Since then, and particularly since 1939, these stands have been relatively free from fire. Although silvicultural treatment has been carried out in some areas (e.g., Bago S.F.) in order to modify the species composition of the forest stand, in most instances this tends to increase the purity of the stand (at Bago S.F. *E. delegatensis*—alpine ash—is the species favoured in this way).

Although defoliation of the ash stands has been at times severe, gums (*E. viminalis* and *E. dalrympleana*) and peppermints (*E. robertsoni*) have been observed being defoliated preferentially. The latter groups of eucalypts refoliate readily, but the ash group does not and deaths have occurred from repeated defoliation. In areas defoliated by *D. violescens* the thinning of the canopy is followed by vigorous growth of grasses (mainly *Poa* spp. snow grass). This has retarded and prevented the establishment of seedling regeneration. Regeneration of gum or peppermint, mainly from lignotubers, has not been retarded similarly. Thus defoliation tends to favour regeneration and survival of the species more favoured as hosts though less desirable as timber producing species.

Forest stands with extensive canopy appear necessary for phasmatid populations both to persist and to increase. Populations occupying small or isolated localities of woodland are soon killed out by bird predators as are those in localities of small or medium-sized regeneration. The chance of survival of nymphs to adults are minimized unless tall trees are relatively abundant in the stand.

P. wilkinsoni occurs in forest stands with a history possibly less well defined than those where *D. violescens* occurs in plague numbers. However, fire has influenced the species composition and age groupings. Major fires have burnt over extensive areas from time to time throughout all these highland forests and these have resulted in many even-aged stands. Some of these areas (Nundle-Walcha and Jenolan-Wallerawang) have a record of phasmatid plagues from the 1890's and no doubt these occurred prior to this date also.

The species composition of these forests differs slightly from those where *D. violescens* predominates, but the gum and peppermint groups are again favoured hosts. However, defoliation of many of these hosts has also been prolonged and severe enough to cause death in a number of instances, but again their regeneration is favoured.

Removal of the tall overstorey trees of a stand at Tuggolo (near Hanging Rock, N.S.W.) leaving the small regeneration may have had an adverse effect on a phasmatid population. Although there was ample food present the population did not persist in high numbers. The causes of this are not fully understood, but it is thought that the limitation of dispersal of the insects because of the lack of tall trees may be a contributing factor.

DISPERSAL

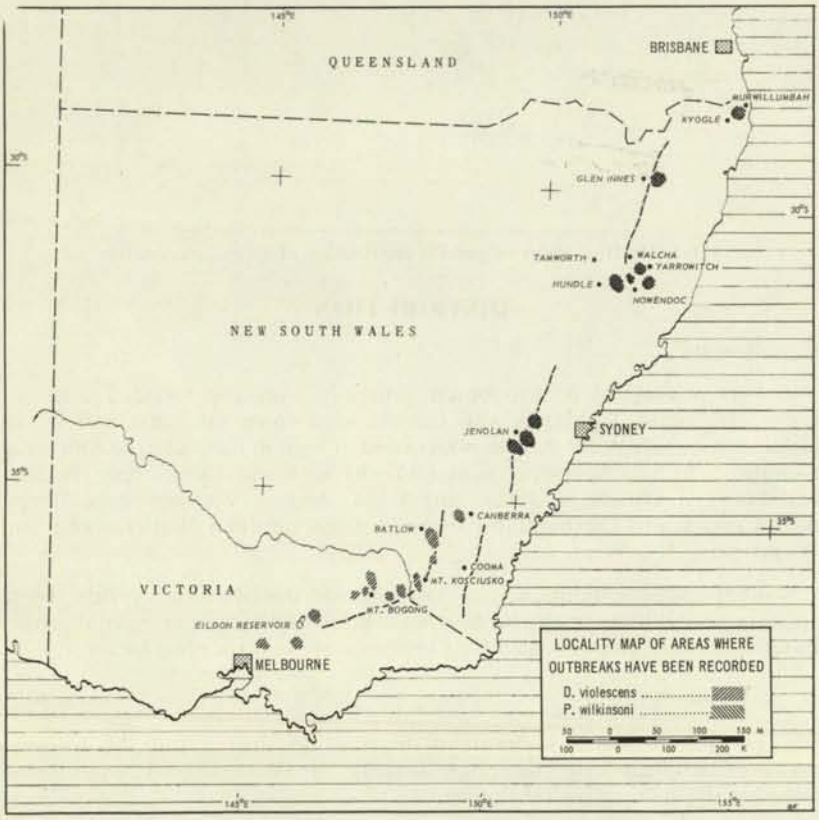
As mentioned previously, horizontal movement by either *D. violescens* or *P. wilkinsoni* within a forest stand is not great unless there are breaks in the canopy or the area is dissected or bounded by steep sided valleys. The adult males of *D. violescens* often fly into open country some distance from a forest margin (particularly downwind) and many of these die,

some being taken by predators. Dispersal of adults down the steep sides of ridges may result in eggs being laid in unfavourable situations as regards altitude and host trees; such dispersal is usually one way, individuals seldom regaining the higher parts of the topography.

Mature but non-gravid females and males of *P. wilkinsoni* can fly readily and even take off from level ground. Even so, as with *D. violescens*, horizontal movement within the forest stand is not great. However, adult *P. wilkinsoni* can cross considerable distances of open country to reach suitable host stands and it is not until the female becomes gravid that there is much differential dispersal of the males.

DISTRIBUTION AND NUMBERS

Areas where outbreaks of the three species of phasmatids have occurred are shown on the following maps.



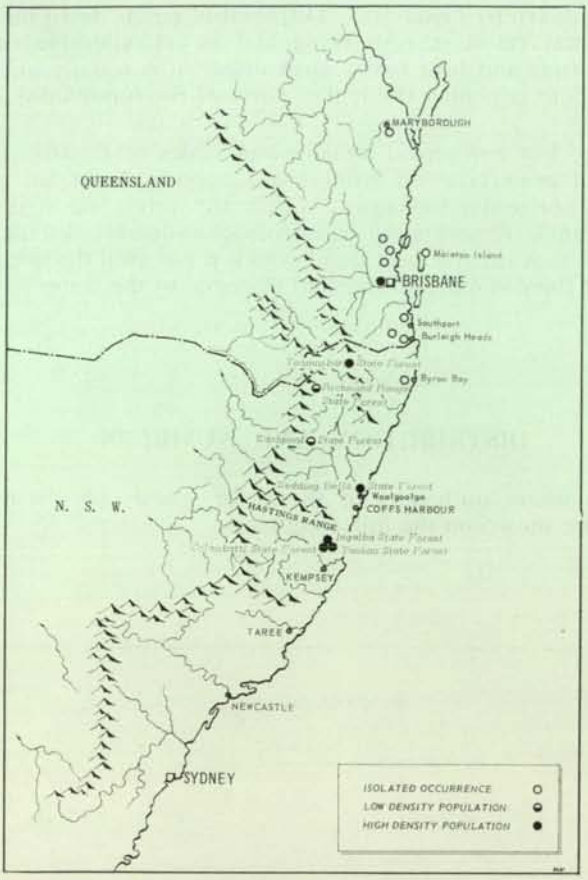


FIGURE II. Maps of general distribution of plague phasmatids

DISTRIBUTION

P. wilkinsoni

This phasmatid is distributed generally over the forested areas of the southeastern highlands and coastal area from northern N.S.W. to Goulburn in N.S.W. It has been recorded in high numbers in the following localities: Mount Warning, near Uki, the highland forests near Walcha and between Walcha and Hanging Rock, Mount Warung State Forest near Coolah and the highland forested areas between Wallerawang and Wombeyan, N.S.W.

The southern boundary of the general distribution of this insect appears to coincide with the northern limit of the winter rainfall zone. Later work has also revealed that temperature is a limiting factor.

D. violescens

This insect has a widespread distribution throughout the forested areas of southeastern Australia, mainly in the highland region and occasionally in the coastal region.

It occurs in association with *P. wilkinsoni* and *P. viridoroseus* at Mount Warning. In the New England Tableland and the central highland forests with *P. wilkinsoni* it has contributed to the defoliation of extensive areas, though in these areas *P. wilkinsoni* has the major role.

On the southern highlands south of Tumut, N.S.W., through the Snowy Mountains and northeastern Victoria, it alone has been responsible for defoliation of hundreds of thousands of acres of highland forest area, some of it commercial forest. Bago S.F. (near Batlow, N.S.W.) has been repeatedly defoliated by this insect since 1953.

C. tessulatus

This phasmatid has been recorded from the coast and coastal highlands from Maryborough (Queensland) to Kempsey (N.S.W.). High numbers of insects have been recorded from Toonumbar S.F. (near Kyogle, N.S.W.), Wedding Bells S.F. (near Woolgoolga, N.S.W.), and Taban, Ingalba and Collombatti S.Fs. (near Kempsey, N.S.W.). Defoliation has been caused to localized areas within forest stands. Extensive defoliation as occurs with the other plague phasmatids does not occur with this insect.

POPULATION STUDIES

In order to study the fluctuations in numbers of these phasmatids, techniques had to be developed so that the various stages of the life cycle could be estimated. The eggs, which are dropped on to the forest floor, are the most readily available; the nymphs and adults which spend most of their lives in the higher parts of the host are less available. If the trees are small, direct counts may be made by cutting off branchlets of a predetermined size and catching and counting the insects. If the trees are over 10 ft in height this method becomes impractical as too many insects escape after the sample is taken or the foliage cannot be reached without special equipment, which is usually unavailable or prohibitive in cost. When the trees are large indirect methods, such as frass measurement, must be used.

1. Egg Stage

The eggs may be sampled directly at any time by collecting the litter down to the mineral soil from a measured area, sorting, sieving, and discarding all material either larger or smaller than the egg and finally removing the eggs. The contents of these may then be examined with the aid of a microscope and the number of viable eggs, those with advanced embryos and those containing parasitic wasps or diseased, determined. Another method (personal communication—J. L. Readshaw—Division of Entomology, CSIRO) of estimating egg numbers is by collecting eggs from a square foot for five minutes and "calibrating" the collector by testing him in localities where the actual density of eggs is known. Allowances are made for the amount of litter, etc., present (i.e., the difficulty of finding the eggs).

All egg sampling must, of course, be done beneath the canopy of a host tree. The intensity of sampling will vary depending on whether a general estimation of the population for, say, prediction of possible plague numbers or whether detailed ecological studies of small units of a population, is desired. Several small samples taken from a locality give a more precise measure of egg numbers present than one large sample covering an equal area, as the density of eggs will vary markedly from place to place even beneath a single host tree.

2. Nymphal and Adult Stages

When the hosts are small the insects may be counted directly or sample branchlets taken as already described. This is rarely possible and indirect methods of estimating numbers are usually necessary where trees are involved.

One effective method is that of measuring the rate of faecal pellet or "frass" production or "frass fall" as it is commonly known. As the insects feed in the crown of the trees, frass produced falls to the ground. This will be small from early instars, increasing in size as the insect grows. The material from which the trap is made must allow for this. To provide accurate measurement the frass is collected at measured intervals, sorted to remove extraneous material and usually dried to constant weight.

To derive actual numbers of insects from the frass collections, known numbers of phasmatids may be held in cages in conditions as near to those in the field as possible and the frass collected from these at measured intervals. A known frass fall per insect per unit of time may be established and used to calculate the number of insects in the field per trap, etc.

The rate of frass fall, i.e., number of pellets per insect per hour may be measured directly and related to the number of insects producing it. The rate varies with the rise and fall of temperature, the number produced at 60° being less than that at 80° F. It varies also with the food tree, sex and in the case of *P. wilkinsoni* slightly with the age of the insect.

For convenience the rate is measured at shade temperatures, though the actual ambient temperature influences the insect's metabolic rate.

The average number of pellets produced per insect per hour of caged insects (5 insects per cage) held at Epping fed on *E. andreana* is shown in the following Table VI.

TABLE VI

P. wilkinsoni

Average number of frass pellets produced per insect per hour

Temperature° F

Instar	50	55	60	70	80	90
2–3 ..	..	1	1	1½	2	3
3–4 <	1	1	1½	2	3	4
4–5 <	1	1	1½	2	3	4
5–6 <	1	1	1½	2	3	4

In the field with a different host the rate may be different and this must be determined for relevant host and site. J. L. Readshaw (personal communication) has found that, in the case of *D. violescens*, the rate is more constant, i.e. 1 at 50°, 2 at 60° and 3 at 70° at all instars.

If the insects are mature and the females ovipositing, a similar comparison of eggs laid in the field and those in cages may be made to estimate field numbers of females and as a check on the frass fall method.

These methods have been found to be of value in control experiments where knowledge of population density before and after application of the control (insecticide, fire or other treatment) is required. Here the

actual number of insects is less important than the proportional effect of the treatment. If sufficient traps are laid a reasonably accurate measure of this may be obtained by these methods. Where accurate figures of numbers of insects are required the number of traps may be increased and more attention given to deriving the frass produced by known numbers of insects. As the frass produced by female insects is larger than that produced by males, particularly when adult, this must also be taken into account when greater accuracy is desired.

It has been apparent from the initial appearance of the plagues that environmental factors were not exerting sufficient influence on the populations of phasmatids to reduce the numbers to a level below that which would produce defoliation and economic loss. Before chemical control was attempted it was necessary to be able to assess the insect population so that the efficacy of any insecticide or method of application could be estimated.

CONTROL BY USE OF INSECTICIDE

Ground spraying

(a) BAGO STATE FOREST

PLATE XI. Severe defoliation by *D. violescens* in 1954-55 at Bago S.F.

In 1954 high numbers of *D. violescens* were thought to be confined to about 600 acres of forest. Ground spraying with a 0·5 per cent aqueous solution of Dieldrin was carried out, prior to emergence of the nymphs from the eggs, in an attempt to reduce the population over this comparatively small area. In September each tree in the area was treated by spraying the ground around its base out to a radius of seven feet and all around the trunk up to a height of seven feet from the ground. This provided a continuous barrier of insecticide over which the newly hatched phasmatids had to cross to reach the foliage.

The results were not estimated quantitatively but from observation the barrier was at least partially effective. Although some insects were present in the foliage, trees within the area sprayed were not so severely defoliated as those outside. It was found later in the season that the 600 acres treated was only a small part of the area where the phasmatids were in high numbers and dispersal of insects by flight from the surrounding forest probably took place.

(b) Jenolan Area

Field trials using organic-phosphate insecticides were carried out near Jenolan Caves at the end of October, 1957, where nymphs of both *D. violescens* and *P. wilkinsoni* were present.

PLATE XII. Death of Eucalypts following repeated defoliations by *D. violescens* and *P. wilkinsoni* at Konangaroo S.F. (near Jenolan)

To simulate the range of droplet sizes which could be expected when spraying solution from an aircraft, a "Swingfog" fogging machine was used to apply a high concentration solution of the insecticide in diesel-distillate oil. Malathion, Trithion and Diazinon were used at concentrations of ½ to 1½ ounces of active ingredient per gallon of oil with an additional test of Malathion at 3 ounces per gallon. Malathion gave significantly better control than the other insecticides at 1½ ounces per gallon, and there was no significant advantage using 3 ounces per gallon. This insecticide has a short residual action under field conditions and also a low mammalian toxicity so that it has certain advantages when used in large scale aerial sprayings of these insects.

Aerial Spraying

(a) BAGO STATE FOREST

(1) In January, 1955, an aerial spraying of about 500 acres of forest was attempted, using a Douglas DC3 (Dakota) fixed-wing aircraft belonging to the Royal Australian Air Force. Dieldrin was applied at the rate of 8 ounces per gallon of diesel fuel oil per acre. A high percentage kill was achieved, but little useful information was obtained because of faults in both the aircraft and spray-dispensing apparatus.

(2) In March, 1957, a De Havilland "Agricultural Beaver" fixed-wing aircraft was used to spray an experimental area of about 500 acres of forest. Two insecticides, Dieldrin and benzene hexachloride, were used for comparison and were to have been applied at a rate of 2 ounces of active ingredient to 2 gallons of diesel distillate per acre. However, due to a technical inability, the aircraft applied only a little over 1 gallon per acre and, although some "knock down" of insects was achieved, the percentage kill was so low that it could not be measured by the frass-fall method used to assess it.

PLATE XIII. Severe defoliation by *P. wilkinsoni* at Nundle/Hanging Rock S.Fs. in 1951-52

(b) NUNDLE STATE FOREST

In January, 1960, a replicated field experiment was carried out using a Bristol "Sycamore" helicopter aircraft. Two insecticides, benzene hexachloride and Malathion were tested both at a concentration of 1½ ounces of active ingredient per gallon of diesel fuel oil. Each insecticide was applied at two rates—two and three gallons per acre, an untreated control being provided for comparison. Each treatment was replicated three times (15 blocks in all) and a total of 350 acres was treated.

Malathion at the rate of 4½ ounces in 3 gallons of diesel fuel oil per acre proved to be most effective. The results of this experiment were used at Bogong.

(c) BOGONG, VICTORIA

In January, 1961, aerial spraying of about 6,500 acres of steep country (elevation 2,000-4,200 ft) in the forested catchments of the east and west Kiewa rivers was carried out to control *D. violescens*. This was done to prevent defoliation of the tree cover by the phasmatids, which might be followed by accelerated erosion of the steep slopes and siltation of the hydro-electric works of the State Electricity Commission of Victoria situated there. A "Sycamore" helicopter was used to apply Malathion at the rate of 5½ ounces of active ingredient in 3 gallons of light fuel oil per acre. Newman and Endacott (1962).

Spraying was stopped as soon as oviposition by the phasmatids commenced. This was done to ensure that this insecticide chosen for its short residual action would have little or no deleterious effects on the emerging wasp parasites. It was hoped that eggs laid by any surviving phasmatids would be dealt with by these biological agents.

Assessment (using the frass-fall method) of the spraying of a 50 acre experimental plot, indicated a high percentage kill of insects and observations showed that a high level of mortality resulted over the whole of the treated area. In this there was no defoliation, but in adjoining unsprayed areas it was severe. A further area of about 7,000 acres previously unsprayed, was treated similarly in 1962-63. This time a "Bell" helicopter was used. Again the treatment was successful and no noticeable defoliation occurred. (R. L. Newman unpublished report S.E.C.V.). From the time of spraying to the present the phasmatid population in the treated areas has remained at a low-density level at a time when in nearby areas of Victoria population density has remained high.

(d) MOUNT BUFFALO, VICTORIA

In late January, 1961, a fixed-wing Wackett "Ceres" aircraft was used to spray 1,000 acres of phasmatid-infested forest with Malathion at the same rate as at Bogong, with similar success.

The successful practical application of the experimental results obtained at Nundle was most encouraging to all concerned.

DISCUSSION

Probable causes of phasmatid plagues

At the present stage of investigation, no final conclusions have been reached as to the causes of phasmatid plagues. High numbers of both *D. violescens* and *P. wilkinsoni* have been present for the last ten years at least, although in 1957 wild fires are considered to have reduced the populations of *P. wilkinsoni* to very low numbers in the central and New England highland forests. It is known in the case of this latter insect, at least, that protracted plagues took place during the early years of this century.

Even though the insects are present at low numbers for some years, they are capable of increasing rapidly in several generations. For a population to maintain its density each female must produce 2 progeny, a male and a female, which must reach adulthood and reproduce similarly. Any reduction in mortality results in an increase in numbers and when the female is capable of producing hundreds of eggs a slight percentage reduction will result in an "explosion" of the population to plague numbers. This must be borne in mind when considering mortality factors, as one which causes only a small proportion of deaths may determine whether or not the insect can persist at all but not the density at which it persists.

Mortality factors

At present the known mortality factors may be considered as:

Parasites, predators, disease.
Dispersal.
Intraspecific competition.
Security of the environment.
Stand factors.

Egg parasites and predators

These account for quite a high percentage of mortalities of the eggs. In most of the phasmatid populations with mainly a two-year life cycle (*P. wilkinsoni* and *D. violescens*) there are two segments of the population, one of which is at a high density (or plague) and the other one at low density. For example, with *D. violescens* at Bago S. F. the high-density segment adults are present during the even-ended years (1954/6/8, etc.), and the low-density segment present during the odd-numbered years (1955/7/9, etc.). There is some slight overlapping of these segments due the the presence of one-year life cycle forms of the insect.

From studies of the wasp parasites, it appears that these have one-year and two-year life cycle forms with the one-year life cycle predominating (at least in the more southern regions). Apparently only eggs with no embryonic development are suitable for wasp oviposition so that opportunities for the parasite to increase in numbers sufficient to reduce the population to low densities are limited. Freshly laid eggs are more available to the parasites as they are not covered by the forest litter as are those laid earlier in the season. As the female is wingless and must search on foot for the eggs amongst the litter, it should be more

efficient at high egg densities than at low. However, higher numbers of wasps produced from eggs of the high-density segment will have relatively few eggs from the low-density segment to parasitize the following year. This will tend to perpetuate this state rather than reverse it. If enough "two-year" wasps have their life cycle "in phase" with the high-density segment they may in time reduce it.

Quite large numbers of eggs fail to develop for undetermined reasons (shown as "diseased or deteriorated" in egg dissection tabulations). Some of these are no doubt unfertilized eggs and some may be infected by disease and the implications of the former will be discussed later. Predation of the eggs by ants, lizards, birds and other animals occurs and mortality of eggs in the field due to these is often considerable.

Nymphal and adult stages

Birds (Crows, Currawongs, Wattle birds, Magpies, etc.), account for large numbers of nymphs and adults, but are seldom present in high enough numbers to exercise effective control. However, several instances (Jenolan and Nundle) where isolated pockets of high numbers of mainly adult phasmatids have been almost completely eliminated by birds, are known.

A red mite *Charltonia* sp. (f. Erythraeidae) is parasitic on nymphs and adults but does not appear to cause much mortality. Sarcophagid flies were noted to be endoparasitic on *D. violescens* at the end of the feeding season of 1959, but are apparently of small significance. Gordion worms accounted for large numbers of *P. wilkinsoni* at Wombeyan, N.S.W., in 1961-62, many deaths occurring in the late nymphal and early adult stages.

Dispersal

Differential dispersal of the sexes in adult insects is commonplace, particularly along margins between forest and open country. Males are better fliers and can move further and movement is much easier away from the forest, as the insects find it difficult to rise from the ground to fly back. Dispersal is more likely to take place downwind and downhill.

Intraspecific competition

Although in a forest the food of phasmatids may appear virtually unlimited, this is sometimes not so. All hosts are not equally favoured, in the case of *D. violescens* and *P. wilkinsoni* the order generally being (1) peppermints; (2) gums; (3) other species, and when numbers of insects are high this is usually the order of severe defoliation. Newly emerged nymphs require relatively tender foliage as food in the early part of their lives. If most of the leaves are old or harsh at this time, mortality of the nymphs due to lack of suitable food may be heavy. The species composition and vigour of the stand, as well as the weather conditions, may influence this.

When the population is very dense, the negatively-geotactic behaviour of the insects causes them to congregate on the most terminal part of the leaf bearing shoots and jostling for feeding positions causes some insects to fall from the tree, which they must then reclimb to recommence feeding. In a few instances *P. wilkinsoni* has eaten or destroyed virtually all the *Eucalyptus* spp. foliage over large areas of the Nundle/Hanging Rock S.Fs., exhausting the food supply before many insects became mature and laid eggs. Numbers in this area were subsequently very low for several generations.

Environmental security

The forested areas where these insects are known to occur, or to have occurred, in high numbers, have probably been subject to "wild" fires at different times over a very long period. The species composition of present forests has been influenced by their past fire history and even-aged stands composed largely of one or a few *Eucalyptus* species are one result. Large-scale fires are obviously unfavourable to tree dwelling species such as the phasmatid nymphs and adults, and if fires have been recurrent at short intervals, low numbers of these insects would be expected. However, smaller fires at periods of the year when only eggs are present may have different effects, perhaps reducing the number of egg parasites relative to those of the phasmatids, or vice versa (Campbell 1961).

There appears to be little doubt that, since fire control and prevention have been more successful during the past 25 years, extensive fires have been rare (except in the previously mentioned instances) on the areas where phasmatids have been present in high numbers and that freedom from fire is an important factor contributing to increase of these insects.

Forest stand factors

It appears that areas of even-aged stands composed of a few species of medium to large-sized trees are favourable to phasmatid increase. Large areas of small regeneration without a number of larger overstorey trees does not appear to favour increase. Whether this affects the successful dispersal of these insects in mating or feeding or renders them more vulnerable to desiccation or predation, has not been established.

To sum up, the probable causes contributing to phasmatid outbreaks are considered to be:

(1) Security of the environment—protection from fire over large areas for lengthy periods;

(2) Food supply not limited;

(3) Stand factors favourable—even-aged, few and favoured species, stands of medium to large trees common over extensive areas;

(4) Cleptid wasp egg parasites "out of phase" with major segment of phasmatid population.

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