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POPULATION BIOLOGY OF *CHLENIAS* SP., A GEOMETRID DEFOLIATOR OF *PINUS RADIATA* IN TASMANIA

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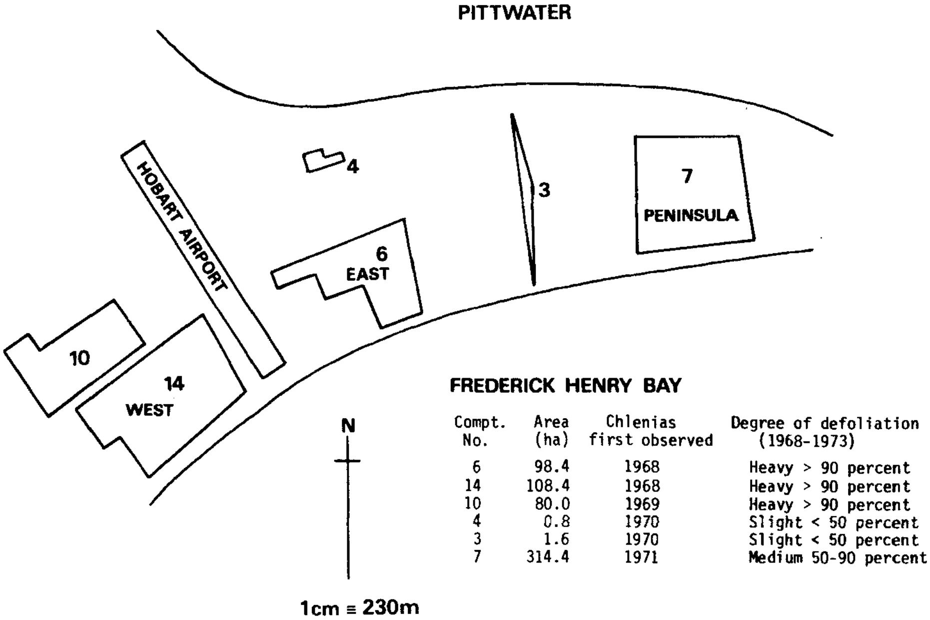
Abstract

An analysis of the factors influencing populations of the moth, *Chlenias* sp., is given with respect to the host tree, parasitism, predation and disease. The phenologies of these various agents are given, together with an account of their general behaviour and effectiveness. Predisposition of the host tree to attack by the woodwasp, *Sirex noctilio* F., following defoliation, is also discussed.

Introduction

The basic biology and behaviour of *Chlenias* sp., a native geometrid defoliator of *Pinus radiata* D. Don, have been described (Madden and Bashford 1977). Adult moths emerge through the litter at Pittwater, Tasmania, from mid-April to mid-July when the dusk temperature is consistently below 4.5°C. Eggs are deposited in batches on the terminal needles and hatch in 6-7 weeks. There are six larval instars, and pupation occurs within a silken-sand cocoon at the soil-litter interface from early November to December. Defoliation becomes increasingly evident when the larvae have reached the fourth and subsequent instars.

This paper describes five populations of the moth in three separate stands of regeneration in 1969-70, 1970-71 and 1971-72, in terms of annual budgets. The outbreak extended from 1968-72. A progressive reduction of suitable food and the action of natural enemies and disease resulted in the virtual disappearance of the moth from the study areas although recoveries of low numbers from other plantation areas have been recorded since that time. Other *Chlenias* species have caused damage in radiata nurseries and plantations in the mainland states (Minko 1965), and South Australia (Bednell *in* Rawlings 1960).



Compt. No.	Area (ha)	Chlenias first observed	Degree of defoliation (1968-1973)
6	98.4	1968	Heavy > 90 percent
14	108.4	1968	Heavy > 90 percent
10	80.0	1969	Heavy > 90 percent
4	0.8	1970	Slight < 50 percent
3	1.6	1970	Slight < 50 percent
7	314.4	1971	Medium 50-90 percent

FIG. 1—Location of experimental areas and summary of defoliation history at Pittwater, Tasmania 1967-1972.

Materials and Methods

The study was carried out in 1-16 year old radiata pine regeneration at Pittwater, Tasmania. The area includes a peninsula of land and is divided by the Hobart Airport and areas of clear felling into three separate areas designated West, East and Peninsula blocks (Fig. 1).

The outbreak commenced in the Western block in 1968-69 and in the next two years spread to the Eastern and Peninsula blocks respectively. Routine weekly sampling of egg and larval populations was commenced in the Western and Eastern blocks in 1969-70 and the Eastern and Peninsula blocks in 1970-71 and 1971-72. No significant population remained in the Western block in 1970-71, nor in any other areas at Pittwater following 1972.

The sample unit was a 15 cm long lateral shoot. Twenty infested shoots were selected at random, removed with secateurs and transferred to labelled plastic bags for detailed census and dissection in the laboratory. A minimum number of 20 shoots per tree was examined for the presence of *Chlenias* sp. before that tree was rejected and a new one chosen. A new tree was selected after the location of an infested shoot. This procedure resulted in a large number of trees being examined in the early and late stages of

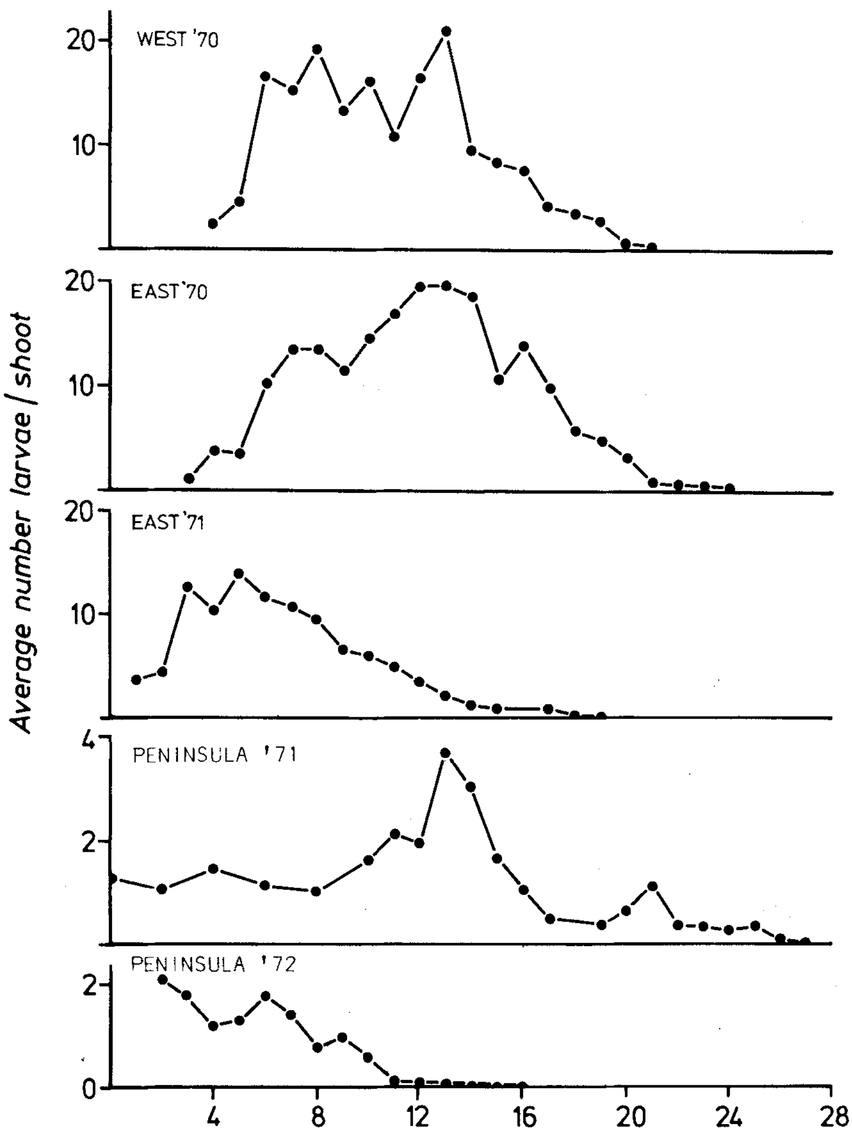


FIG. 2—Seasonal trends in five populations of *Chlenias* sp. larvae at Pittwater, Tasmania, 1970-1972.

the larval period, whereas in mid-season only 20 trees were required to obtain the requisite number of 20 samples from each study area.

Egg clusters within the samples were held separately in the laboratory to evaluate survival and parasitism, while larvae from each twig sample were counted, width of head capsules measured and thereby allocated to instar, and dissected for estimating parasitism and/or disease.

Adult emergence was followed in 10 × 1 m^2 field cages placed on the litter beneath defoliated trees and in batches of pupae previously collected from 1 m^2 areas and held in the laboratory in stoppered bottles. Avian predation of adult moths was assessed by counting the numbers of wings occurring on 1 × 12 m strips on roads within the regrowth.

Estimates of tree density were obtained by counting the number of trees in 16 m^2 plots. Levels of defoliation were subjectively assessed into percentage classes. The behaviour of the parasitoids was observed directly in the field and the laboratory. Potentially diseased larvae were dissected and tissue and lymph samples examined under high magnification and micrographs of the disease producing entity were obtained.

Results

The outbreak area was grossly overstocked and averaged 30,000 seedlings ha^{-1}. The course of the outbreak was such that population changes in the three study areas over the three seasons reflected a sequence of increasing regulation by natural enemies. These population trends are shown in Fig. 2.

Eggs were parasitized by a scelionid, *Aholcus* sp., (Scelionidae: Teleonominae) and larval stages by a braconid, *Protomicroplitis* sp. and a tachinid, *Chlorotachina* sp. (Tachinidae: *Ernestinii*). Late stage larvae were increasingly prone to infection by a polyhedrosis virus disease. Incidental predators of larvae included ants, reduviids, spiders, chrysopids and pentatomids, and pupae were attacked by the ichneumonids, *Theronia viridicans* and *Echthromorpha intricatoria.*

The Raven (*Corvus coronoides*) was observed to scratch and disturb the litter and prey on both healthy and diseased pupae in the Peninsula block in 1971 and 1972.

Adult moths were attacked chiefly by two bird species. Silver Eyes (*Zoosterops harmaturina*) fed on instars I to III from May through to October, and adult moths were taken also by this predator and the Blue Wren (*Malurus cyaneus*) as they rested on the foliage during the day. Plot counts of wings taken during the period of peak adult emergence in the Eastern block during 1970 and 1971 averaged 3.3 moths. $m.^{-2}$ day^{-1}, or 33,000 ha^{-1}. Average emergence of adults from the litter at this time was 4.0 moths. $m.^{-2}$ day^{-1}.

At least 2 generations of *Aholcus* sp. attack *Chlenias* eggs, the average development period being 40-60 d. This parasitoid was not species specific as it was recovered from the egg clusters of other moths (families: Geometridae, Lasiocampidae, Lymantriidae) at other times of the year. Average parasitism per parasitized egg cluster was 82%.

The braconid, *Protomicroplitis* sp. chiefly attacked the 3rd instar *Chlenias*, although a small number of 1st and 2nd instars were also attacked. Although multiple parasitism occurred, encounter and combat between highly mandibulate first instar larvae resulted in only one parasitoid per host. There were three larval instars and

TABLE 1
STAGE OCCUPANCY OF SHOOTS. PERCENTAGE OF SHOOTS OCCUPIED BY *CHLENIAS* SP. LARVAE IN FIVE POPULATIONS SAMPLED AT PITTWATER, TASMANIA, 1970-1972

Instar	Population				
	West 1970	East 1970	East 1971	Peninsula 1971	Peninsula 1972
I	64.0	76.0	49.0	32.0	46.0
II	64.0	46.0	44.0	42.0	24.0
III	70.0	41.0	49.0	10.0	14.0
IV	78.0	31.0	44.0	12.0	9.2
V	21.0	34.0	15.0	12.0	1.8
VI	14.0	26.0	5.0	8.4	0.4
Average	51.8	42.3	34.3	21.1	15.9

TABLE 2
THE BUDGETS OF FIVE POPULATIONS OF *CHLENIAS* SP. EVALUATED AT PITTWATER, TASMANIA FROM 1970 TO 1972. DENSITY EXPRESSED ON FREQUENCY. SHOOT^{-1} BASIS[1]

Stage	Population	West 1970		East 1970		East 1971		Peninsula 1971[3]		Peninsula 1972	
	Mortality Factors	Frequency	Proportional Reduction	Frequency	Proportional Reduction	Frequency	Proportional Reduction	Frequency	Proportional Reduction	Frequency	Proportional Reduction
Egg Clusters (Ave. 112 Eggs/Cluster)		0.09		0.16		0.08		0.025		0.020	
Eggs		9.99		17.80		8.88		2.78		2.22	
	AHOLCUS SP.		0.17		0.43		0.42		0.42		0.70
	DESICCATION PREDATION DISPERSAL ON HATCH[2]		0.33		0.30		0.38		0.37		0.18
Larvae I		3.15		5.10		1.88		0.18(0.59)		0.48	
	PROTOMICROPLITIS SP.		0.00(9)		—		0.006		0.21		0.30
	PREDATION DISPERSAL		0.29		0.70		0.010		?		0.50
Larvae II		2.20		1.48		1.85		0.22(0.47)		0.17	
	PROTOMICROPLITIS SP.		0.02		—		0.370		0.26		0.18
	POLYHEDROSIS PREDATION		0.08		0.52		0.490		?		0.12
Larvae III		1.98		0.72		0.69		0.23(0.35)		0.12	
	PROTOMICROPLITIS SP.		0.26		—		0.500		0.25		0.35
	POLYHEDROSIS PREDATION		0.37		0.17		0.170		?		0.23
Larvae IV		1.04		0.60		0.29		0.26		0.05	
	PROTOMICROPLITIS SP.		0.46		0.01(9)		0.674		0.30		—
	POLYHEDROSIS PREDATION AND DISPERSAL		0.02		0.10		0.470		0.39		0.92
Larvae V		0.55		0.53		0.05		0.11		0.00(4)	
	PROTOMICROPLITIS SP.		0.41		0.01(6)		0.780		0.32		—
	POLYHEDROSIS		0.23								
	TACHINID AND PREDATION		0.16		0.56		0.82		0.47		0.75

Larvae VI		0.11		0.23		0.02		0.04		0.00(1)	
	POLYHEDROSIS		0.20		0.10		0.25		0.40		0.70
Pupae		0.09		0.21		0.01(5)		0.01(4)		0.00(03)	
	POLYHEDROSIS		0.17		0.01		0.27		0.40		0.90
		0.07		0.20(8)		0.01(1)		0.01(4)		0.00(003)	
Status of Larval Food Supply		PROGRESSIVE TO COMPLETE DEFOLIATION WITH DEATH OF MANY TREES. MORTALITY 0.74.		COMPLETE DEFOLIATION OF MANY SMALL TREES AND SOME CROWNS. MORTALITY 0.11.		PROGRESSIVE TO COMPLETE DEFOLIATION WITH DEATH OF MANY TREES. MORTALITY 0.59.		MEDIUM DEFOLIATION OF CROWNS AND NEW LATERAL GROWTH.		CONTINUED DESTRUCTION OF NEW GROWTH—NO DEATH OF TREES.	

[1] The values for proportional reduction preceded by parentheses were estimated from the difference between survival expected following parasitism (or disease) and the observed survival.

[2] Madden and Bashford (1977) reported that the bulk of egg clusters were deposited on shoots between 2-4 m in 7 m high trees. The positive phototactic response of *Chlenias* sp. larvae would result in a nett movement of larvae from the base of the trees. All shoot samples were taken from 1-2 m high.

[3] Values for instars I-III underestimated, as intensive weekly sampling was not commenced until 30/9. Figures in parenthesis are estimates derived by backworking parasitism from instar IV estimate—the difference 0.37 (0.82 individuals. $shoot^{-1}$) should be distributed through instars I-III.

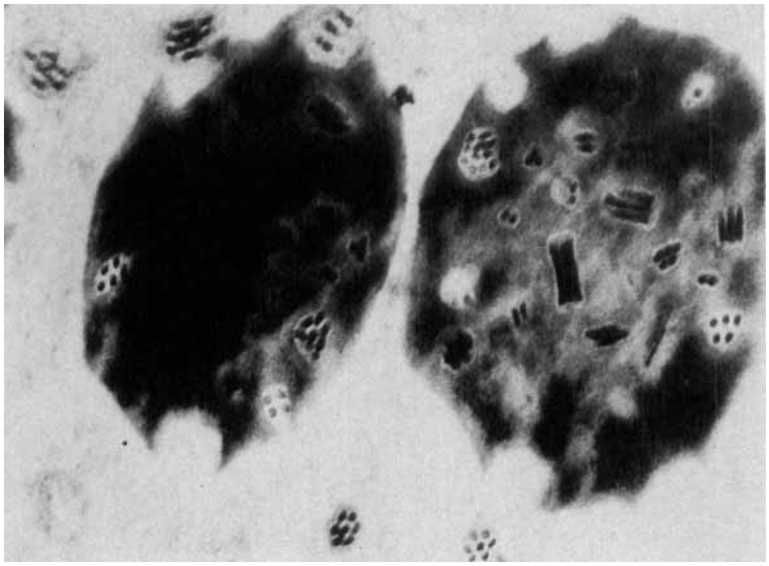


FIG. 3—Nuclear polyhedrosis disease of *Chlenias* sp. larvae—polyhedral bodies with inclusion of virions (maximum number 7). Magnification 44,000×.

the larvae remained within the host until it had reached the 5th instar. The parasitoid then emerged through the dorsal wall between the 6th and 7th abdominal segments to pupate on the host.

The caudal vesicle ensured that the parasitoid larva remained attached to the host until the pupal case was constructed. The pupal case was spun in two sections—the dorsal half of the pupal case was spun first on the ventral surface of the larva. After completion, the larva leant away from the section and, by arching its body, lifted the section onto its dorsal surface. The ventral half was then spun and loosely attached to the dorsal section at the pleural margins. When the larva was completely enclosed it moved into the framework to consolidate the walls and complete the case. The entire construction period was 120-180 min. The parasitized *Chlenias* sp. larva moved, with the attached *Protomicroplitis* sp. pupa, toward the bottom of the tree and died within 48 h of parasitoid emergence and pupation. The parasitoid pupa eventually fell to the litter. The adult braconid emerged from the litter nine months later although a small number emerged in the laboratory within 10 weeks. Two species of chalcid super parasites of *Protomicroplitis* pupae were found to occur at low frequency.

The parasitoid tended to favour open and sunny situations and adults basked on the foliage of pine and other vegetation, e.g. *Acacia* sp. Parasitoids searched the foliage for hosts and upon location slowly approached until the extended antennae touched the host surface. The parasitoid then sprang forward and thrust the ovipositor into the host which responded by writhing and dislodgment of the parasitoid.

The tachinid parasitoid, *Chlorotachina* sp.* was confined to the peripheral regions of the study sites with the exception of the heavily defoliated and well illuminated Western blocks. Eggs were deposited on the surface of the host and as many as four larvae were found in single hosts. However, only one or sometimes two emerged to pupate in the soil.

The virus disease was first observed in late stage larvae in the Western block in 1970 and subsequently in all other blocks at a time when food was in short supply and larvae were migrating between trees. Apparently healthy larvae were collected from an area with a high incidence of disease. After 36 h, the majority of larvae were

*Crosskey (1973) lists Hesperiidae as hosts of this genus.

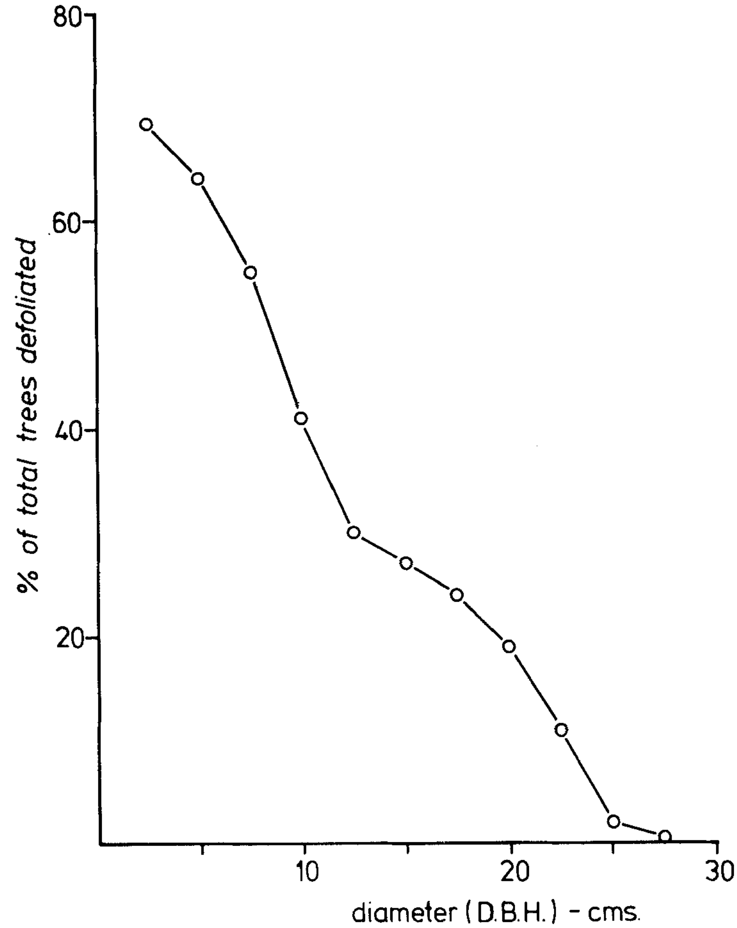


FIG. 4—Susceptibility of *P. radiata* regeneration to defoliation by *Chlenias* sp. larvae with respect to tree size. Size measured by diameter at breast height (d.b.h.) i.e. 1.25 m above ground. Compartment 6 (East), Pittwater, Tasmania 1971.

inactive with a limited movement of the thoracic legs and anal claspers. Larvae remained in this condition for the next 48 h at which time movement was observable only beyond segment 6. The larvae became denser and began to shrink to complete collapse during the following 24 h. The infection bodies are illustrated in Fig. 3.

Shoot occupancy varied throughout the season (Table 1) and declined from an average 51.8% in West 1970 to 15.9% in Peninsula 1972. Occupancy progressively declined through the instars with the exception of the populations of West 1970 and East 1971 in which occupancy increased during the 3rd instar. Egg cluster and larval numbers and shoot occupancy data were adjusted to a 20 infested shoot basis which, in combination with estimates for parasitism and disease, provided a series of budgets (Table 2). Overall survival from egg to pupae was 0.74, 1.17, 0.12, 0.005 and 0.001% for West 1970, East 1970, East 1971, Peninsula 1971 and 1972 respectively.

High mortality occurred in the egg-instar I stadia and the chief mortality agents were *Aholcus* sp., desiccation, predation and failure to locate suitable feeding sites. Both desiccation and the inability to locate food were more prevalent in late hatching eggs and in previously defoliated areas. First instar larvae were also attacked by *Protomicroplitis* in Peninsula 1971 and 1972, but whether these parasitoids would have survived is unknown.

Second to fifth stage larvae were increasingly attacked by *Protomicroplitis*, virus

TABLE 3

DEGREE OF DEFOLIATION AND DIAMETER. DEFOLIATION WITH RESPECT TO TREE DIAMETER IN TWO COMPARTMENTS OF DIFFERENT STOCKING INTENSITIES

A. EAST 1970 COMPARTMENT 6—ESTIMATED NUMBER OF TREES 8000.ha^{-1}

Degree of defoliation	Diameter at 1.25 m (cms) 2.5	5.0	7.5	10.0	12.5	15.0	17.5	20.0	22.5	25.0	Total	Nos attacked by *S. noctilio*	Proportion
Heavy ≃ 90-100%	287	193	29	15	3						527	96	.182
Medium 60-90	25	33	18	11	—						87	10	.115
Light* 10-60	32	32	15	11	7	2	2				104	5	.050
Healthy* < 10%	71	47	31	31	17	18	5	3	4	1	228	39	.171
TOTAL	415	305	93	68	27	20	7	3	4	1	943		

* Defoliation confined to apical regions in these trees.

B. WEST 1970 COMPARTMENT 10—ESTIMATED NUMBER OF TREES 80 000.ha^{-1}

Degree of defoliation*	Diameter at 1.25 m (cms) 2.5	5.0	7.5	10.0	12.5	15.0	17.5	20.0	22.5	25.0	Total	Nos attacked by *S. noctilio*	Proportion
Heavy ≃ 90-100%	199	155	69	11	3						437	32	.073
Medium	1	1	2	4	–						8	3	.375
Light	1	2	5	–	–						8	1	.125
Healthy	8	6	4	2	1						21	–	—
TOTAL	209	164	80	17	4						474		

* Majority of trees defoliated to some extent in previous season

and avian predators. Tachinid parasitism was generally confined to groups of larvae in the more open Western and Peninsula areas and was low overall.

Sixth instar larvae were free of parasitoids but prone to virus disease and predation and all populations with the exception of East 1970 had high levels of virus infection which was carried over into the pupal population to remain latent until the following season.

The preference of adults to deposit egg clusters on younger shoots was reflected in the extent of defoliation in trees of different sizes (Fig. 4). Surveys in areas with differing densities of trees indicated that excessive overstocking of seedling trees in the Western block provided optimal conditions for the development of the outbreak. Defoliation resulted in the death of many trees, while many survivors were so physiologically stressed that they were prone to *Sirex* attack in the following summer months (Table 3).

Discussion

Excessive overstocking with seedling trees provided dense young foliage for the establishment of a *Chlenias* sp. population in the Western block in 1967-68, which in the absence of significant parasitism and disease grew and dispersed to other areas resulting in defoliation, death and predisposition of trees to *Sirex* attack.

The greater attractiveness of apparently healthy trees to *Sirex* emphasizes the importance of *Chlenias* sp. and the reaction of the host tree to infestation. Small diameter trees were able to overcome the defoliation effect and the regeneration of shoots resulted in high survival. In contrast, defoliation of larger trees resulted in irreversible alterations in water relationships and new shoots withered and died. Trees which died in the spring were unattractive to *Sirex* during the summer but moribund trees were attractive. Madden (1977) reported that slight damage to the crown of the host tree resulted in changes in its physiological status and increased the probability of *Sirex* attack. Therefore, defoliation by *Chlenias* sp. resulted in physiological stress, the duration of which increased with tree size and many slightly defoliated, large diameter trees were attractive to *Sirex* in the summer following the defoliation.

The budgets describe a pattern of increasing control by egg mortality, *Protomicroplitis* and polyhedrosis. The virus disease becomes increasingly evident following the marked increase in defoliation by fourth and subsequent instar larvae and, with the exception of East 1970, all populations were undoubtedly experiencing a shortage of food as late stage larvae moved from tree to tree in search of food. Fragmentation

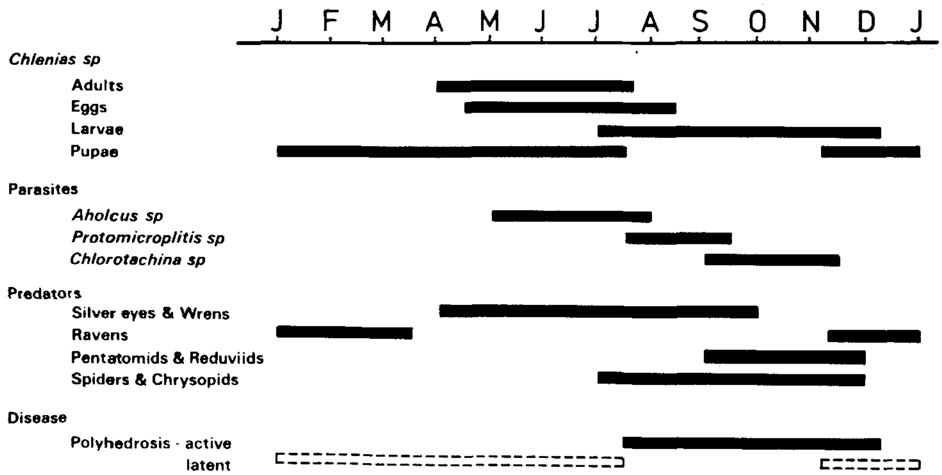


FIG. 5 The seasonal incidence of all stages of *Chlenias* sp. and active stages of its natural enemies at Pittwater, Tasmania.

of diseased pupae within the litter would lead to the contamination of the general environment with virus particles. Many broken pupae were found during sampling and predation by small rodents and insect larvae was suspected.

The effect of avian predators was not fully assessed, however, larval and pupal predation together with the removal of adult moths would be collectively significant.

A similar pattern of control was observed in the attack of hedged *Cupressus macrocarpa* at Queenborough Oval, Sandy Bay, Tasmania, by another species of *Chlenias* in 1970-71. Parasitism by *Aholcus*, *Protomicroplitis* and an unidentified tachinid together with a granulosis disease resulted in the disappearance of this moth at the end of its second season. A high larval population was observed again in October, 1976.

The populations sampled represented a succession from decline (West 1970), establishment (East 1970, Peninsula 1971) and decline (East 1971, Peninsula 1972), and no active stages were found in these areas after 1972 despite intensive sampling and light trapping during the adult period. The increase in shoot occupancy by 3rd and 4th instar larvae in West 1970 and 3rd instar larvae in East 1971 was the result of the dispersal of larvae from defoliated shoots. Trees in both of these areas had been defoliated the previous season and the following season's shoots were small and therefore rapidly defoliated by the 1st and 2nd stage larvae. The sequence of natural enemies and disease ensured that all stages of *Chlenias* sp. were attacked and the host population suppressed within an area after two-three generations.

An abundance of suitable food, such as found in high intensity nursery stock or unmanaged natural regeneration, appears to be a necessary prerequisite for an outbreak of *Chlenias* sp. Under plantation conditions populations are regulated by the quality and quantity of larval food and this regulation is reinforced by such agencies as *Aholcus*, *Protomicroplitis*, polyhedrosis and avian predation. The seasonal incidence of the natural enemies with respect to the host is shown in (Fig. 5).

Acknowledgments

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