

The Sirex woodwasp:  
ecology and control of an  
introduced forest insect

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Introduction

In the northern hemisphere siricid woodwasps, which infest both softwoods and hardwoods (Cameron 1965; Wolf 1967), have developed an interesting symbiotic association with basidiomycetous fungi (Büchner 1928). Although in their natural habitat the woodwasps are regarded as secondary pests attacking dead or dying trees, one species, *Sirex noctilio* F., which was accidentally introduced into New Zealand and Australia, has been responsible for serious damage in plantations of the predominant exotic softwood, *Pinus radiata* D. Don.

Historical and pest status

*S. noctilio* was found in the North Island of New Zealand as far back as 1900 (Miller and Clark 1935). It was 'by no means a common species' for many years, but in 1927, because of its 'abnormal abundance' in plantations of exotic conifers, steps were taken to locate and introduce parasites for its control. From 1940 to 1949 abnormal mortality due to *S. noctilio* occurred in *P. radiata* plantations (Rawlings 1948; Rawlings and Wilson 1949).

In March 1952 *S. noctilio* was discovered in a private plantation of *P. radiata* at Pittwater, near Hobart Airport (Gilbert and Miller 1952). Unsuccessful attempts were made to eradicate it, and by 1959 tree mortality in the plantation had reached about 40%.

Late in 1961, the pest was discovered in Victoria (Irvine 1962), which greatly increased the possibility of its spreading to the large plantations in western Victoria and South Australia. A meeting of Commonwealth and State ministers in January 1962 decided to set up a National Sirex Fund, to which all States contributed approximately in proportion to the area of their plantations of *Pinus* spp., and their total contributions were matched by the Commonwealth Government. Private forest owners also contributed. The Fund was administered by a committee that coordinated research activities and 'search and destroy' operations in Victoria.

The research program that followed has attracted world-wide interest as an example of a multidisciplinary approach to a national problem. *Sirex noctilio* and all its host trees in Australia were endemic to the northern hemisphere, the principal host, *P. radiata*, being restricted to a limited natural habitat in California. As none of its natural enemies was present in Australia the possibility of biological control was given high priority, and a large-scale search for insect parasitoids was initiated in 1962 by the Division of Entomology, CSIRO. The program was later extended to include a search for parasitic

nematodes, first discovered in New Zealand in 1962 (Zondag 1969). The Division also studied the ecology and behaviour of *S. noctilio* and its parasitoids both in Tasmania and (with other siricids) overseas. The Forest Research Institute, Forestry and Timber Bureau (now Division of Forest Research, CSIRO) studied aspects of tree physiology, relationships between the tree and the symbiotic fungus, and tree breeding. The Waite Agricultural Research Institute, University of Adelaide, undertook studies on insect/fungus relationships and investigated the possibility of using chemical control combined with chemical attractants. Others involved were the Forests Commission, Victoria; the Forestry Commission of Tasmania; the Commonwealth Institute of Biological Control; the Forest Research Institute, New Zealand; the University of Tasmania; and the Division of Building Research, CSIRO.

*S. noctilio* occurs naturally throughout Europe, reaching its greatest density in the Mediterranean zone, and it is more or less specific to *Pinus* spp. (Spradbery and Kirk 1978). It is unique amongst the European siricids in that it is able to kill living trees (Spradbery 1973), and events in New Zealand, Tasmania and Victoria have clearly shown that, given favourable conditions, it can cause serious losses.

### Life-cycle

In southern Tasmania, where most of the research has been done, *S. noctilio* emerges from January through to May, with peaks in late January and late March. Males begin to emerge before females, and form swarms around the tops of the tallest trees. Females, after emergence, enter these swarms and mating takes place on the upper foliage.

*S. noctilio* is arrhenotokous, that is, males result from unfertilized eggs, and females from fertilized eggs.

After an initial period of flight activity, the females begin to oviposit in suitable trees by drilling holes through the bark into the sapwood. The adults do not feed, so the females are totally dependent upon fat-body reserves. When these are exhausted they die, sometimes with their ovipositors still inserted in a tree, and usually with some eggs still unlaidd. In the field, adults live only a few days. At the time of oviposition, the females introduce the symbiotic fungus, *Amylostereum areolatum* (Fr.) Boidin, and a mucus, which is toxic to the tree (Coultts 1969b).

When they hatch from the eggs, the larvae chew up or down in the wood, feeding upon the fungus which by then has invaded the wood cells surrounding the oviposition site. In the third or fourth instar, they begin to tunnel more deeply into the wood.

Before pupation the larvae turn back towards the bark, to enter a prepupal stage, usually within about 5 cm of the bark surface. Many individuals do not pupate until the second or even the third year after hatching, particularly in cooler and wetter climates. After pupation it is usually about three weeks before the adult insect emerges.

The symbiotic relationship does not end with the siricid, the fungus and the tree. The parasitic nematode, *Deladenus siricidicola* Bedding, is totally dependent (in nature) upon both the siricid and the fungus (Bedding 1972), and the parasitoids locate their host, in part at least, by the odour of the active fungus (Madden 1968b, and see p. 240).

### Insect-fungus-host tree relations

The females of *S. noctilio* do not attack trees indiscriminately, and a necessary prerequisite to attack is that the tree be attractive. Madden (1968a, 1977) showed that the basis of this attraction was the release of monoterpene hydrocarbons from the phloem or cambial sap through the bark following changes in its permeability. This occurred in parts of physiologically stressed trees where there was a decline in osmotic pressure and growth had temporarily ceased.

Madden (1971) found that felled trees in the field were most attractive to *S. noctilio* 5-7 days after felling, and that this attraction persisted, though reducing in intensity, for periods up to three weeks. In electroantennogram bioassays of volatiles emanating from *P. radiata* after felling, Simpson and McQuilkin (1976) found that there was an increase in antennal response coinciding with an increase with time, up to three weeks, or oxygenated components (camphor, pinocamphone, isopinocamphone and transpinocarveol), while the pinenes remained relatively static. This suggests that the oxygenated components either repel *S. noctilio* or mask the effect of the monoterpene hydrocarbons (Madden, personal communication).

When attacking a tree *S. noctilio* females assess the suitability of the wood, lay their eggs if its condition appears suitable and inoculate with the mucus secretion together with arthrospores of the symbiotic fungus, *A. areolatum*. Madden (1974) found that newly emerged females were photopositive and only became ovigerous after a period of flight activity or mating. Coutts and Dolezal (1969) showed that the kind of drill made through a single hole in the bark varied from a single up to multiples of five or six. Single drills, and the drill made before the removal of the ovipositor, usually contained only the arthrospores and mucus, eggs being found mainly in the other drills. Where osmotic pressures of the phloem sap were high, only single drills were made initially (Madden 1974). 'The combined effect of the contents of these drills acting with the initial stressor was to reduce osmotic pressure progressively so that increasingly higher proportions of multiple drills were made in time' and, in consequence, greater numbers of eggs were deposited' (Madden and Coutts 1979). After dissecting over 1300 drill sites, Madden (1974) found that the average number of eggs was 0.04, 0.70, 1.6 and 2.3 for single, double, treble and quadruple drill sites respectively.

The number of females attacking individual trees varies with the size and availability of the field population. Madden and Coutts (1979) state that sometimes small trees (less than 2.5 cm dbh) were attacked and killed by only one female whereas as many as 50 females were observed attacking and sometimes killing dominant trees.

#### *Susceptibility and resistance*

Coutts (1969a) showed that many attacked trees became chlorotic in the apical region 10-14 days after attack, and that the progress of the chlorosis throughout the foliage depended upon attack intensity and the tree's susceptibility to attack. He found that no systemic toxic effects could be attributed to the fungus, which appeared to cause the sapwood to dry out in advance of the mycelium, thus restricting sap supply. Further experiments (Coutts 1969b) showed that when a mucus secretion from the female *S. noctilio* was injected into the sapwood of *P. radiata*, physiological changes and chlorosis were rapidly induced in the crown, symptoms characteristic of trees attacked by *S. noctilio*. The presence of the mucus was also shown by Kile and Turnbull (1974) to aid in localized drying in the vicinity of oviposition drills following germination of arthrospores of the fungus.

The susceptibility of a tree is related to the rate of respiratory activity of the phloem tissue. Madden (1974) stated that 'under conditions of stress the overall respiration of the tree increases, hence an exhaustion of respiratory substrate with a subsequent decline in osmotic pressure occurs first in the region of maximum rate [of respiratory activity] and it is this region which is first attacked under field conditions'. Working in natural regeneration at Pittwater, Tasmania, he found that the maximum rate of respiratory activity occurred at a height which was proportional to tree size.

In plantations in northern Tasmania, on better sites with higher and more dependable rainfall, the decline in osmotic pressure appears to occur in very localized regions of the

stem not clearly related to tree size; also, in the following year(s), a limited zone at a lower level (which might still be quite high on the trunk) is attacked (Taylor, unpubl. data).

A high level of successful attack occurred over the full length of the trunks of many trees in a plantation near Mansfield in Victoria during the drought year of 1976 (McKimm, personal communication). This indicates low water saturation deficit in the phloem tissue (Madden 1974) and low osmotic pressure throughout the trunks, i.e. severe water stress.

In general, a healthy vigorous tree has adequate physical and chemical reserves to resist attack by *S. noctilio*. Coutts and Dolezal (1966) described two resistance mechanisms:

- flooding of the oviposition drills with resin resulting in egg and larval mortality. The efficiency of this mechanism apparently depends upon the genetic constitution of the host tree as well as upon its vigour. Kile and Turnbull (1974) also demonstrated that resin had inhibitory or toxic effects on *Amylostereum areolatum*, due, at least in part, to chemical factors;
- isolation of the symbiotic fungus by a barrier of polyphenols.

They also showed by preventing translocation to sections of bark, that polyphenol formation was greatly reduced in those sections. They suggested that polyphenols in the outer growth ring were produced from photosynthesis, translocated from the crown, but that stored reserves could also be used. Either way, the tree could not use such materials without adequate supplies of water to maintain turgor. Any factors which cause susceptibility in a tree by reducing turgor and translocation also suppress the operation of its resistance mechanisms (Madden and Coutts 1979). The physical and chemical reserves in a healthy tree may become exhausted after large numbers of females have attacked the tree (Coutts and Dolezal 1966).

Coutts (1969b) found great variation in the ability of trees to tolerate injections of mucus, and this led to studies on genetic resistance with the ultimate object of breeding resistant stocks of *P. radiata* (Kile *et al.* 1974). Obviously a long-term project, this work is still in progress.

The precise role of the mucus and fungus is still not clear in some trees, which, although attacked in summer or autumn, do not die until the following spring or summer (see below).

#### *Larval development and survival*

Madden (Madden and Coutts 1979) found that eggs hatched only when the drills containing them, and the surrounding xylem, were invaded by hyphae of the symbiotic fungus. The first and some second instar larvae fed exclusively on the fungus before entering the wood. The initiation of hatching was therefore related to water content of the wood immediately surrounding the site, since growth of the fungus will not begin until some drying has occurred.

It has been found (Taylor, unpubl. data) that in some trees in northern Tasmania viable eggs were still present in the wood 12 months after the trees had been attacked by *S. noctilio*. At Pittwater, where the rainfall is lower, unhatched eggs have been found in the wood (Taylor and Madden, personal communication) in September and October, but not later.

Larvae of later instars feed by chewing their way through the fungus invaded wood. Madden (personal communication) found that if the wood retained sufficient moisture to sustain fungal growth, some individuals passed through 12 instars. Lack of moisture

in the xylem, which stopped fungal growth, led to pupation, provided that the larva had reached at least the seventh instar. Fungal growth is impeded by excess or scarcity of water. Thus there are very marked differences in size between adult insects emerging from different trees or experimental billets. Even larvae hatching from eggs in the same oviposition drill 'but encountering different conditions of wood moisture, and thus fungal growth and activity, were significantly different in size' (Madden and Coutts 1979).

In samples from some trees studied, the larval galleries penetrated to the centre of logs more than 20 cm in diameter; yet in some experimental billets, in which the core remained very wet, no galleries penetrated to a depth greater than 2-3 cm.

There is no doubt that some trees are more suitable for siricid development than others. In some, survival of larvae, calculated either as a percentage of the estimated number of eggs laid, or as a percentage of those which hatched, is very low (Taylor, unpubl. data). This type of tree is normally found in plantations where mortality of trees has been high for several years. In freshly invaded areas the survival rate of *S. noctilio* is usually high, and the emerging insects large.

Each generation emerges over a period of two or three years, but the relative proportions of the total which emerge in the first, second or third year vary at different sites. For example, at Pittwater, Tasmania, about 85% of the siricids emerge one year after the tree is killed, and most of the remaining 15% a year later, with a few carrying over to the third year. In northern Tasmania about equal numbers emerge in years 1 and 2, again with a small carryover to year 3. In a plantation near Mansfield in Victoria most of the population emerges in the first year, with only a few in the second (McKimm, personal communication).

These differences are almost certainly related to the climates at the three sites concerned and the rate of drying in the wood as it affects the cessation of fungal growth and, consequently, of larval feeding.

#### *Insect-fungus relationships*

The mechanisms involved in the mutualistic roles of the fungus and the siricid are a remarkable example of co-evolution. Büchner (1928) noticed two intersegmental organs, invariably containing arthrospores of a basidiomycetous fungus, at the base of the valvulae of the siricid ovipositor. Cartwright (1929) showed that spores were inoculated into the tree during oviposition and that the mycangia contained arthrospores before the females emerged from the trees.

Parkin (1942) discovered structures, which he called hypopleural organs, on the posterior aspect of the first abdominal segment of the larvae. These contained arthrospores embedded in brittle wax platelets. They did not occur on all larvae and Parkin suggested that those bearing these organs were females. This was later confirmed by Rawlings (1951). Thus a mechanism was established whereby the fungus could be collected by the larvae as they chewed through the fungus-infected wood, but Parkin (1942) found no evidence of fungus in the pupae. It was Francke-Grosmann (1957) who showed that the fungus was released from the hypopleural organs in the final larval exuviae by reflex movements of the ovipositor while the female was emerging from the pupal skin. The wax platelets are transported to the base of the ovipositor by the alternating movements of the stylets.

#### **Adult biology and behaviour**

##### *Emergence of adults from trees*

The pattern of emergence varies considerably, although at all sites where records have been kept in Tasmania and Victoria it begins in early to mid summer. McKimm (personal

communication) reports that in parts of Victoria emergence begins in mid-December and ends in June. In northern Tasmania it begins in mid- to late January, whereas at Pittwater it begins at any time from late December to late January, depending upon the season, and usually ends in mid-May.

Throughout the investigation at Pittwater there have been two peaks of emergence in summer and autumn each year, the first in late January, and the second, which is almost invariably the greatest, in the second half of March. The two peaks are related to the cessation of feeding between and within trees. In some trees the majority of the siricids emerge early; in others emergence does not begin until mid-March; but in many individual trees there are two distinct peaks of emergence.

Weather clearly plays a part in the actual emergence of adult *S. noctilio*. Maximal emergence seems to occur on days when the temperature is above average and the barometric pressure falling (K. L. Taylor, unpubl. data). Adults may remain in the wood for several days, with their emergence holes cut, if weather is adverse.

#### *Dispersal*

Evidence on the dispersal of *S. noctilio* is very scanty. Bedding and Akhurst (personal communication), using a flight mill, found that large females were capable potentially of flying up to 160 km. Madden (unpubl. data) found that the flight of medium-sized females was predominantly upwind, but that when wind velocity exceeded  $9.3 \text{ km h}^{-1}$  they ceased flying and remained on the trees.

In the Scottsdale district, nematode-infected trees were found in 1976 up to 13 km from the point where the nematodes were released in 1970. Infected *S. noctilio* females probably flew that distance in one year because there were few, if any, *Sirex*-infested trees between the several plantations. There is also always a possibility of females being carried from place to place on logging or other vehicles.

#### *Sex ratio and its relationship to population density*

The male/female ratio of *S. noctilio* at the study areas in Tasmania has varied within the range of 1.5 : 1 and 16.5 : 1 since 1962. When the work began at Pittwater the siricid population was declining rapidly, and the ratio in 1962 was 16.4 : 1 in the mature trees. In the regeneration it was 6.6 : 1 in 1964 and declined to 2.8 in 1967. At all other sites, where samples were first taken within 2-3 years of invasion by *S. noctilio*, the ratio was low initially (range 1.5-3.6); it increased as the population increased (up to 10.6). Similar trends were recorded in New Zealand by Morgan and Stewart (1966).

Each year at Pittwater there was wide variation in sex ratio between trees. In most years, only males emerged from at least 5% of the trees sampled, while in a few other trees females predominated.

Although no firm conclusions can be drawn from the data, it appears that there might be a relationship between sex ratio and the degree of susceptibility of the host trees. However, Madden (personal communication) has suggested that at Pittwater the sex ratio might also have been affected by selective predation of male swarms by nomadic birds, thus reducing the probability of females mating.

#### **Factors other than natural enemies regulating the population of *S. noctilio***

It will be clear from the section on insect-fungus-host tree relation that the host trees are a major factor controlling the population, but there are several factors, affecting their ability to do so.

Site quality and forest management

In some *P. radiata* plantations in northern Tasmania, where adult siricids have been observed, no evidence has ever been found that trees were killed by *S. noctilio*. All of these plantations are on sites of good quality.

In two other plantations on similar sites *S. noctilio* has killed up to 15 trees per ha. This is still not a serious loss and it has been associated in these plantations with wind damage and delayed thinning, yet there are examples to show that delayed thinning and wind damage alone do not necessarily lead to high tree mortality.

The plantation at Pittwater was on a very sandy soil close to the sea. There, in the original plantation, it was estimated that 40% of the trees were killed: that is, about 100 per ha. However, in this plantation the dominant, least susceptible trees had been selected for the initial harvesting in 1946-47 (Madden 1975a). Thus, when *S. noctilio* first became established there must have been a high proportion of susceptible trees, made more so by logging damage.

Age and vigour of trees

In all infested Tasmanian plantations (as distinct from natural regeneration) it was found that the trees were usually not attacked until they were 13 or more years old.

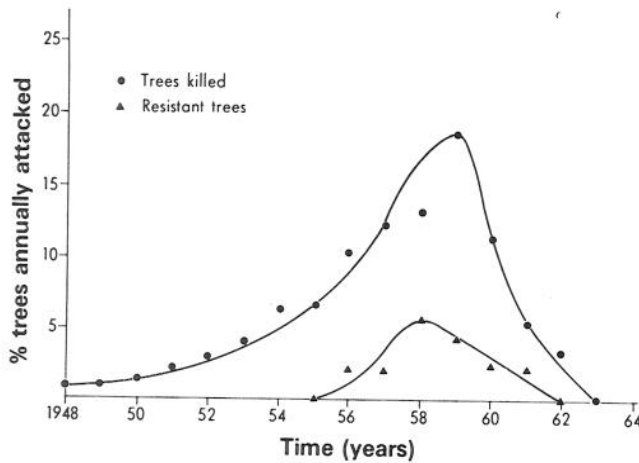


Fig. 1. Annual incidence of *Sirex* attack at Pittwater, Tas., 1948-64, resulting in killed and resistant trees. (After Madden 1975.)

In northern Tasmania, serious tree mortality due to *S. noctilio* occurred only in compartments in which the first thinning was delayed until the trees were 18 or more years old. After the second thinning at 22-25 years tree mortality was almost non-existent.

Madden (1975a) traced the development of the outbreak of *S. noctilio* at Pittwater by analysing the growth rings of killed and surviving trees. The study showed that there was an increase in the proportion of trees resisting attack as the outbreak progressed (Fig. 1), and that survival of insects within the killed trees declined with the years. As a result of the siricid killing susceptible trees there was 'an increase in vigour of the remaining trees accompanied by an increase in the proportion of trees possessing natural resistance'. The first two parasitoids intended to control the pest were introduced into this plantation in 1957 and 1959 respectively, but it is clear from Fig. 1 that the outbreak had already begun to decline before they could have had any significant effect.

*Climatic factors*

Kirk (1974) showed 'that all localities in which *P. radiata* is grown in Australia have bioclimatic counterparts in the northern hemisphere where ... *S. noctilio* is indigenous', although this siricid 'also occurs in colder areas which have no climatic homologues with Australian *P. radiata* areas'. Kirk used the UNESCO bioclimatic maps (UNESCO-FAO 1963), in which the mediterranean climate (within the warm temperate or temperate category) is defined as one with a definite dry period of 1-8 months coincident with the period of longest daylight. In the absence of a recognizable dry period the climate is termed 'axeric'.

Kirk did not discuss the relative severity of *S. noctilio* attack in localities falling within different bioclimatic designations. However, he designated some localities as 'dynamic bioclimatic' and it is interesting to note that of those Tasmanian localities classified as axeric serious damage has occurred only at Pittwater, which is dynamic. That is, it experiences 'more or less long dry spells once every three or four years thus becoming temporarily sub-mediterranean'.

It may be significant that in 1967 the climate at Mt Helen State Forest, with a dry spell of three months, became 'temporarily sub-mediterranean', for the only time between 1960 and 1977. However, the summers of 1966 and 1968 were also drier than average. Tree mortality in the Mt Helen plantation apparently began to increase from 1967 (unpubl. plot data), and reached a peak in 1972. Rawlings and Wilson (1949) described a similar sequence of events, beginning with the 1945-46 drought, at Kaingaroa Forest in New Zealand.

The plantation near Mansfield in Victoria is designated sub-mediterranean; that is, a definite dry period is normally experienced there every summer. Very high mortality occurred in unthinned parts of this plantation in 1976, a year in which the dry period was longer and more severe than normal.

Experience in Tasmania and Victoria (and in New Zealand) suggests that although *S. noctilio* can establish itself in plantations over a wide range of climatic conditions, its population will normally remain at a low level, causing little or no economic damage, particularly in axeric bioclimatic areas. However, Madden's (1974) experiments and the history of a number of outbreaks indicate that in any climate the susceptibility of the trees increases greatly when summer rainfall is below normal for a long period (three months or more). The resulting stress favours survival of *S. noctilio* within the trees, leading to large populations in the following season. Tree mortality may continue at a level above normal for several years, perhaps as a result of root damage. Also, with an increase in the siricid population, oviposition pressure can cause the death of trees which would not normally succumb to a light attack.

Although it appears that the trees are more likely to be at risk in the long dry summers of sub-mediterranean or mediterranean climates, particularly if the dry period is longer than normal, several plantations designated sub-mediterranean in north-eastern Victoria have not suffered high mortality. Climatic factors alone are not necessarily responsible for serious damage by *S. noctilio*.

**Natural enemies**

Details of the collection, rearing and liberation of the natural enemies imported were given by Taylor (1967a, 1976) and Bedding and Akhurst (1974).

*Insect parasitoids - species introduced and their origin*

Two parasitoid species were introduced to Tasmania and released in the plantation at Pittwater before the large scale research program began in 1962 (see Taylor 1967a).



*Rhyssa persuasoria* (L.) (Ichneumonidae) was received in 1957 and *Ibalia leucospoides* Hochenw. (Cynipoidea) in 1959 and 1960, both from New Zealand, where they had been reared from stocks obtained from England some years earlier.

Further stocks of these two species were introduced from throughout their range in the northern hemisphere (both are holarctic) between 1962 and 1973. Nineteen other species were introduced, but only eight of them were successfully reared for release (Taylor 1976). Most of the remainder were associated with other host siricids in different genera of host trees (e.g. *Abies* and *Picea*).

Four more species are definitely established: *I. rufipes drewseni* Borries and *Odontocolon geniculatus* Kreichbaumer (Ichneumonidae), which are palaeartic in origin and *Megarhyssa nortoni* (Cresson) (Ichneumonidae) and *Schlettererius cinctipes* Cresson (Stephanidae), both of nearctic origin. One other, *Rhyssa hoferi* Rohwer, from the arid zone of the U.S.A., is probably established but this awaits confirmation.

#### Characteristics of the parasitoid complex

The established parasitoids should complement one another rather than compete for the available host larvae. The first five may be divided into two 'guilds' (*sensu* Root 1967): (a) *Ibalia* spp. and (b) *Rhyssa*, *Megarhyssa* and *Schlettererius*.

The two species of *Ibalia* attack the host before or after eclosion, and may parasitize first or second instar siricid larvae. They are apparently not attracted to the drill of *S. noctilio* before the larva is fully developed and ready to hatch (Madden 1968b; Spradbery 1974). They are endoparasitic until the third instar, which emerges from the host larva to become ectoparasitic (Chrystal 1930). *I. leucospoides* emerges more or less over the same period as its host (see Fig. 2). Thus it can only attack *S. noctilio* if the eggs hatch within a few weeks after oviposition, i.e. in trees or at sites on trees where stress is high (Madden 1974). The nearctic subspecies *I. l. ensiger* Norton emerges a little later in summer than *I. l. leucospoides*, and its addition to the complex appears to have improved the efficiency of the species as a controlling agency. On the other hand, *I. rufipes drewseni* emerges in spring so that it can only attack the host when hatching of the eggs is delayed. The two species therefore do not compete directly even though they attack the host at the same stage in its development.

Members of the second ('rhyssine') guild all attack more advanced larvae of the host. They emerge mostly in late spring or early summer (Fig. 2), by which time the wood has dried out considerably, and many of the siricid larvae are moving back towards the bark to pupate. The females of these parasitoids all possess a long ovipositor which is inserted through the wood to sting the siricid larva and paralyse it (Taylor 1967b; Hocking 1968; Spradbery 1970). The parasitoid egg is laid upon the host, and the larva feeds as an ectoparasite. It destroys the host within a few weeks and then enters a pre-pupal stage, which usually overwinters. However, a small proportion of each generation pupates almost immediately, to emerge in early summer and attack the same generation of host larvae as that from which it emerged. This proportion is usually greater in *M. nortoni* than in the other two species.

In the adult stage, the ichneumonids feed on honey-dew (Hocking 1967a), and in some plantations availability of honey-dew may be limited, which would reduce the efficiency of species of *Rhyssa* and *Megarhyssa*. However, no evidence has yet been found in any study area that the adults were not obtaining adequate food, although the source of their food has not been ascertained, and the quantity available may be below the optimal level.

As with the *Ibalia* species, the three members of the rhyssine guild are more or less complementary, although there must be some competition between them. Unpublished work by the author has shown that the ratio *M. nortoni* : *R. persuasoria* increases directly

with the diameter of the tree trunk, the density of the two normally being about equal at 9.0 cm diameter. *S. cinctipes* usually emerges later in the season, well after the peak emergence of the other two species (Taylor 1976) (see Fig. 2).

The other two exotic species should also act in a complementary rather than competitive fashion. *O. geniculatus* is a small insect, emerging in spring; it has a short ovipositor, and probably attacks late-hatching host larvae that are still close to the surface. It also attacks beetle larvae (Spradbery, personal communication). *R. boferi* seems to be confined to the arid zone in the U.S.A., so if it becomes established it should be well adapted for the drier, hotter conditions in South Australia and Western Australia which might prove less favourable for the other rhyssines.

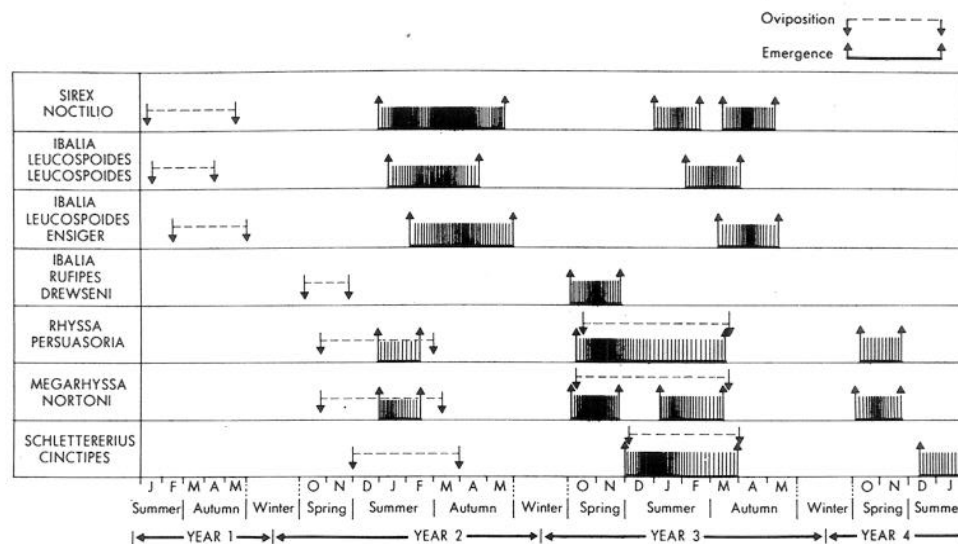


Fig. 2. Diagram showing periods of oviposition and emergence by *S. noctilio* and its parasitoids throughout one generation of the host at Pittwater, Tas. A few individuals of *S. noctilio* and *S. cinctipes* would also emerge during the summer of year 4.

One native ichneumonid, *Certonotus tasmaniensis* Turn., the natural hosts of which are apparently weevils, has been found to parasitize *S. noctilio* in Tasmania (Hocking 1967b) and Victoria. It has emerged from samples collected at many points throughout the range of *S. noctilio*, and levels of parasitization up to 15% have been recorded (Taylor 1976). The sporadic nature of the occurrence of *C. tasmaniensis* in Sirex-killed trees suggests that it is unlikely to play an important part in the control of *S. noctilio*.

#### Host-finding by the parasitoids

Madden (1968b) showed that the symbiotic fungus *A. aerolatum* was implicated in the attraction of *I. leucospoides*, *R. persuasoria* and *M. nortoni* to their host larvae. *I. leucospoides* females showed a preference for cultures of *Amylostereum* 2-3 weeks old, and for *S. noctilio* drills 2-3 weeks old in test logs. Spradbery (1970) found that the attractiveness of cultures of *Amylostereum* to *R. persuasoria* increased with age up to three or four months. *R. persuasoria* and *M. nortoni* respond to a different threshold concentration of extracts from fungal cultures (Madden 1968b), which would tend to reduce competition between them for the same larvae.

Madden (1975b) demonstrated the presence of yeasts (principally *Saccharomyces*) and bacteria in the moist frass immediately behind feeding siricid larvae, and showed that the yeast enhanced the attractiveness of the frass to the rhyssines. It appears that both yeasts and *Amylostereum* (reactivated by the moist frass) are involved in the production of attractants for these parasitoids.

The symbiotic fungus is also involved in the location of emerging females by *M. nortoni* males (Madden 1968b).

#### Parasitic nematodes

Zondag (1969) discovered in 1962 that *S. noctilio* was parasitized by a nematode that caused the host female to lay infertile eggs. Investigations began in 1965 at the CSIRO Sirex Unit at Silwood Park, England, on nematode parasites of various siricids and of their parasitoids. Between 1965 and 1973 seven species of *Deladenus* (Neotylenchidae) were collected and described by Bedding (1968, 1974), but only one, *D. siricidicola* Bedding, has been found suitable for use in the biological control of *S. noctilio* (Bedding and Akhurst 1974). Many strains of *D. siricidicola* were screened, and some were unsuitable because they did not sterilize the host female.

Bedding (1967, 1972) described the unusual life-cycle of these nematodes, which involves extraordinary female dimorphism; a free-living mycetophagous and an entomophagous life-cycle (Fig. 3). When a larva of *S. noctilio* is parasitized by an effective strain, it contains 1-100 nematodes and the reproductive system of the nematode(s) expands rapidly with the onset of pupation in the host; the juvenile nematodes are released ovoviviparously into the haemocoel of the host pupa and migrate into its reproductive organs. The female is sterilized, but although the testes are invaded the male remains fertile. Parasitized females oviposit normally, introducing into the trees the symbiotic fungus and egg shells, which each contain up to 200 juvenile nematodes. These migrate into the wood and feed on the developing fungus. They grow into adult free-living nematodes laying many eggs within the tracheids close to the oviposition holes of *S. noctilio*.

As the wood dries and the fungus spreads within it, the nematodes feed upon it and breed, the juveniles developing only into mycetophagous forms except in the vicinity of healthy *S. noctilio* larvae, which, of course, are the progeny of uninfected females attacking the same tree. There bacteria are present (Madden 1975b), and Bedding (1979) states that 'in the vicinity of *S. noctilio* larvae, ... where bacteria abound, juvenile nematodes may develop into adult infective females ...'. These mate with males which have microspermatozoa, and then penetrate the siricid larvae to begin the parasitic cycle again.

Bedding and Akhurst (1974) reported that early competition for fungal food between *S. noctilio* larvae and nematodes probably resulted in smaller adult siricids. When the density of nematodes in the wood is very high, some siricid larvae may die from starvation, and the data from nematode-infected trees in Tasmanian study areas suggest that many host larvae die before they reach the third instar.

Different strains of *D. siricidicola* have been released throughout Sirex-infested areas of Tasmania and Victoria, and the nematode is well established throughout the range of *S. noctilio*. It is still being reared and released in parts of Victoria where the host density is greatest.

#### Birds

Studies by Madden at Pittwater (personal communication) showed that changes in the total bird population closely paralleled the seasonal emergence of *S. noctilio*. He

released large numbers of male *S. noctilio* and found that this resulted in an immediate local concentration of actively preying birds. It seems unlikely that birds will exercise any effective control of the siricid, but the attraction of large migratory birds such as dusky wood swallows, spine-tailed swifts and ravens, to prey preferentially on the males, could cause significant changes in the sex ratio (Madden, personal communication, see also p. 236).

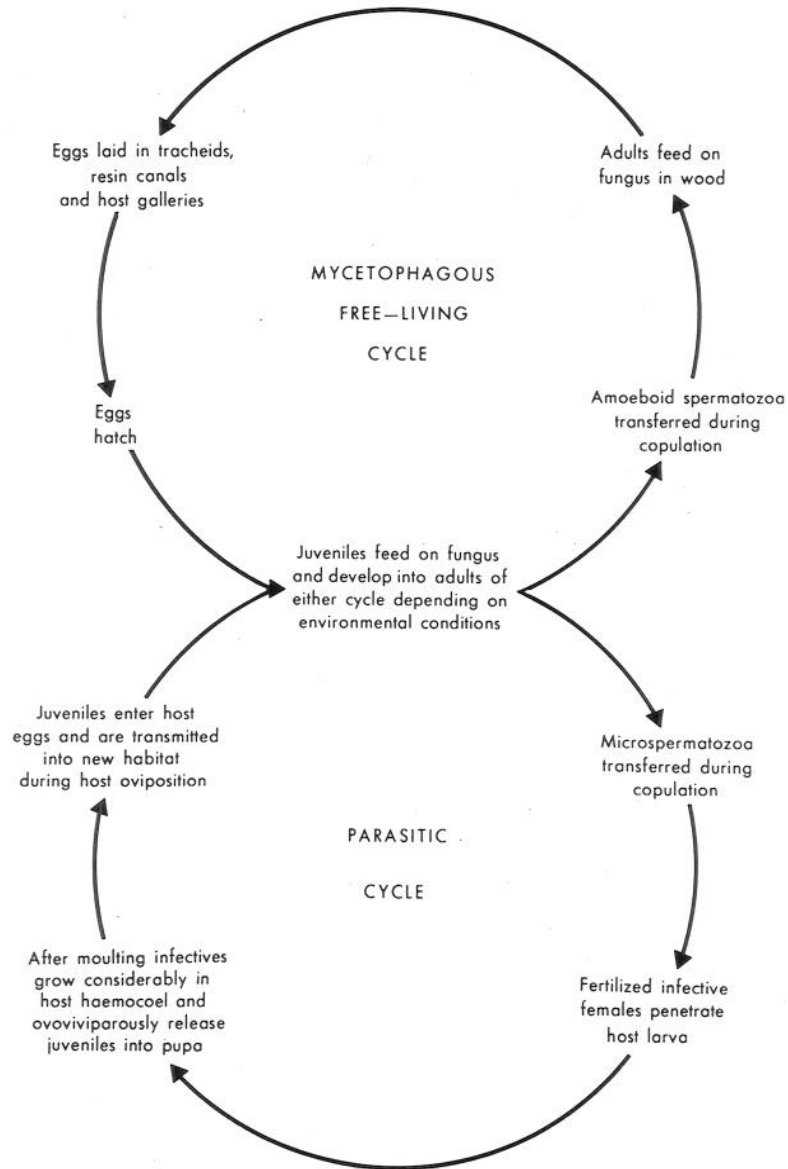
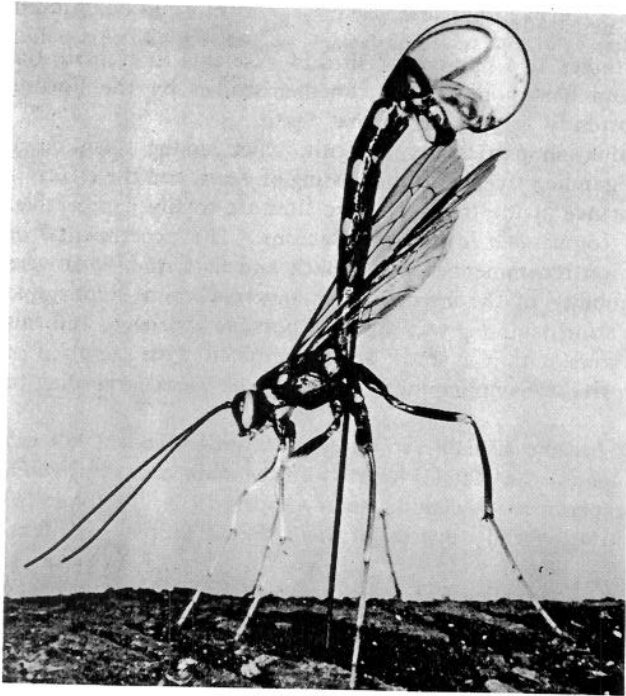
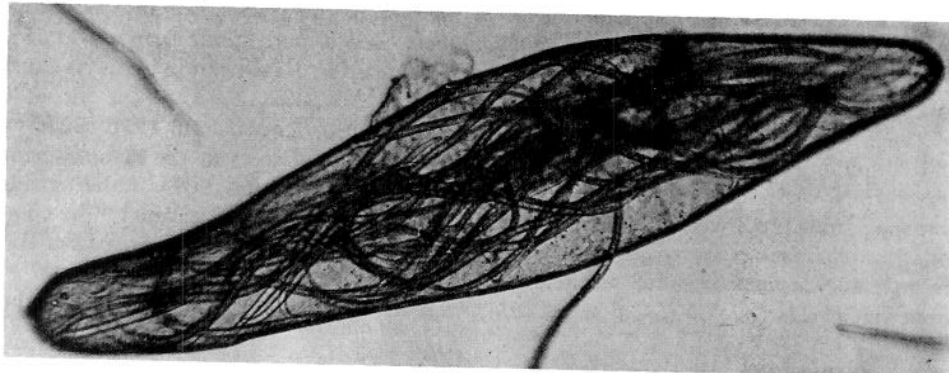
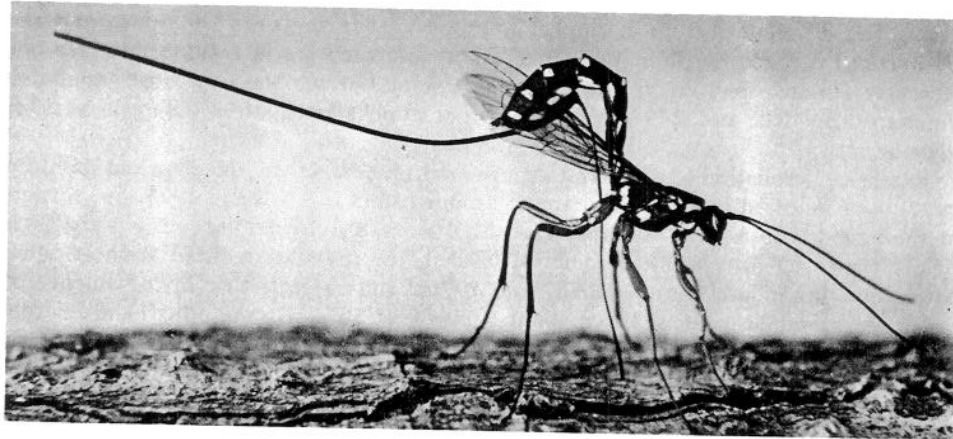


Fig. 3. Diagram of the life history of *Deladenus siricidicola*. (After Bedding 1972.)



Females of *Megarhyssa nortoni* (left) and *Rhyssa persuasoria* (below) probing to locate siricid larvae.  
(Bottom) Egg of *S. noctilio* invaded by juvenile nematodes of *Deladenus siricidicola*. Infected female siricids are sterilized by these nematodes.



### Impact of the parasitoids and nematodes

CSIRO is still undertaking studies at a number of sites in Tasmania to evaluate the effect of the natural enemies on host populations. Further studies by the Forests Commission of Victoria, are currently in progress in that State.

Many factors make this evaluation particularly difficult, chief among them being the increasing resistance of the standing trees with the passing of years, and the effects of seasonal conditions on the resistance of the trees. No two sites are totally comparable, nor are the same sites totally comparable in different seasons. The experimental or comparison methods of evaluation recommended by DeBach and Bartlett (1964) were not practical because of the mobility of the insects within any area where comparable plots could be selected. Population sampling was the only possible approach, and this involved sampling of infested trees within a study area, combined with sampling of insect populations within those trees. Sampling methods had to be varied according to circumstances.

The study sites in Tasmania became available at different times between 1962 and 1971 as *S. noctilio* spread throughout the island. Apart from the main site at Pittwater, releases at each site were made experimentally (Bedding and Akhurst 1974; Taylor 1976) to obtain information on colonization and dispersal of the different species, and interactions between them.

Pittwater is the only area where sampling has been in progress for long enough to enable any firm conclusions to be drawn about the interactions of the parasitoids (Taylor 1978) and it is still too early to evaluate fully the nematode and *S. cinctipes*. Figure 4a shows the relative numbers of all species emerging from the *Sirex*-killed trees in this forest for the years 1965 to 1975 inclusive; and the estimated total numbers emerging during the different seasons is shown in Fig. 4b. The rhyssines (*R. persuasoria* and *M. nortoni*) are combined in these figures because they are in fact operating as one mortality factor: they emerge at the same time and attack the same host population simultaneously (see pp. 239-40). *S. cinctipes* attacks later, after the main peak of rhyssine attack.

Extensive defoliation of this forest by a geometrid, *Chlenias* sp. (Madden and Bashford 1977), was followed by *S. noctilio* attack on most trees in 1970 and 1971, but survival of the siricid within them was very low (Taylor 1978). Nevertheless, Fig. 4 indicates clearly that after *M. nortoni* became established, the rhyssines reduced the host population to a lower level between 1967 and 1970; and suggests that in the absence of nematodes it would have oscillated about a level near 30%. On the other hand *I. leucospoides* is apparently density-independent at this site, the availability of the host to it being regulated by conditions within the tree.

Until 1974 at Pittwater the impact of the nematode *D. siricidicola* and the parasitoid *S. cinctipes* (released there in 1973 and 1970 respectively) was negligible. Figure 4 shows a dramatic decrease in the population of *S. noctilio* in the trees killed in 1975, with increased infection of the siricids by *D. siricidicola* (hence more sterile females) to 58% from 21% in 1974. This was accompanied by an increase in parasitization by *C. cinctipes* to 23% from 2% in 1974.

The first experimental liberation of *D. siricidicola* near Scottsdale in 1970 (Bedding and Akhurst 1974) resulted in over 90% of the *Sirex*-killed trees in the compartment where they were liberated being infected within two years, and 90% of the siricids emerging from these were infected. At Mt Helen State Forest, parasitization by the combination of *I. leucospoides*, *I. r. drewseni*, *M. nortoni*, *R. persuasoria*, *S. cinctipes* and the native *C. tasmaniensis* had reached 64% in 1972 and was still rising. In that year 700 *Sirex*-killed trees (out of an estimated 2100) were inoculated with *D. siricidicola*. Of the

trees killed in 1973, 94% were infected by the nematodes. In 1974 only about 30 *Sirex*-killed trees were found in the whole forest; in 1975 only 3, and none could be found in 1976.

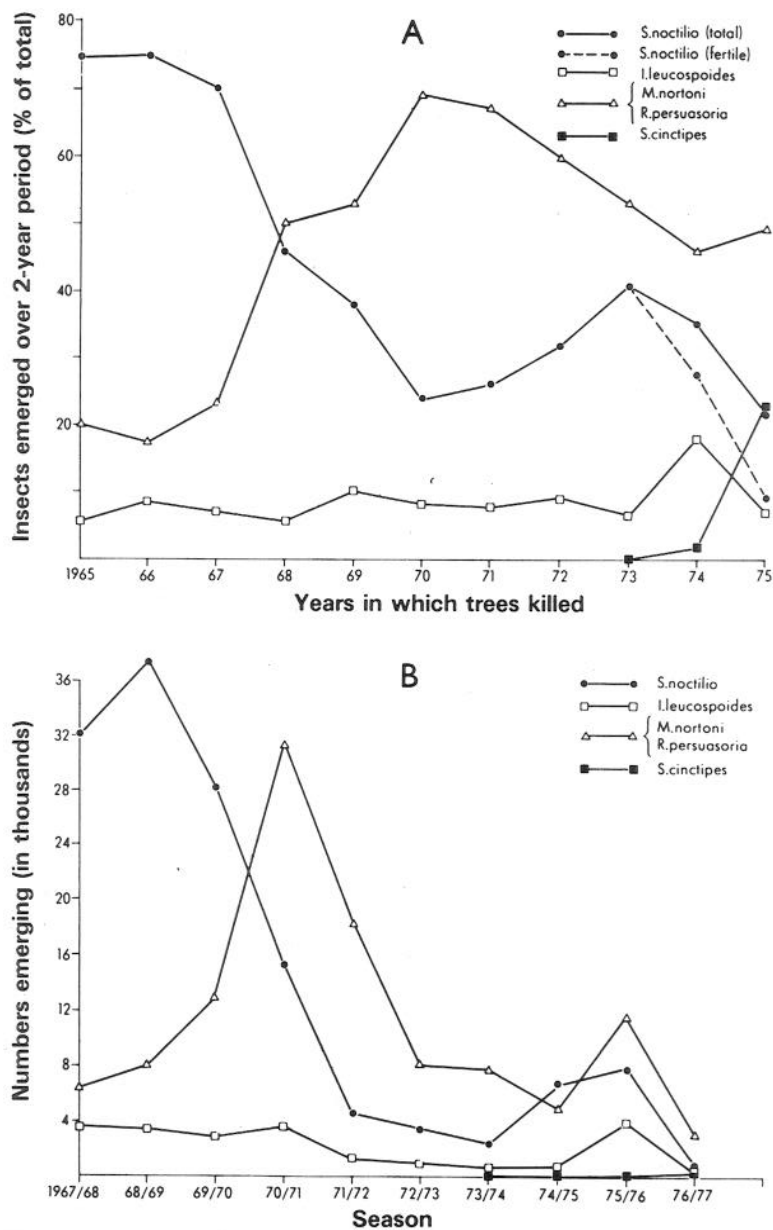


Fig. 4. Observed changes in the density of *S. noctilio* and its parasitoids in *P. radiata* regeneration at Pittwater, Tas., following releases of the parasitoids. (a) Relative numbers (above) emerging from trees killed each year, 1965–75. Broken line for 1974 and 1975 represents fertile *S. noctilio*, i.e. not parasitized by *Deladenus siricidicola*, which was released in 1973. (b) Estimated total numbers (below) emerging in the study area each season, i.e. from trees killed in the previous two seasons – see Fig. 2. Of the *S. noctilio* emerging in 1976–77, 58% were sterile.

The results from these two important study sites clearly indicate that the combination of *D. siricidicola* and the parasitoids has reduced the population of *S. noctilio* to a very low level. It is even possible that the nematode would have achieved the same result without the parasitoids. However, it is clear from the section on factors regulating the population of *S. noctilio* that it might have been declining anyway, and therefore these results should be interpreted with caution.

From the results of these studies and from parasitoid recoveries in Tasmania and Victoria it is known that *I. leucospoides* will disperse over long distances (Taylor 1967a), probably as rapidly as its host. *M. nortoni* has been recorded at distances up to 19 km from the nearest liberation point, but the greatest distance so far recorded for *R. persuasoria* is 7.2 km (Taylor 1976). No information is available yet on the dispersal of *S. cinctipes* or *I. r. drewseni*.

#### Conclusion — a successful biological control attempt?

Although evaluation must continue for several years in order to cover a range of sites in different climatic areas and a series of wet and dry years, there is no doubt that the population of *S. noctilio* will be controlled to some degree by the natural enemies that have been introduced. At all study sites in Tasmania, the parasitoids have reached a level at which between 60 and 80% of the *S. noctilio* population is destroyed, and because one or more species at each site has still not reached an equilibrium level, the full potential of the whole complex is still not known. The nematode appears to have had a dramatic effect in reducing the host population at two sites, but other factors have contributed, in part at least, to the collapse.

There are so many variable factors involved in the ecosystem that, without more data, firm conclusions cannot be drawn about the role of any one in the control of *S. noctilio*. At each study site in Tasmania where the biological control agents appear to have reduced the population of *S. noctilio* to a very low level, the trees have shown few signs of water stress since the population started to fall. It is still too early to assess whether the nematode will keep the host population at a low equilibrium level indefinitely, and through wide seasonal fluctuations, following a collapse. Perhaps this will prove to be the role of the insect parasitoids. The complex of parasitoids which is, or is likely to become, established, is well balanced: species like *I. rufipes drewseni* and *S. cinctipes* can take advantage of departures from normal in the host life cycle, resulting from seasonal fluctuations or changing susceptibility of the trees, which might act to the detriment of the more numerous species.

The plantation near Mansfield, Victoria, where the trees were heavily attacked in 1976 and 1977, will provide a good test for the natural enemies. The rhyssines and *D. siricidicola* had not been established long enough to have reached equilibrium and limited data are available so far to permit their evaluation. However, the level of parasitization by *I. leucospoides* is much higher there than at Pittwater (McKimm, personal communication).

Whatever the final conclusions might be on the success of the project as a biological control attempt, the associated research has produced overwhelming evidence to confirm that trees suffering from physiological stress are at great risk from *S. noctilio*. This will be minimized if *P. radiata* plantations are restricted to good quality sites and properly managed to maintain health and vigour, thus reducing the possibility of high tree mortality in the initial stages of an outbreak.

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# The Ecology of Pests

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