Oecologia (Berl.) 32, 1–10 (1978)

Oecologia

# Evaluation of the Insect Parasitoids of *Sirex noctilio* (Hymenoptera: Siricidae) in Tasmania

K.L. Taylor

Division of Entomology, CSIRO,
Stowell Avenue, Hobart, Tasmania 7000, Australia

**Summary.** Sampling of *Sirex noctilio* F. and the insect parasitoids released in a forest of *Pinus radiata* D. Don near Hobart, Tasmania, has shown that the rhyssines, *Megarhyssa nortoni* (Cresson) and *Rhyssa persuasoria* (L.) were mainly responsible for reducing the level of the population of *S. noctilio* between 1965 and 1974. Parasitic nematodes were not present during this period. Key factor analysis indicates that in this forest the two species act as one delayed density-dependent factor, whereas *Ibalia leucospoides* Hochenw. is apparently density-independent, its ability to parasitize the host being regulated by conditions within the tree.

## Introduction

The assessment of the effect of insect parasitoids and nematodes introduced for the biological control of *Sirex noctilio* F. in Australia (Taylor, 1976) was commenced in 1964 in Tasmanian plantations of *Pinus radiata* D. Don. Evaluation is difficult because of great variation in the suitability of the host tree for siricid development, the effect of seasonal conditions, the long host life-cycle, and other factors including sampling problems.

The work has now been in progress for 13 years in a stand of natural regeneration in a pine forest at Pittwater, near Hobart. The data from trees killed each year from 1965 to 1974 inclusive can be conveniently summarized in the form of a life table, from which appreciation of the role of the parasitoids can be obtained by graphical methods. Changes in the relative numbers of the various species from year to year strongly suggested that the rhyssine parasitoids were mainly responsible for reducing the population of *S. noctilio* and holding it at a lower level.

Varley and Gradwell's (1968) key factor method was suggested as a convenient method of analysing the data, and the results of the analysis are presented in this paper.

0029-8549/78/0032/0001/$02.00

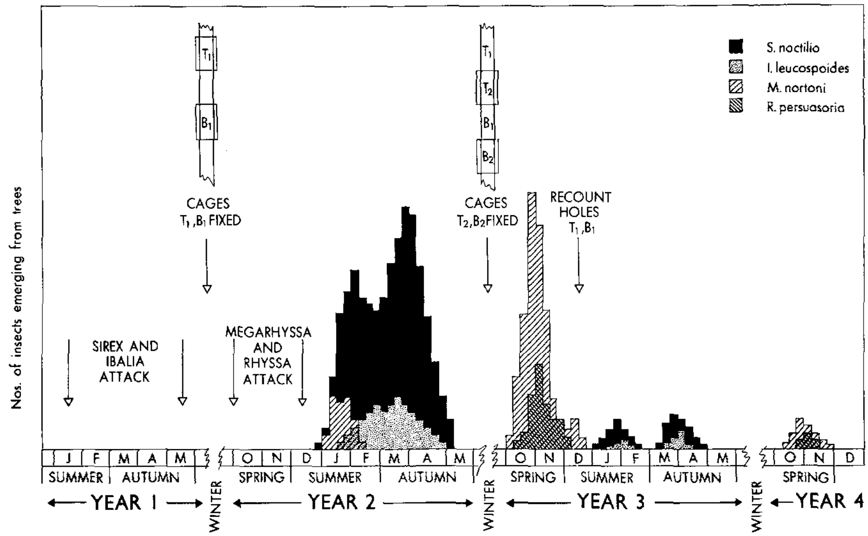


**Fig. 1.** Diagrammatic representation of the life cycles *S. noctilio, I. leucospoides, R. persuasoria,* and *M. nortoni* to show the sequence of events through the three seasons following death of the tree

## Life Cycles

The life cycles of the four main species are shown in Figure 1. At Pittwater only a small proportion of each generation of *S. noctilio* remains in the wood after Year 2 (i.e. the first season of emergence). These emerge as adults in Year 3, two years after oviposition. *Ibalia leucospoides* Hochenw. attacks fully-developed eggs and first or second instar larvae of *S. noctilio*; adults emerge in Year 2, and a few in Year 3, more or less at the same time as their host. During the spring of Year 2 *Rhyssa persuasoria* (L.) and *Megarhyssa nortoni* (Cresson) parasitise siricid larvae which are then in an advanced stage of development and several centimetres deep in the wood. The rhyssine larvae destroy the host within a few weeks; some of them pupate immediately, to emerge as adults in early summer (of Year 2), but the majority enter larval diapause to emerge the following spring (Year 3). The larvae of *S. noctilio* adults emerging in Year 3 are, of course, exposed to attack by *R. persuasoria* and *M. nortoni* during the preceding spring, and therefore limited numbers of these parasitoids will emerge in the third spring (Year 4).

## Methods

### *Sampling*

*Trees.* The density of trees in the regeneration at Pittwater varied considerably, from over 12,000 stems per acre to less than 400 in a few patches. This made sampling very difficult. J.L. Madden (unpublished data) carried out random sampling for trees killed by *S. noctilio* from 1963 to 1971, to obtain an estimate of the number of trees killed. The majority of these, in the first few years at least, were less than 5 cm DBH and therefore too small for sampling by the method used in this study, i.e. fixing cages to the trees.

Each year the area was searched extensively to find Sirex-killed trees greater than about 5 cm DBH, to which cages could be fixed. Up to 1968 the search was continued only until about 60 suitable trees were found with a reasonable range of diameters and well distributed over the whole area. In 1969 and in subsequent years (with the exception of 1971) all or most of the dead trees were located.

**Table 1.** Number of *S. noctilio* eggs laid and emergence of Sirex and parasitoids[a] per square metre of bark surface on sampled trees at Pittwater, 1966–1974

| | 1966 | 1967 | 1968 | 1969 | 1970 | 1971 | 1972 | 1973 | 1974 |
|---|---|---|---|---|---|---|---|---|---|
| Estimated no. of eggs laid | 164 | 212 | 214 | 221 | 147 | 79 | 104 | 224 | 244 |
| Total insects emerged | 102 | 138 | 151 | 153 | 59 | 34 | 40 | 81 | 101 |
| Survival % | 62 | 65 | 71 | 69 | 40 | 43 | 38 | 36 | 41 |

[a] Each parasitoid represents one host larva, and therefore one of the original host population

Estimates of the total number of Sirex-killed trees in the area were made from these two sets of data, using 1970 as the year in which they could be correlated. Thus for 1965–1968 and to a lesser extent 1969 and 1971 the estimates were mainly based on Madden's figures. From 1972 it was assumed that all trees were found each year.

Madden's estimate of dead trees for 1971 was 6–7 times greater than that for 1970. In the years 1969–1971 the area was seriously defoliated by a geometrid, *Chlenias* sp. and the effect of defoliation in 1969 is reflected in the lower density of oviposition and much lower survival rate in the trees attacked in 1970 (see Table 1). Defoliation in 1970 was much more severe, and most of the trees were attacked by *S. noctilio* in 1971, including many that were already dead. Those sampled, from which the figures for 1971 in Table 1 were derived, were the most suitable that could be found. The numbers of the remaining dead trees, and the population density of insects within them, were very difficult to estimate. Therefore the margin of error in the estimate for 1971 was much greater than in any other year.

Most of the dead trees were felled in thinning operations in 1971–1972, so in 1972 and later years the freshly killed trees were easy to find.

*Adult Insects.* Sampling for adult insects was done on about 60 trees selected each winter from those killed by *S. noctilio* during the previous summer. Two cages (each about 76 cm long) were fixed on each tree in the winter of Year 1 (see Fig. 1), and the insects emerging in the cages during summer and autumn of Year 2 were removed and counted at weekly intervals. The cages were moved up or down on the tree trunks during the winter of Year 2 (see Fig. 1) to trap insects emerging from sections of the bark which had been fully exposed to all insects during the preceding season.

When the cages were moved, emergence holes were counted and marked in all four cage positions, which are referred to as T1 (top cage 1st Year), T2 (top 2nd Year), B1 and B2 (the corresponding bottom cages). The emergence hole counts in T1 and B1 served only to check the numbers of insects recorded from within those cages during Year 2; in T2 and B2 the holes represented the total insects which emerged in those positions during Year 2, but the relative numbers of each species were unknown.

In spring *M. nortoni* females were observed probing through the wire mesh into the trunk within the cages. Also small numbers of *M. nortoni* (the non-diapausing component of the progeny of the females which oviposited through the cages) emerged in the first year cages.

Because of this, in late December of Year 3 (i.e. at the end of the main emergence season for *R. persuasoria* and *M. nortoni*) fresh holes in cage positions T1 and B1 were counted. The only insects which would emerge in spring are *M. nortoni* and *R. persuasoria*. In the latter, the proportion of non-diapausing to diapausing larvae is smaller than in *M. nortoni*, and because *R. persuasoria* has a shorter ovipositor, females of this species cannot oviposit so freely through the cages. Hence for practical purposes all of the fresh emergence holes were assumed to be those of *M. nortoni*.

At the end of the Year 3 the cages were removed and the emergence holes in all four positions were counted, as a check against the number of insects recorded from them.

The relative numbers of each species emerging from the trees killed in any one year were calculated as shown in Table 2. The calculations are based on emergences in cages T2 and B2.

**Table 2.** Insect emergence from trees killed in 1972 at Pittwater, Tasmania

| Cages | *S. noctilio* | *I. leucospoides* | *M. nortoni* | *R. persuasoria* | Total | Emergence holes | December holes (DecH) |
|---|---|---|---|---|---|---|---|
| *Year 2* | | | | | | | (Year 3) |
| 1. T1, B1 | 883 (A) | 260 (B) | 68 (C) | – | 1211 | | 288 (D) |
| 2. T2, B2 | – | – | – | – | – | 556 (E) | |
| *Year 2 adjusted* | | | | | | | |
| [=insects estimated to have emerged in Year 2 in T2 and B2: *M. nortoni* ratio=0.236 (see text)] | | | | | | | |
| 3. T2, B2 | 350 (J) | 103 (K) | 103 (L) | – | 556 (=E) | | |
| *Year 3* | | | | | | | |
| 4. T2, B2 | 55 (F) | 11 (G) | 436 (H) | 240 (I) | 742 | | |
| *Total emerged* (sum of 3 and 4) | | | | | | | |
| T2, B2 | 405 (J+F) | 114 (K+G) | 539 (L+H) | 240 (I) | 1298 | | |
| | 31.2% | 8.8% | 41.5% | 18.5% | 100% | | |

The emergences from T1 and B1 in Year 2, together with the fresh holes (DecH) in those positions counted in December of Year 3, are used only to give the proportions of each species which emerged in positions T2 and B2 during Year 2. The figures used in the calculations are labelled A to I in Table 2 to simplify the description of the method.

First, the ratio C:D (i.e. non-diapausing *M. nortoni:* diapausing *M. nortoni*) was calculated. The number of *M. nortoni* emerging in Year 3 in cages T2 and B2 (*H*) was then multiplied by this ratio to give *L*, which is thus an estimate of the non-diapausing *M. nortoni* which emerged in the T1 and B1 positions. The figure *L* was subtracted from the number of Year 2 holes (*E*) in positions T2 and B2, and the result divided between *S. noctilio* and *I. leucospoides* in the same proportion as they emerged in the cages T1 and B1. Thus

$$\textit{S. noctilio}\ (J)=(E-L)\times\frac{A}{A+B},$$

and

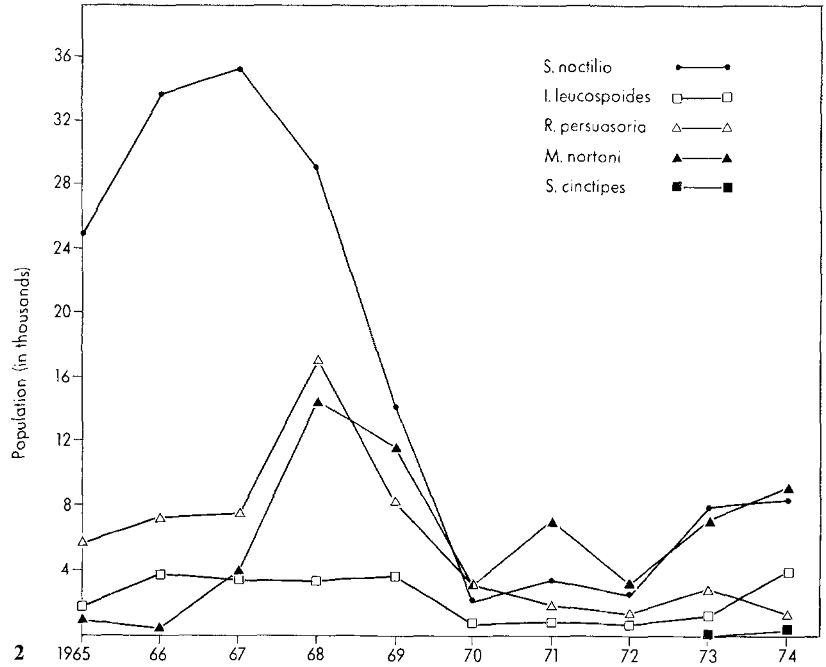
$$\textit{I. leucospoides}\ (K)=(E-L)\times\frac{B}{A+B}.$$

Year 3 emergences in cages T2 and B2 were then added (as shown in Table 2), and the resulting numbers of each species expressed as a percentage of the total two year emergence.

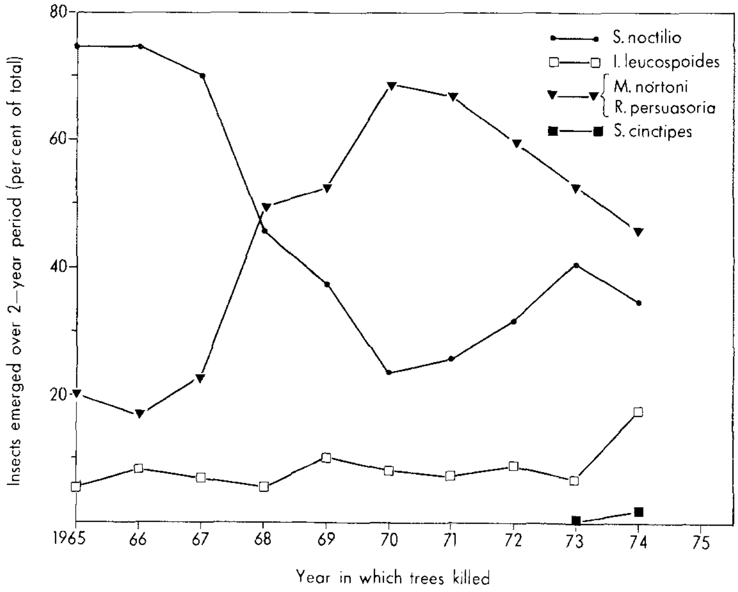
The total population which emerged in each of the sampled trees was measured at the end of Year 3 from samples (7.6 cm bands around the trunk) taken at intervals of 61 cm for the full length of the trunk. Emergence holes were counted in each sample and the total was multiplied by 8 to give an estimate for the whole tree.

Having obtained an estimate of the mean numbers of insects in the trees sampled, an estimate was made each year of the total numbers from all trees killed by *S. noctilio* in that year. During the search of the area, after 1968, all trees found were rated according to size and suitability for the development of *S. noctilio* (unpublished data). The numbers of insects each would yield were estimated in relation to the mean numbers in the average tree sampled.

These figures made it possible to estimate the total population of insects (all species) within the study area (*Ni* in Table 3).



**2**



**3**

**Fig. 2.** Estimated numbers of insects emerging from trees killed by *S. noctilio* in study area at Pittwater, 1965–1974

**Fig. 3.** Relative numbers of 5 species emerging from trees killed by *S. noctilio* at Pittwater, 1965–1974, expressed as a percentage of total insects emerging

*Oviposition.* Oviposition could only be measured after the bark was removed. Consequently this was not done until the end of Year 3. Two samples, each consisting of a 7.6 cm band around the trunk, were taken within each cage area.

After removal of the bark from each sample, the oviposition drills of *S. noctilio* were counted and classified according to the number of drills (1–4) in the group. From data collected at Pittwater, Madden (1974) found that the mean number of eggs laid per group was 0.042, 0.684, 1.550 and 2.220 in groups with 1, 2, 3 and 4 drills respectively. In this study, the number of eggs laid in each sample was estimated by using the factors 0.04, 0.7, 1.5 and 2.2.

The oviposition data and the emergences from cages T2 and B2 were converted to numbers per square metre of bark surface (Table 1). Using the ratio from Table 1 between the estimated number of eggs laid and the total insects emerged, it was then possible to estimate the total number of eggs laid (*EL* in Table 3) in all new trees killed each year within the study area.

## Results

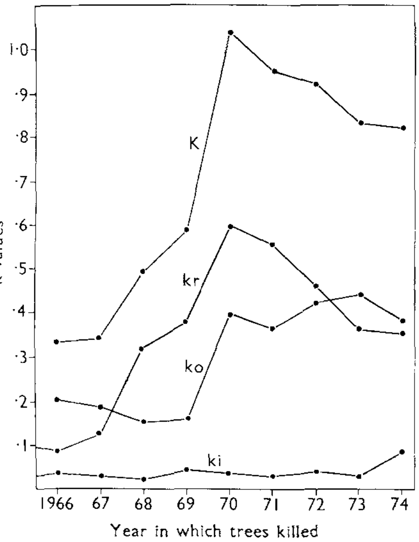
Figure 2 shows the estimated total numbers of each species emerging from all of the trees within the study area each year from 1965 to 1974, and Figure 3 shows their relative numbers expressed as a percentage of the total insects which emerged from the trees killed in each of those years. The parasitoid *Schlettererius cinctipes* (Cresson) was only recently established and had no significant bearing on the analysis up to and including 1974.

Both figures strongly suggest that the rhyssines are mainly responsible for reducing the *S. noctilio* population. To test this, the key factor method of Varley and Gradwell (1968) has been used for further analysis.

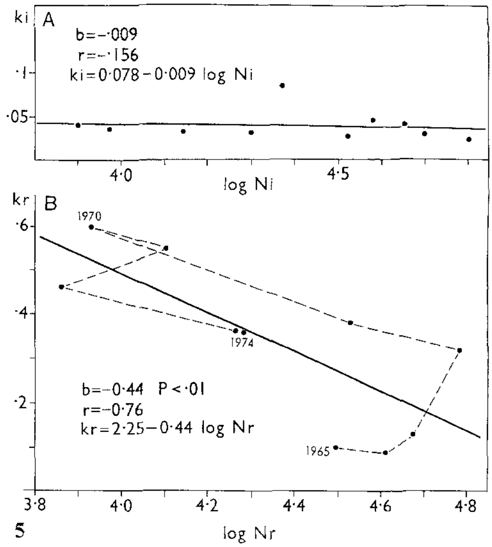
Table 3 shows the logarithms of the estimated numbers each year of eggs laid (*EL*); the siricid populations available to *I. leucospoides* (*Ni*); the siricid populations available to the rhyssines (*Nr*) and the surviving host populations (*S*). The $k$-values $k_0$, $k_i$ and $k_r$ are the differences between the logarithms of the populations before and after the mortality factors act, and $K$ is the sum of the three $k$-values (see Varley and Gradwell, 1968). For this analysis the total number of insects which emerged from the trees killed each year was assumed to be the number of eggs which hatched, that is, *Ni*. In fact $k_0$ represents not only egg mortality, but also a number of other mortality

**Table 3.** Life table of *Sirex noctilio* at Pittwater, Tasmania

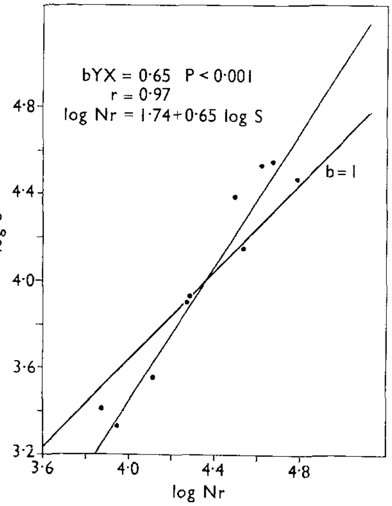
| Year | log *EL* | $k_0$ | log *Ni* | $k_i$ | log *Nr* | $k_r$ | log *S* | $K$ |
|---|---|---|---|---|---|---|---|---|
| 1965 | – | – | 4.520 | 0.024 | 4.496 | 0.102 | 4.394 | |
| 1966 | 4.859 | 0.206 | 4.653 | 0.038 | 4.615 | 0.088 | 4.527 | 0.332 |
| 1967 | 4.887 | 0.186 | 4.701 | 0.031 | 4.670 | 0.123 | 4.547 | 0.340 |
| 1968 | 4.958 | 0.152 | 4.806 | 0.023 | 4.783 | 0.320 | 4.463 | 0.495 |
| 1969 | 4.738 | 0.160 | 4.578 | 0.046 | 4.532 | 0.380 | 4.152 | 0.586 |
| 1970 | 4.370 | 0.399 | 3.971 | 0.036 | 3.935 | 0.600 | 3.335 | 1.035 |
| 1971 | 4.504 | 0.364 | 4.140 | 0.032 | 4.108 | 0.554 | 3.554 | 0.950 |
| 1972 | 4.325 | 0.421 | 3.904 | 0.040 | 3.864 | 0.461 | 3.403 | 0.922 |
| 1973 | 4.735 | 0.439 | 4.296 | 0.031 | 4.265 | 0.361 | 3.904 | 0.831 |
| 1974 | 4.752 | 0.384 | 4.368 | 0.085 | 4.283 | 0.352 | 3.931 | 0.821 |



4



5



6

**Fig. 4.** Changes in the mortality of *S. noctilio*, expressed as *k*-values, in the years 1966–1974 (from Table 3). *K* total mortality; $k_0$ mortality due to causes other than parasitism; $k_i$ mortality due to *Ibalia leucospoides*; $k_r$ mortality due to rhyssines (*R. persuasoria* and *M. nortoni*)

**Fig. 5.** Values for $k_i(A)$ and $k_r(B)$ plotted against the host densities (*Ni* and *Nr* respectively from Table 3) upon which they acted

**Fig. 6.** Test for density dependence of the rhyssine parasitoids. For explanation of *Nr* and *S* see Table 3

factors which could not be measured, such as mortality of host and parasitoid larvae within the wood due to unknown causes.

Following Varley and Gradwell (1968, p. 134) the $k$-values from Table 3 are plotted in Figure 4 against the years. The form of the line $k_r$ is very similar to that of $K$, which indicates that mortality due to the rhyssines is the key factor causing population change in *S. noctilio*.

It should be noted here that in this analysis the rhyssines are treated as one mortality factor because both act upon the same host population at the same time. Although *M. nortoni* was liberated for the first time in 1964, and could not have played a significant role in the mortality of *S. noctilio* before 1968 (see Fig. 2), there is evidence (Taylor, in prep.) that the ratio *R. persuasoria*: *M. nortoni* is reduced as the diameter of the tree trunk increases. This is reflected in the relative numbers of the two species as shown in Figure 2, particularly from 1970 to 1974.

The test for density relationships (Varley and Gradwell, 1968, p. 135) is shown in Figure 5A and B where the $k$-values $k_i$ and $k_r$ respectively are plotted against the logarithms of the populations upon which they acted. The slope of the regression for $k_i$ does not differ significantly from $b=0$, indicating density independence; but the slope of the regression for $k_r$ differs significantly from $b=0$ and is negative, indicating inverse density dependence. When the individual points for each year are linked serially they form an anticlockwise spiral (Fig. 5B) indicating delayed density dependence.

To provide proof of density dependency (Varley and Gradwell, 1968, Fig. 3), in Figure 6 log $S$ (the surviving population) is plotted against log Nr (the initial population). The regression slope differs significantly brom $b=1$ at the 0.1% level.

## Discussion

Figure 2 strongly suggests that the rhyssines were responsible for reducing the host population between 1967 and 1970, and that they will hold it at a relatively low level. Figure 3 reveals a tendency for the *S. noctilio* and rhyssine populations to oscillate approximately in antiphase as one would expect when the parasites are density-dependent. Key factor analysis indicates that under the conditions at Pittwater the rhyssine complex appears to act as a delayed density dependent factor whereas *I. leucospoides* appears to be density independent. These indications are consistent with our knowledge of the biology of the insects concerned.

Luck (1971) points out that Varley and Gradwell's method is best suited to univoltine populations. At Pittwater on average about 15 per cent (range 7–25) of each generation of *S. noctilio* emerge in Year 3, so that the rhyssines in Year $n$ act upon the bulk of the host population of Year $n$-1 plus about 15 per cent of that of Year $n$-2. Likewise the rhyssines present in the field in Year $n$ emerge mostly from the trees killed in Year $n$-2 with some from Year $n$-3. In addition *M. nortoni*, and to a lesser extent *R. persuasoria*, is partly bivoltine. The nondiapausing component of each generation acts upon the same generation of the host as that from which it emerges. These complicated relationships are being examined in more detail.

The regression for $k_i$ (Fig. 5A) indicates density independence (Varley and Gradwell, 1968, p. 135). The apparent density independence of *I. leucospoides* under the conditions prevailing at Pittwater may well be due to the reaction of the trees to attack by *S. noctilio.*

The attraction of *I. leucospoides* to the oviposition drills of *S. noctilio* coincides with hatching of the host eggs (Madden, 1968); it is dependent upon drying in the wood and is therefore related to water stress (Madden, 1974). In highly stressed trees most of the host eggs will hatch during the flight season of *I. leucospoides,* but at Pittwater, where few of the remaining trees suffer from more than mild stress in normal, non-drought summers, the eclosion of many *S. noctilio* eggs is frequently delayed until the following spring (Taylor, 1976).

In areas where a high proportion of the trees are very susceptible and there is little or no reaction from them to attack by *S. noctilio* the relationship between *I. leucospoides* and its host may prove to be density dependent. It is probably significant that in parts of Victoria which experience long dry summers and where most of the *S. noctilio* population emerges one year after the trees are killed, the level of parasitism by *I. leucospoides* is much higher than at Pittwater (R.J. McKimm, personal communication).

The values for $k_0$ (other sources of mortality) are also density independent but in the period 1969–1970 a marked elevation in $k_0$ was recorded. This can be attributed to the effects of the geometrid defoliator, *Chlenias* sp., on the suitability of the trees for siricid development. Before the defoliation $k_0$ was consistently between 0.15 and 0.2, indicating little variation in mortality of stages within the tree; whereas after defoliation the trees were apparently less suitable for *S. noctilio.* In 1970 $k_0$ doubled, and it has remained between 0.36 and 0.44 ever since. Thus mortality of stages within the tree has remained high since the defoliation, although in 1973 the estimated number of eggs laid (see Table 1) returned to the level of 1969.

This analysis covers only the first phase of the evaluation study at Pittwater. The parasitoid *Schlettererius cinctipes* and the parasitic nematode *Deladenus siricidicola* Bedding (see Bedding and Akhurst, 1974) were both released quite recently at Pittwater and had made no significant impact on the *S. noctilio* population prior to 1975.

Early results of evaluation studies in northern Tasmania and in Victoria make it clear that the overall economic impact of the parasitoids cannot be assessed effectively unless detailed studies similar to those made at Pittwater are carried out at other sites and in different bioclimatic areas.

*Acknowledgments.* I am grateful to Mr. R.J. Akhurst, Dr. J.L. Readshaw, Dr. R.D. Hughes, and particularly to Dr. J.L. Madden, for advice and constructive criticism of the manuscript; to Mrs. E. Longmore for help in analysing the data; and to Mrs. G. Palmer for preparing the figures. I also thank the many assistants who have taken part in the painstaking work of gathering the data, in particular, Mr. R. Bashford, Mr. J.G.T. Moss, and Mr. B.V.W. Reynolds.

Until 1974 the work was supported by the Australian National Sirex Fund.

## References

Bedding, R.A., Akhurst, R.J.: Use of the nematode *Deladenus siricidicola* in the biological control of *Sirex noctilio* in Australia. J. Aust. Entomol. Soc. **13**, 129–135 (1974)

Luck, R.F.: An appraisal of two methods of analyzing insect life tables. Can. Entomol. **103**, 1261–1271 (1971)

Madden, J.L.: Behavioural responses of parasites to the symbiotic fungus associated with *Sirex noctilio* F. Nature **218**, 189–190 (1968)

Madden, J.L.: Oviposition behaviour of the woodwasp, *Sirex noctilio* F. Aust. J. Zool. **22**, 341–351 (1974)

Taylor, K.L.: The introduction and establishment of insect parasitoids to control *Sirex noctilio* in Australia. Entomophaga **21**, 429–440 (1976)

Varley, G.C., Gradwell, G.R.: Population models for winter moth. In: Insect abundance (T.R.E. Southwood, ed.). Symp. R. Ent. Soc., Lond. **4**, 132–142 (1968)

*Received August 17, 1977*