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Avian Predation of the Woodwasp, *Sirex noctilio* F., and its Parasitoid Complex in Tasmania

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Abstract

More than 50% of the bird species occurring in a plantation of *Pinus radiata* at Pittwater, Tas., were implicated in the predation of the introduced woodwasp, *Sirex noctilio*, and its parasitoids. The dusky woodswallow, the raven and the spine-tailed swift attacked mating swarms at the tops of trees; an indirect effect was the abnormally high sex ratios of emergent insects in the following generations, which indicate a serious disturbance to mating frequency. Estimates of predator success, through the controlled release of large numbers of *Sirex*, and estimates of gross feeding, by bird census and numbers of *Sirex* in the stomach contents of the major predators, indicated that avian predation supplemented the effect of other biocontrol agents. The behavioural response of birds to their insect prey is described, and measures recommended which could be taken to maximize the beneficial effects of birds.

Introduction

The exotic woodwasp *Sirex noctilio* F. was discovered in plantations of *Pinus radiata* D. Don in Tasmania and Victoria in 1952 and 1960 respectively (Gilbert and Miller 1952; Irvine 1962), and more recently in the States of South Australia and New South Wales (Anon. 1981). The continued spread of this pest constitutes a serious threat to Australia's softwood industry, because a successful attack results in the death of trees. Both insect parasitoids and entomophagous nematodes have been introduced and released as biological control agents (Taylor 1967; Bedding and Akhurst 1974).

Birds are regarded as potentially important predators of forest pests (Dickson *et al.* 1979) and their role in affecting the dynamics of *Sirex* and parasitoid populations was investigated during 1965-71 and 1978-80.

The aims of the investigation were: (1) to identify bird species attacking *Sirex* and its parasitoids; (2) to estimate the impact of predation on insect densities, either directly or indirectly through preferential attack on mating swarms which could alter resulting sex ratios through disturbance of mating frequency; (3) to consider the effects on predatory activity of defoliation by geometrid larvae.

Methods and Materials

The major study area was 42 ha of *P. radiata* regeneration 10-15 y old at Pittwater, Tas. The plantation area was surrounded by extensively thinned mature trees and open *Eucalyptus-Acacia* associations.

A number of birds were collected during the *Sirex* flight season and their stomach contents examined for woodwasps. Two predator individuals were trapped, and held in laboratory cubicles (2·5 by 2·0 by 2·0 m) for feeding trials with *Sirex*.

The general activity and census of birds was assessed from 1968 to 1971 by making 5-min observations three times each week between 1100 and 1200 h at each of 10 sites within and around the study area. The census commenced in early December, before the emergence of *Sirex*, and was continued through to its completion. Birds frequenting the tops of trees were counted directly; estimates of numbers of birds frequenting the ground and lower canopy were obtained by recording the birds crossing the observer's line of vision over a transect of *c.* 100 m at each of the 10 sites. These latter, relative estimates of activity were in turn related to estimates of numbers of nesting pairs of the sedentary species.

Prey abundance and ovipositional activity were determined in each season from the weekly emergence of *Sirex* and its parasitoids into cages attached to 60 representative trees attacked by *Sirex*; the trees were subsequently collected for detailed dissection and all data adjusted with respect to the total study area (Taylor 1978).

Batches of 100–300 male *Sirex* from insectary stock were released within the study area, so that predation by birds could be observed and assessed. The majority of released insects flew to the tops of trees; the time lapse between release and the arrival of predators was recorded, together with the number of attacks made by the predators. The general activity of birds within the release area before, during and after 20 of these releases was obtained on playback from a Sony C80 tape recorder. General weather conditions were also obtained.

Predation on *Sirex* females was assessed in an experiment in which females found during daily examinations on 84 trees, preconditioned to *Sirex* attack by ringbarking (Madden 1971), were marked with a colour code and their subsequent longevity followed.

Sex determination in both *Sirex* and the parasitoids is by the haplo-diploid mechanism (White 1964). Unfertilized eggs result in male progeny and fertilized eggs in female progeny. Therefore, preferential removal of males before mating would be expected to result in alterations of the sex ratio of emergents in the following season. The sex ratios of emergents from the 60 caged trees were examined for this effect.

Consumption of prey by predators was assessed by multiplying the average weekly numbers of birds by seven times the average daily consumption of prey, taken as the mean number of prey per stomach examined. This value was compared with the incidence of successful attack obtained from the released batches of prey, times the average weekly number of emergents obtained from the caged trees.

Results

The apparency of *Sirex* and its parasitoids to potential predators is influenced by their seasonal abundance and behaviour following emergence. The following paragraphs summarize these features.

S. noctilio emerges during the summer months (December–May). Emergents fly to the tree tops, and aggregate into swarms at the tops of the highest trees in a stand. This aggregative response is presumably facilitated by sound, because the wing beat is distinctly audible. Mating occurs on the upper branches, after which females reenter the understory to locate suitable trees in which to oviposit. Males remain at the tops of the trees.

The parasitoid *Ibalia leucospoides* (Hochenw.), which parasitizes *Sirex* eggs and young larvae, emerges with *Sirex* (January–March); the larval parasitoids *Rhyssa persuasoria* L. and *Megarhyssa nortoni nortoni* Cresson emerge to attack mature larvae during the spring (September–November). Despite the difference in their seasonal incidence the post-emergence behaviour is similar. Male parasitoids are attracted to trees similar to those from which they emerged; males form aggregations at sites on the bark surface from which females are likely to emerge.

Hence, *Sirex* aggregate at the tops of trees whereas the parasitoids remain within the understory.

Experimental Results

Predation was confined chiefly to the period 0900–1200 h, as after this emergence and subsequent flight were suppressed through the onset of a cool sea breeze. *Sirex* flight and predation during the cooler afternoons was only rarely observed, although surviving insects could be seen on the treetops.

Forty-two species of birds were recorded in the study area and 22 (52%) of these species were implicated in predation. The major predators of *Sirex* were the dusky woodswallow *Artemus cyanopterus*, the forest raven *Corvus tasmanicus*, and the migratory spine-tailed swift *Hirundapus caudacutus*, all of which attacked the mating swarms.

Table 1. Avian predators of *S. noctilio* at Pittwater in 1966–71, in order of their effectiveness, and the stomach contents of the major species collected at peak emergence of *Sirex*

Common name	Number sampled	Number of *Sirex* in stomach			
		Mean	Range	No. males	No. females
Dusky woodswallow	15	8	2–11	117	3
Forest raven	7	8	4–16	52	4
Spine-tailed swift[A]	–	–	–	–	–
Grey butcherbird	2	5	–	10	–
Grey shrike-thrush	8	3	1–5	8	16
Golden whistler	5	2	1–4	3	7
Welcome swallow	5	2	0–4	8	2
Wattlebird[A]	–	–	–	–	–
Dusky robin[A]	–	–	–	–	–
Scarlet robin[A]	–	–	–	–	–
Flame robin[A]	–	–	–	–	–
Silvereye[A]	–	–	–	–	–
Black-faced cuckoo-shrike[A]	–	–	–	–	–
Yellow-throated honeyeater[A]	–	–	–	–	–

[A] Observed but not collected.

Table 1 shows the average numbers of *Sirex* found within the stomach contents of the major predators. Both the dusky woodswallow and the spine-tailed swift fed exclusively on *Sirex*, whereas the raven contained *Sirex*, other insects (Coleoptera, Blattodea), mammal remains and pine seeds. This last species also differed in its feeding habits, preferring to perch on the upper branches of trees and feed on insects flying around the tree or resting on the foliage. Two captured ravens, starved for 24 h, consumed an average of 230 immobilized male insects during 60 min; in another trial 300 active insects were pursued and captured during 120 min.

Predation of released batches of *Sirex* males averaged 36·4% (range 7·0–88·0%; $n = 26$) and the average time for predators to locate released insects which aggregated at the tops of trees was 6·9 min after release ($n = 16$).

Coincident with the release of males was an increase in the frequency of calls made by smaller, generally non-predaceous birds, e.g. finches, wrens, etc. This enhanced calling was temporarily suppressed on the arrival of the predators but remained above pre-release levels until the predators had left the area. Observed changes in bird number and diversity and calling frequency before, during and after predation are summarized in Table 2.

Table 2. Numbers and diversity of birds before, during and after release of 250 male *Sirex* on each of three occasions in *Pinus radiata* regeneration at Pittwater in 1971

M, many. Asterisk indicates that attack and feeding were observed

	12 February 1045–1245 h	15 February 1145–1245 h	4 March 1145–1245 h
Temperature (°C)	21–22	25–28	20–21
Conditions	Cloudy, bright	Sunny, bright	Sunny, bright
Wind	Light north-east	Light north-east	Light south-east
	Before release (15 min)		
Hawk	–	–	1
Robins	–	2	2
Flame robin	1	–	–
Fairy-wrens	–	6	4
Goldfinch	7	–	–
Forest raven	–	–	–
	During release (20 min)		
Hawk	–	1	–
Swifts	107*	4*	5*
Flame robin	3*	–	–
Scarlet robin	–	2*	–
Dusky robin	–	2*	–
Grey shrike-thrush	2*	–	–
Fairy-wrens	–	8	1
Pardalote	1	–	–
Silvereye	14*	12*	–
Goldfinch	13*	6*	1
Woodswallow	1*	4*	2*
Forest raven	4*	1*	2*
	After release (25 min)		
Swifts	–	4	–
Welcome swallow	10	–	7*
Scarlet robin	M*	2*	–
Dusky robin	–	2*	1*
Golden whistler	2*	–	–
Grey shrike-thrush	–	–	1*
Fantail	–	–	1
Fairy-wrens	M	8	–
Thornbills	M	–	2
Pardalotes	M	–	–
Silvereye	M*	15*	–
Goldfinch	M*	6*	3*
Woodswallow	10*	4*	8*
Butcherbird	–	–	1*
Forest raven	–	6*	1*

The average number of birds observed within the study area increased at the beginning of the *Sirex* emergence season and remained at high levels throughout the season, to decline rapidly at its completion. The functional response of prey numbers relative to *Sirex* prey is depicted in Fig. 1. The regression of log estimated consumption to log expected consumption was significant in 1968–69 ($P<0\cdot05$,

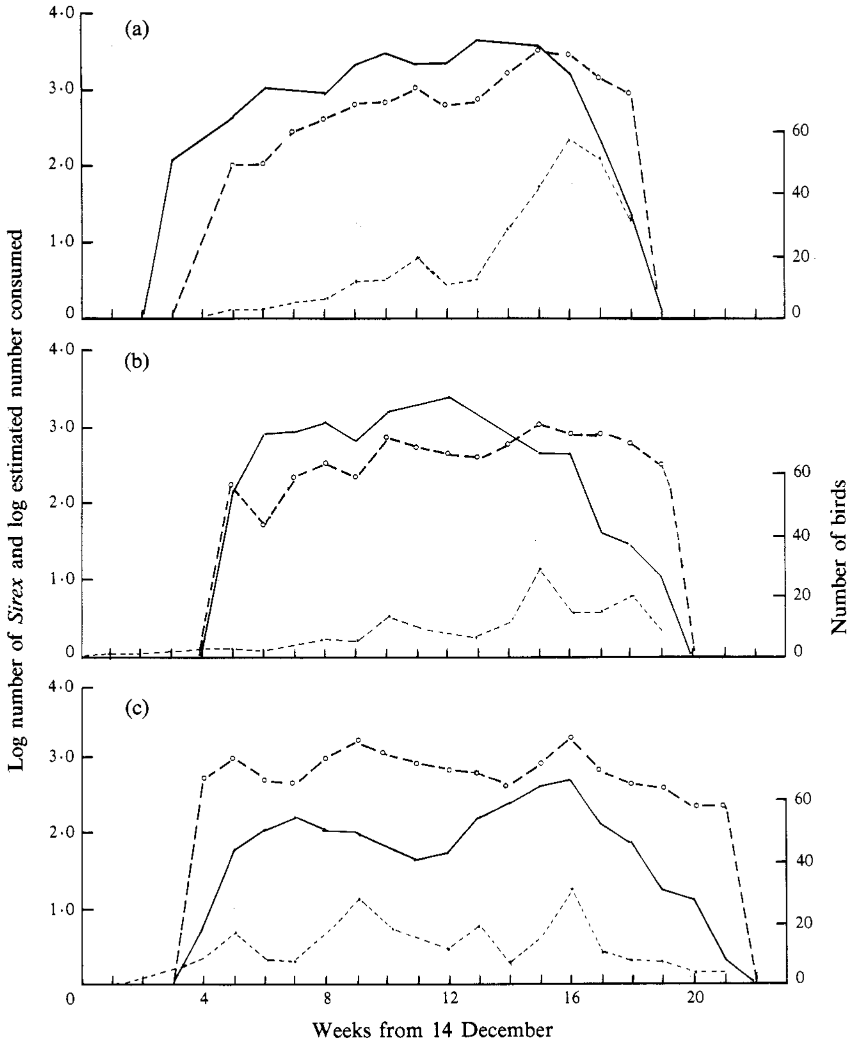

Fig. 1. Seasonal emergence of *Sirex* from trees (————), the incidence of major bird predators (- - - - -), and their estimated consumption of *Sirex* (-O- - - -O-) for the three seasons of study. (*a*) 1968–69. (*b*) 1969–70. (*c*) 1970–71.

$r=0\cdot84>0\cdot60$ critical value) but fell in the following two seasons ($r=0\cdot56<0\cdot67$, and $r=0\cdot35<0\cdot63$ respectively) (Fig. 2). The accumulated weekly totals of predators over these three seasons were 315, 160 and 246; those of *Sirex* were 29,040, 14,190 and 2213 respectively.

The sex ratio of emergents from individual trees was variable, and males significantly outnumbered females. A similar trend was observed in the sex ratios of the parasitoids (Table 3; Fig. 3).

Predation of the parasitoids was observed only rarely. However, the release of insectary stock within the study area was followed by predation by, notably, the golden whistler *Pachycephala pectoralis*, grey shrike-thrush *Colluricincla harmonica*, and three species of robins, together with the dusky woodswallow and the welcome swallow, *Hirundo neoxena*. Predators of the parasitoid complex, and numbers of parasitoids found in their stomachs after collection in normal field conditions, are summarized in Table 4.

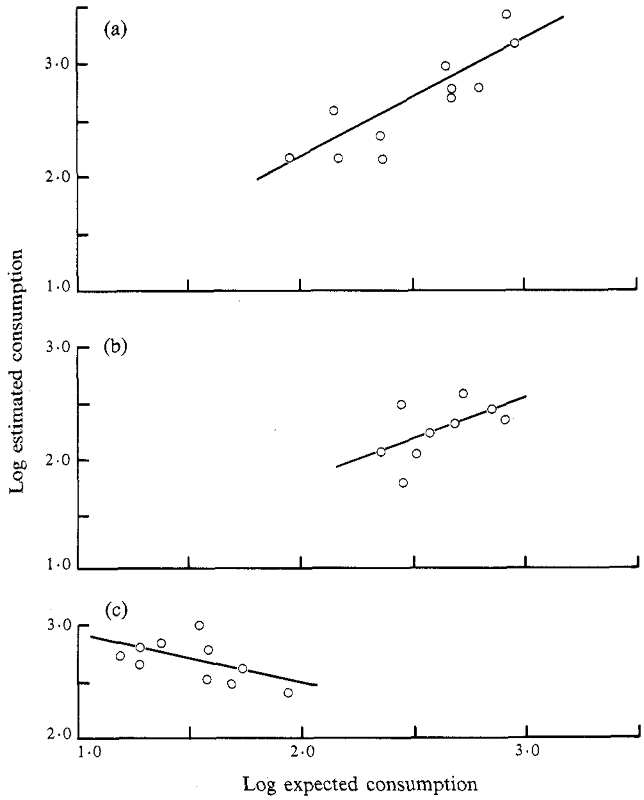

Fig. 2. Correlations of estimated with expected consumption of *Sirex* prey for the three seasons of study. (*a*) 1968–69. Regression equation: $\log y = -0\cdot06 + 1\cdot01 \log x$; $r = 0\cdot84$, $P < 0\cdot05$.
(*b*) 1969–70. Regression equation: $\log y = -1\cdot26 + 0\cdot48 \log x$; $r = 0\cdot56$, NS.
(*c*) 1970–71. Regression equation: $\log y = 3\cdot36 - 0\cdot45 \log x$; $r = 0\cdot35$, NS.

Predation of ovipositing females was evidenced by the remnants of oviposition within trees, and 13% of the observed number of females were taken. However, 58% of the total females disappeared, and on the basis of observations it is assumed that these were also taken by birds as they walked over the bark surface. Consequently, 63% of females on trees were taken by birds. The average duration of a female's stay on a tree before predation was 1·70 days, compared to 2·60 days for those that disappeared and 2·70 for those that remained and died on the trees (Table 5). In 1979–80, at Dulverton in north-west Tasmania, a total 41 *Sirex* ovipositors were

Table 3. The sex ratios of *S. noctilio, I. leucospoides, R. persuasoria* and *M. nortoni* emerging from individual trees attacked during study seasons

Values are means ± standard deviations, with numbers of trees in parentheses. Trees with emergents of only one sex excluded

Season	*S. noctilio*	*I. leucospoides*	*R. persuasoria*	*M. nortoni*
1968–69	5·40 ± 4·59 (*56*)	0·88 ± 0·57 (*26*)	4·78 ± 7·67 (*47*)	2·95 ± 3·02 (*37*)
1969–70	5·30 ± 4·27 (*58*)	1·79 ± 1·59 (*46*)	5·74 ± 6·27 (*48*)	5·28 ± 5·75 (*43*)
1970–71	5·40 ± 8·15 (*49*)	1·52 ± 1·06 (*33*)	5·33 ± 4·39 (*33*)	2·33 ± 1·55 (*31*)

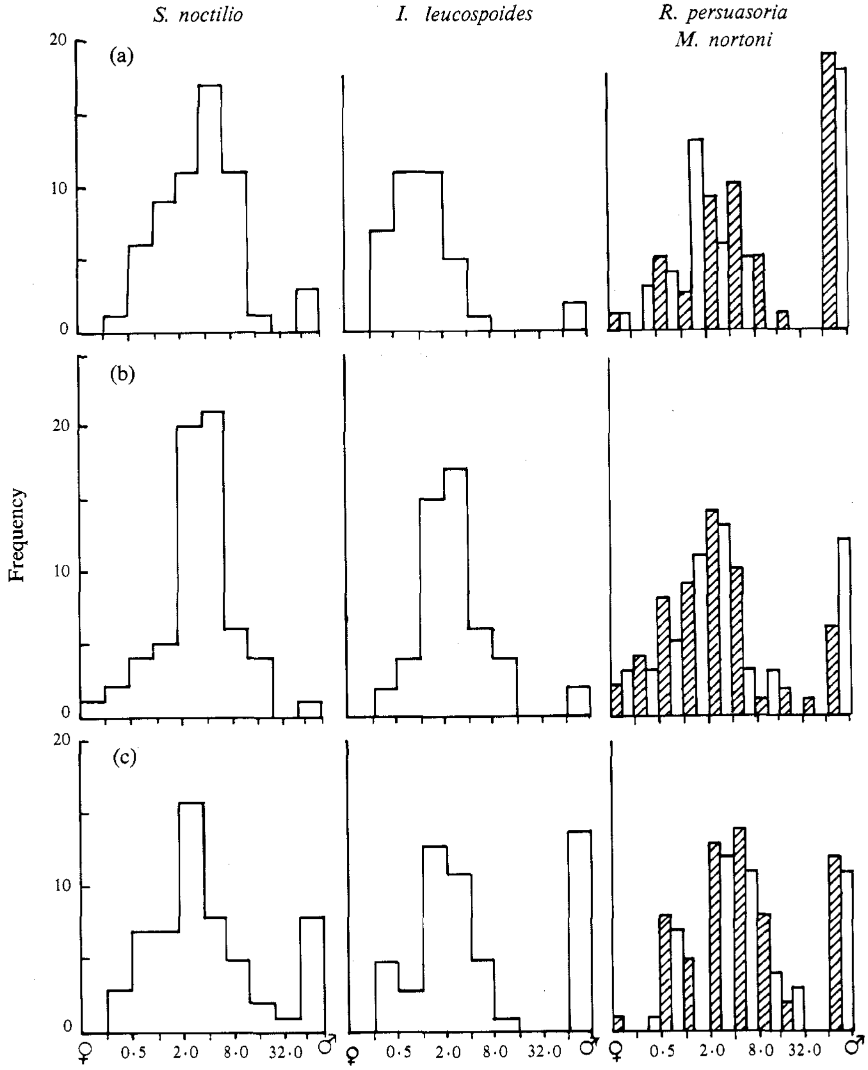

Fig. 3. Frequency distributions of sex ratios of *S. noctilio* and its parasitoids *I. leucospoides*, *R. persuasoria* (hatched) and *M. nortoni* emergent from individual trees over the three seasons of study. (*a*) 1968–69. (*b*) 1969–70. (*c*) 1970–71. Sex ratios are grouped in geometric series. Female and male symbols refer to the incidence of trees from which individuals of only one sex emerged.

found in the stems of 38 trees; in this infestation the average number of females observed per attacked tree was $2 \cdot 40 \pm 0 \cdot 68$ ($n = 20$ trees).

Table 4. Avian predators of the parasitoids of *S. noctilio* at Pittwater, in 1966–71, in order of their effectiveness, and the stomach contents of some major species collected at peak emergence of the respective parasitoid species

Common name	No. sampled	*I. leucospoides* Males	*I. leucospoides* Females	No. sampled	*R. persuasoria* Males	*R. persuasoria* Females
Silvereye	5	5	15	0[C]	0	0
Golden whistler	5	2	16	3	15	6
Grey shrike-thrush[A]	8	8	4	2	8	3
Fantail	2	1	6	0[C]	0	0
Dusky woodswallow	15	3	4	0[C]	0	0
Welcome swallow	5	8	3	0[C]	0	0
Dusky robin[B]	–	–	–	–	–	–
Scarlet robin[B]	–	–	–	–	–	–
Flame robin[B]	–	–	–	–	–	–
Goldfinch[B]	–	–	–	–	–	–
Pallid cuckoo[B]	–	–	–	–	–	–
Brown thornbill[B]	–	–	–	–	–	–
Superb fairy-wren[B]	–	–	–	–	–	–
Blackbird[B]	–	–	–	–	–	–

[A] Observed to take *Megarhyssa*. [B] Observed but not collected.
[C] Not observed (Sept.–Oct.)

Table 5. The fate of marked *Sirex* females on experimental trees at Pittwater in 1968

Fate	Number	Percentage	Mean time observed (days)
Disappeared from trees	106	58·0	2·60
Attacked by birds	10	5·0	1·70
Dying on tree	65	36·0	2·65
Attacked by pentatomid	1	1·0	1·00

Discussion

Estimates of predation of *S. noctilio* by birds at Pittwater during 1968–69 averaged 36% of males and a minimum of 13% of females. The selective predation of *Sirex* aggregations at the treetops resulted in a reduction of numbers of *Sirex*, with the probable consequence that mating frequency was disturbed. The overall bias in favour of males in the sex ratios of emergent *Sirex* over the three seasons contrasts markedly to the ratio reported by Spradbery and Kirk (1968) for European populations of *S. noctilio*, viz. $1 \cdot 0 : 1 \cdot 82$ ($n = 7032$ insects).

A similar phenomenon can be proposed for the abnormally higher sex ratios of the parasitoid complex, which in Europe were found by the above authors to be $1 \cdot 0 : 1 \cdot 2$ for *I. leucospoides* ($n = 6470$) and $1 \cdot 0 : 2 \cdot 9$ for *R. persuasoria* ($n = 7587$).

Taylor (1978) in a key factor analysis of the role of insect parasitoids, provided a series of annual budgets from which, with allowance for sex ratios, the numbers of eggs deposited per female *Sirex* per season were 12·75 and 10·31 for 1968–69 and 1969–70 respectively, which indicated a loss in potential of approximately 90% from the average egg content of 140 in newly emerged *Sirex*. In 1970–71 the loss in potential fell to 35%, which could have resulted from the dispersal of the *Sirex* population onto the large numbers of trees predisposed to attack by *Chlenias* sp. (Madden and Bashford 1977). That is, spatial dispersal of the prey reduced the risk of predation, as has been demonstrated in the predation of other forest pests (Otvos 1979).

Differences in the seasonal patterns of bird activity and abundance were not related to *Sirex* abundance. Progressive defoliation of the study area by a geometrid defoliator, *Chlenias* sp., (Madden and Bashford 1977) resulted in a drastic alteration in the habitat of many of the sedentary bird species. In 1970–71 mortality of nestlings was observed as a result of nests being exposed, due to defoliation, to weather and predators.

The frequency of wing beat of *Sirex* males is of the order of 20 Hz (unpublished information) and quite audible. The collective noise from a swarm of *Sirex* generated an immediate disturbance reponse in small birds, which continued until the *Sirex* had been removed and the predators had left the area.

The disturbance response and increased frequency of calling initiated by the presence of flying insects presumably provided the cue to which the predator species responded, as 80% of the swarms were located within 7 min of release; this indicates that the activities of non-predator species of birds may be utilized by predators in the location of prey.

This study illustrates that birds, acting opportunistically, are capable of feeding on large numbers of *Sirex* throughout a season, and that their effects on mating frequency may result in changes which would have a considerable effect on succeeding generations of *Sirex* through reducing the numbers of females. This in turn would supplement the activity and effect of the insect parasitoids. However, predation on the parasitoid complex may reduce their overall effect.

In terms of *Sirex* control and forest management, this study emphasizes the importance of maximizing the effects of birds. The interruption of pure stands with corridors of natural vegetation would, where feasible, be a first approach as it reduces the ratio of perimeter to area and ensures a diversity of birds and their access to the insects' habitat.

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