

Life cycle and biological control of the *Eucalyptus* snout beetle (Coleoptera, Curculionidae) by *Anaphes nitens* (Hymenoptera, Mymaridae) in north-west Spain

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- Abstract**
- 1 *Gonipterus scutellatus* is a weevil that has become a pest in most *Eucalyptus* plantations in Africa, America and Europe. The egg parasitoid *Anaphes nitens* has been introduced into many countries as a biological control agent. Even if control has been successful in most countries no detailed study of the interactions between both species has been published.
 - 2 *Gonipterus scutellatus* was detected in 1991 in north-west Spain and *A. nitens* was introduced in early 1994. Here we report on the results of a 2-year study of parasitism in a field plot and a survey of 16 localities in North-west Spain. In 1996, parasitism was so intense (80–100% of eggs) that *G. scutellatus* became locally extinct, and as a consequence *A. nitens* disappeared. In 1997, *G. scutellatus* recolonized the area and was followed by its parasitoid, but parasitism was low in spring, probably because the parasitoid population needed 3 weeks to achieve a similar size as in 1996. Consequently, damage to the trees was extreme in 1997. We interpret these results as population fluctuations due to parasitoid–host interactions and suggest that parasitoids should not be so effective as to locally extinguish their host to be useful for biological control.
 - 3 The analysis of parasitism level in 16 localities indicates that *A. nitens* is highly efficient in finding *G. scutellatus* egg-masses. At a small spatial scale (single trees) positive density dependence was detected where parasitism was low and inverse density dependence where parasitism was high.

Keywords *Anaphes nitens*, biological control, *Gonipterus scutellatus*, local extinction, parasitoid density-dependence, population oscillations.

Introduction

Biological control is the regulation by natural enemies of another organism's population density at a lower average than would otherwise occur (DeBach & Rosen, 1991). Kidd & Jervis (1997) review the impact of parasitoids on forest insects and indicate that in 20 out of 32 detailed studies of forest pests, natural enemies were the main factor regulating pest populations. Many examples of biological control studies indicate that a detailed knowledge of the ecology of parasitoid–pest interactions is necessary to achieve successful control (Caltagirone, 1981; DeBach & Rosen, 1991; Murdoch & Briggs, 1996).

The *Eucalyptus* snout beetle (*Gonipterus scutellatus* Gyll.) is a weevil native to south-east Australia, where it is a rare insect that feeds exclusively on *Eucalyptus*, although attacks on apple trees have been reported (Tooke, 1955). It remained largely ignored until it was found in South Africa in 1916, where populations reached pest status in a few years. Damage to the *Eucalyptus* plantations was so extreme that in 1926 the South African Government decided to send F. G. C. Tooke to Australia, to search for natural enemies of the pest. In only 10 days, he found the mymarid *Anaphes nitens*, a parasitoid of *Gonipterus* eggs. This led to the introduction of *A. nitens* into South Africa and the start of one of the most impressive examples of biological control ever reported (Mossop, 1929; Tillyard, 1931; Tooke, 1942, 1955). The parasitoid has subsequently been introduced to New Zealand (Clark, 1931), Zimbabwe (Mossop, 1955), Mauritius (Moutia & Vinson, 1945; Williams *et al.*, 1951),

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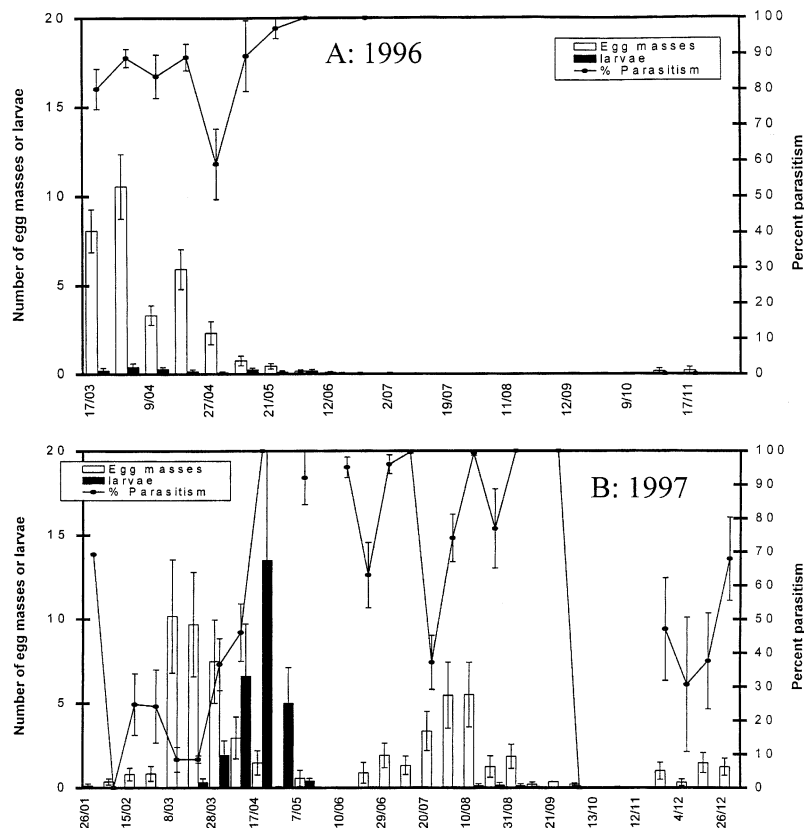


Figure 1 Phenology of *G. scutellatus* at Lourizán (average number of egg masses or larvae per tree \pm SE) and parasitism by *A. nitens*. In 1996 only one main egg-laying period was observed, while two were clearly detected in 1997. Note that parasitism was higher in the spring of 1996 than in 1997, but the density of egg masses was similar.

Madagascar (Frappa, 1950), Argentina (Marelli, 1928), Italy (Arzone, 1985), France (Pinet, 1986) and Spain (Mansilla & Pérez, 1992). There are also plans to introduce it into California (Cowles & Downer, 1995). In most cases control was highly effective, and this is the only biological control example where an egg parasitoid acting alone was able to control a pest successfully (DeBach & Rosen, 1991).

Given the above historical account, it is surprising that no detailed study seems to have been made of the interaction between *G. scutellatus* and *A. nitens*. Published estimates of parasitism are reduced to range values from a large geographical area or point values from different localities at a single or several dates, without systematic sampling. For example, *A. nitens* was first introduced into South Africa in 1926, and about 736 000 parasitoids were liberated by the end of 1933 (Tooke, 1955). The action of this parasitoid was spectacular: in May 1928 parasitism was 3–13%; in summer 1929 0.1–31%; between 1929 and 1930 it reached 60–90% and by December 1930 it rose to 77–98% (Tooke, 1955). Nevertheless, subsequent studies in South Africa have shown that *A. nitens* is unable to control the weevil in very susceptible tree species and outbreaks have been detected in areas where good control was previously reported. A search for more parasitoids has started (Anon, 1987).

Gonipteris scutellatus lays egg masses that have an average of eight eggs, covered by a dark secretion mainly composed of faeces. These egg masses are easily found on young leaves, and parasitism by *A. nitens* can be estimated by counting the number of beetle larvae and parasitoids emerged from field-collected egg masses.

We present a study of the phenology of *G. scutellatus* and parasitism by *A. nitens* at one locality in north-west Spain during 2 years, and the incidence of parasitism in 16 localities in the same area. Our aim was to study the interaction of the parasitoid and its host, and to determine whether *A. nitens* acts in a spatially density-dependent way, a behaviour that is considered useful for biological control agents (Walde & Murdoch, 1988; Murdoch & Briggs, 1996; but see Rohani *et al.*, 1994).

Methods

The experimental plot was established in a young *Eucalyptus globulus* stand on 17 March 1996, located at Lourizán (Pontevedra, North-west Spain), in the area where *G. scutellatus* had first been found in 1991 (Mansilla, 1992). We selected 25 small trees randomly (2–3 m high at the start of the experiment), marked them and removed every egg mass found. At intervals of about 10 days we collected all the egg masses found on the trees,

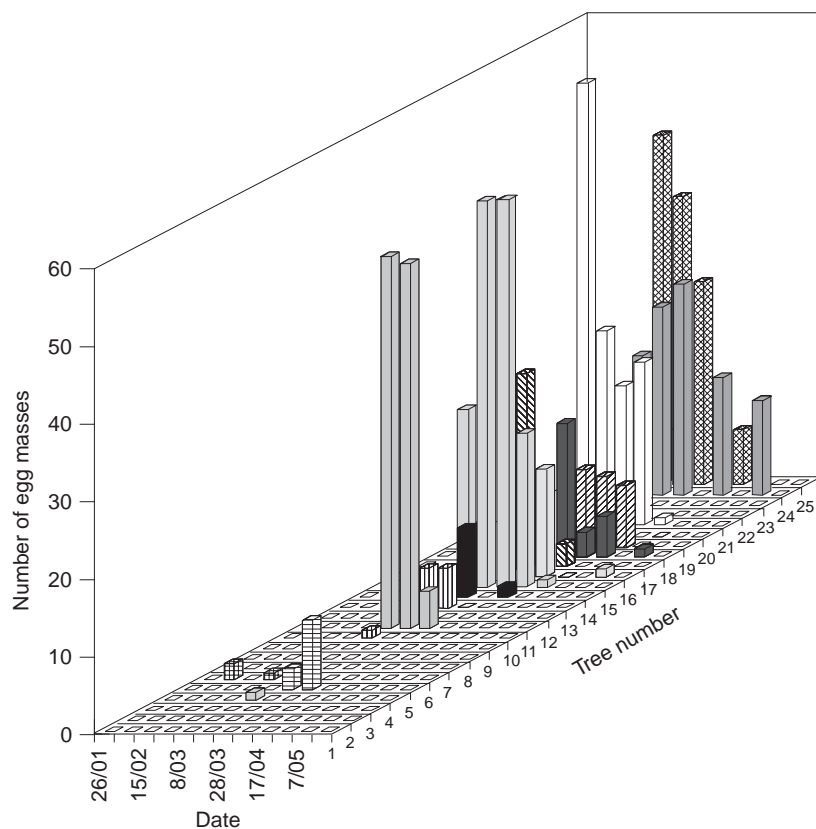


Figure 2 The number of egg masses found in individual trees at Lourizán plot during spring 1997. Note that some trees never received eggs, while others (most of them with adult leaves) were heavily attacked.

transported them to the laboratory and placed them in plastic tubes (6×1 cm). We collected a total of 2289 egg masses during 2 years. We also counted the number of adults and larvae found on the same trees. This was done not to estimate their abundance (because we collected egg masses from these trees), but to estimate the number of larvae that emerged from egg masses that we did not find. A lapse of 10 days was selected because larvae of *G. scutellatus* emerge after about this interval at 20–23°C.

Tubes were examined every day for 1 month and the number of beetle larvae and parasitoids emerged was counted. We estimated parasitism as parasitoids/(parasitoids + beetle larvae). Unless otherwise indicated, parasitism was averaged over eggs within trees and over trees within the plot. We assume that every egg produced one parasitoid or one beetle larvae. We tested this assumption by dissecting 50 randomly chosen egg masses. In 25 cases egg masses were empty (suggesting all the eggs hatched), 9 had 1 or 2 dead *Anaphes* inside and 16 had an average of 1.6 eggs (range 1–5) in different stages of development. These eggs could be infertile or dead embryos that were superparasitized, and all *Anaphes* larvae died (Tooke, 1955). In very rare cases do two adults of *A. nitens* emerge from one *Gonipterus* egg (Clark, 1931), and the few that do tend to be half-size. Therefore our estimates of parasitism are probably an underestimate, due to parasitoids dying inside the egg mass as adults or larvae. Sampling continued until the end of December 1997, but no samples were collected during December 1996. Two trees died

during the sampling period and were substituted by the nearest tree. On 20 September 1997 all but two trees were destroyed by a forest fire. Therefore, on 21 September we selected 23 new trees at about 50 m from the previous ones, and these were sampled until the end of 1997.

To test whether *A. nitens* acted in a spatially density-dependent way, we calculated the regression between egg mass density and parasitism (angular transformation).

In spring 1997 we visited 16 localities and counted the number of adults, larvae and egg masses of *G. scutellatus* found in 50 randomly selected young trees (1–4 m high). We always selected young trees to facilitate sampling, because *G. scutellatus* concentrates on the top of the trees. To examine the tree it was carefully inclined. At each locality we also collected at least 30 egg masses to estimate parasitism. Most localities were sampled only once.

Results are presented as means \pm SE (n). Statistical analyses were made with SPSS.

Results

In 1996, the egg-laying period of *G. scutellatus* had already started when we collected the first sample of egg masses on 17 March. Mating pairs were very common. Figure 1a shows the average number of egg masses and larvae found in sampled trees during 1996. Eggs were found during spring, but not thereafter.

Table 1 The slope of the relationship between parasitism (angular transformation) and number of egg masses per tree. The null hypothesis is that the slope is zero. Only slopes calculated from at least 20 egg masses and five trees are included. The Bonferroni correction for type I errors indicates that slopes are significantly different from zero if $P < 0.002$.

Date	Trees	Slope
1996		
17 Mar.	23	0.008444
3 Apr.	24	-0.003602
9 Apr.	20	-0.015351
18 Apr.	22	-0.004051
27 Apr.	15	-0.008766
1997		
15 Feb.	5	0.052061
26 Feb.	9	0.020844
8 Mar.	15	0.005977
18 Mar.	12	0.006187***
28 Mar.	11	0.010207
7 Apr.	7	0.026137
19 Jun.	11	-0.007741
29 Jun.	8	-0.052148***
11 Jul.	10	0.001776
20 Jul.	11	-0.009052
30 Jul.	10	0.000479
10 Aug.	6	-0.012327
21 Aug.	9	-0.029093
25 Nov.	8	0.063260
14 Dec.	7	0.006234
26 Dec.	10	0.042874

*** $P < 0.001$

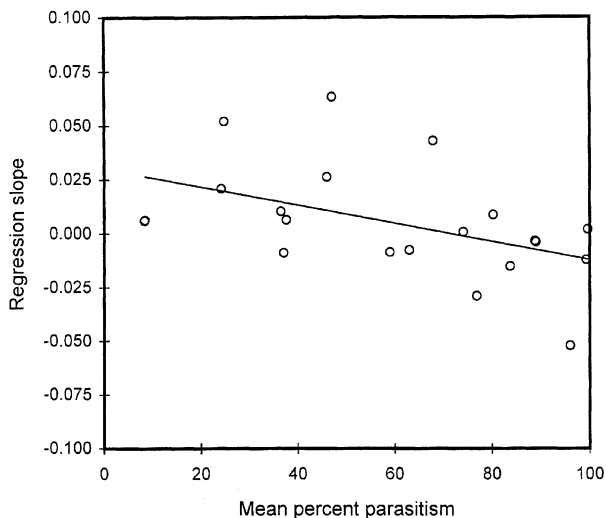


Figure 3 The relationship between parasitism and the slope of the regression between parasitism and egg mass density. The regression equation is $y = 0.03005 - 0.00042x$, $F = 5.642$, d.f. 1, $P = 0.028$.

Larvae were rarely found on the trees, and the adults were almost non-existent from June: only three individuals were found between June and October. A few egg masses were again found in November. Nevertheless, in 1997 the life cycle of

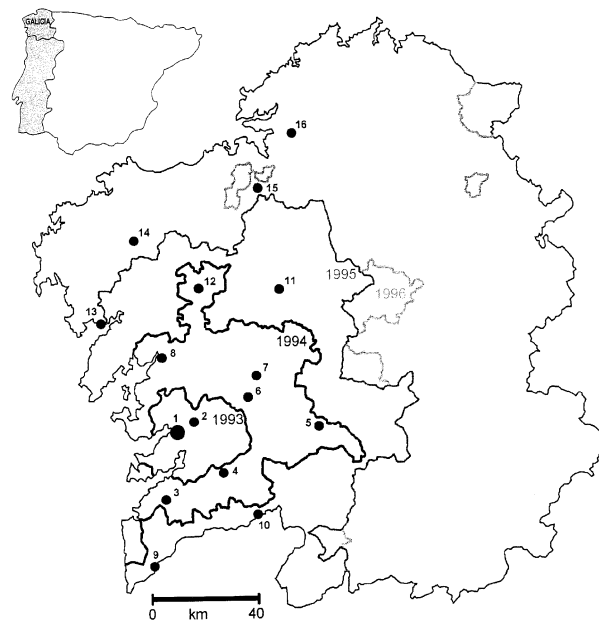


Figure 4 Map of Galicia (north-west Spain) showing sampled localities. Lines indicate the area colonized by *G. scutellatus* until different years (from Mansilla & Pérez, 1996; J. P. Mansilla, pers. com.).

G. scutellatus was completely different (Fig. 1b): there was the first egg-laying period in spring and a clear second egg-laying period in June–August. Many trees were almost defoliated in April, with a maximum of 124 mature larvae in our experimental trees, from which we collected egg masses. This was due to some eggs hatching between samplings (they probably took less than 10 days to develop due to high temperatures). It is also possible that some larvae migrated from trees whose canopy was in contact with the experimental trees. Nearby trees whose egg masses had not been collected were totally defoliated by larvae. Adults were regularly observed. A third and smaller egg-laying period started at the end of November.

Figure 1 also shows the relationship between parasitism and egg mass density. In 1996, most eggs were parasitized, reaching 80–89% parasitism even when the number of eggs per tree reached a maximum. Parasitism was reduced to 59% at the end of April, but achieved 90–100% in May–June, when egg density was very low. From the nine egg masses found in November no parasitoids emerged. In 1997, the first sample was collected on 26 January: only three egg masses were found and were 69% parasitized. No parasitoids emerged from the nine egg masses found on 6 February. Afterwards, *G. scutellatus* laid eggs at a high rate and egg mass densities increased from 0.84 ± 0.34 (25) egg masses per tree on 26 February to 10.16 ± 3.37 (25) on 8 March. Apparently this 'explosive' breeding allowed most eggs to escape parasitism and only 8% were parasitized. This is surprising because on 3 April 1996 the number of egg masses was almost the same but parasitism achieved 89%. Parasitism grew to 46% on 7 April and 90–100% on most subsequent dates, and showed again two minima on 19 June and 20 July. Most egg masses were completely parasitized at high parasitism rates, but

Table 2 Parasitism of *G. scutellatus* egg masses by *A. nitens*, in 16 localities of Galicia (north-west Spain) in early 1997. Localities are ordered from its distance to the locality where *G. scutellatus* was first found (loc. 1). Numbers in parenthesis after localities refer to Fig. 4.

Locality	Date	% Parasitism*		Mean number per tree (\pm SE)**		
		By egg mass Mean \pm SE (N)	By plot	Egg masses	Larvae	Adults
Pontevedra (1)	18 Feb.	45.7 \pm 8.0 (34)	40.6	–	–	–
	22 Feb.	43.6 \pm 8.4 (31)	41.7	1.26 \pm 0.35	0.00 \pm 0.00	0.42 \pm 0.11
Bora (2)	8 Feb.	57.3 \pm 7.2 (42)	52.5	–	–	–
Vigo (3)	21 Feb.	34.6 \pm 6.4 (51)	27.9	1.38 \pm 0.59	0.08 \pm 0.08	0.34 \pm 0.12
	14 Mar.	2.7 \pm 2.4 (36)	2.3	10.66 \pm 2.24	0.80 \pm 0.38	0.24 \pm 0.10
Mondariz (4)	15 Feb.	100.0 (1)	100	0.03 \pm 0.03	0.00 \pm 0.00	0.03 \pm 0.03
	2 Mar.	15.8 \pm 5.2 (46)	18.6	3.52 \pm 0.61	0.00 \pm 0.00	0.18 \pm 0.07
Maside (5)	23 Mar.	2.6 \pm 1.8 (69)	2.5	15.60 \pm 3.11	13.70 \pm 3.17	0.82 \pm 0.27
Folgosos (6)	22 Feb.	0.0 (1)	0	0.04 \pm 0.03	0.00 \pm 0.00	0.20 \pm 0.06
	7 Mar.	0.0 \pm 0.0 (34)	0	2.56 \pm 0.69	0.00 \pm 0.00	1.20 \pm 0.35
	8 Apr.	5.8 \pm 2.5 (61)	4.9	15.26 \pm 3.11	81.40 \pm 20.86	0.28 \pm 0.17
Candán (7)	26 Mar.	0.0 \pm 0.0 (45)	0	9.36 \pm 1.39	2.74 \pm 0.86	0.12 \pm 0.05
Catoira (8)	9 Mar.	34.3 \pm 0.5 (36)	27.4	3.11 \pm 1.15	0.08 \pm 0.06	0.19 \pm 0.10
Goíán (9)	1 Mar.	86.4 \pm 4.1 (52)	83.1	2.58 \pm 0.76	0.00 \pm 0.00	0.02 \pm 0.02
	6 Apr.	87.7 \pm 4.3 (48)	87.3	9.02 \pm 0.98	4.04 \pm 0.75	0.02 \pm 0.02
Arbo (10)	2 Mar.	26.4 \pm 5.5 (51)	28.4	9.38 \pm 2.31	0.24 \pm 0.24	3.28 \pm 1.00
	13 Apr.	71.5 \pm 14.7 (8)	76.1	2.94 \pm 0.62	19.52 \pm 4.19	0.20 \pm 0.07
Arzúa (11)	26 Mar.	1.4 \pm 1.1 (44)	1.9	4.38 \pm 0.82	8.02 \pm 1.67	0.06 \pm 0.03
Santiago (12)	16 Mar.	70.9 \pm 5.3 (54)	69.5	4.46 \pm 0.93	0.24 \pm 0.13	0.10 \pm 0.08
Muros (13)	30 Mar.	32.2 \pm 8.0 (32)	21.5	0.84 \pm 0.26	0.30 \pm 0.30	0.00 \pm 0.00
Sta Comba (14)	30 Mar.	26.2 \pm 7.6 (31)	19.7	0.12 \pm 0.05	0.26 \pm 0.19	0.00 \pm 0.00
Mabegondo (15)	28 Mar.	99.0 \pm 0.6 (34)	99.0	0.68 \pm 0.16	0.26 \pm 0.13	0.00 \pm 0.00
Pontedeume (16)	1 Jul.	100.0 \pm 0.0 (2)	100	0.04 \pm 0.04	0.00 \pm 0.00	0.00 \pm 0.00

* Percent parasitism was calculated by egg mass and afterwards averaged per plot, or directly by plot taking the total number of larvae and parasitoids emerged.

** Density of *G. scutellatus* was estimated from 50 trees by plot, except at Mondariz plot on 15 February, when we examined only 33 trees.

in spring 1997, when parasitism was low, many egg masses were partially parasitized.

Some trees received consistently higher number of egg masses (Fig. 2). The main cause of this variability was whether trees had mature leaves or not. Egg density was significantly higher in trees with mature leaves (Mann–Whitney *U*-test 1996: $z = -2.06$, $P = 0.039$; 1997: $z = -3.369$, $P < 0.001$).

The slope of the regression between egg mass number (per tree) and parasitism was calculated for all dates when a minimum of 20 egg masses from at least five trees were collected (Table 1). Spatial density-dependent relationships were only found on two dates (Table 1). Nevertheless, there was a negative relationship between the slope and mean parasitism (Fig. 3): negative slopes were common at high parasitism levels and positive slopes at low parasitism levels ($b = -0.0004239$, $P = 0.028$).

Table 2 presents the parasitism and density of *G. scutellatus* estimated in 16 localities sampled in 1997 (see Fig. 4). *Anaphes nitens* was originally liberated at Pontevedra (locality 1) in 1994 (Mansilla & Pérez, 1996) and in three more localities in 1996. In 1997 it was liberated in many places by the paper industry to achieve biological control (P. Mansilla, pers. com.). We failed to find the parasitoid in only one locality (Serra do Candán), but only one sample was taken there. In general, parasitism was higher in the areas nearer to the point of introduction of *G. scutellatus* and in northern plots (Table 2 and Fig. 4), but this could be due to timing of sampling, temperature, or other factors.

There was a high variability between samples taken in the same locality at different dates, which is in agreement with the above results for the Lourizán plot. At Muros, Mabegondo, Santa Comba and Pontedeume, the egg mass density was so low that a careful search in 50 trees did not yield the minimum of 30 egg masses that we decided to collect. Trees were not damaged and the adults of *G. scutellatus* were very rare. Nevertheless, parasitism was high in these localities. The extreme cases were Mabegondo where *G. scutellatus* was very rare but parasitism reached 99% and Pontedeume, where we were able to find only two egg masses, both completely parasitized.

Discussion

Arzone & Meotto (1978) indicate that *G. scutellatus* has two egg-laying periods in Italy, the first generation (hibernating adults) lays eggs in February–May and the second generation in July–October. In contrast, Mansilla & Pérez (1996) indicate that *G. scutellatus* lays eggs in March–June and October–December in North-west Spain, with an aestivation period during July–September. Our results indicate that *G. scutellatus* had only one main egg-laying period in 1996 but two in 1997. The difference between both years seems due to the parasitism by *A. nitens*.

Ecological theory predicts that host density can be reduced by the action of parasitoids, but subsequently this effect should

reduce parasitoid density due to the lack of hosts (Begon *et al.*, 1996). In 1996, parasitism was so high that the snout beetle population became locally extinct. Very few larvae were found and adults disappeared from June to November. This long period with no egg masses available (more than 5 months) probably led to the local extinction of *A. nitens*. Therefore, when *G. scutellatus* recolonized the area in November 1996, no parasitoids were found. Unfortunately we could not sample during December 1996, when, probably, the first parasitoids arrived. In January 1997, the parasitoid population was probably very low, and it needed about 3 weeks to achieve a similar degree of control as was observed in 1996. This time-lag is characteristic of parasitoid–host interactions (Begon *et al.*, 1996) and allowed many weevil eggs to escape parasitism.

An alternative explanation is that the weevils entered aestivation in 1997 but not in 1996. This hypothesis cannot be completely refuted by our data, but the available evidence does not support this idea. First, *G. scutellatus* has one spring and one summer generation in Australia and South Africa (Tooke, 1955), Argentina (Marelli, 1928) and Italy (Arzone & Meotto, 1978). The climatic conditions of north-west Spain are very similar to south-east Australia, humid and not very hot, and so unlikely to promote aestivation. Second, preliminary observations in 1998 indicate that *G. scutellatus* lays eggs in summer in some plots, but not in others that are only a few kilometres away, suggesting that a climatic explanation for this lack of synchronization is unlikely. Finally, there are many examples of population oscillations in other parasitoid–host complexes (DeBach & Rosen, 1991), even in tropical climates (Godfray & Hassell, 1989).

This study is the first to suggest the existence of fluctuations between *G. scutellatus* and *A. nitens* populations. Tooke (1955) indicated that at high altitudes in South Africa the first generation of *G. scutellatus* is poorly controlled by the parasitoid, and suggested that a low winter survival of *A. nitens* was the cause of this poor control. Nevertheless, over the years it has become evident that *G. scutellatus* in South Africa becomes a problem not only in the highlands in spring, but also at lower altitudes in both spring and summer, requiring the use of insecticides to control it (Atkinson, 1995). We suspect that recent South African outbreaks are in part due to population oscillations such as those we have found in north-west Spain. When parasitism reaches such high levels, local extinctions of host and parasitoid will follow, and the next year the control will be poor until parasitoid populations recover. Although it seems paradoxical, a highly effective parasitoid is not a good biological control agent. Similar local extinctions of parasitoids have been reported in other biological control projects (Murdoch *et al.*, 1985; DeBach & Rosen, 1991). Such population oscillations had been hypothesized by Mossop (1929). If this hypothesis is correct, then the first generation of *G. scutellatus* should be controlled by *A. nitens* in some years (as in 1996) but not in others (as in 1997), while low winter survival of the parasitoid should produce poor control of the first generation every year. A practical application of this study is clear: if parasitoids are highly effective, then the next year some artificial liberations of the parasitoid would be necessary to achieve good control, unless the parasitoid has a high dispersal ability. We are currently following parasitism in several localities to test the ability of *A. nitens* to recolonize field plots.

Gonipterus scutellatus dispersed in north-west Spain from Pontevedra until it colonized all *Eucalyptus* plantations from 1991 to 1997 (Fig. 4; Mansilla & Pérez, 1996; authors' pers. obs.). Therefore, the snout beetle density is higher in the areas colonized in 1991 than in the areas colonized recently (Table 2). *A. nitens* colonized most localities, in part due to the artificial liberations but also thanks to its natural dispersal. The dispersal ability of *A. nitens* was demonstrated in South Africa, where it colonized areas 160 km away from the nearest liberation point (Mossop, 1929), in Kenya (Kevan, 1946) and in Zimbabwe, where it appeared spontaneously after snout beetle detection (Mossop, 1955). In north-west Spain it has been able to colonize the Cíes islands, at 1 km from the coast. The low parasitism observed in eastern Galicia is probably due to a combination of low winter temperatures, no artificial liberations and low density of *G. scutellatus* (*Eucalyptus* are rare far from the coast).

Anaphes nitens is highly efficient in finding and parasitize *G. scutellatus* egg masses. We found that, between plots, parasitism does not follow egg-mass density, which is not surprising given that the life span of the individual parasitoid is only a few days. Even in localities where *G. scutellatus* was very rare, egg masses were completely parasitized (Table 2). This explains why the action of this parasitoid has been so impressive in South Africa (Tooke, 1955), New Zealand (Clark, 1931), Kenya (Kevan, 1946), Madagascar (Frappa, 1950), Mauritius (Williams *et al.*, 1951), Argentina (Marelli, 1928; Quintana, 1963), Italy (Arzone, 1985), France (Pinet, 1986) and Spain (Mansilla & Pérez, 1996). It also explains why *G. scutellatus* is a rare species in Australia (Tooke, 1955).

Our results indicate that, at a small spatial scale, *A. nitens* shows a tendency for positive spatial density dependence when parasitism is low and negative spatial density dependence when parasitism is high (Fig. 3). This suggests that parasitoids remain at high density patches (trees where egg masses are recruited at a high rate) only when parasitoid density is low. When there are too many parasitoids, the risk of superparasitism is so high that females gain more by dispersing and searching for patches with a lower density of egg masses. Tooke (1955) indicates that superparasitism is common in *A. nitens* at the end of summer, when parasitoid density is maximum, and as many as 17 first-instar larval parasitoids have been found in one *G. scutellatus* egg. Given that the emergence of more than one adult of *A. nitens* per egg of *G. scutellatus* is very rare (Clark, 1931), the usual result of superparasitism is that all parasitoid larvae die. Therefore, there should be a high selection pressure in female *A. nitens* to avoid parasitized eggs, an ability previously found in *Anaphes iole* (Conti *et al.*, 1997). The behaviour of *A. nitens* is currently under examination to test these ideas.

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