

# Impact and oviposition behaviour of *Ageniaspis fuscicollis* (Hymenoptera: Encyrtidae), a polyembryonic parasitoid of the apple ermine moth, *Yponomeuta malinellus* (Lepidoptera: Yponomeutidae)

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## Abstract

The distribution and extent of parasitism of the apple ermine moth *Yponomeuta malinellus* Zeller by the polyembryonic encyrtid parasitoid *Ageniaspis fuscicollis* (Dalman) were examined in a three year field study and related to oviposition behaviour in the laboratory. *Ageniaspis fuscicollis* attacks egg batches of its host and kills the final instar larvae, which feed gregariously from within tents. Host population densities in the field were low, from 1.5 to 2.2 tents per 100 leaf clusters, and parasitism increased from 7.8% to 18% over the three year period. Parasitism was independent of host density at the whole tree scale, but at the individual tent scale, the probability of a tent containing parasitized host larvae increased and percent parasitism decreased with the number of host larvae per tent. Observations on the oviposition behaviour of *A. fuscicollis* in the laboratory revealed that parasitoids distributed their eggs randomly within host egg batches. On average, they spent almost two hours on an egg batch and laid 44% of their egg load of 132 eggs into the first egg batch visited, leading to a mean of 1.4 eggs laid per host egg through frequent self-superparasitism of hosts. The percentage of eggs receiving one or more ovipositions was independent of the size of an egg batch, contradicting our field observations of inverse density dependence. Factors that might account for the differences in rates of parasitism and attack distributions between laboratory and field data are discussed.

## Introduction

The importance of parasitoids in the regulation of host populations and their potential in the biological control of insect pests have been reported frequently in the literature (e.g. Waage & Mills, 1992; van Driesche & Bellows, 1996). There remains much debate, however, about which characteristics of a parasitoid are most likely to be correlated with

success as a biological control agent (Waage, 1990). For example, Hawkins *et al.* (1993) have argued that success in biological control is determined by the extent to which the pest has a refuge from attack by the parasitoid, and Hawkins & Cornell (1994) demonstrated that the maximum percent parasitism in the region of origin of the pest correlates well with the degree of success.

Alternatively, much of the recent theoretical literature has focused on the spatial distribution of parasitism between host patches (Mills & Getz, 1996). Interestingly, heterogeneity in parasitoid attack can be a powerful stabilizing force in

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discrete-time host-parasitoid models, although greater stability leads to increased host abundance (Mills & Getz, 1996). In contrast, heterogeneity in parasitoid attack is not a general stabilizing mechanism in continuous-time host-parasitoid models, but aggregative responses of parasitoids to local host density can reduce the equilibrium density of a pest (Murdoch & Briggs, 1996). More than a decade ago, Lessells (1985) demonstrated how parasitoid foraging behaviour affects the spatial distribution of parasitoid offspring. Using a simple optimal foraging model she noted that parasitoids should generate density-dependent parasitism across a set of patchily distributed hosts to maximize their rate of fitness gain. Lessells (1985) also investigated how egg and time limitation of parasitoids should affect the pattern of density dependence. Parasitoids limited by their egg supply should produce inverse density dependent parasitism, while time-limited parasitoids may generate patterns that vary from density independence to inverse density dependence. There is considerable evidence from both field and laboratory observations that parasitoid responses to local host density range from positive density dependence through density independence to inverse density dependence (Lessells, 1985; Walde & Murdoch, 1988; Pacala & Hassell, 1991). However, Murdoch & Briggs (1996) emphasize that the most effective parasitoids for use in biological control are likely to be those that concentrate their attacks in patches with more hosts, i.e. that show positive density dependence.

In this paper we present detailed observations on parasitism of the apple ermine moth, *Yponomeuta malinellus* Zeller (Lepidoptera: Yponomeutidae), by the egg-larval parasitoid *Ageniaspis fuscicollis* (Dalman) (Hymenoptera: Encyrtidae) to provide some insight into the potential of this parasitoid as a biological control agent of its host that has recently invaded western North America (Unruh *et al.*, 1993; J. Cossentine, personal communication). We first examine the extent of parasitism in the field, to estimate the existence of any refuge from parasitism, and the spatial pattern of parasitoid attack at two spatial scales. We then present detailed laboratory observations on the oviposition behaviour of *A. fuscicollis* to examine the degree to which individual host egg batches are exploited by the parasitoid. Finally, we discuss to what extent the oviposition behaviour of *A. fuscicollis* could account for the spatial distribution of parasitism observed in the field.

## Material and methods

### *Study organisms*

The apple ermine moth, *Y. malinellus*, is a univoltine species that feeds gregariously on apple. It lays its eggs in distinct batches on the bark of apple twigs in late summer. The larvae hatch and enter diapause within a hibernaculum formed on the surface of the egg batch. In spring, the overwintered larvae firstly mine apple leaves and subsequently spin a tent from which they emerge to feed externally on the apple leaves (Junnikkala, 1960). The parasitoid *A. fuscicollis* is also univoltine and is the only known species of the parasitoid community of *Y. malinellus* that attacks the host in the egg stage. The parasitoid eggs do not hatch until the host has reached the third larval instar. The parasitoid then develops polyembryonically and produces over 80 larvae from a single parasitoid egg (Junnikkala, 1960). Parasitized host

larvae become swollen and are killed in the fifth instar by mummification as the parasitoid larvae pupate. Adults emerge synchronously from the mummified host larvae (Martin, 1914). The host range of *A. fuscicollis* is probably restricted to the genus *Yponomeuta* (Blackman, 1965; Affolter & Carl, 1986; Dijkerman *et al.*, 1986; Kuhlmann, unpublished data). Mating and oviposition begin immediately after emergence of parasitoid adults (Marshall, 1904) and mean longevity is one week (Marshall, 1904; Martin, 1914; Junnikkala, 1960). Sitenko (1962) found that honey-fed females laid 61–224 eggs, whereas unfed females laid only nine eggs. According to Blackman (1965) female *A. fuscicollis* lay single eggs into host eggs and Martin (1914) reported that only those parasitoid eggs which are inserted into the embryo of the host develop successfully, while those placed into the yolk degenerate without causing any harm to the host.

### *Field studies on the impact of A. fuscicollis on Y. malinellus*

Studies were carried out in an apple orchard located near Giessen-Wettenberg in western Germany to determine the density of *Y. malinellus*, the impact and distribution of parasitism by *A. fuscicollis*, and the frequency of single and mixed sex broods of the parasitoid in 1993–1995. This orchard contained rows of unpruned, 3–4 m high trees that were evenly spaced (10 m), in a resident vegetation ground cover. Ten trees selected at random were sampled. Since *Y. malinellus* eggs are very difficult to detect in the field and younger instar larvae are difficult to rear without high rates of mortality, only the later developmental stages were sampled. Sampling occurred once at the peak of the fifth instar and again at the peak of the prepupal stage when the pupal cocoon is formed. Each tree crown was divided into eight equal sampling sections by cardinal direction and upper and lower canopy. From each section, a single branch was selected at random and 30 leaf clusters were examined for *Y. malinellus* tents. Branches were marked to avoid recollection at the next sampling interval. Tents found during sampling were removed (branch and tree were recorded) and reared under outdoor conditions in Delémont, Switzerland, to assess rates of parasitism. In 1995, clusters of first instar larval mines of *Y. malinellus* were additionally sampled and successfully reared until mummified by *A. fuscicollis* to verify the rates of parasitism. The clusters of *Y. malinellus* mines were reared individually in Petri dishes (12 cm diameter) in an incubator at  $20 \pm 1^\circ\text{C}$  and a photoperiod of 16L : 8D. Petri dishes were checked every two days to supply fresh apple foliage, if necessary, until *Y. malinellus* larvae were mummified by *A. fuscicollis*.

Percent parasitism by *A. fuscicollis* was based on mummified *Y. malinellus* larvae which are easily discernible. Parasitism by *A. fuscicollis* was examined at two spatial scales (tree and egg batch) and two levels of resolution (the probability of an egg batch or tent being attacked and the percent parasitism of individual eggs or larvae). For the tree scale, the two independent samples collected from different trees in each year were used, and for the egg batch scale each larval tent was considered separately. In all cases, parasitism was arcsin transformed for statistical analysis.

To determine the sex of the emerged parasitoid brood, mummified *Y. malinellus* larvae from tents collected in 1994 were placed separately in small plastic tubes. After

emergence of the adults, the sex of ten randomly selected individuals per brood was determined. Broods were divided into three groups: (i) pure male broods; (ii) pure female broods; and (iii) mixed broods containing both females and males.

*Laboratory studies on the oviposition behaviour of A. fuscicollis on Y. malinellus egg batches*

In order to produce egg batches of *Y. malinellus* for experiments on the oviposition behaviour of *A. fuscicollis*, 325 mated female moths were kept in groups of five individuals in sleeve cages on several apple trees at Delémont, Switzerland. Sleeve cages (35 × 20 cm) enclosed two-year-old twigs, the preferred oviposition site of *Y. malinellus*, and were checked daily for new egg batches. Egg batches of similar age, at the pink stage of development (Junnikkala, 1960), were used for experiments. The number of eggs in each batch was counted.

Parasitoids were reared from mummified *Y. malinellus* larvae collected in the field. Following emergence, adults were kept in a group in screen cages (50 × 30 × 30 cm) with honey and water for two days at 22 ± 1°C to allow mating before being used for behavioural observations. The females of *A. fuscicollis* used in the laboratory study had no contact to its host prior the experiment.

In a first series of observations, a single naive female parasitoid was gently released onto an unenclosed egg batch. Twigs pruned to 4 cm length and carrying the experimental egg batch were fixed under a dissecting microscope with 16-fold magnification. Behaviour of female parasitoids was continuously monitored until she left the egg batch. Behavioural observations of 26 female *A. fuscicollis* were conducted between 08:00 and 20:00 h on consecutive days at 22 ± 1°C, each on a different egg batch of *Y. malinellus*. From these observations, the following parameters were measured: (i) time spent on the egg batch (batch residence time); (ii) time spent searching; (iii) time spent ovipositing (from insertion to withdrawal of ovipositor); (iv) time spent resting; (v) number and rate of ovipositions; and (vi) number of unsuccessful ovipositor probings (insertion of ovipositor, but no egg laid, distinguished by a much shorter duration than an oviposition event). To indicate whether only a single egg was laid during an oviposition event, we compared the initial egg load of a subset of 26 two-day-old-female parasitoids with the remaining egg load of those females used in the oviposition experiments. Parasitoids were killed and egg load was determined by crushing the abdomen in a drop of water under a coverslip on a microscope slide so that the eggs could be counted easily under phase contrast.

In a second series of observations, we focused on the spatial distribution of parasitoid eggs within host egg batches and monitored individual egg batches under a dissecting microscope equipped with a video camera at 25-fold magnification. The entire egg batch was visible on the screen of the television monitor. A single naive female was released onto an egg batch and her behaviour videotaped until she left the batch. The exact position of each oviposition (an egg laid) and probing event was recorded on a 21.0 × 29.5 cm transparency sheet that was taped to the monitor screen. The two activities could easily be distinguished by the duration of insertion of the ovipositor into the *Y. malinellus* egg. Using this method it was possible to determine the number of

hosts attacked, the number of eggs laid, and the distribution of parasitoid eggs among available hosts.

## Results

*Field studies on the impact of A. fuscicollis on Y. malinellus*

The density of *Y. malinellus* tents remained remarkably constant over the three year study period at 0.46 to 0.65 tents per 30 leaf clusters (table 1). With a mean of 20.4 ± 0.5 SE (n = 80) leaf clusters per metre of branch this translates into an average distance of 2.3 to 3.3 m of branch between tents of *Y. malinellus*. The number of *Y. malinellus* per tent in 1995 was higher for the sample collected at the leaf-mining stage compared to the combined fifth instar-prepupal stage (table 1,  $P = 0.035$ , Mann Whitney U-Test), indicating that 17% larval mortality occurred in the field over this part of the life cycle. However, there was no change in the rate of parasitism between developmental stages (table 1,  $P = 0.491$ , Mann Whitney U-Test), verifying that there was no inaccuracy in the estimation of the impact of *A. fuscicollis* from tents collected at the later stages of development. Parasitism increased over the three years investigated, but averaged 13.5% ± 1.1 SE.

The distribution of attack by *A. fuscicollis* was examined at two spatial scales (i.e. trees and tents of *Y. malinellus*) and two resolutions (i.e. the probability of *Y. malinellus* tents being attacked and percent parasitism of *Y. malinellus* larvae). At the tree scale, the probability of a *Y. malinellus* tent containing at least one parasitized larva did not vary with the density of tents per tree in two out of three years, but a weak positive density dependent response occurred in 1994 (fig. 1A). However, the percent parasitism of *Y. malinellus* larvae was not related to the density of tents per tree in any of the three years (fig. 1B).

At the scale of individual *Y. malinellus* tents it was necessary to group the tents into four size classes (1–15, 16–30, 31–45 and 46–60 larvae per tent) in order to estimate the probability of an egg batch being attacked. As this provides only four estimates for each year, the data were pooled across the three years to examine the relationship between the probability of an egg batch being attacked and the number of larvae per tent. The combined data, weighted by sample size, show that the larger the size of an egg batch, the greater its probability of being attacked by *A. fuscicollis* ( $F_{1,10} = 12.15$ ,  $P = 0.006$ ,  $y = 0.25 + 0.017x$ ,  $r^2 = 0.59$ ). In a multiple regression analysis, that included year as a second independent variable, neither the coefficient for year

Table 1. The abundance of apple ermine moth and the extent of parasitism by *Ageniaspis fuscicollis* at Giessen-Wettenberg in 1993–1995. Samples of first instar larvae were collected in 1995 only.

Year	<i>Y. malinellus</i> tent density/30 leaf cluster (±SE, n = 160)	No. <i>Y. malinellus</i> /tent (±SE)	% Parasitism by <i>A. fuscicollis</i> /tent (±SE)	n tents
1993	0.65 ± 0.03	22.6 ± 1.6	7.8 ± 1.3	107
1994	0.46 ± 0.04	23.5 ± 1.9	15.5 ± 1.9	90
1995	0.52 ± 0.04	28.2 ± 1.8	18.1 ± 1.8	95
1995*	0.54 ± 0.06	34.1 ± 2.6	16.5 ± 2.9	44

\*First instar larvae of *Y. malinellus* in mines collected.

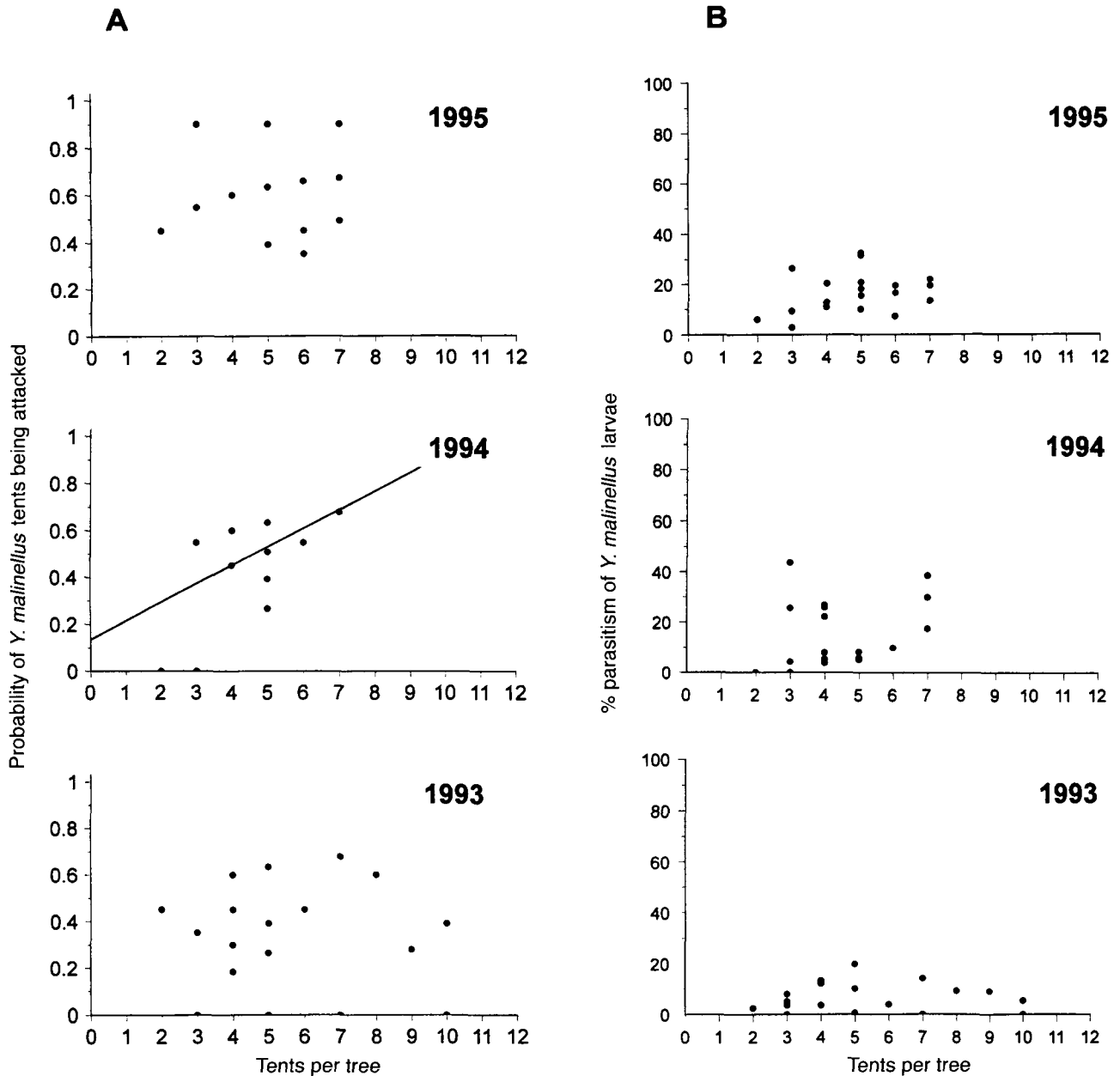


Fig. 1. (A) The probability of tents of the apple ermine moth being attacked by *Ageniaspis fuscicollis* as a function of the density of host tents per tree from samples in 1993–1995. Linear regressions: 1993,  $F_{1,18} = 0.082$ ,  $P = 0.778$ ; 1994,  $y = 0.135 + 0.079x$ ,  $F_{1,18} = 8.80$ ,  $P = 0.008$ ,  $r^2 = 0.33$ ; 1995,  $F_{1,18} = 0.083$ ,  $P = 0.776$ . (B) Percent parasitism of apple ermine moth larvae by *A. fuscicollis* in relation to the density of host tents per tree from samples in 1993–1995. Linear regressions: 1993,  $F_{1,18} = 0.011$ ,  $P = 0.918$ ; 1994,  $F_{1,18} = 1.17$ ,  $P = 0.293$ ; 1995,  $F_{1,18} = 1.89$ ,  $P = 0.186$ .

( $t_{10} = 1.41$ ,  $P = 0.20$ ) nor the coefficient for the size by year interaction ( $t_{10} = -0.67$ ,  $P = 0.52$ ) were significantly different from zero. This indicates that the increased probability of larger-sized egg batches being attacked by *A. fuscicollis* is independent of the year of sampling.

In contrast, percent parasitism by *A. fuscicollis* within attacked tents of *Y. malinellus* (i.e. excluding tents that were not attacked) was inversely dependent on the number of hosts per tent in all three years (fig. 2). Thus the highest rates of parasitism were reached in small tents. Yet, even in low

density tents, the rate of parasitism exceeded 60% only in a single case. This suggests that egg batches of *Y. malinellus* cannot be fully exploited by *A. fuscicollis* and so may benefit from a partial refuge from parasitism. The mean percent parasitism within attacked *Y. malinellus* tents was  $22.0 \pm 2.4$  SE ( $n = 67$ ) in 1993,  $23.3 \pm 2.7$  SE ( $n = 59$ ) in 1994, and  $25.2 \pm 1.7$  SE ( $n = 89$ ) in 1995.

We also tested the frequency distribution of mummified larvae within tents of *Y. malinellus* and thus the pattern of parasitoid attack across *Y. malinellus* tents. In all three years



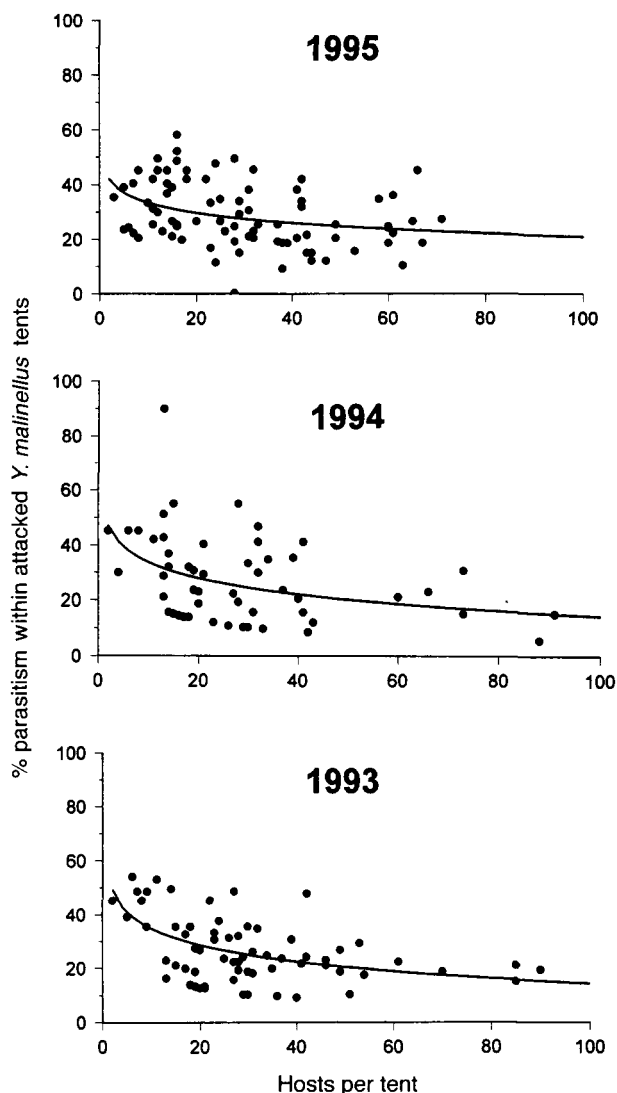


Fig. 2. Percent parasitism of apple ermine moth larvae by *Agenisps fuscicollis* in relation to the number of hosts within attacked tents from samples in 1993–1995. Logarithmic regressions: 1993,  $F_{1,67} = 23.79$ ,  $P < 0.001$ ,  $y = 55.37 - 8.93(\ln x)$ ,  $r^2 = 0.26$ ; 1994,  $F_{1,57} = 9.42$ ,  $P = 0.003$ ,  $y = 53.03 - 8.39(\ln x)$ ,  $r^2 = 0.14$ ; 1995,  $F_{1,87} = 11.57$ ,  $P = 0.001$ ,  $y = 45.83 - 5.37(\ln x)$ ,  $r^2 = 0.12$ .

of investigation the distribution of mummified larvae was highly aggregated and followed a negative binomial distribution with clumping factors of  $k$  well below 1 (1993:  $k = 0.25$ ,  $\chi^2 = 3.86$ ,  $df = 5$ ,  $P = 0.57$ ; 1994:  $k = 0.48$ ,  $\chi^2 = 8.88$ ,  $df = 8$ ,  $P = 0.35$ ; 1995:  $k = 0.7$ ,  $\chi^2 = 14.06$ ,  $df = 10$ ,  $P = 0.17$ );  $k$  estimated by maximum likelihood procedure (Elliot, 1983;  $\chi^2$  tests for the goodness of fit of the observed distribution with a negative binomial distribution).

An analysis of the sex ratio of parasitoids emerging from 54 individual larvae of *Y. malinellus* revealed that parasitoid individuals of both sexes emerged from 22% of the mummified host larvae, indicating that individuals developed from at least two eggs. Pure male or pure female broods, which may develop from single or multiple eggs, emerged from 41% and 37% of the hosts, respectively.

#### Laboratory studies on the oviposition behaviour of *A. fuscicollis* within egg batches of *Y. malinellus*

The 26 egg batches of *Y. malinellus* used in the first series of observations, contained an average of  $43.9 \pm 4.1$  SE eggs (range 12 to 91). The mean residence time of *A. fuscicollis* on an individual egg batch was  $1\text{ h }54\text{ min} \pm 12\text{ min SE}$ . The egg batch residence time of *A. fuscicollis* was strongly related to the number of host eggs within the egg batch, over the entire range of egg batch sizes ( $F_{1,24} = 57.5$ ,  $P < 0.001$ ) (fig. 3A). The majority of the time (78%) was spent ovipositing, 21% was spent searching for host eggs, and only 1% of the time was spent resting. On average, parasitoid females oviposited  $63.1 \pm 6.3$  SE times into a host egg batch and the number of unsuccessful probings was  $2.5 \pm 0.7$  SE, leading to a mean of  $1.4 \pm 0.1$  SE ovipositions per host egg and an oviposition rate of  $0.6 \pm 0.03$  SE eggs per min. Like the residence time, the total searching time ( $F_{1,24} = 43.9$ ,  $P < 0.001$ ) (fig. 3B) and the number of ovipositions ( $F_{1,24} = 168.5$ ,  $P < 0.001$ ) (fig. 3C) were dependent on the number of host eggs in an egg batch. The handling time per host egg was  $1.3 \pm 0.06$  SE min.

Dissection of a control group of *A. fuscicollis* females revealed an initial egg load of  $132\text{ eggs} \pm 5\text{ SE}$  ( $n = 26$ ). After completing a single visit to an egg batch  $74 \pm 5$  SE ( $n = 26$ ) eggs per female remained, indicating that 44% of the initial egg supply was laid in the egg batch encountered. Thus the observed mean number of ovipositions per female (63 ovipositions) closely matched the estimated drop in egg load from an egg batch visit (58 eggs), suggesting that only a single parasitoid egg was inserted into a host egg at each observed oviposition event.

The distribution of parasitoid eggs across host eggs within an egg batch was analysed from the second series of observations with similar average egg batch size ( $44.3 \pm 2.4$  SE,  $n = 26$ ) and oviposition frequency ( $57.6 \pm 3.7$  SE,  $n = 26$ ). The number of ovipositions by *A. fuscicollis* was again strongly related to the number of host eggs per batch ( $F_{1,24} = 36.9$ ,  $P < 0.001$ ,  $r^2 = 0.61$ ,  $y = 5.19 + 1.18x$ ) and exceeded the number of available eggs in 23 of the 26 replicates. The observed frequency distribution of ovipositions per host egg closely matched that of a Poisson series with the same mean (table 2), indicating that ovipositions were randomly distributed and that parasitoid females do not avoid self-superparasitism. As a consequence of the random distribution of parasitoid eggs, there was a strong linear relationship (fig. 4) between the number of eggs attacked and the number of hosts per egg batch ( $F_{1,24} = 67.5$ ,  $P < 0.001$ ) which resulted in a constant 71% parasitism  $\pm 9.6$  SE ( $n = 26$ ) that was independent of the number of hosts per egg batch ( $F_{1,24} = 0.003$ ,  $P = 0.956$ ).

#### Discussion

*Agenisps fuscicollis* is a consistent parasitoid of *Y. malinellus* in Europe, and is an important candidate for the biological control of this pest in North America (Unruh *et al.*, 1993). In this study we have examined the extent and distribution of parasitism by *A. fuscicollis* in the field and its oviposition behaviour in the laboratory, to determine the potential of this parasitoid as a biological control agent. In the study area at Giessen-Wettenberg, tent density of *Y. malinellus* per 100 leaf clusters varied from 1.5 to 2.2 in 1993–1995. These densities were generally below the tradi-

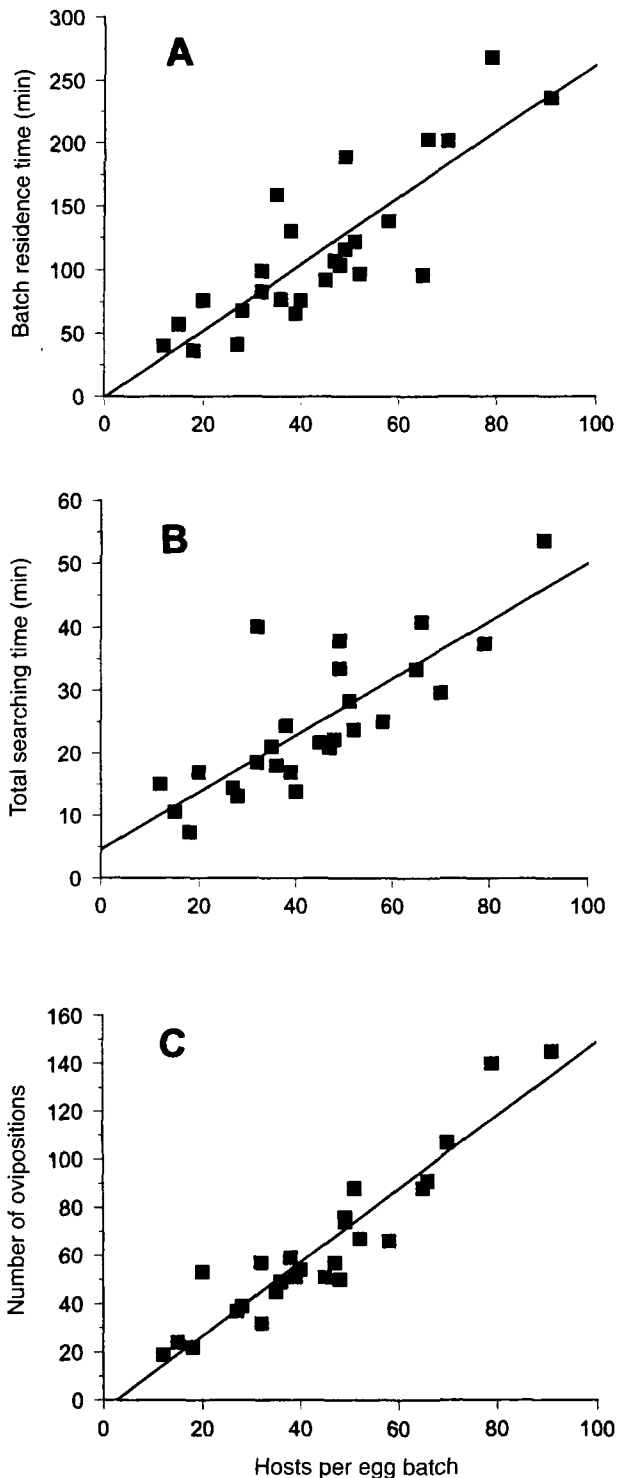


Fig. 3. Residence time (A), time spent searching (B), and number of ovipositions (C) by *Ageniaspis fuscicollis* females on a single host egg batch in relation to host density recorded in the laboratory at 22°C ( $n = 26$ ). Linear regressions: (A)  $y = -0.99 + 2.63x$ ,  $P < 0.001$ ,  $r^2 = 0.71$ ; (B)  $y = 4.61 + 0.45x$ ,  $P < 0.001$ ,  $r^2 = 0.65$ ; (C)  $y = -4.22 + 1.53x$ ,  $P < 0.001$ ,  $r^2 = 0.88$ .

tional control threshold of 3–5 apple ermine moth larval tents per 100 leaf clusters (Baggiolini *et al.*, 1980).

#### Extent of parasitism

Previous studies of *Y. malinellus* have recorded between 2% and 77% parasitism by *A. fuscicollis* (Junnikkala, 1960; Kot, 1964; Nenon & de Merleire, 1972; Mamedov, 1977; Aleksidze & Abashidze, 1983; Dijkerman *et al.*, 1986). In this study, mean percent parasitism increased from 7.8% in 1993 to 18% in 1995, although the density of *Y. malinellus* tents remained remarkably constant, suggesting that the observed increase in parasitism had little influence on the dynamics of the *Y. malinellus* population. More importantly, however, up to 100% of the *Y. malinellus* egg batches in a tree had been attacked by *A. fuscicollis* (fig. 1A) but only a maximum of 60% of the individuals within an egg batch were parasitized (with the exception of 100% parasitism in a single relatively small egg batch, fig. 2). By analysing maximum observed rates of parasitism from field samples in the region of origin of 58 parasitoid species used in classical biological control, Hawkins & Cornell (1994) found that parasitoid introductions failed to control the target pest when rates of parasitism fell below a lower threshold of 32%. The maximum realized rate of parasitism of *Y. malinellus* tents within trees was 100%, suggesting that egg batches have no refuge from discovery by *A. fuscicollis*. However, the maximum realized rate of parasitism within tents was 60%, indicating that *Y. malinellus* may experience a partial refuge from parasitism within egg batches. A maximum 60% rate of parasitism by *A. fuscicollis* corresponds to a 24% probability of success in the classical biological control of *Y. malinellus* (Hawkins & Cornell, 1994), although there is a substantial level of variability in the predictive relationship indicating that other factors can also influence the probability of success.

#### Distribution of parasitism

The distribution of parasitism by *A. fuscicollis* was studied at two spatial scales, trees and egg batches. Neither the probability of a tent containing at least one mummified larva nor the percent parasitism within an attacked tent showed any consistent response to the density of tents per tree. In contrast, however, the probability of an egg batch being attacked increased, and the percent parasitism within an attacked tent decreased, with the density of individuals per tent. This suggests that the parasitoid is generally unable to respond to variation in the density of egg batches between trees, and that there is a trade-off in the effect of egg batch size on parasitism. The larger the egg batch, the more likely it is to be found, but the greater the refuge from parasitism due to incomplete exploitation.

The inability of *A. fuscicollis* to show a positive response to host density at the tree scale suggests that it is unlikely to suppress *Y. malinellus* to low equilibrium densities as effectively as would a parasitoid that exhibits direct density dependence (Murdoch, 1990; Murdoch & Briggs, 1996). However, a similar lack of response to host density has been found in about half of the cases reviewed by Walde & Murdoch (1988). From theory we would expect an optimally-foraging parasitoid to forage longer and parasitize proportionately more hosts in patches of higher host density (Charnov, 1976; Comins & Hassell, 1979; Lessells, 1985), although an inverse response to host density can be generated by either egg or time limitation (Lessells, 1985). The field data indicate that *Y. malinellus* egg batches are, in general, not completely exploited by *A. fuscicollis*, and that the extent

Table 2. Frequency distribution of the mean number of ovipositions by *Ageniaspis fuscicollis* in individual eggs of the apple ermine moth within a single egg batch at  $22 \pm 1^\circ\text{C}$  ( $n = 26$ ). The observed distribution is compared to a Poisson series with the same mean number of ovipositions per host ( $\chi^2$ -test).

Distribution	Mean frequencies of <i>Yponomeuta malinellus</i> eggs containing the following number of ovipositions by <i>Ageniaspis fuscicollis</i>					$\chi^2$
	0	1	2	3	4–8	
Observed	12.8	15.1	9.9	4.3	2.2	$\chi^2 = 0.1$ , $df = 3$ $P = 0.992$
Expected	12.1	15.7	10.2	4.4	1.9	

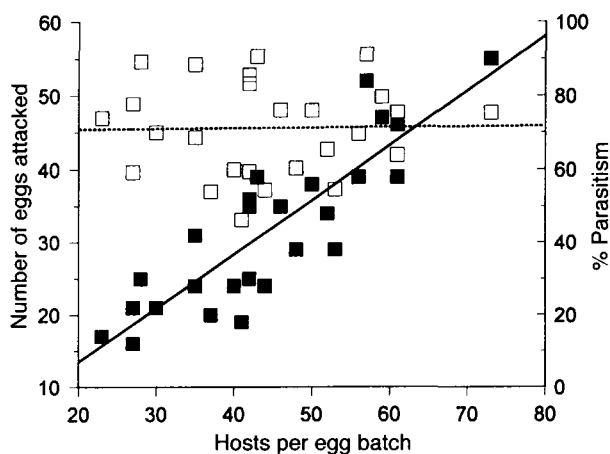


Fig. 4. The number ( $y_1$ , solid squares, solid line) and percentage ( $y_2$ , open squares, dashed line) of apple ermine moth eggs attacked by *Ageniaspis fuscicollis* on a single egg batch in relation to host density obtained from a laboratory experiment at  $22^\circ\text{C}$  ( $n = 26$ ). Linear regressions:  $y_1 = -1.44 + 0.74x$ ,  $P < 0.001$ ,  $r^2 = 0.74$ ;  $y_2 = 70.6 + 0.01x$ ,  $P = 0.956$ .

of parasitism declines with egg batch size. To determine whether this is likely to be due to egg or time limitation we conducted more detailed laboratory observations of the oviposition behaviour of *A. fuscicollis*.

#### Oviposition behaviour

On average, an *A. fuscicollis* female, with an initial egg load of 132 eggs, spent nearly two hours foraging on a single egg batch of *Y. malinellus*, containing 44 eggs, and randomly oviposited 63 times to achieve 71% parasitism. Both the total residence time and the number of ovipositions increase with increasing egg batch size. The number of ovipositions exceeded the number of available host eggs, and self-superparasitism was frequent. These observations suggest that, in contrast to the majority of parasitoids (Salt, 1961; van Lenteren, 1981), *A. fuscicollis* shows no oviposition constraint on previously parasitized hosts (but see Visser *et al.*, 1992a for rearing conditions of parasitoids in which it is most likely that self-superparasitism will occur). While conspecific superparasitism is adaptive under a wide range of environmental conditions that limit access to host insects (van Alphen & Nell, 1982; Charnov & Skinner, 1984; Iwasa *et al.*, 1984; van Alphen & Visser, 1990; van der Hoeven & Hemerik, 1990; Speirs *et al.*, 1991; Weisser & Houston, 1993), self-superparasitism in solitary parasitoids is adaptive only

under a very limited set of conditions (Puttler, 1974; Bakker *et al.*, 1985; Visser, 1993).

*Anagrus delicatus* Dozier (Hymenoptera: Mymaridae), is a solitary parasitoid that attacks egg batches of its host, but leaves an egg batch after only a few ovipositions (Cronin & Strong, 1990, 1993). This early patch departure has been interpreted as a means to avoid the costs of self-superparasitism for a solitary parasitoid that is unable to discriminate between parasitized and unparasitized hosts and is frequently egg limited in the field (Rosenheim & Mangel, 1994; but see Bouskila *et al.*, 1995).

For polyembryonic and gregarious parasitoids, where more than a single parasitoid larva per host can develop successfully, the fitness consequences of self-superparasitism are not so restrictive (Ode & Strand, 1995). Mixed broods, developing from separate eggs, are quite common in *A. fuscicollis* and a number of other polyembryonic parasitoid species (Clausen, 1940; Godfray, 1994). *Copidosoma floridanum* (Ashmead) (Hymenoptera: Encyrtidae) lays either a single egg (male or female) or two eggs (always one male plus one female) during a single oviposition bout into eggs of plume moth (Lepidoptera: Noctuidae) (Strand, 1989a,b). In the present study on *A. fuscicollis* it was not determined whether mixed broods are produced by multiple females laying a single egg or single females laying multiple eggs into a host egg.

Although the costs of self-superparasitism may be less for a polyembryonic parasitoid, such as *A. fuscicollis*, than for a solitary parasitoid, such as *A. delicatus*, there may be other adaptive explanations for the long residence time and high oviposition rate of *A. fuscicollis* on host egg batches. A parasitoid should stay longer and parasitize more hosts in a patch when its egg load is high (Rosenheim & Mangel, 1994), the travel time between patches is high (Charnov, 1976), the mortality risk is higher while travelling between patches than within a patch (Weisser & Houston, 1993; Rosenheim & Mangel, 1994), or when it experiences competition for hosts within a patch (Visser *et al.*, 1992b). *Ageniaspis fuscicollis* has a much greater egg load (132 eggs) than *A. delicatus* (33 eggs, Cronin & Strong, 1993) and, as egg batches of *Y. malinellus* were from 227 to 328 cm apart on the apple trees, travel time for *A. fuscicollis* may also be high (but see Corbett & Rosenheim, 1996 for the mobility of a similarly sized parasitoid). However, we have no data that address relative mortality rates or levels of competition experienced by *A. fuscicollis* in the field.

#### Oviposition behaviour and parasitism

The mean level of parasitism of *Y. malinellus* by *A. fuscicollis* over the three years of sampling in western Germany was 14%, despite the fact that *A. fuscicollis* has a relatively

large initial egg load (132 eggs) and polyembryonic development such that each egg produces over 80 progeny. The observed levels of parasitism result from the combined probability of an egg batch being discovered by the parasitoid and the percent parasitism of the eggs within each egg batch. The density of egg batches per tree had no influence on either the discovery or the exploitation of egg batches. In contrast, larger egg batch size increased the probability of discovery, but reduced the level of exploitation.

Observations of the oviposition behaviour of *A. fuscicollis* in the laboratory indicated that ovipositions occurred at random within an egg batch such that the 1.4 ovipositions per host egg resulted in a constant 71% parasitism independent of egg batch size. Under these controlled conditions, the level of exploitation of an egg batch by *A. fuscicollis* was limited by the random nature of the ovipositions rather than by time or egg load. However, we also made the assumption that one or more ovipositions into an egg will result in the successful parasitism of the host. Martin (1914), from dissections of host eggs, determined that the probability of survival of parasitoid eggs was 17%, as parasitoid eggs must be inserted into the embryo of the host to develop successfully and *A. fuscicollis* frequently inserts eggs into the yolk where they soon degenerate. Assuming that only 17% of ovipositions result in successful parasitism, our initial estimate of 71% parasitism of eggs in an egg batch would be reduced to 12%. This value is somewhat lower than the average 23% parasitism observed in the field for egg batches of a comparable size (fig. 2). The survival rates of eggs laid by parasitoids in the field may be greater than that estimated by Martin (1914) in the laboratory, and is likely to vary with the age of an egg batch discovered by a parasitoid. Further studies are needed to clarify the influence of age on the suitability of eggs for parasitism by *A. fuscicollis*.

From the oviposition behaviour of *A. fuscicollis* under laboratory conditions, we would expect parasitism to be independent of egg batch size, as the parasitoids adjust their batch residence time and number of ovipositions to match the size of an egg batch. However, observations of parasitism by *A. fuscicollis* in the field suggest an inverse density dependent response to egg batch size. The inverse response in the field largely results from greater levels of parasitism of egg batches with less than 20 eggs (fig. 2). Our laboratory observations indicate that there is no structural refuge from parasitism that increases with egg batch size (Braune, 1982), no egg limitation that could reduce the exploitation of larger egg batches, and no reason to suspect that the random oviposition behaviour of the parasitoid should result in reduced success in the parasitism of larger egg batches. The most likely explanation for this discrepancy between field and laboratory observations is that the parasitoid females are unable to stay long enough on larger egg batches to exploit them to the same extent. Either predators (substantial predation of egg batches in the field has been documented by Kuhlmann *et al.*, 1998) or variation in abiotic conditions may introduce time limitation by interrupting oviposition and promoting early egg batch departure by *A. fuscicollis*. However, this needs to be verified through detailed observations of *A. fuscicollis* oviposition on egg batches under field conditions.

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# African Cereal Stem Borers: Economic Importance, Taxonomy, Natural Enemies and Control

*Edited by A Polaszek, International Institute of Entomology, UK*

An assemblage of approximately twenty moth species belonging to the families Crambidae, Pyralidae and Noctuidae constitute the most important cereal pests in many parts of Africa. The caterpillars of these moths bore into the stems of maize, sorghum, millet and rice, often killing the plant, and are commonly known as stem or stalk borers. The cereals attacked are grown by smallholders to feed themselves and their families and are of great importance as the staple food for the population in most parts of Africa. Complex control measures, including the use of chemicals, are often inappropriate.

This book provides fundamental information necessary for formulating integrated pest management of African cereal stem borers, in particular any natural enemy component. Firstly, the economically important species are characterized regionally and according to their biology and host plants, both wild and cultivated. The taxonomy of the moths, their larvae and their natural enemies is examined in detail and techniques of rearing are described. Illustrated keys are provided for their recognition, and their distributions and hosts are listed. Finally, the control measures currently in use and those being investigated, are summarized.

This book is essential reading for applied entomologists, agronomists and extension workers with an active interest in cereal production in Africa and will be of value to all those concerned with integrated pest management in the tropics.

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