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Host specificity and comparative foraging behaviour of *Aenasius vexans* and *Acerophagus coccois*, two endo-parasitoids of the cassava mealybug

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Abstract

Two encyrtid parasitoids, *Aenasius vexans* Kerrich (Hymenoptera: Encyrtidae) and *Acerophagus coccois* Smith (Hymenoptera: Encyrtidae), were compared for their degree of dietary specialisation and the impact this has on their foraging strategies. Both parasitoid species are significant for biological control of the cassava mealybug, *Phenacoccus herreni*, Cox & Williams (Homoptera: Sternorrhyncha) a major Latin American pest of cassava, *Manihot esculenta* Crantz, an important root crop. Host acceptance and parasitism were analysed in seven mealybug species (with different levels of polyphagy) occurring in and around cassava fields. Results demonstrate that, in this ecosystem, *An. vexans* is a specialist for *P. herreni* while *Ac. coccois* is a generalist on the first and second trophic level. Of the seven mealybug species, *P. herreni and P. madeirensis* Green were the most acceptable hosts for *Ac. coccois*, followed by *Ferrisia virgata* Cockerell. *Ac. coccois* did not accept the other four mealybug species. The foraging and oviposition behaviour of individual parasitoids was observed in bioassays with cassava leaves infested by *P. herreni*. The two species used different strategies to locate their host. *Aenasius vexans* spent significantly more time walking and standing on an infested leaf and examined a host longer than did *Ac. coccois*. *Acerophagus coccois*, in contrast, spent more time for oviposition. As a consequence *An. vexans* parasitised more hosts in a given time than did *Ac. coccois*. Because the rate of offspring production of the two species did not differ, we conclude that the gregarious *Ac. coccois's* strategy to deposit several eggs at once might compensate for its relatively low number of ovipostitions, compared with the solitary *An. vexans*. These findings suggest that, given the advantages and limitations of each species, a multi-species approach to biological control of *P. herreni* may yield best results.

Introduction

Comparative studies of species with related or even overlapping niches allow to assess how differences in behavioural traits may influence parasitoid performance. Comparison of niche-related species has been applied to interpret functional differences in foraging behaviour of parasitoids (Wiskerke & Vet, 1994; Brodeur et al., 1998), based on the hypothesis that the degree of dietary specialisation affects foraging strategies (Vet & Dicke, 1992).

Generally, for biological control purposes, natural enemies with a narrow host spectrum (specialists) are assumed to be more effective than those with a broad host spectrum (generalists) (Futuyma & Moreno, 1988; Sheehan, 1986), and safer to non-target organisms in the ecosystem (McEvoy, 1996; Secord & Kareiva, 1996). Dietary specialisation of parasitoids can be assigned to both the herbivore level and the plant level. We define a specialist as a parasitoid that is specialised at both the herbivore and the plant level, whereas a generalist is specialised neither

at the herbivore nor at the plant level (Vet & Dicke, 1992).

For biological control, once parasitoids are released, successful host searching in the field becomes a key process to achieving high levels of parasitism in a pest population. Analysis of behavioural traits of control agents, together with the use of life tables, is an important prerequisite to predicting their effectiveness and reliability in a more ecological context (Dorn, 1996). In addition, the foraging success of parasitoids seems to differ between parasitoid species of different host specificity levels (Vet & Dicke, 1992) because different host finding behaviour may result in differences in encounter rates with hosts (Vet & Bakker, 1985). Specialists may be more efficient foragers than generalists (Futuyma & Moreno, 1988) and more selective as they are supposed to have an efficient host detection system (Vet & Dicke, 1992). Specialist parasitoids are assumed to use more specific information about their hosts than generalists do, because the wide host range makes the detection of a particular host less important. However, even though generalist parasitoids can develop in various host species, these species may differ in their suitability as hosts (Brodeur et al., 1998).

In this study we investigated the relationship between parasitoid specificity and foraging behaviour in a tritrophic system consisting of cassava (*Manihot esculenta* Crantz), its herbivorous pest *Phenacoccus herreni* (Cox & Williams) (Homoptera: Pseudococcidae) and the two larval parasitoids *Aenasius vexans* (Kerrich) (Hymenoptera: Encyrtidae) and *Acerophagus coccois* (Smith) (Hymenoptera: Encyrtidae). Cassava is a long-season, subsistence crop, grown throughout the tropics for its starchy roots (FAO, 1997). It is often intercropped with cash crops such as beans (A. Bellotti, pers. commun.), and surrounded by wild vegetation including fern (B. Dorn, pers. obs.). Cassava mealybug is a major pest in seasonally dry ecosystem, causing yield losses up to 80% (Bellotti et al., 1999). Its control relies primarily on the mass-release of antagonists, because no resistant cassava germplasm is available for this sucking pest and the low economic return of the cassava crop restricts investments by farmers (Bellotti et al., 1999).

Aenasius vexans is a solitary, and *Ac. coccois* a gregarious larval endoparasitoid of mealybugs, mainly on *P. herreni*. The two parasitoids appear to have different degrees of host specialisation, with *Ac. coccois* being more generalist than *An. vexans* (Bertschy et al., 1997). *Aenasius vexans* was frequently recorded on *P. herreni* on cassava, but occasionally on other *Phenacoccous* species on other host plants in different habitats (Noyes & Ren, 1995).

We used a comparative approach to evaluate (1) the host range of the two encyrtid parasitoids *An. vexans and Ac. coccois* and their capability to parasitise and develop successfully in different mealybug species in the cassava ecosystem, (2) the relative host suitability of different mealybug species, and (3) the host-location behaviour of both parasitoid species on cassava leaves infested by *P. herreni*.

Material and methods

Parasitoids

Aenasius vexans and *Acerophagus coccois* were continuously reared at CIAT on cassava plants (cv. CMC 40), infested by *Phenacoccus herreni*. Both colonies were initiated with insects collected in Venezuela in 1990. The colonies were kept in cages in a glasshouse at 28–35 °C under natural light conditions (at 5° N, about L12:D12). On emergence, the parasitoids were transferred to a Plexiglas cylinder (6 cm × 4 cm) with a screen-lidded window (5.5 cm × 4 cm) where wasps were kept for two days for egg-maturation and mating. They were fed with sugar-water.

Plants

All plant species were grown in a glasshouse at 32 ± 5 °C and 62 ± 15% r.h. under natural light conditions (at 5° N, about L12:D12). Individually potted cassava plants (cv. CMC 40) were used once they carried eight to 17 leaves (about six weeks after planting). Potted bean seedlings (*Phaseolus vulgaris* Linn cv. Rio Tibagi) were used when they were two weeks old. Each pot contained four seedlings. Fern plants (*Nephrolepis biserrata* var. *furcans*) were potted and grown by the Associated Workers' Enterprise, CIAT.

Egg-load

The egg-load of each parasitoid species was evaluated in order to establish the potential host density in the experiment on host specificity, and to determine the age of the parasitoids for bioassays.

Bioassay

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described above.

Bioassay

Upon emergence, parasitoids were removed from the rearing unit and released in a screened cage (40 cm × 40 cm × 60 cm). They were separated into four groups based on diet and the age at the time of evaluation of egg-load. Females were (1) supplied with sugar-water for 24 h, (2) supplied with sugar-water for 24 h, kept in a Plexiglas cylinder for further 48 h, (3) allowed to parasitise mealybugs on infested cassava plants for 24 h, or (4) allowed to parasitise mealybugs on infested cassava plant for 24 h, and then kept in a Plexiglass cylinder for further 48 h. Plants were infested with mealybug ovisacs, as described by Van Driesche et al. (1987). Parasitoids were subsequently killed by deep-freezing. Their egg complement ($n = 20$) was obtained by dissecting the ovaries under a stereomicroscope (*An. vexans*) or after crushing the wasps with a cover slide in distillated water (*Ac. coccois*).

Statistical analysis. The Mann–Whitney U-test was used to compare the egg complement of each species for each feeding treatment (Zar, 1984).

Host specificity and host suitability

Mealybug collection and rearing. Different mealybug species were collected in the field and in greenhouses at CIAT (Cali, Colombia) in spring 1998. The mealybug colonies were reared as follows:

Phenacoccus herreni Cox & Williams, ex. *M. esculenta*, *Phenacoccus madeirensis* Green, ex. *M. esculenta*, *Pseudococcus jackbeardsleyi* Gimpel & Miller, ex. *M. esculenta*, and *Ferrisia virgata* Cockerell, ex. *M. esculenta* were reared on potted cassava plants (cv. CMC 40) at CIAT. Plants were infested weekly with mealybug ovisacs, as described by Van Driesche et al. (1987) and separated in different cages based on the age of the mealybugs they carried.

Planococcus citri, ex. *Clitoria fairchildiana* and *Pseudococcus* sp. near *importatus* McKenzie, ex. *Desmodium strycifolium*, were reared on potted bean plants (cv. Rio Tibagi). Weekly, two to three ovisacs were transferred to a two 2-week old bean plant. *Pseudococcus longispinus* Targioni Tozzetti, ex. *Nephrolepis biserrata*, was reared on fern *N. biserrata* (var. *furcans*) with a procedure similar to that described above.

Bioassays

Phenacoccus herreni, P. madeirensis, P. jacksbeardsleyi *and* F. virgata. A leaf of a potted cassava plant was enclosed in a Petri dish (15-cm diameter) which itself was supported by the loop of an iron wire anchored in the soil of the pot so that the leaf would remain in its natural position. Two holes of 10-cm diameter were cut in each half of the Petri dish and sealed with nylon screen. A hole of 1-cm diameter on the vertical side of the Petri dish served to introduce the plant petiole.

Fifty third-instar female mealybugs were transferred from an infested cassava plant onto the upper side of a leaf enclosed in a Petri dish. The dishes were sealed with Parafilm to prevent mealybugs from escaping.

After the mealybugs had settled and started to feed (24 h), one female parasitoid was introduced from a small glass vial into the Petri dish and removed after further 24 h. Plants with the parasitised mealybugs were kept in a glasshouse at 32 ± 5 °C and 62 ± 15% r.h. under natural light conditions (at 5N, about L12:D12). To test whether host acceptance was influenced by the host plant, the polyphagous species *F. virgata* was parasitised on both cassava and bean.

Phenacoccus citri/ P. *sp. near* importatus. A trifolium of a bean plant was introduced in a Petri dish, as described for the cassava leaf. Bean plant infestation and parasitoid introduction were conducted as described for cassava.

Phenacoccus longispinus. The tip of a fern leaf was introduced into a Petri dish. Plant infestation and parasitoid release was conducted as described for cassava.

As soon as parasitised mealybugs mummified, they were removed and kept individually in a gelatine capsule until parasitoid emergence. Parasitoid emergence was monitored daily, and emerged parasitoids removed. The effect of the different mealybug hosts on the number of mummies produced, on the parasitoids developmental time from oviposition to mummy formation and from mummy to adult emergence, and the total number of progeny per wasp was determined. Three replicates were made, each with eight female parasitoids, for a total of 24 parasitoids per mealybug species.

Statistical analysis. T-test (normally distributed data) or Mann–Whitney U-test (not normally distrib-

uted data) were used to compare the relative effectiveness of *An. vexans* and *Ac. coccois* on *P. herreni*. One-way ANOVA (normally distributed data) followed by Student-Newman-Keuls pairwise multiple comparison was Kruskall-Wallis one-way ANOVA on ranks (not normally distributed data) followed by Dunn's pairwise multiple comparison used were used to compare the relative suitability of different mealybug species for *Ac. coccois* (Zar, 1984).

Foraging behaviour

Bioassay. The host location behaviour of parasitoids was observed on a cassava leaf lobe infested by mealybugs placed upside down in a Petri dish (15 cm diameter). Just before the experiment, all but 12 third instar female mealybugs were removed. The leaf area and the position of the mealybugs were mapped. Observations took place in a climate controlled room at 26 ± 0.5 °C, 70 ± 20% r.h., and 1015 ± 2 mbar atmospheric pressure.

A single wasp was released from a small glass vial on the distal end of the leaf lobe. Continuous behavioural recording, using the computer software package 'The Observer' (Noldus, 1991), started immediately after introducing the parasitoid and lasted for 90 min. The duration of different behavioural activities was measured. The behavioural parameters were 'walk on leaf', 'walk in experimental arena', 'stand on leaf', 'stand in experimental arena', 'examination of unparasitised host', 'examination of parasitised host', 'oviposition in unparasitised host', and 'oviposition in parasitised host'. In addition, the frequency and duration of oviposition were recorded. Because of *Ac. coccois*'s small size, only types of behaviour that were visible to the eye were measured. The observation stopped when the parasitoid did not encounter a host for more than 45 min.

Parasitised mealybugs were immediately labelled with luminous marking powder (Channel luminous materials). After each experiment, parasitised mealybugs were removed and reared individually in a leaf cage on cassava plants to confirm successful oviposition at mummification. Mummies were collected in gelatine capsules until parasitoid emergence. Parasitism success, developmental time, and number of offspring of each parasitoid were recorded.

For each replicate, a new cassava lobe and a new female parasitoid were used. Females of both species were bioassayed on the same day. A total of 15 *An. vexans* and 15 *Ac. coccois* females were tested throughout several experimental days.

Table 1. Egg-load of the parasitoids *An. vexans* and *Ac. coccois* at different ages and with different feeding treatments. Different letters close to means are significantly different at P=0.05 (Mann-Whitney U-test) within each species and each feeding treatment. Values represent mean number of eggs ± s.e.

	Age (h)	*An. vexans*	*Ac. coccois*
Sugar-water	24	10.75 ± 1.68 a	4.75 ± 1.39 a
	72	6.90 ± 1.62 a	10.10 ± 1.49 b
Mealybugs	24	1.20 ± 0.28 a	2.25 ± 0.65 a
	72	7.20 ± 0.61 b	8.10 ± 1.60 b

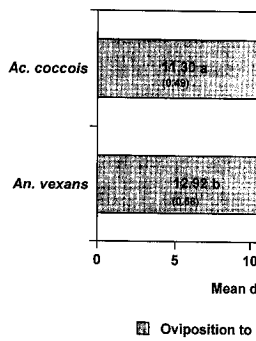
Statistical analysis. T-test or Mann–U-test were used for pairwise comparison of duration and frequency of each behavioural parameter for the two species (Zar, 1984).

Results

Egg-load

The egg-load of *An. vexans* and *Ac. coccois* is shown in Table 1. Newly emerged *An. vexans* females, provided with sugar-water, but with no hosts, carried on average the same amount of eggs within three days from emergence (Mann–Whitney U-test, T = 476.5, P = 0.074). When newly emerged wasps were allowed to oviposit, they depleted nearly all their eggs. After 48 h, the number of eggs increased significantly up to their original supply (7.20 ± 0.61 eggs, Mann-Whitney U-test, T = 213.0, P < 0.0001). *Aenasius vexans* can be considered a pro-synovigenic species (*sensu* Quicke, 1997).

Newly emerged *Ac. coccois* females, provided with sugar-water but with no hosts, carried on average significantly more eggs after three days than at emergence (Mann–Whitney U-test, T = 306.0, P = 0.005). When newly emerged wasps were allowed to oviposit, they depleted only part of their eggs and matured up to eight new eggs within the next 48 h (Mann–Whitney U-test, T = 316.0, P = 0.01). *Acerophagus coccois* therefore can be considered a synovigenic species (*sensu* Quicke, 1997). These results were used to determine the number of hosts provided in the following bioassays, which were thus at least twice as high as the



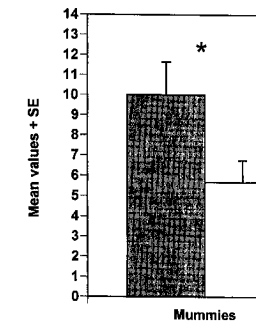


Figure 1. (A) Developmental t
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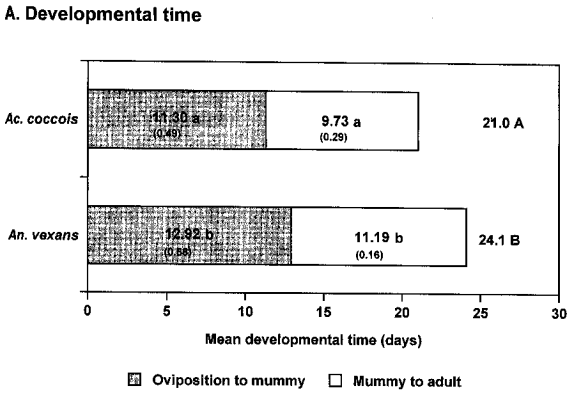


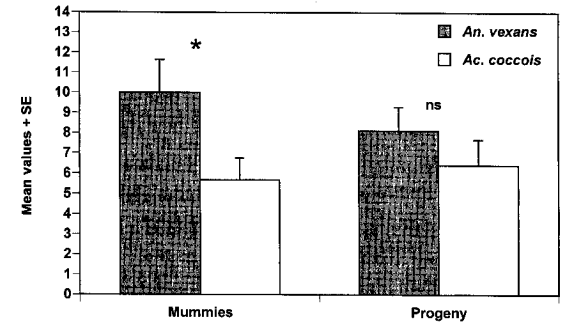
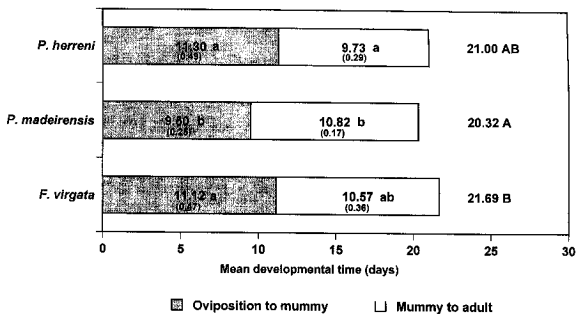


Figure 1. (A) Developmental time of *An. vexans* and *Ac. coccois* on *P. herreni*. Means followed by different letters indicate significant differences between parasitoid species at $P = 0.05$ (Mann–Whitney U-test). Values represent mean number of days ± s.e. (B) Reproductive success of *An. vexans* and *Ac. coccois* on *P. herreni*. The asterisc indicates significant differences between the two parasitoid species ($P < 0.05$, T-test). Values represent means ± s.e.



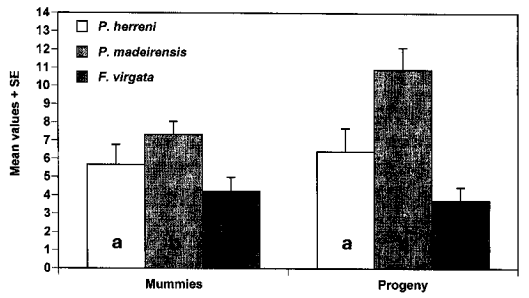


Figure 2. (A) Developmental time of *Ac. coccois* on *P. herreni*, *P. madeirensis* and *F. virgata*. Means followed by different letters indicate significant differences among different host species (Kruskal–Wallis one-way ANOVA followed by Dunn's pair-wise multiple comparison, $P<0.05$). Values represent mean number of days ± s.e. (B) Reproductive success of *Ac. coccois* on *P. herreni*, *P. madeirensis* and *F. virgata*. Means followed by different letters indicate significant differences among different host species ($P<0.05$, Kruskal–Wallis one-way ANOVA).

number of hosts that the two parasitoid species were able to parasitise in one day.

Host specificity and host suitability

Host specificity. *Aenasius vexans* accepted and completed development in only one mealybug species, *P. herreni*. In contrast, *Ac. coccois* developed in three of the seven mealybug species tested, *P. herreni*, *P. madeirensis* and *F. virgata*. Apparently, host acceptance did not depend on the host plant because *Ac. coccois* parasitised *F. virgata* on both cassava and bean in equal proportions.

Comparative effectiveness of An. vexans *and* Ac. coccois. Total developmental time in days from oviposition to adult emergence for *An. vexans* was significantly longer than for *Ac. coccois* (Mann–Whitney U-test, 423.0, $P < 0.0001$; Figure 1A). *Aenasius vexans* had longer developmental time from oviposition to mummy (Mann–Whitney U-test, $T = 496.0$, $P = 0.001$) and from mummy to adult emergence (Mann–Whitney U-test, $T = 420.5$, $P = 0.0001$). The parasitoids' reproductive outcome is different for the two species as well (Figure 1B). *Aenasius vexans* produced significantly more mummies on *P. herreni* than *Ac. coccois* (t−test, $t = 2.2$, d.f. = 46, $P = 0.0328$). Parasitism rate in this bioassay was 20% for *An. vexans* and 11.3% *for Ac. coccois*. However, the number of progeny that emerged did not differ between the two parasitoid species (t-test, $t = 1.92$, d.f. = 34, $P = 0.3557$).

Host suitability. The relative host suitability is shown for three different mealybug species from the cassava ecosystem accepted by *Ac. coccois* (Figure 2A). The total developmental time differed depending on the host species (Kruskal–Wallis one-way ANOVA, H = 9.21, d.f. = 2, P = 0.01). Developmental time of *Ac. coccois* was shorter on *P. madeirensis* than on *F. virgata*, but both did not differ from the developmental time on *P. herreni* (Dunn's pairwise comparison, $P < 0.05$). *Acerophagus coccois* produced significantly more mummies (Kruskal–Wallis one-way ANOVA, H = 8.18, d.f. = 2, P = 0.0167) and more progeny (one-way ANOVA, F = 11.3, d.f. = 2, $P < 0.0001$) on *P. madeirensis* than on the other two mealybug species (Figure 2B). Parasitism rate was 14.7% on *P. madeirensis*, 11.3% on *P. herreni*, and 8.4% on *F. virgata*.

Foraging behaviour

The mean duration of the the foraging behaviour parameters is shown in figure 3. The pie surfaces reflect the total foraging time spent on the infested leaf lobe. The two parasitoid species differed in the duration of their foraging activities during the observation period. As compared to *Ac. coccois*, *An. vexans* spent more time walking on the infested cassava leaf (*t*-test, $t = -3.75$, d.f. = 28, P = 0.0008), walking (Mann–Whitney U-test, T = 119.0, P = 0.018) and standing in experimental arena (Mann–Whitney U-test, T = 167.0, P = 0.007). *Aenasius vexans* examined both unparasitised (Mann–Whitney U-test, T = 120.0, $P \leq 0.0001$) and parasitised (Mann–Whitney U-test, T = 86.0, P = 0.002) mealybugs for a significantly longer time than *Ac. coccois*. In contrast, *Ac. coccois* spent more time ovipositing in both unparasitised (Mann–Whitney U-test, T = 324.0, $P \leq 0.0001$) and previously parasitised hosts (Mann–Whitney U-test, T = 156.5, $P \leq 0.0001$) as compared to *An. vexans*. In fact, this parasitoid species allocated over half of the active foraging time to oviposition. The average duration of an oviposition was 28.1 s for *An. vexans* and 885.9 s for *Ac. coccois*, and this was significantly different (Mann–Whitney U-test, T = 122.0, $P \leq 0.0001$). The parasitism rate was 76.6% for *An. vexans* and 32.2% for *Ac. coccois*.

Searching efficiency and parasitism success. Figure 4 depicts the average number of hosts parasitised and progeny obtained from *An. vexans* and *Ac. coccois* within the 90 min of the behavioural observations. Under our experimental conditions, *An. vexans* attacked significantly more hosts (*t*-test, $t = 5.89$, d.f. = 28, P = 0.0001) than *Ac. coccois* and produced significantly more mummies (Mann–Whitney U-test, T = 345.0, P = 0.0001). However, the number of progeny produced per individual by each species did not differ significantly because *Ac. coccois* is gregarious and deposited several eggs in to a single host. (Mann–Whitney U-test, T = 251.5, P = 0.443).

Discussion

Host specificity depends both on the behavioural abilities of the adult parasitoid and on the physiological capability of the immature parasitoid. Adult females must locate and accept their host. The ovipositing female must recognise suitable herbivores and the developing parasitoid must avoid host defence in order to survive (Vinson & Iwantsch, 1980). Specialisation is often a flexible attribute of a population that is responding to features of its particular community. In our approach, we determined the host specificity of two mealybug parasitoid species testing plant and mealybug species occuring in and around cassava fields. We chose mealybugs displaying different degrees in polyphagy. *Aenasius vexans* was able to parasitise and develop only in one mealybug species, a herbivore that is known to be monophagous on cassava (Williams & Willink, 1992). *Aenasius vexans* has been most frequently recovered in the cassava ecosystem on *P. herreni*. However, in a few occasions it was recorded on other mealybug species feeding on plants belonging to different ecosystems (Noyes & Ren, 1995). *Aenasius vexans* therefore can be considered to be a specialist in the cassava ecosystem, both at the plant and at the herbivore level. In contrast, *Ac. coccois* showed a broader host range as it parasitised and developed in three different mealybug species – the monophagous *P. herreni* and the two polyphagous *P. madeirensis* and *F. virgata*. *Acerophagus coccois* accepted *F. virgata* on both cassava and on beans in equal proportion. In addition this species was also recovered from *Oracella acuta* (Homoptera: Pseudococcidae) feeding on Loblolly Pine (*Pinus taeda* L.) (Clarke et al., 1990). Therefore we conclude that *Ac. coccois* is a generalist at the plant and at the herbivore level.

Higher host suitability for parasitoids can be characterised by a more rapid developmental time and by a higher production of offspring (Rivers & Denlinger,

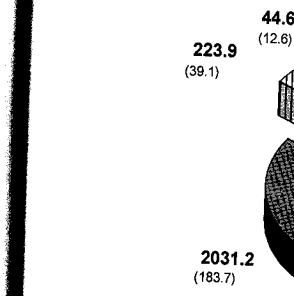


Figure 3. Comparison of for
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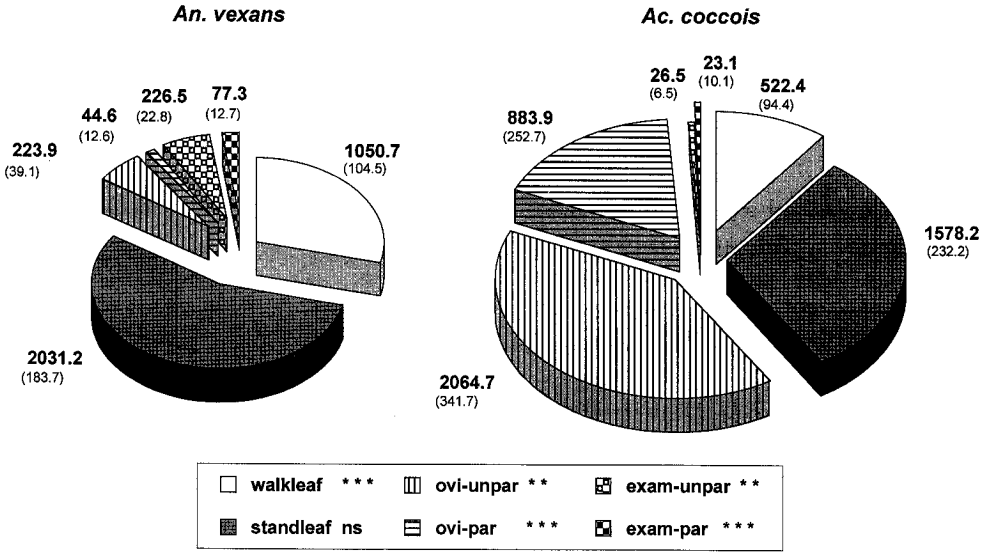

Figure 3. Comparison of foraging activities of *An. vexans* and *Ac. coccois* females on mealybug infested cassava leaves. Pie surfaces indicate the total active foraging time. Bold numbers close to slices indicate average duration of each behaviour in seconds (s.e. in parenthesis). Asteriscs close to abbreviations of behavioural parameters indicate significant differences between *An. vexans* and *Ac. coccois* in the duration of each behavioural parameter. *P<0.05; **: P<0.01; ***: P<0.001, n.s.: not significant (Mann–Whitney U-test). Abbreviations: walkleaf = walk on infested cassava leaf; standleaf = stand on infested cassava leaf; ex-unpar = examination of unparasitized mealybugs; ex-pa = examination of parasitized mealybugs; ovi-unpar = oviposition in unparasitized mealybugs; ovi-par = oviposition in parasitized mealybugs. Behaviours in the experimental arena are not shown.

1995). In the present study, *Ac. coccois* accepted three different mealybug species. However, their suitability, measured in terms of developmental time, mummy production, and progeny emergence differed. The number of mummies produced and the resulting progeny was smaller in *F. virgata* than *P. herreni* and *P. madeirensis*. The suitability of the three species could be ranked as *P. madeirensis* > *P. herreni* > *F. virgata*. Effects of different host species on life-history parameters of other parasitoid species have been reported. For example, the generalist parasitoid *Cotesia glomerata* (Hymenoptera: Braconidae) develops in three different *Pieris* caterpillar species, but with significant differences in survival, development, sex-ratio, and size of parasitoid progeny (Brodeur et al., 1998).

Having established that the two encyrtid species have different degrees of dietary specialisation, we tested whether females of *An. vexans* and *Ac. coccois* differed in host location and oviposition behaviour on mealybug infested cassava. Both parasitoid species exploit the same host in the same ecological niche. We observed that the solitary specialist *An. vexans.* spent more time on the infested cassava leaf than the gregarious generalist *Ac. coccois*. Differences in time allocation could probably be attributed to the host

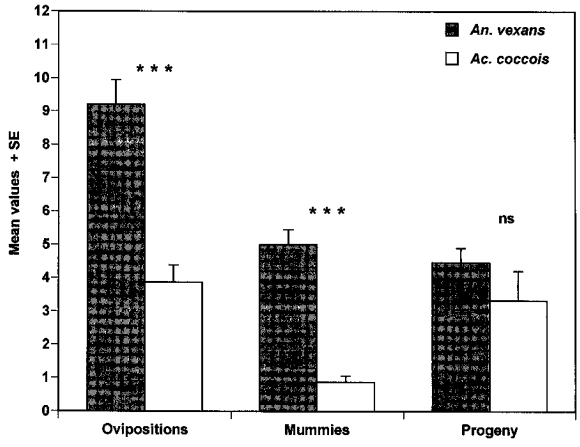

Figure 4. Number of ovipositions, mummies and progeny produced by *An. vexans* and *Ac. coccois* during the foraging behaviour experiment. Asterisks indicate significant differences (P<0.001, T-test and Mann–Whitney U-test).

specificity level of the two species and also to the behavioural parameter 'solitary' and 'gregarious'. *Aenasius vexans* had a longer host examination phase probably because it must discriminate effectively between suitable and unsuitable hosts. On the other hand, *Ac. coccois* does not need to rely on the abundance of a particular host. This species allocated most of the for-

aging time to oviposition, probably because it deposits several eggs per host. Such differences in host searching behaviour may provide a means by which the two species can co-exist, as observed for other parasitoids (Vet & Bakker, 1985).

Parasitisation rates for both species were lower in the experiment on host specificity than in the foraging behaviour experiment. This difference probably reflects a sacle effect of the experimental set-up, as the parasitoids searched the whole leaf in the first experiment but only a leaf lobe in the second. A similar quantitative decrease in ovipositions with increasing environmental complexity was observed for *Aphidius rosae* (Hymenoptera: Aphidiidae) searching for *Sitobion fragariae* (Homoptera: Aphididae) on rose bushes (Völkl, 1994), and for *Aphidius funebris* (Aphidiidae) searching for *Uroleucon jaceae* (Homoptera: Aphididae) on *Centaurea jacea* (Weisser, 1995).

Our study showed that *An. vexans* and *Ac. coccois*, differ in their host specificity level and in their host searching strategies and oviposition behaviour. Specialists are assumed to be more effective competitors (Fox & Morrow, 1981) and more effective in controlling pest populations (Sheehan, 1986). Generalists on the other hand are expected to be good explorers (Sheehan, 1986). Hence, both specialist and generalist parasitoids have their advantages and limitations. To increase efficiency of a biological control program a combination of various natural enemies may be used as as the species might complement each other (Hassan & Rost, 1993). Such an approach was adopted for a predatory species, *Hyperaspis notata* Mulsant of the cassava mealybug in Africa, *Phenacoccus manihoti* Mattile-Ferrero (Staeubli Dreyer et al., 1997). As observed for other species (e.g., the generalist *Cotesia glomerata* and the specialist *C. rubecula*, Brodeur et al., 1998) the two cassava mealybug parasitoids may co-exist in the cassava ecosystem through host instar and host species segregation and through different foraging strategies. For biological control of *P. herreni*, a multi-species approach using a highly efficient specialist, *An. vexans*, and a species with a moderately narrow host range, *Ac. coccois*, may be considered.

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