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Searching at different spatial scales: the foraging behaviour of the aphid parasitoid *Aphidius rosae* in rose bushes

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Abstract The searching patterns of the aphid parasitoid *Aphidius rosae* were analysed at three different spatial scales: leaves, shoots and bushes. Parasitoid females searched aphid-infested leaves and shoots intensively and remained on average more than twice as long on infested than on uninfested shoots. Patch times and oviposition numbers per shoot were highly variable both between females and for different shoot visits within females. However, at the shoot and bush level low oviposition numbers were generally found. The time spent on different behavioural patterns (searching, resting, feeding, host handling) changed significantly during subsequent shoot visits of individual females but oviposition success was not influenced by this change. Parasitoids searched individual leaves and shoots mainly by walking, while moving between shoots occurred exclusively by flight. The travel time between shoots (i.e. flight time) accounted for less than 1% of the residence time in a bush. At the bush level foraging was characterized by a high ability to localize infested shoots and consequently little time was wasted in searching on uninfested shoots. The pattern of resource exploitation of individual females was consistent with the distribution of *A. rosae* larvae in field samples taken from individual rose bushes.

Key words Parasitoid foraging · Different spatial scales
Searching patterns · Individual variability
Pre-patch experience

Introduction

In the field, parasitoid females have to search for hosts on a hierarchy of spatial scales. In a broad sense, we can distinguish two levels. On a large scale, the parasitoid is searching between patches in its habitat. On a small scale, the parasitoid is foraging for hosts within patches, where a patch is defined as a section of the parasitoid's environment, the borders of which, when crossed by a foraging individual, elicit a change in its behaviour (Hassell and Southwood 1978; Waage 1978; Bell 1990). Most recent studies on parasitoid foraging behaviour have focused on small spatial scales, either analysing the foraging behaviour in single patches (e.g. Cook and Hubbard 1977; Waage 1979; Morrison and Lewis 1981; Weis 1983; Price and Clancy 1986; Jones and Hassell 1988; Cronin and Strong 1993) or on single small host plants (e.g. Waage 1983; Ayal 1987; Cloutier and Baudouin 1990; Romstöck-Völkl 1990; Maini et al. 1991; Völkl 1994), and most of these studies were carried out in the laboratory. In contrast, few studies have analysed foraging behaviour on large scales under field conditions where the parasitoid females' movements were not restrained by cages (e.g. Thompson 1986; Casas 1989; Ives et al. 1993).

The present study deals with the foraging behaviour of the aphid parasitoid *Aphidius rosae* (Haliday)(Hymenoptera: Aphidiidae) in rose bushes (*Rosa canina* L.). *A. rosae* is a solitary koinobiont endoparasitoid whose main hosts are the aphid species *Macrosiphum rosae* (L.) and *Sitobion fragariae* (Walker)(Homoptera: Aphididae) on their primary host plant, rose (Mackauer and Stary 1967; Stary 1973). Both aphid species suck mainly on current-year shoots, in particular on the developing leaves at the tip of the shoot, and on the petioles and veins of the lower side of the first and second leaf pairs (Zwölfer et al. 1984). The structure of rose bushes is very complex on several spatial scales, e.g. leaf, shoot and bush level, which may be searched in different manners by foraging parasitoids. *A. rosae* females usually visit more than one shoot with an aphid colony during their stay in a rose bush. Since *A. rosae* is a comparably large aphidiid species (body length 3–4.5 mm), it is not only possible to observe females while they are searching on a shoot but also to follow their search flight between shoots within single rose bushes.

I tested whether (1) searching patterns and patch time allocation differed for different spatial scales, i.e. on

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leaves, shoots and bushes, (2) whether resource exploitation and patch time allocation were influenced by the female's prior experience (Visser et al. 1992; Hemerik et al. 1993) and if they changed during subsequent shoot visits, and (3) whether patterns of parasitism in the field can be explained by the foraging patterns of individual females.

Materials and methods

General methods

Mummies of *A. rosae* were collected in mid-May 1990 in the vicinity of Bonn from rose bushes (*Rosa* spp.) only infested by *S. fragariae*. All mummies were kept singly in gelatine capsulae until the adult parasitoid emerged. Subsequently, males and females were given a chance to mate in small cages containing rose leaves. All parasitoids were supplied daily with honey and water and kept in small plastic cages at 20°C. For the experiments, 3- to 4-day-old females, which had had a previous opportunity for oviposition but had been deprived of hosts for 24 h before the experiment, were used.

Study site, host plant characters and hosts

The field experiments were carried out from end May to mid-June 1990 near Bonn, Germany. During this period, there was remarkably constant sunny weather with almost no wind, high humidity and air temperatures varying between 21°C and 26°C during each trial.

The experimental rose bushes were growing on the side of a hedge with a southerly exposure. They measured about 1.0–1.5 m in height and 1 m in diameter, and were separated from each other by hawthorn and blackthorn bushes. The total number of current-year shoots per bush ranged between 39 and 56, and the number of shoots infested with *S. fragariae* between 8 and 11. The distances between all infested shoots were measured and shoots were ranked according to their distance from the shoot on which the parasitoid was currently searching. This procedure was repeated after each parasitoid flight to a new colony. Uninfested shoots were included in this sequence only if they were visited by the parasitoid.

All aphids on a particular shoot were considered to belong to the same colony. Colony size ranged between 19 and 42 individuals. All colonies were founded by winged females (i.e. all bushes were free of fundatrices and fundatrix-borne colonies) and had a similar age structure, with third- and fourth-instar larvae being the dominant stages. The total number of *S. fragariae* per bush ranged between 187 and 402 aphids (mean±SE=286±74).

Foraging behaviour of *A. rosae* in rose bushes in the field

Single *A. rosae* females were released onto the tip of a rose shoot infested with *S. fragariae* and continuously observed until they left the bush. The shoot structures searched were classified as (1) upper leaf side, (2) lower leaf side or (3) shoot stem and tip with unfolding leaves. The following parasitoid behavioural patterns were distinguished: (a) *Searching* – the parasitoid searched the shoot but had no contact with aphids (b) *Feeding* – the parasitoid fed on aphid honeydew which was distributed around the colony (c) *Cleaning* – the parasitoid intensively cleaned its antennae, legs and/or its ovipositor (d) *Resting* – the parasitoid sat motionless on the shoot at least 2 cm away from an aphid colony (e) *Host handling* – the parasitoid located a potential host and tapped it with its antennae or showed a behavioural pattern connected with oviposition (waiting with bent abdomen, attacking the host or ovipositing). An oviposition was characterized by an ovipositor insertion for 1–2 s in the aphid's body and a strong and jerky withdrawal of the ovipositor. Cases of assumed oviposition were confirmed by dissecting the stung aphid 4 days after the experiments.

My experimental design involved the risk of females foraging in colonies that contained hosts that had already been parasitized. Contacts with previously parasitized hosts may affect patch times (Charnov 1976; van Alphen and Visser 1990), since *A. rosae* is able to distinguish between unparasitized and parasitized hosts (W. Völkl, unpublished work) and usually avoids superparasitism. This possibility was considered to be negligible for two reasons. Firstly, foraging in such colonies should be common in nature, and one aim of this work was to study the foraging behaviour of *A. rosae* under field conditions. Secondly, the incidence of parasitism prior to the experiments proved to be very low. Only very few aphidiid larvae were found when aphids that had not been stung during a trial were dissected. This indicates that almost no parasitoids had been present in the experimental rose bushes before the experiments.

Field samples

To evaluate the distribution of aphidiid larvae within rose bushes and the degree of parasitization within particular colonies, all *S. fragariae* colonies on 25 bushes growing in the vicinity of the study site were collected in mid-June. All aphids were dissected and the number of parasitoid first-instar larvae were counted.

Developing larvae of *A. rosae* only remain in the first instar for about 1 day (Mackauer 1990; W. Völkl, unpublished work). I therefore assumed that all first-instar larvae recorded from a particular bush originated from oviposition events occurring within 1 day. The number of first-instar larvae should therefore be suitable for comparing experimental data on the searching behaviour of individual parasitoids with the distribution of parasitism in the field. I used the number of aphid colonies with one or more first-instar parasitoid larvae as a rough estimate of the parasitoid's searching efficiency within bushes, and the number of first-instar parasitoid larvae per colony as an estimate of parasitoid resource exploitation.

Results

Patch time allocation and resource exploitation at shoot and bush level

Females remained on aphid-infested shoots for on average 1591±114 s (n=50) but only for 557±66 s (n=12) on uninfested ones (Wilcoxon paired sample test, W=150, n=62, P<0.001). The residence time on infested shoots was not correlated with aphid colony size (Table 1a). There was considerable variation in time allocation within individual females. However, this variability in residence time was not correlated with the sequence in which shoots were visited (Table 1a), i.e. the residence time did not significantly increase or decrease during subsequent shoot visits and did not not depend on the number of shoots visited previously. Mean residence times did not differ significantly between females (Kruskal-Wallis ANOVA: χ^2=4.674, df=9, P=0.862).

Females laid on average only 2.8±0.3 eggs per colony. No egg was laid in seven colony visits (14%). The number of ovipositions was significantly correlated with residence time but not with aphid colony size (Table 1a). Consequently, the parasitization rate decreased with increasing aphid colony size (r_s=-0.463, n=50, P=0.0007).

Table 1 Correlation matrix for different parameters on the (*a*) shoot level and (*b*) bush level for searching *Aphidius rosae* females. The shoot visit sequence begins with shoot visit 1 for each female

	Sequence in which shoots were visited	Colony size	Residence time
a. Shoot level (*n*=50)			
Residence time	r_s=–0.034 *P*=0.813	r_s=0.067 *P*=0.642	– –
No. ovipositions	r_s=0.039 *P*=0.786	r_s=–0.082 *P*=0.569	r_s=0.665 *P*<0.001
Oviposition rate	r_s=0.064 *P*=0.660	r_s=–0.248 *P*=0.083	r_s=–0.122 *P*=0.340

	No. shoots visited	Aphids/bush	Residence time
b. Bush level (*n*=10)			
Residence time	r_s=0.881 *P*<0.001	r_s=0.506 *P*=0.135	– –
No. ovipositions	r_s=0.718 *P*=0.019	r_s=0.267 *P*=0.455	r_s=0.804 *P*=0.005
Oviposition rate	r_s=0.072 *P*=0.843	r_s=-0.315 *P*=0.375	r_s=0.171 *P*=0.636

There was also no relationship between the number of ovipositions and the sequence in which shoots were visited (Table 1a). Again, there was high variability within females but the mean number of ovipositions per colony did not differ significantly between females (Kruskall-Wallis ANOVA: χ^2=5.298, *df*=9, *P*=0.791). The average oviposition rate was 6.6±0.6 eggs/h. This rate was not correlated with aphid colony size (Table 1a) or with the sequence in which shoots were visited (Table 1a).

The wasps' oviposition success was influenced by the shoots' structural complexity: 17.3±2.6% of the attacks took place while the *A. rosae* female was standing on a different plant structure than that on which the aphid was feeding, such as a nearby spine, basal leaflet or petiole, and these attacks resulted in ovipositions more often than attacks originating on the same structure on which the aphid was feeding (other structure: 29.1±2.9%; same structure: 15.5±1.4%). In total 37.0±4.8% of all ovipositions per colony were made from spines, basal leaflets or petioles.

Females remained on average for 8684±786 s (*n*=10) in a bush and visited on average 6.2±0.6 shoots during their stay. They spent 91.3±2.4% of their total residence time on infested shoots and only 8.7±2.4% on uninfested ones. The residence time per bush was correlated with the number of shoots visited but not with the estimated total number of aphids per bush (Table 1b).

Females laid on average 14.1±1.6 eggs (range 4–26) per bush. The number of ovipositions was correlated with residence time and thus with the number of shoots visited but not with the estimated total number of aphids per bush (Table 1b). The average oviposition rate per bush was 5.8±0.5 eggs/h. This rate was not correlated with residence time (Table 1b). The lower overall rate of oviposition on bushes than on individual shoots is the result of time "wasted" on uninfested shoots during the search. Percent parasitism on the bush level averaged only 5.0±0.6%. This rate was considerably lower than that at the colony level, since no female visited all colonies.

Table 2 Proportion of time (%; mean±SE) spent by *A. rosae* females in different behavioural patterns on infested and uninfested shoots

Pattern	Infested shoots	Uninfested shoots
Searching	35.5±2.3	99.4±2.9
Tip	50.0±2.0	10.3±1.3
Upper leaf side	13.4±1.3	83.0±3.1
Lower leaf side	37.3±1.8	8.5±2.0
Resting	23.0±2.2	0.9±1.7
Feeding	7.8±0.8	–
Host handling	22.2±1.6	–
Cleaning	12.2±1.1	–

Time partitioning at shoot level

Time partitioning was significantly different for females on uninfested and infested shoots. On uninfested shoots, they spent most of their time on the upper sides of leaves where normally no hosts can be found, and hardly rested or fed (Table 2). On infested shoots, by contrast, females spent on average only 35.5% of their patch time in searching, but searched the aphids' feeding sites most intensively, i.e. the tip of shoot and the lower side of the leaves (Table 2).

Time partitioning on infested shoots changed during a visit to a bush. While the proportion of time spent in searching decreased from an average of 49% to c. 25% (r_s=-0.333, *n*=50, *P*=0.018), the proportion of time spent in feeding (r_s=0.317, *n*=50, *P*=0.025) and resting (r_s=0.468, *n*=50, *P*=0.006) increased in parallel (Fig. 1).

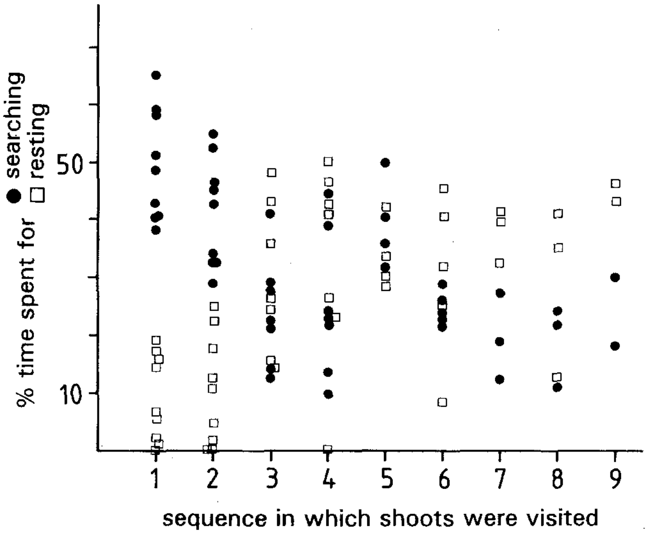

Fig. 1 The proportion of time spent by the parasitoid *Aphidius rosae* in searching (*circles*) and resting (*squares*) during sequential visits (=sequence in which shoots were visited beginning with visit 1 for each female) within rose bushes. Note that the number of shoot visits, and thus the number of data points per individual shoot visit, differed between females

This pattern was consistent for all females. However, the increase in resting and feeding intervals did not influence the average number of eggs laid or the oviposition rate (see above), and consequently there was no relationship between the proportion of time spent in host handling (r=–0.281, n=50, P=0.048) or cleaning activities (r=–0.093, n=50, P=0.519; see also Table 2), which are connected with host handling, and the sequence in which shoots were visited.

Searching patterns of *A. rosae* females on different spatial scales

The searching movements of *A. rosae* females differed significantly on the leaf/shoot and bush level. Females travelled between leaflets or between leaves mainly by walking along the leaf or shoot stem, respectively, but short-range search flights occurred occasionally (3.6%) when females moved from the shoot tip to the first leaf pair. They examined significantly more leaves for hosts on uninfested than on infested shoots (Table 3). Furthermore, the number of leaflets searched per aphid-free leaf was significantly higher on uninfested shoots, while the number of leaflets searched did not differ for infested and aphid-free leaves on infested shoots (Table 3; Wilcoxon test, P>0.05). Single leaves and leaflets were in general searched by walking.

Table 3 Mean numbers (±SE) of leaves and leaflets searched by *A. rosae* females on aphid-infested and uninfested rose shoots. Within each row, means differ significantly at P<0.05 (Wilcoxon test)

	Infested shoot	Uninfested shoot
No. leaves searched	2.30±0.16	4.33±0.35
No. leaflets searched/ uninfested leaf	2.65±0.20	3.77±0.21
No. leaflets searched/ infested leaf	2.80±0.19	–

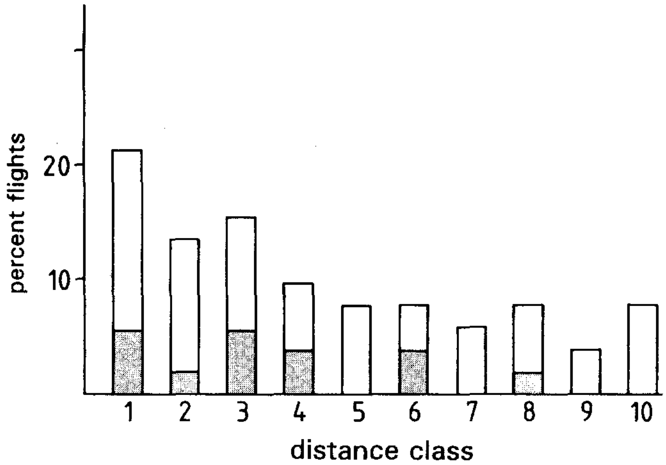

Fig. 2 The proportional distribution of landings of *A. rosae* in different colony distance classes (*shaded areas* indicate the proportion of flights to uninfested shoots)

Fig. 3 Relationship between *Sitobion fragariae* colony size on *Rosa canina* shoots and the number of first-instar larvae of *A. rosae* recorded in field surveys

After a particular shoot was left, new host patches were searched for exclusively by flight. The search flight can be described as approximately U-shaped: the female flies away from the plant up to a distance of c. 30 cm, then turns and lands, always on the tip of a shoot. Search flights lasted on average only 3.6±1.0 s (n=52). Their lengths did not vary significantly between individual females (Kruskal-Wallis ANOVA: χ^2=6.763, n=10, P=0.343) and were independent of the distance class between two shoots (Kruskal-Wallis ANOVA: χ^2=6.113, n=50, P=0.383), which is a rough estimate of the flight distance. Thus, travelling between shoots accounted for less than 1% of the total time females spent in a bush.

Females landed significantly more often on infested shoots (5.6±0.3) than on uninfested shoots (1.6±0.5) (U=8.0 n=63, P<0.001) and visited on average 45.2±3.6% of the infested shoots per bush but only 2.7±0.5% of the uninfested ones. The probability that a flight would end on an infested shoot was 0.76 although the average proportion of infested shoots within the bush was only 15.9±0.7%. There was a slight tendency for flying females to land on a nearby shoot belonging to one of the first three distance classes (Fig. 2). However, this trend was not significant (χ^2=12.615, df=9, P=0.181).

Females always left bushes in a straight flight, which seemed to differ in speed from the search flight, although exact measurements were not possible.

Field studies

Parasitized aphid colonies were found in 14 out 25 rose bushes (=56%). In these bushes, on average 4.1±0.7 colonies on particular shoots contained one or more first-instar larvae of *A. rosae*. This number was the same as that found in the experiments, where females laid at least one egg in 4.3±0.5 colonies per bush (U=60, n=24, P=0.554).

The mean number of first-instar larvae of *A. rosae* per colony (2.6±0.3) was not correlated with aphid colony size (Fig. 3: r_s=0.095, n=57, P=0.482). It was significantly lower than the mean number of ovipositions per colony in the experiments if only colonies with at least one egg laid are considered (3.3±0.2)(U=848.5, n=100, P=0.007). The rate of parasitism decreased significantly with increasing aphid colony size (r_s=-0.475, n=57, P=0.0002). This decrease did not differ significantly from the decrease found in the experiments (ANCOVA: F=0.02, df=1, P=0.900).

Discussion

Considering movement patterns and foraging behaviour, the environment of *A. rosae* may be divided into three hierarchical spatial scales. A shoot and its leaves together represent the smallest scale, where the parasitoid mainly moves by walking and generally avoids flying. This level may form what Ayal (1987) called the "elementary unit of foraging", since it provides all essentials of life for the parasitoid, i.e. hosts, food and sheltered places for resting. Searching within a bush differed from searching on shoots since parasitoids moved between shoots exclusively by a typical search flight. These flights differed in speed and flight curve from the straight flight by which the parasitoid left the bush. Thus, a particular bush seems to represent a higher level of the parasitoid's environment and may be regarded as a intermediate scale between the shoot and the higher level, e.g. a hedgerow with many rose bushes.

The search pattern and time partitioning on the smallest spatial scale, the leaf and shoot level, were strongly influenced by the presence of hosts. Females searched more leaves and leaflets, and thus a larger area, on uninfested shoots but spent significantly less time there than on infested shoots. The upper sides of the leaves, where host-associated contact kairomones like honeydew (Budenberg 1990) may accumulate, were searched most intensively, but females made almost no resting or feeding pauses even if honeydew was found on some leaves. Search behaviour was different on infested shoots. *A. rosae* females always located the first hosts shortly after landing on the tip of the shoot. They searched fewer leaves and leaflets, spent only a minor proportion of their time on the upper side of the leaf, and remained mainly in the vicinity of their hosts (Table 2). This behaviour resembled the "area restricted search" seen in many parasitoids and predators (e.g. Laing 1937; Dixon 1959; Evans 1976; Waage 1979; Carter and Dixon 1982; Nakamuta 1985).

A. rosae females seem to be able to locate aphid-infested shoots within a rose bush during the search flight, since more than 80% of the search flights led to an infested shoot although 90% of the shoots bore no aphid colony. It is likely that females use mainly aphid-borne host-location cues for orientation, e.g. honeydew and aphid cornicle secretion (Hagvar and Hofsvang 1989; Grasswitz and Paine 1992; Guerrieri et al. 1993). This directed search from shoot tip to shoot tip provides three major advantages for the foraging female. Firstly, in combination with the U-shaped flight curve it may reduce the risk of being caught in a spider web, which can reach high densities within rose bushes (Zwölfer et al. 1984). Secondly, the travel time between shoots occupies only a negligible proportion of the total residence time (<1%), while searching for new hosts by walking from shoot to shoot would be much more time consuming. Thirdly, flying from tip to tip ensures that the female lands close to hosts, which feed preferentially in the distal region and on the tip of the shoot.

Searching behaviour and patch time allocation of parasitoids are of crucial importance in understanding the population dynamics of host-parasitoid systems because of the direct link between successful searching and parasitism (Comins and Hassell 1979). The foraging and oviposition behaviour of *A. rosae* females was generally characterized by a low degree of resource utilization (i.e. on average less than 10% of the available hosts). This pattern, which is typical for many aphidiid wasps (Mackauer and Völkl 1993), was consistent at the shoot and bush levels. Both patch times and oviposition number were independent of aphid colony size, resulting in an inversely density-dependent parasitization rate on both shoot and bush level. Theoretical models of parasitoid foraging behaviour showed that patch residence time and oviposition number per patch should decrease with decreasing travel time and the expected concomitant decrease in travel mortality risks for the female (Weisser et al. 1994). The low patch residence times and oviposition numbers of *A. rosae* correspond with very low travel times between patches. Thus, the predictions of the model of Weisser et al. (1994) are consistent with the behaviour of *A. rosae* females in the field.

Both patch times and oviposition numbers of *A. rosae* showed high individual variability within and between females. The source of this variability may be sought both in the external environment, e.g. in differences in host-plant structure (Andow and Prokrym 1990; Maini et al. 1991), host distribution (Gardner and Dixon 1985; Völkl 1990) or host behaviour (Völkl 1991; Mackauer and Völkl 1993), and also in a female's pre-patch experience (Visser et al. 1992; Grasswitz and Paine 1993) or in "internal state variables" such as egg load or age (Völkl and Mackauer 1990; Rosenheim and Rosen 1991; Weisser 1994). In the present study,an effort was made to keep the internal state variables egg load, age and mating status constant and thus they should have had only a small effect on the variability in foraging patterns. Collins and Dixon (1986) found that oviposition activity of the parasitoid *Monoctonus pseudoplatani* (Marshall) decreased during sequential patch visits under laboratory conditions. Both patch time allocation and oviposition numbers varied considerably within *A. rosae* females but showed no relation to the sequence in which shoots were visited and thus to pre-patch experience. However, the patterns of time partitioning changed significantly during a female's stay in a bush. Females allocated more time to searching for hosts during earlier than later shoot visits, while feeding and resting intervals increased. This decrease in relative searching time had, however, no significant effect on the number of ovipositions or on the oviposition rate, and thus on reproductive success in subsequent shoot visits. The number of ovipositions per colony was also influenced by the plant's structural complexity, since many ovipositions took place while the female was sitting on a nearby spine, basal leaflet or petiole where it was out of reach of the aphids' physical defense.

There was a significantly higher number of parasitoid progeny per colony in the experiments than in the field surveys. Two (not mutually exclusive) explanations may account for this observed difference. One possible explanation is differences in internal state variables of females foraging in the field population. Alternatively, different weather conditions may have influenced foraging behaviour of experimental and other females (Roitberg et al. 1993). However, the overall pattern of resource exploitation did not differ significantly between field and experimental data, either on the bush or on the shoot level. Thus, general patterns of parasitization at the population level can largely be explained by the foraging strategy of the individual parasitoids.

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