



Host and food searching in a parasitic wasp *Venturia canescens*: a trade-off between current and future reproduction?

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Whether to invest in current or future reproduction is an important trade-off in life history evolution. For insect parasitoids, this trade-off is determined, among other factors, by the decision whether to search for hosts (immediate gain of fitness) or food (delayed fitness gains). Although host searching has been well studied, food sources, cues that parasitoids use to search for food and how insects modify their feeding behaviour have not. To address these questions, we investigated the food- and host-searching decisions made by the parasitoid *Venturia canescens* in both laboratory (olfactometer experiments) and field conditions (choice experiments). The wasps detected chemical cues associated with food, as well as those associated with hosts, and moved towards one or the other according to their nutritional state. Females used as food sources the same fruits that harboured hosts and detected the olfactory cues that would direct them to these fruits. Field results were consistent with those obtained in the laboratory. By integrating responses to infochemicals related to host and food, *V. canescens* might reduce the costs associated with food searching, so that more time and energy can be allocated to foraging for hosts. This behaviour should result in an adaptive advantage over parasitoids that incur additional costs by searching for hosts and food in different locations.

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An animal's lifetime reproductive success depends on two factors: its potential reproductive output and the probability of surviving long enough to realize this potential. A potential trade-off will arise whenever these factors depend on a common resource. For instance, in many parasitoids feeding and reproduction are mutually exclusive activities: they search for hosts (generally other insects) where their offspring develop, thus gaining immediate fitness, or they increase survival and/or future reproductive output (Idris & Grafius 1995; Siekmann et al. 2001) by searching for food (Roff 1992; Sirot & Bernstein 1996). Other factors such as clutch size determine this trade-off: animals might have to choose between laying more eggs on a host or saving some of them for later and potentially better conditions. Solving such trade-offs requires that animals detect and integrate information

on resource availability and distribution, and that flexible behavioural processes allow them to take decisions according to their internal state (such as the level of metabolic resources).

Parasitoids are particularly suitable for the study of the adaptive flexibility of behaviour (Vet et al. 2002) required to settle the trade-off between current and future reproduction (i.e. between immediate and delayed fitness rewards). Typically, hosts have a patchy distribution and, to lay their eggs, females of numerous species travel from one patch to another mostly by flight. Flight is a very energy-expensive activity in insects (Harrison & Roberts 2000); it rapidly reduces energy reserves and, consequently, life expectancy. Therefore, many parasitoid species also feed during the adult phase. Some feed on the hosts themselves (Jervis & Kidd 1986; Heimpel & Collier 1996; Gilbert & Jervis 1998; Jervis 1998), others feed on pollen, nectar and/or honeydew (Leius 1960; Jervis et al. 1993; Lee & Heimpel 2003; Wäckers & Steppuhn 2003) and some do both (e.g. Heimpel et al. 1997).

In the nonhost-feeding parasitoids, two situations can be distinguished: one in which the food sources are near the hosts, as in aphid parasitoids feeding on honeydew

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produced by their hosts (Jervis & Kidd 1996), and one in which food and hosts are independently distributed. In the first case, the decision to feed or oviposit need not be taken before arrival on the host patch. In the second case, however, the insects have to commute between food and host patches, and searching for food would clearly interfere with foraging for hosts. Sirot & Bernstein (1996) developed a state-dependent model to explore how non-host-feeding parasitoids should allocate their time between searching for food and searching for hosts when these resources are in separate locations. Their results suggest that the optimal decision to search for hosts or food strongly depends on the energy reserves of the animal and the probability of finding food sources. At intermediate probabilities of finding food, if its energy reserves are high the parasitoid should always search for hosts. If energy reserves are intermediate, it should search for hosts unless it is already on a food patch. In the latter case, it should keep replenishing its reserves until satiation. A level is then reached at which searching for hosts is the only available strategy. At low energy reserves the parasitoid should exclusively search for food. At extreme probabilities of finding food parasitoids should search for hosts. Differences in mortality risk shift the boundaries of these strategies, but the general pattern of predictions remains the same (see Figure 1 in Sirot & Bernstein 1996). Despite the important fitness consequences of food acquisition (Stapel et al. 1997; Thompson 1999), knowledge of the processes by which parasitoids search for food, the cues they use, and the influence of physiological state on their food foraging decisions remains limited, especially in field conditions (Wäckers 1994a; Jervis & Kidd 1996; Lewis et al. 1998; Jacob & Evans 2001; Sisteron & Averill 2002).

Our aim was to examine the food- and host-searching strategies of *Venturia canescens* Gravenhorst, depending on its nutritional state in both laboratory and field conditions. *Venturia canescens* is a non host-feeding parasitoid, known to feed actively in the field (Casas et al. 2003). We also investigated the cues *V. canescens* uses to find resources and the food sources it uses in field conditions.

To address this question, we first studied the influence of nutritional state on survival in *V. canescens*. Next, we tested whether this wasp could detect volatile cues from food and host sources and how her response was modified by nutrition. We then investigated whether sites that harbour hosts in the field also provide food and investigated the odour preference of fed or hungry wasps for single (host or food) or mixed (host and food) resource sites. Finally, we tried to confirm our findings in a field experiment where we analysed the resource-searching strategy of *V. canescens* according to its nutritional state.

METHODS

Cultures

We used a thelytokous strain (i.e. females produce daughters without egg fertilization) of *V. canescens* (Gravenhorst) collected in the field in 1999 in the southeast of

France (Antibes). *Venturia canescens* is a synovigenic parasitoid (Jervis et al. 2001). The adults emerge with only some of their total mature egg complement and produce up to 250 eggs (Harvey et al. 2001). There is no egg resorption in this species (Eliopoulos et al. 2003). The host range is fairly broad (Salt 1976) and includes lepidopterans that are pests in granaries and flour mills such as *Corcyra cephalonica* Stainton, *Ephestia kuehniella* Zeller and *Plodia interpunctella* Hübner (Salt 1976). In natural conditions, however, *V. canescens* finds its hosts in dried fruits such as figs, carobs, medlars and dates (Driessen & Bernstein 1999). As a host, we used *E. kuehniella* (Lepidoptera: Pyralidae) and cultures were maintained in a constant environment of $25 \pm 1^\circ\text{C}$ and $75 \pm 5\%$ relative humidity on a 16:8 h light:dark regime. *Venturia canescens* attacks its hosts in their second to fifth instar and responds strongly to the odour of a host mandibular gland secretion deposited in host food medium (Thorpe & Jones 1937). This odour guides the parasitoids to the hosts. Biochemical analyses have shown that *V. canescens* consumes food in the field (Casas et al. 2003). Beling (1932) also suggested that *V. canescens* feeds on nectar or honeydew, far from their oviposition sites. In laboratory conditions, adult feeding increases the fecundity of *V. canescens* through its effect on longevity (Harvey et al. 2001; Eliopoulos et al. 2003).

Experiment 1: Influence of Food Access on Survival

Our aim in this experiment was to study the influence of nutritional state on the life expectancy of *V. canescens*. Four groups of newly emerged parasitoids were placed individually into plastic tubes (7.5×2 cm) and assigned to one of the following treatments: (1) fed ad libitum (FA, $N = 48$); (2) fed every 48 h (F48, $N = 30$); (3) fed every 96 h (F96, $N = 48$); and (4) food deprived (UF, $N = 50$). Food consisted of a droplet of 50% water-diluted honey, and females (F48 and F96) were allowed to feed for up to 20 min. All the wasps in the F48 and F96 treatments started feeding as soon as food was offered. We inspected the tubes hourly between 0800 and 1900 hours to register time of death of the parasitoids. We considered the wasps found dead at first inspection in the morning as having survived until 0130 hours (the mean time between 1900 and 0800 hours). These data were not considered as censored, because this would mean discounting some of the available information, namely the period when these wasps died. The experiment was conducted under controlled conditions at $25 \pm 1^\circ\text{C}$ ($75 \pm 5\%$ relative humidity and 16:8 h light:dark regime).

Experiment 2: Olfactory Detection of Resources

In this experiment we assessed whether wasps actively search for food or host depending on their metabolic reserves by using volatile cues. For this test we used a Y-tube olfactometer. The base of the Y-tube was connected

to an air pump that produced an airflow through the arms of the tube to the base. Each arm of the tube was connected to a plastic box in which odour sources could be placed. The air inlets of the plastic boxes contained carbon filters. The base of the Y-tube was 50 cm from the junction of the two arms and this junction was 25 cm from the odour sources. The airspeed inside each arm of the olfactometer was kept constant at 1 m/s. The olfactometer was placed in the centre of a white-painted wooden box (200×140 cm and 70 cm high). This ensured that the environment in which wasps were tested was symmetrical and devoid of any feature that could attract them. Observations were made through a small window in one of the walls of the box. Experiments were done in a climate room (25 ± 1°C, 75 ± 5% relative humidity) between 1000 and 1630 hours.

The food odour source consisted of a petri dish 5 cm in diameter filled to the rim with 50% water-diluted honey. The host odour source consisted of a 1-ml kairomone solution deposited on a piece of filter paper (4×4 cm) that was left to dry for 5 min before use. We prepared the kairomone solution by washing host-contaminated semolina from the host culture with a mix of 50% acetone and 50% ether (Mudd & Corbet 1973; Castelo et al. 2003). We prepared a stock quantity of this solution before all experiments started, which ensured a constant kairomone concentration throughout the experiments. Parasitoids readily attempted oviposition in pieces of paper treated with this solution. We replaced the paper impregnated with the kairomone every 30 min (the time to test three wasps) to limit a potential decrease in the olfactory stimulus and a bias from pseudoreplication (Ramirez et al. 2000).

We tested two types of females, fed and food deprived, for their preference for the two odour sources. Food-deprived wasps were 48 h old and had had no contact with food sources since their emergence. Fed wasps were also 48 h old but had had permanent access to a drop of 50% water-diluted honey. Wasps were individually introduced through a hole near the base of the Y-tube. We observed each foraging female until it had reached the end of one of the arms (i.e. the entrance of the plastic box) after which we removed it. Wasps that did not reach the end of an arm within 10 min were removed and scored as 'indecisive'. The position of the odour sources (left or right arm of the olfactometer) was alternated every five trials and we randomly assigned fed or food-deprived wasps to each trial. Every 10 trials, the Y-tube was carefully washed with water and detergent.

Experiment 3: Host Fruits as Feeding Resource

In field conditions, carob fruits and figs harbour a host of *V. canescens*, *Ectomyelois ceratoniae* (Driessen & Bernstein 1999). To investigate whether these fruits could also provide food for the parasitoids, we compared the survival up to 48 h of wasps that had access to fruits with that of females that had access only to water. For this, we introduced four groups of wasps into plastic cages (30×30×30 cm) containing a petri dish with a piece of wet cotton wool. The females used (0–2 days old) had emerged from the stock

cultures with no access to food. Two of the cages also contained fruits collected in the field (either carob fruits or figs). The other two cages were taken as controls. The experiments were done in pairs, a cage containing fruits and a control. After 48 h, at 25 ± 1°C and 16:8 h light:dark regime, we counted the dead and living wasps.

Experiment 4: Choice of Odour (Food, Host or Both)

Since we found that fruits that harbour potential hosts can also provide food for *V. canescens* (see results of experiment 3), we then tested whether females prefer the combination of the odours of both host and food or the odours of a single resource. In the olfactometer, fed and food-deprived females were tested in two situations. In the first (experiment 4a), females had the choice between the odour of hosts and the combined odours of food and hosts. In the second (experiment 4b), wasps had the choice between the odour of food and the combined odours of food and hosts. For the preparation of the odour sources and other details see experiment 2. We obtained the combination of odours by placing the two odour sources in the same plastic box.

Experiment 5: Food Searching in the Field

Experiment 4 showed that in an olfactometer, food-deprived wasps would prefer the association of odours (host and food) rather than the single odour of food (see below). To see whether these findings reflected the behaviour of the animals in nature, we conducted a large-scale field experiment. We tested whether food-deprived *V. canescens* were preferentially attracted by sites where food was combined with hosts (Hosts + Food sites) rather than by sites containing only food (Food sites). The basic procedure consisted of releasing colour-marked fed and food-deprived wasps in an environment containing the two types of sites. As in the olfactometer experiment, fed wasps were used as a control.

The wasps were released in the middle of a star-shaped grid of 97 equidistant (10 m) wooden poles, 1 m long (Desouhant et al. 2003). All poles (except the central one) contained food patches, while each alternate pole also held a host patch (Fig. 1). Each pole had four stands at a height of around 60, 70, 80 and 90 cm, respectively. Food patches consisted of petri dishes (5 cm diameter) filled with cotton wool saturated with a water-diluted honey solution. They were placed on the stands, yielding four food patches per pole. Host patches consisted of honeycomb-like-structured pieces of cardboard (2×5×5 cm) containing fifth-instar *E. kuehniella* larvae settled in their food medium (semolina). They were installed at the top of the poles. We placed host and food patches on the poles a few minutes before releasing the wasps. Green or red, nonpoisonous baker's dyes had been added to the honey. Previous tests showed that these dyes could be seen through the transparent parts of the wasp's abdomen 10–20 s after feeding and lasted for at least 2 h. Food patches on the poles containing a host patch were

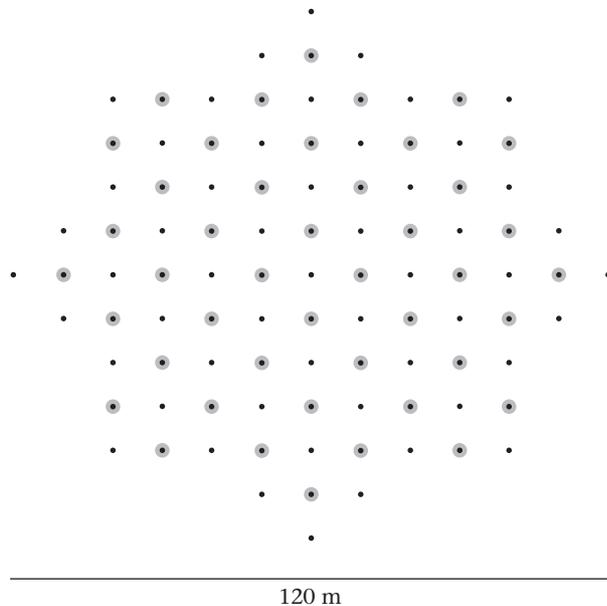


Figure 1. Position of the 97 poles composing the grid for the mark-release experiment (experiment 5) in the Botanical garden, Antibes. Black circles: poles with food only (50% water-diluted honey dyed red); grey and black circles: poles with host patch and food (50% water-diluted honey dyed green); wasps were released next to the central pole (pole without food and host); 10 m between each pole.

dyed green, while those on the poles without a host patch were dyed red. We assessed whether a recaptured wasp had fed, and on which type of patch, by checking the colour of its abdomen. Red and green dyes in the abdomen of parasitoids were readily and equally visible. Previous tests in the laboratory revealed no preference for red- or green-dyed 50% diluted honey in 38 females of *V. canescens* (E. Desouhant, unpublished data).

Study Site, Treatments and Experimental Procedures

We did the experiment in the botanical garden 'Jardin Thuret', Antibes. This heterogeneous forest-like garden contains bushes, trees and small open grass lawns. At the time of the experiment, feeding and ovipositing sites were virtually absent from the study area, except for the experimental sites (for further details see Desouhant et al. 2003).

We used wasps from the stock culture (0–2 days old), randomly assigned to two groups (fed and food deprived). Individuals of each group were given a different colour mark. For marking, the wasps were anaesthetized with CO₂ for less than 5 min and we placed a dot of acrylic paint on the thorax. After marking, the wasps were kept individually in clear plastic tubes (7.5 × 2 cm) in the same conditions as the cultures. After emergence both fed and food-deprived wasps were given an initial meal: they were allowed to feed for 2 h on a droplet of 50% water-diluted honey. Food-deprived wasps were not fed further, whereas fed wasps were fed each day, until 4–2 h before release (i.e. 48 h after the initial meal).

Two hours before release, we individually transferred the wasps to opaque plastic tubes. All the tubes were

opened gently in the field, next to the central pole, at 1115 hours. This procedure avoided interference during the wasps' departure from the release point (Desouhant et al. 2003). We released 99 food-deprived and 100 fed wasps. After release, we inspected each host and food patch every 15 min to check for wasps that had arrived. The 15-min interval between the inspection of the poles was short enough to allow us to capture all the wasps visiting the patches (Desouhant et al. 2003). We recaptured the wasps with a pooter and noted the time, place in the grid and on the pole (on food patch, on host patch or between these patches) and colouration of the abdomen. Recapturing continued until 1800 hours, the time at which the garden closed. By this time recapture rates had dropped to almost zero.

The experiment was carried out on 19 September 2001, a time of the year falling within normal periods of activity of *V. canescens* in the south of France (June to mid-October). Weather conditions were sunny with occasional clouds, mean temperature was 23.3°C and winds were light (range 0.08–0.49 m/s).

RESULTS

Experiment 1: Influence of Food Access on Survival

Figure 2 shows Kaplan–Meier survival curves of the wasps according to their feeding treatments. There was a significant effect of the feeding treatment on life span (overall comparison, log-rank test: $\chi^2_3 = 170$, $P < 0.0001$). There was no significant difference in the life span between wasps fed ad libitum (median survival time: 635 h) and wasps fed every 48 h (F48, median survival time: 654 h; log-rank test: $\chi^2_1 = 1.2$, $P = 0.26$). Similarly, no difference was detected in the life span of food-deprived females (UF) and females fed every 96 h (F96; median survival time: 80 and 88 h, respectively; log-rank test: $\chi^2_1 = 0.3$, $P = 0.61$). The median life span of the

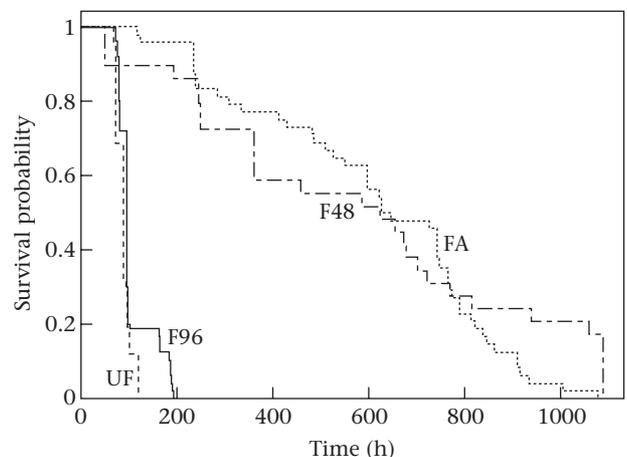


Figure 2. Survival curves of *Venturia canescens* according to four feeding treatments (food deprived: UF; fed ad libitum: FA; fed each 48 h: F48; fed each 96 h: F96). Data are represented by Kaplan–Meier curves.

wasps in the first two treatments was about six times longer than that of those in the other two. The first deaths were recorded after 48 h of food deprivation. Food-deprived females and F96 females died rapidly after this period. A single meal every 48 h was sufficient to keep the insects in good feeding conditions. For these reasons, in subsequent experiments, we took 48 h as the starvation period for the wasps that would be deprived of food.

Experiment 2: Olfactory Detection of Resources

With the exception of one 'indecisive' female in each treatment, all fed wasps ($N = 38$) moved towards the host odour source, whereas 77% of the food-deprived females ($N = 43$) moved towards the food odour source. The influence of the nutritional state of the females (fed or food deprived) and of the position of the odour source in the olfactometer (right or left arm), was tested by means of a generalized linear model (logit link, binomial distribution of errors). The dependent variable was the proportion of wasps that chose the host source, (i.e. those that reached the end of one of the olfactometer arms). Nutritional state and position of the odour sources were considered as factors. The position of the odour source did not influence the decisions made by the wasps ($\chi^2_1 = 0.67$, $P = 0.41$), but the choice was strongly dependent on nutritional state ($\chi^2_1 = 65.41$, $P < 0.0001$). The restricted number of residual degrees of freedom precludes testing the interaction between choice and position.

Experiment 3: Host Fruits as Feeding Resource

In the presence of fruits (figs or carobs) collected in the field, 92% ($N = 137$) of wasps were still alive after 2 days. Conversely, almost all the wasps (96.7%, $N = 120$) that had access only to water were dead at the end of the same period. Fruits and/or honeydew on these fruits thus provide a food source and can prolong the life span of *V. canescens*.

Experiment 4: Choice of Odour (Food, Host or Both)

When presented with the alternative between the host odours alone or a combination of host and food odours, fed females did not show a preference for either arm of the olfactometer, whereas food-deprived females moved preferentially to the combination of odours (Table 1, experiment 4a). When presented with the odour of food alone or a combination of host and food odours, females moved towards the combined odours, independently of their feeding state (Table 1, experiment 4b). A comparison of these results with those from experiment 2 shows that fed wasps always preferred host odours whether or not they were associated with food odours (Table 1, experiment 4a), whereas food-deprived wasps were able to detect food odours, even when they were mixed with the host odours (Table 1, experiment 4a) and preferred the combined

Table 1. Number of fed and food-deprived *V. canescens* females that chose either a single odour (H: host; F: food; experiment 4a and 4b, respectively) or a combined odour of hosts and food (H-F) in a Y-tube olfactometer

	Experiment 4a				Experiment 4b			
	H	H-F	I	P	F	H-F	I	P
Fed	13	11	1	0.25	1	23	1	0.001
Food deprived	3	20	2	0.001	3	22	0	0.001
Fisher's test	$P = 0.005$				$P = 0.60$			

The wasps that did not reach the end of one of the arms of the olfactometer in 10 min were considered 'indecisive' (I) and were ignored in the subsequent statistical analysis. P : Probability value of the binomial tests used to verify whether the results obtained for each row are the consequence of a random choice (equal probability) between the arms of the olfactometer. Fisher's exact tests were used to assess the independence of the choice from the feeding status of the wasps.

odours rather than the odour of food alone (Table 1, experiment 4b).

Experiment 5: Food Searching in the Field

All the recaptured wasps (45.7% of those released) were caught on sites with both host and food patches (Hosts + Food sites). A larger proportion of food-deprived than fed wasps had a green abdomen, showing that they had fed on dyed honey associated with a host patch (Table 2; 14.0 versus 4.0%, respectively; Fisher's exact probability test: $P = 0.014$). This difference is not altered by including in the statistical analysis the wasps that had fed on both green and red honey (one food deprived) and/or those that were caught while feeding and whose abdomen was not yet coloured (four food deprived and four fed). Significantly, more food-deprived than fed wasps were captured (57.0 versus 34.3%, respectively: $\chi^2_1 = 9.37$, $P = 0.002$).

DISCUSSION

Our results show that, under laboratory conditions, wasps that had access to food at least once every 48 h, lived six times longer than those that fed every 96 h or at longer

Table 2. Number of fed and food-deprived *Venturia canescens* that were recaptured on hosts and food sites, according to whether they had fed on dyed honey in the field

Colour of dye in abdomen	Fed	Food deprived
Green	4 (4.0)	14 (14.0)
Red	0	0
No dye	30 (30.3)	42 (42.0)
Red and green	0	1 (1.0)
Number of wasps released	99	100

Honey patches with green dye were associated with host patches, whereas honey patches with red dye were not. The dye was visible in the wasp's abdomen after feeding. Percentages are given in parentheses.

intervals. We also showed that *V. canescens* could detect chemical cues associated with food and hosts and move towards one or the other according to its nutritional state. Females were able to use fruits that may harbour hosts as a food source and this considerably prolonged their life span. Furthermore, they could distinguish, at a distance, between patches containing both hosts and food and those containing food only. If food deprived and given a choice, they preferred sites where both food and hosts were present. The results of the olfactometer experiment in which wasps had to choose between the odours of host plus food or food on its own were confirmed by our large-scale experiment in the botanical garden.

The food- or host-searching strategy in *V. canescens* should depend on the relative spatial distributions of food and hosts. Food and hosts can be separated in space or occur at the same location. The behaviour of *V. canescens* has evolved to cope with both situations. For instance, females that lay their eggs in anthropic conditions (granaries, mills) may leave the buildings (Beling 1932; J. Lukas, V. Stejskal & C. Bernstein, personal observation) to find food and have been reported to return to them with food droplets in their mandibles (Beling 1932). Food and hosts may also be close together or even in the same location. For example, we have observed *V. canescens* feeding on exudates or honeydew produced by homopterous insects such as *Metcalfa pruinosa* on the leaves of trees that generally harbour hosts (C. Bernstein, E. Desouhant, G. Driessen, personal observation). In conditions with no available food in the stands of trees, it would be surprising if a strong flyer such as *V. canescens* did not search for food in nearby gardens or stands of flowers. Finally, the wasps are also able to feed on dried fruits such as figs and carobs where hosts are normally found (Driessen & Bernstein 1999). The nutritional value of the various food sources will affect the potential trade-off between immediate and future fitness but if fruits harbouring hosts and other food sources are close together and have similar nutritional values, *V. canescens* does not necessarily face such a trade-off.

In contrast, when food and host locations are distant from each other, wasps do face the trade-off between immediate and future fitness rewards (Sirot & Bernstein 1996). For instance, walnut husks and almonds frequently harbour hosts (mostly one per husk; Driessen & Bernstein 1999), but they do not provide food resources for adults. When resources are distant, in order to take adaptive decisions, animals are predicted to search for hosts and food in a nonrandom manner (i.e. by detecting them at a distance) and to use this information according to their nutritional state. This is precisely what we found in *V. canescens*: wasps used volatile cues to discriminate between food and host odours and adapted their choice according to their feeding history. The preference for food rather than hosts in hungry parasitoids enables them to live longer and increase energy reserves for dispersal and future host searching. Our results are consistent with studies showing that nutritional state influences the choice between food and host searching (reviewed in Lewis et al. 1998). For instance, in *Cotesia rubecula*, nutritional state and visual preference modified the

preference for odour cues (Wäckers 1994b). In *Microplitis croceipes* (Cresson), individuals are able to learn two different volatile cues associated with food and hosts. They are attracted by the volatile associated with food when food deprived and by the chemical associated with the host when satiated (Lewis & Takasu 1990; Takasu & Lewis 1993).

Our results also showed that the food provided by fruits that may harbour hosts prolongs the life of *V. canescens*, relative to wasps that had access only to water. Other evidence of the suitability of fruits as food sources is given by previous work (e.g. Waage 1979), in which *V. canescens* adults were routinely fed on split raisins. By using the same fruits for host and food foraging, parasitoids avoid facing the trade-off between the two activities. Indeed, this strategy would cancel the travel time between the two resources and the associated energy costs. In other species, such as food-deprived *Phanerotoma franklini* in field conditions, travel time between food sources can reach 25% of the total foraging time (Sisteron & Averill 2002). An example of the adaptive competitive advantage of foraging for host and food in the same site is given by Eijs et al. (1998): three of the four species of drosophilid parasitoids of the genera *Asobara* and *Leptopilina* they studied feed on their natural breeding substrates. These species gain energy from these substrates and economize on food searching.

Venturia canescens would profit from the association between host and food sites only if females were able to detect the association of resources at a distance and if their preference depended on their nutritional state. This is what our results show. Although well-fed females moved towards the odour of hosts independently of whether it was associated with the odour of food, food-deprived wasps were able to detect the combined odours of the two resources and preferred this association to the odour of food on its own. In general terms, the combination of different cues, when they are both valuable at the same time, may enhance the overall foraging efficiency of females. For instance, the use of different sources of information enhances host location (Wäckers & Lewis 1994; Fisher et al. 2001; Meiners et al. 2003), host acceptance (Battaglia et al. 2000) and mate location (McAuslane et al. 1990).

Our conclusions from the laboratory experiments held under field conditions. When fed and food-deprived wasps had to choose between food sources presented alone and food sources combined with hosts, all wasps were caught in traps combining the two resources. Not surprisingly, the wasps released after a period of food deprivation were the ones that fed most often during the experiment.

When taking decisions, parasitoids are known to acquire and integrate a variety of cues, revealing the characteristics of the environment and/or their internal state (Godfray 1994). *Venturia canescens* females are able to use as food sources the same fruits that may harbour hosts and to detect the cues that might direct them to these fruits. The ability to use food sources either on their own or associated with hosts is a clear form of adaptive plasticity. Our study also highlights the parasitoids'

capacity to integrate and respond to different external (e.g. resource odours) and internal (e.g. physiological state) information in their food-searching process. These results open new experimental and theoretical perspectives to unravel how insects integrate the different kinds of information that they acquire and the evolutionary and population dynamics consequences of differences in food-searching strategies.

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