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ORIGINAL PAPER

Small but smart: the interaction between environmental cues and internal state modulates host-patch exploitation in a parasitic wasp

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Abstract The reproductive success of insect parasitoids depends on two activities, searching for hosts to obtain immediate fitness rewards (offspring) and searching for food to extend life span and enhance future reproductive opportunities. Models suggest that to deal with this trade-off and to cope with the variability of the resources they depend on, parasitoids should simultaneously integrate information originating from three distinct sources: host and food availabilities in the environment (environmental information) and the metabolic reserves of the parasitoid (internal information). We tested whether, in the parasitic wasp *Venturia canescens*, these three types of information are perceived simultaneously and interact during host-patch exploitation. Experiments were performed with strains originating from two different geographical locations and with individuals of the two reproductive modes, arrhenotoky and thelytoky. We hypothesised that there would be differences between modes of reproduction as they thrive in different ecological conditions. Our results show that metabolic state, food availability and the number of ovipositions performed simultaneously modulate patch residence time in *V. canescens* of both populations and reproductive modes. Unfed wasps left their host patch earlier than fed ones. The tendency to leave the patch increased with an increasing probability of finding food. Our study confirms that globally, each oviposition increases the patch-leaving tendency (decremental mechanism). This effect was modulated by both the metabolic reserves and food availability, and the relationship depended on the geographic origin of populations. Individuals of one of the populations switched from a decremental to an incremental patch-leaving mechanism depending on the presence or absence of food in the vicinity. Differences between reproductive modes in the responses to environmental cues can be explained by the different ecological conditions they live in.

Keywords Cognitive ecology · Patch residence time · Food and host searching · Parasitoids · *Venturia canescens*

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Introduction

The availability of the resources that animals depend upon for growth, reproduction and maintenance is highly variable, both in time and space. To cope with such variability, animals need to rely on the information they gather both from the environment and their internal condition (Dall et al. 2005).

The reproductive success of insect parasitoids crucially depends on two kinds of resources: hosts, to obtain immediate fitness rewards (offspring), and metabolic resources, to extend life span and obtain further reproduction opportunities (Tenhumberg et al. 2006; Sirot and Bernstein 1996). The metabolic resources of an adult parasitoid originate from nutrient reserves accumulated during larval development and from the food they obtain either from hosts themselves, in host-feeding species (Jervis and Kidd 1986) or from vegetable sources (nectar, honeydew or sap, containing mainly carbohydrates) in other species (Jervis et al. 1993; Wäckers and Steppuhn 2003). Some parasitoids feed on both types of resources (e.g. Heimpel et al. 1997). When searching to oviposit, parasitoids are known to use both chemical and physical cues for both patch and host selection and exploitation (Vet et al. 2002; van Alphen et al. 2003). For instance, when dispersing, parasitoids use visual cues that guide them to locations that are likely to contain host patches (Desouhant et al. 2003) and subsequently use chemical cues that inform the animal about patch quality (Wäckers 1994). Once the individual is on the host patch, mechanisms incorporating different sources of information (successful ovipositions, metabolic reserves, perception of hosts chemicals, presence of conspecifics, weather conditions, etc.; Heimpel et al. 1998; Ueno 1999; Goubault et al. 2005; Amat et al. 2006; Wajnberg 2006) modulate the time devoted to host exploitation (patch residence time). In spite of their importance, however, much less is known about the cues that guide parasitoids to food sources and on the information used in their exploitation. Nevertheless, parasitoids are known to use chemical cues that guide them to food sources (Desouhant et al. 2005), and host-feeding parasitoids are known to modulate the use of hosts as food sources or for reproduction, depending on their metabolic condition (Jervis and Kidd 1996).

The ability of parasitoid females to find food, for survival and hosts to realise their potential reproductive output—two mutually exclusive activities—might depend on limited resources (time for instance). Thus, a trade-off should arise between feeding and reproduction, which affects both current and future reproductive success. Dealing with such a trade-off requires that parasitoid females are able to: (1) acquire and integrate information on the availability of both food and hosts on which survival and reproduction depend, and (2) modulate their searching for food or hosts according to their nutritional state (Desouhant et al. 2005).

Some parasitoids find food and hosts in the same location, whereas for others, the two resources are distant and independently distributed (Jervis and Kidd 1996). In this last case, travelling between hosts and food implies costs and risks that amplify the trade-off between the two mutually exclusive activities: ovipositing or feeding. The decision to commute between the two types of resources is likely to depend on both external (environmental) and internal (individual-specific) information that the parasitoid perceives.

Theoretical studies on the role of acquired information in the resolution of the trade-off between reproduction and feeding mainly considered host-feeding parasitoids (Chan and Godfray 1993; Briggs et al. 1995; Heimpel and Collier 1996). For non-host-feeding parasitoids, two theoretical studies, based on dynamic programming models, analysed situations in which resources are found in separate locations: Tenhumberg et al. (2006) and Sirot and Bernstein (1996). Both models consider the same general problem but make specific assumptions inspired by different biological models. The first one was parameterised for *Cotesia rubecula* whereas the latter was inspired by *Venturia canescens*, the parasitoid studied here. These two state-dependent models predict how parasitoids should allocate their time budget between host and food searching. The results of both models suggest that optimal decisions depend on three kinds of information: host and food availabilities in the environment and the metabolic reserves of the parasitoid. Both studies predict that, when food is available, the time invested in host exploitation should increase with increasing metabolic reserves and decrease with an increasing probability of finding food. Thus, these models require that if the forager is non-omniscient, it should perceive and integrate information on these three key resources simultaneously. Experimental work in this field is scant and both the assumptions and predictions of these models remain to be tested experimentally.

The aim of this work was to explore whether information on host availability in the current patch, metabolic reserves and food availability in the environment are actually integrated simultaneously by foraging parasitoid females to influence their behavioural decisions. More specifically, we aimed at determining whether the level of metabolic reserves (internal information) and the presence of food (environmental information) interact whilst parasitoid females *V. canescens* exploit a host patch. To achieve this, we compared the influence of food availability and nutritional status on the time invested exploiting a host patch. *V. canescens* represents a unique opportunity to compare the effect of selection pressures on the host and food exploitation strategies used by two very similar organisms that differ in the ecological conditions of their preferred environment (Schneider 2003; Amat 2004; Amat et al. 2006). Two modes of reproduction are known in this species (Beukeboom et al. 1999; Schneider et al. 2002): obligatory thelytoky (populations consist exclusively of females reproducing parthenogenetically) or obligatory arrhenotoky (haplodiploid reproduction common to most Hymenoptera). Populations exhibiting both modes of reproduction coexist under natural conditions but are separate entities, and gene flows between both are suggested to be rare events (Haccou and Schneider 2004). Under natural conditions, where arrhenotokous reproduction prevails (Schneider et al. 2002), *V. canescens* feeds frequently (Casas et al. 2003), and food is abundant as this species potentially exploits fruit and leaf exudates and nectar (Desouhant et al. 2005). Conversely, in indoor conditions such as mills or granaries, where only thelytokous populations thrive, food is scarce or totally absent. Consequently, thelytokous and arrhenotokous populations living in different environments are expected to evolve different strategies of food and host exploitation (Amat et al. 2006; Pelosse et al. 2007; Thiel et al. 2006). Arrhenotokous parasitoids would be expected to evolve a strategy in which they repeatedly move between both kinds of resources and exploit them probably in relatively short visits. Thelytokous wasps that need to leave their habitat to search for food face a risky journey and would be expected to invest more time in host exploitation. Hence, to further analyse the influence of the information on food availability on host-patch exploitation, we compare the behaviour of animals of both reproductive modes in conditions akin to those found in the two types of habitat.

Materials and methods

Cultures and biological details

V. canescens Gravenhorst (Hymenoptera: Ichneumonidae) is a solitary (a single adult parasitoid emerges from a parasitised host), koinobiont (host larval development continues after parasitism), endoparasitoid of the caterpillars of different species of pyralid moths (Salt 1976), many of which are pests in granaries, mills and orchards. Wasps used in this study were reared on larvae of the flour moth *Ephestia kuehniella* Zeller (Lepidoptera: Pyralidae) maintained in semolina (food medium), in a constant environment of 25(±1)°C and 75(±5)% relative humidity. Light/Dark regime was 12 hL:12 hD). The hosts used originated from a mass rearing facility (Biotop) located in Valbonne, France. The host larvae are attacked when in their second to fifth instar. Whilst on a patch, *V. canescens* searches for hosts by probing the host-contaminated substrate with its ovipositor (Waage 1978, 1979). Ovipositions can be recognised by a characteristic movement of the abdomen, ‘cocking’, whereby the female places a new egg at the tip of her ovipositor in preparation for the next oviposition (Rogers 1972). Experimental results (Amat et al. 2003) show that, at least in 82% of the cases, a cocking movement is associated with an egg being deposited inside a host.

V. canescens females are known to integrate and use both information on their internal state and (external) from their environment (Driessen et al. 1995; Bernstein and Driessen 1996; Driessen and Bernstein 1999; Amat et al. 2006). Volatile cues are known to be used by *V. canescens* to locate food sources and food searching to depend on the nutritional state of the animal (Desouhant et al. 2005). At least under laboratory conditions, access to food results in a four- to sixfold increase in life span (Sirot 1996; Desouhant et al. 2005). *V. canescens* is also known to use environmental information, e.g. visual cues, to select habitats that are likely to contain host patches (Desouhant et al. 2003). Once in a potentially suitable habitat, females are known to use odour of host mandibular gland secretions (kairomones) deposited by host larvae in their food medium to locate host patches (Thorpe and Jones 1937; Waage 1978). Besides guiding parasitoids to hosts at short distances, these substances allow the parasitoids to estimate host density in the patch and influence the decision of when a parasitoid should leave a patch (Waage 1979; Driessen et al. 1995). In spite of theoretical considerations, nothing is known about the combined influence of environmental food availability, host-patch-related cues and metabolic reserves on host-patch exploitation behaviour.

Arrhenotokous *V. canescens* are often reluctant to mate under laboratory conditions. Thus, to ensure that all arrhenotokous wasps have the same mating status, we used unmated females. Mated and unmated females have the same oviposition rate (Metzger, unpublished data). To ensure that our results can be generalised to other *V. canescens* populations, we used strains of both reproductive modes originated from wasps collected in 2002 in the field in two geographically different locations in South-East France: Antibes (43.58°N; 7.12°E) and Valence (44.93°N; 4.90°E). Experiments were performed in a controlled room (temperature 25±1°C, 75±5% RH) between 10.00 and 16.00 h.

Experimental design

The aim of the experiment was to assess whether information on food availability in the environment (external information), information on the host patch (sampling through ovipositions) and on metabolic reserves (internal information) influence host-patch exploitation by *V. canescens*. To do so, patch residence time (henceforth called PRT) and the number of eggs laid by females that differ in nutritional status (fed vs unfed) were recorded in three environments that differ in food availability (high, medium or none, see below for details).

During trials, both host and food patches were placed in a Plexiglas box (500×165×95 mm) with two removable walls that could be placed at different distances from each other. The experiments were performed in the central section of the box to change the concentration of chemical stimuli. We mimicked different conditions of food availability in the environment by changing the distance between food and host. We therefore changed the positions of the removable walls; hence, trials were conducted in different volumes in the central section of the box. In the environment with high food availability (henceforth called “High”), the food patch was 40 mm distant from the host patch, and the distance between removable walls was 165 mm. The two patches were placed in opposite corners on a diagonal of the box. In the environment with medium food availability (“Medium”), the distance between both patches was 200 mm and 500 mm between walls. In conditions of zero food availability (“Null”), no food was present in the box and the distance between walls was 500 mm. To create a symmetrical environment for the females to forage for hosts, the host patch was placed at the centre of the box, and was flanked by two externally similar patches: a food patch and an empty one for the high and medium conditions and two empty patches in case of no food availability. The position of the food patches (right and left side of the host patch) alternated after each trial. After each trial, the Plexiglas box was carefully washed and the patches were replaced.

Food patches consisted of 5-cm-diameter Petri dishes filled to the rim with 1/2 diluted honey. The Petri dishes were covered with a band of white paper to prevent the parasitoid from using visual cues to distinguish between the food and the empty patches. Host patches were standardised and consisted of 5-cm-diameter Petri dishes, filled up to 2 mm to the rim with Paris plaster, the rest filled with a layer of semolina containing eight third-stage unparasitised host larvae (21±2 days old). Host larvae were kept in the patch for 10 days before trials. This ensured that the substrate was marked by the host’s kairomones. Host patches were covered with a fine cloth to prevent host larvae from escaping (see Amat et al. 2006). For the trials, the host patch was placed at the centre of a larger Petri dish (9-cm diameter) filled with clean semolina. The small dish was embedded such that its surface was flush with the surrounding clean semolina. The small patch served as the host patch. Trials were initiated by introducing a single female into the host patch. Observations started just after we closed the lid of the box. During a host-patch visit, *V. canescens* regularly makes short excursions outside the patch. PRT was defined as the total time spent on the host patch between entering the patch for the first time and the last time the patch edge was crossed before the insect left the large dish surrounding the patch. The duration and/or timing of different kinds of behaviour (entering and leaving the host patch, cocking, and leaving the large outer dish) of each individual were recorded with a microcomputer. Before starting the experiments, we had set the maximum observation time per wasp to 30 min, but in fact, PRT of all wasps was shorter than this period. There were thus no censored data.

We used 48-hour-old wasps of the two reproductive modes. Newly emerged females were kept individually in plastic tubes (7.5×3 cm) in a room free of any host or food odours (temperature 25±1°C, 75±5% RH, L/D=16:8). At emergence, females were randomly assigned to two feeding treatments: fed and unfed. Fed individuals had permanent access to a droplet of one-half diluted honey, and unfed females had no access to food since their emergence. Forty-eight hours of food deprivation ensured that fed and unfed individuals differed in metabolic levels (Desouhant et al. 2005).

On each day of the experiment, 12 females, each belonging to one of the 12 combinations of a factorial design (3 levels of food availability, 2 feeding status, 2 reproductive modes), were tested. The sequence of the combination of different factors in a given day was randomly drawn. Twenty-five replicates for each combination were performed, leading to a total of 300 females observed. Two series of trials were conducted, from January the 5th to February the 6th 2004 for the Antibes population and from March the 1st to April the 2nd 2004 for Valence population. Experiments with individuals of the two populations were conducted at different periods to limit the number of interactions in the statistical analyses (e.g. interaction *population* × *food availability*).

Data analysis

The influence of food availability (High, Medium or Null), feeding status (fed vs unfed), reproductive mode (sexual vs asexual) and the number of ovipositions (recorded as the number of cockings) on PRT of the foraging female was analysed using Cox’s proportional hazards model (Cox 1972). The number of ovipositions is known to influence patch-leaving decisions in *V. canescens*; each cocking increases the patch-leaving tendency (Driessen and Bernstein 1999; van Alphen et al. 2003). The parasitoid is said to use a decremental mechanism. Mechanisms are named ‘incremental’ or ‘decremental’ in terms of their effect on PRT. The simultaneous use of three sources of information by the wasps could have been tested statistically using three-way interactions. However, the biological meaning of three-way or higher-order interactions is most often considered to be difficult to interpret (Sokal and Rohlf 1981). As a consequence, we decided to restrict our analysis to the double interactions between food availability, reproductive mode, feeding status and the number of ovipositions (that was entered in the model as a time-dependent covariate) only. Two different analyses were performed, one for each population.

A Cox regression assumes that the leaving tendency (or hazard rate = $h[t]$), the probability per unit of time that a wasp would leave the patch given that it is still on it, is the product of a baseline leaving tendency ($h_0[t]$) and a factor representing the joint effect of the p covariates (explanatory variables) $\left(\exp\left\{\sum_{i=1}^{p}\beta_i z_i\right\}\right)$. t represents the time elapsed since the wasps entered the patch. The β values (the regression coefficients) express the contribution of each explanatory variable (z_i) to the overall leaving tendency. These coefficients are interpreted through the exponential term, the hazard ratio. A hazard ratio higher than unity indicates that the corresponding covariate has an increasing influence on the tendency of a wasp to leave, i.e. it reduces its PRT. Conversely, a hazard ratio lower than one corresponds to an increase in PRT (Wajnberg 2006).

Cases corresponding to a medium food availability, asexual model of reproduction and fed animal were arbitrarily assumed to be the reference level corresponding to the baseline hazard with parameters set to zero. Regression coefficients were estimated by maximisation of the partial likelihood (for details, see Kalbfleisch and Prentice 2002). The significance of the covariates was tested by an iterative standard likelihood ratio test (Wajnberg et al. 1999). Finally, the fit of the model was assessed by plotting deviance residuals (Wajnberg et al. 1999).

Results

The influence of food availability and nutritional state on PRT

The amount of time wasps of both populations spent on the host patch was significantly influenced by both food availability and nutritional condition (feeding status). For both populations, unfed individuals leave the patch faster than fed ones, and the tendency to leave increases with food availability in the vicinity. For the individuals from the Valence population, a significant interaction between the two factors reveals that this tendency is stronger for unfed individuals than for those that had permanent access to food (χ^2=18.5, 2 *df*, P<0.0001; Fig. 1a). For females from the Antibes population, external cues and internal state have additive effects (food availability: χ^2=10.0, 2 *df*, P=0.007, feeding status: χ^2=17.1, 1 *df*, P<0.0001, Fig. 1b; interaction: NS).

The influence of the interactions between nutritional state, food availability and the number of ovipositions on PRT

In the Valence population, the interaction between food availability and the number of ovipositions significantly affects PRT (χ^2=16.03, 2 *df*, P<0.0001). The log-hazard ratio (±SE) for a cocking for null, medium and high food availabilities are, respectively, −0.68 (±0.23), 0.20 (±0.08) and 0.37 (±0.21). These results indicate that the effect of the number of cockings on PRT changes with food availability; in the absence of food, the effect is incremental but decremental when food is available in the vicinity. In the individuals from Antibes, the influence of the number of cockings on the patch-leaving tendency is independent of food availability, with cockings having an overall decremental effect on PRT (log [hazard ratio]=0.321±0.054 1 *df*, χ^2=34.15, P<0.0001; interaction between number of cockings and food availability: χ^2=2.706, 2 *df*, P=0.258).

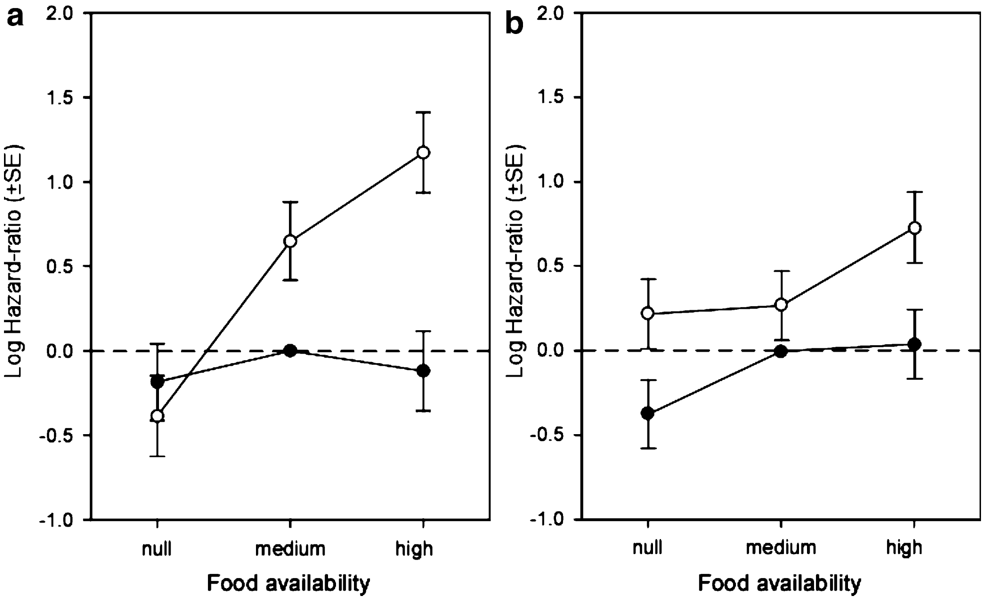
The female's feeding status also appears to modify the overall decremental effect of each cocking. For the Antibes population, this effect is stronger for fed than for unfed individuals (interaction between feeding status and cocking: χ^2=44.48, 2 *df*, P<0.0001, Fig. 2b). No significant effect was observed for the Valence population in which the effect of the number of cockings in itself remains highly decremental (log [hazard ratio] = 0.301±0.060, χ^2=24.26, 1 *df*, P<0.0001, Fig. 2a), independent of the feeding status.

The influence of the reproductive mode on PRT

The increasing tendency to leave the patch as food availability increases (see above) is independent of the reproductive mode of the females (interaction reproductive mode × food availability; for the Valence population: χ^2= 1.38, 1 *df*, P=0.239, for the Antibes population: χ^2=4.32, 2 *df*, P=0.115). However, the combined effect of feeding status and reproductive mode differs between the two populations. For the Valence population, a significant interaction between the two factors (χ^2=7.5, 2 *df*, P= 0.024) suggests that asexual wasps are more sensitive to their nutritional status; unfed individuals leave the patch earlier than fed ones whilst the patch leaving tendency of sexual individuals is not affected by feeding status (Fig. 3a). For the Antibes population, reproductive mode and feeding status have simple additive effects: both sexual reproduction and low metabolic reserves increase the tendency to leave the patch (χ^2=12.05, 1 *df*, P<0.001 and χ^2=17.13, 1 *df*, P<0.0001, respectively, interaction: χ^2= 1.01, 1 *df*, P=0.293; Fig. 3b).

The effect of the number of cockings on PRT (see above) is differently affected by the mode of reproduction, depending on the origin of the animals. For the wasps from Antibes, the decremental effect of each cocking is stronger in asexual wasps than in sexual ones (interaction between reproductive mode and cockings: χ^2=7.05, 1 *df*, P=0.008; Fig. 4b). In the wasps from Valence, the effect of the number of cockings is independent of the reproductive mode (interaction between reproductive mode and the number of cockings: χ^2=1.50, 1 *df*, P=0.220, Fig. 4a).

Fig. 1 Host-patch-leaving tendency, expressed by logarithm of the hazard ratio (±SE), as a function of food availability in the environment (High, Medium or Null) for fed (*close circles*) and unfed (*open circles*) *V. canescens* females originated from Valence (**a**) or Antibes (**b**) populations. A positive log-hazard ratio indicates an increasing patch-leaving tendency. Negative values indicate a decreasing tendency



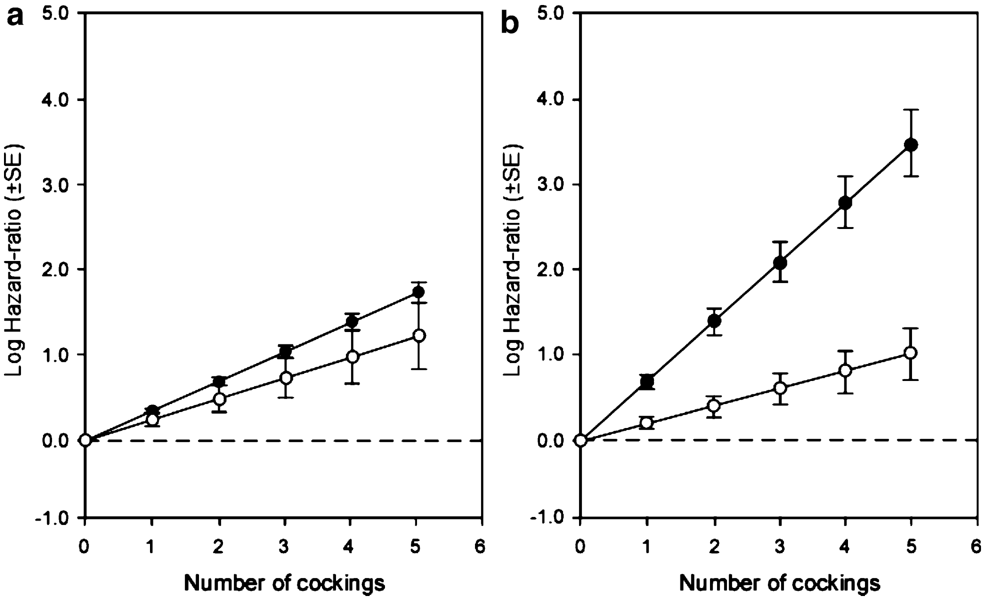
Discussion

Host and food searching: trade-off and information acquired

Models exploring how parasitoids should deal with the trade-off between metabolic resource acquisition and host-patch exploitation make the unrealistic assumption of omniscient parasitoids (Sirot and Bernstein 1996; Tenhumberg et al. 2006). Most empirical studies of patch-leaving decisions have tested the use of relatively simple information emanating mainly from hosts (chemicals deposited by hosts, host encounters, rejections, etc.; Vet et al. 2002; van Alphen et al. 2003; Wajnberg 2006). Here, we analyse the more complex situation in which, whilst deciding when to leave a host patch, the parasitoid should appraise the changes in host availability, its internal state and the probability of finding food. Our results show that the parasitoid *V. canescens* modulates its host patch-leaving decisions according to these three sources of information. This cognitive ability (perception, integration and use of information) exists in both populations studied and in the two reproductive modes observed in this species. These results also imply that *V. canescens* uses information related to one term (metabolic reserves) of the trade-off between current and future reproduction (Sirot and Bernstein 1996; Tenhumberg et al. 2006) and to make decisions regarding behaviours related to the other term: host exploitation.

The intensity of the trade-off between host and food search depends partially on the ability of the parasitoids to

Fig. 2 Host-patch-leaving tendency, expressed by the logarithm of the hazard ratio (±SE), for different numbers of cockings (i.e. ovipositions) for fed (*close circles*) and unfed (*open circles*) *V. canescens* females originated from Valence (**a**) or Antibes (**b**) populations. A positive log-hazard ratio indicates an increasing patch-leaving tendency. Negative values indicate a decreasing tendency



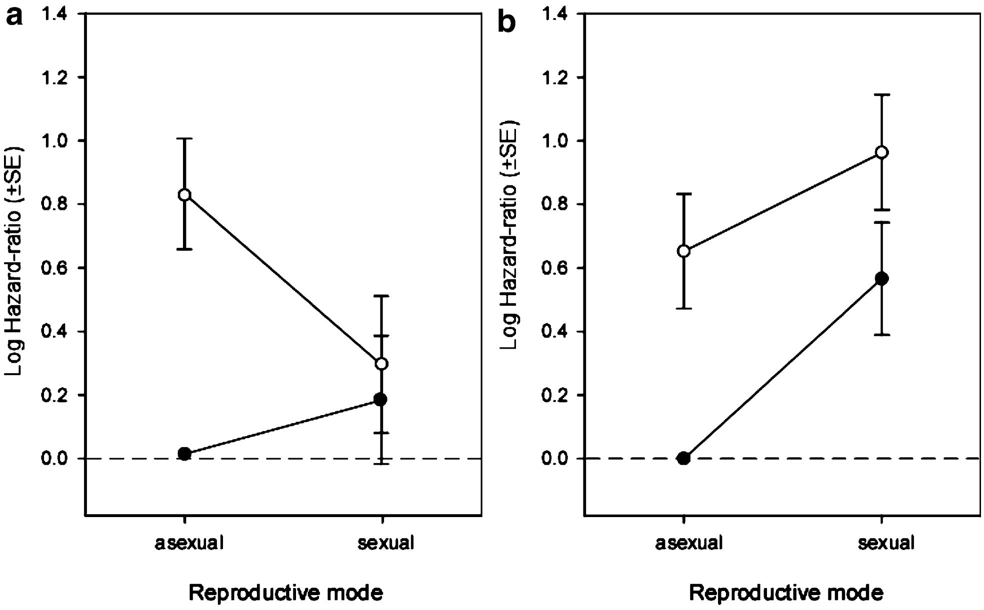


Fig. 3 Host-patch-leaving tendency expressed by the logarithm of the hazard ratio (±SE) according to reproductive mode (asexual and sexual) for fed (*close circles*) and unfed (*open circles*) *V. canescens* females originated from Valence (**a**) or Antibes (**b**) populations. A positive log-hazard ratio indicates an increasing patch-leaving tendency. Negative values indicate a decreasing tendency

detect both resources (Tenhumberg et al. 2006). The fact that the wasps are able to detect cues associated with food whilst foraging for hosts should increase the efficiency of their searching activities. In the presence of food, unfed individuals leave host patches sooner than individuals that are not starved, and this tendency still increases with food availability (Fig. 1). In our design, treatments with High and Medium food availability differ both in the distance between host and food patches and in the volume of the box in which the two patches were placed (see "Experimental design"). Presumably, both factors alter the concentration of the volatile chemicals of food perceived by the wasps. It is difficult to identify the contribution of changes in distance between patches and changes in the structure of the environment on the recorded differences in PRT. However, when the effect of Null and Medium availabilities is compared, the volume is identical. Therefore, at least in this case, the changes in host-patch exploitation can be ascribed to the distance between patches.

Access to food has a crucial influence on parasitoid survival and hence on future opportunities of finding new suitable host patches (Siekmann et al. 2001). In our experiment, after leaving the host patch, the wasps moved to the food patch within 5 min (PL, personal observations). In contrast, exploiting a host patch is energetically costly (Desouhant and Bernstein, unpublished data) thus contributing to resource exhaustion and low survival rates. Casas et al. (2003) showed that, in nature, *V. canescens* feeds frequently on sugar sources suggesting that the nutritional strategy used by this wasp aims at maintaining a target level of metabolic reserves. Our results contribute to an understanding of how external cues interact with state dependency in influencing host exploitation decisions by the parasitoid.

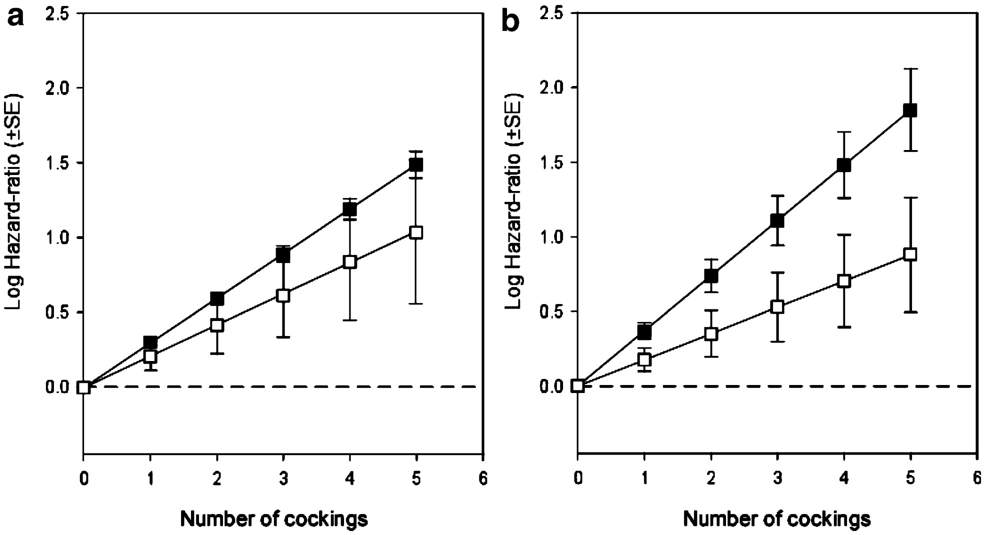


Fig. 4 Host-patch-leaving tendency expressed by the logarithm of the hazard ratio (±SE) according to the number of cockings (i.e. ovipositions) for asexual (*close squares*) and sexual (*open squares*) *V. canescens* females originated from Valence (**a**) or Antibes (**b**) populations. A positive log-hazard ratio indicates an increasing patch-leaving tendency. Negative values indicate a decreasing tendency

Although there is abundant evidence (see Dukas 1998; Shettleworth 1998; Godfray 1994; van Alphen et al. 2003; Wajnberg 2006 for parasitoids) that, in general, foragers are able to estimate the value of resources (prey and hosts availability, food quantity food, etc.), the insects' ability to modulate the exploitation of one resource (e.g. hosts) in terms of the availability of another resource (e.g. food) has rarely been investigated. Exceptions are the experimental studies performed in the context of biological control in field conditions that have shown that parasitism level is positively correlated with the presence of food sources (Leius 1967; Lavandero et al. 2005).

Host-patch devaluation and metabolic resources

Our results show that, as previously reported for *V. canescens* (Driessen and Bernstein 1999; Driessen et al. 1995), each cocking increases the patch-leaving tendency. The parasitoid is said to use a decremental mechanism. Our results also show that this effect is modulated by both the metabolic reserves and food availability, and somewhat surprisingly, our results depend on the geographic origin of strains (Valence or Antibes) used.

For the same feeding status, the increase in the tendency to leave the patch with increasing number of cockings is either independent of (Antibes) or positively correlated with food availability (Valence). In the absence of food, PRT for individuals from the Valence population increases with the number of cockings (i.e. incremental mechanism). This observation suggests that *V. canescens* might switch from a decremental to an incremental patch-leaving mechanism. Incremental and decremental mechanisms have been described as being optimal in different environmental conditions (Iwasa et al. 1981; Driessen and Bernstein 1999; van Alphen et al. 2003). The capacity to switch from one mechanism to another further adds to the plasticity of behavioural responses of parasitoids. Further studies are needed to ensure that apparent switching behaviours correspond to actual biological processes and do not result from a limitation of the statistical method.

We are aware of only a single example of this kind of behavioural flexibility in patch-leaving mechanisms. The parasitoid *Aphidius rhopalosiphi* decreases its tendency to leave host patches after each oviposition. However, after having laid several eggs, females gradually switch from such incremental mechanism to a decremental one. This switch between mechanisms is interpreted as a means to decrease the risk of superparasitism once the animal has attacked several hosts (Outreman et al. 2005).

Globally, the decremental effect of ovipositions is either independent of the feeding status (Valence population) or higher for fed individuals (Antibes population, Fig. 2). The latter observation is not in contradiction with the fact that unfed wasps have a higher tendency to leave the host patch. It indicates that each oviposition devalues the host patch more in fed that in unfed wasps. This can be explained by the higher metabolic reserves that fed individuals have, which allows them to travel more between patches compared with unfed individuals. Fed wasps can therefore leave the patch earlier.

Modes of reproduction and preferred environments

Our results show differences between reproductive modes in the responses of wasps to environmental cues and suggest that such potential differences can be ascribed to differences in preferred habitat.

The increasing tendency to leave the patch as food availability increased is independent of the reproductive mode. Conversely, the combined effect of reproductive mode and feeding status seems to differ between the two populations (Fig. 3). For the Antibes population, both factors have an additive effect, the tendency to leave being higher for unfed individuals and sexual populations. This latter observation confirms the hypothesis that living in an environment where food availability is high and host-patches are poor, sexual individuals should leave host patches more frequently than if they inhabited an environment where food availability is low and host abundance high as experienced by asexual females. This is at odds with the observation that, for the Valence population, unfed asexual individuals have a higher tendency to leave than their sexual counterparts. Finally, for the same feeding status and food availability, individuals of the two populations differ in how the tendency to leave depends on the number of cockings. This tendency is also affected by the mode of reproduction (Fig. 4). For the individuals from the Antibes population, the decremental effect associated to each cocking is stronger in asexual than in sexual wasps. Moreover, there is the same (non-significant) tendency for the Valence population. The results for Antibes suggest that, under the same conditions of feeding status and food availability, the attractiveness of their current patch is reduced faster in asexual individuals as it becomes poorer. This might be explained by the fact that food sources are most rare in indoor conditions where asexual *V. canescens* preferentially thrives. In the presence of food sources, the alternative of finding food becomes more valuable for these individuals if their current patch becomes depleted. We cannot ruled out that, in our experiment, sexual wasps that were unmated, i.e. deprived of spermatozoids, left the host patch earlier in search of males than mated females would have.

Differences between populations

Our results show some differences between populations originating from different localities with respect to the effect of feeding status or mode of reproduction on the decremental effect associated to each cocking. Other results, such as the significant interaction between the mode of reproduction and feeding status on patch-leaving tendency, are more radical. Although members of the same species can respond differently to the same environmental cues depending on their physiological state, previous experience or genetic differences (Wajnberg et al. 1999, 2004; van Alphen et al. 2003), our present knowledge of the environments in which these populations thrive does not yet allow for the interpretation of the observed differences in terms of genetic differences.

Our results show the capacity of parasitoids to acquire and integrate complex information emanating from different sources into their decision to leave a patch. The results also show a phenotypic plasticity rarely described in host-patch exploitation by parasitoids (but see studies on learning Papaj and Lewis 1993). The ability to combine complex information raises the question of how these animals integrate information and how a hierarchy is established between information of different reliability. Finally, the results suggest that the patchiness of the environment as it is perceived by the animals (e.g. distance to food), an aspect that can have a large influence on decision-making, results from both the characteristics of the environment and the cognitive abilities of the animal.

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