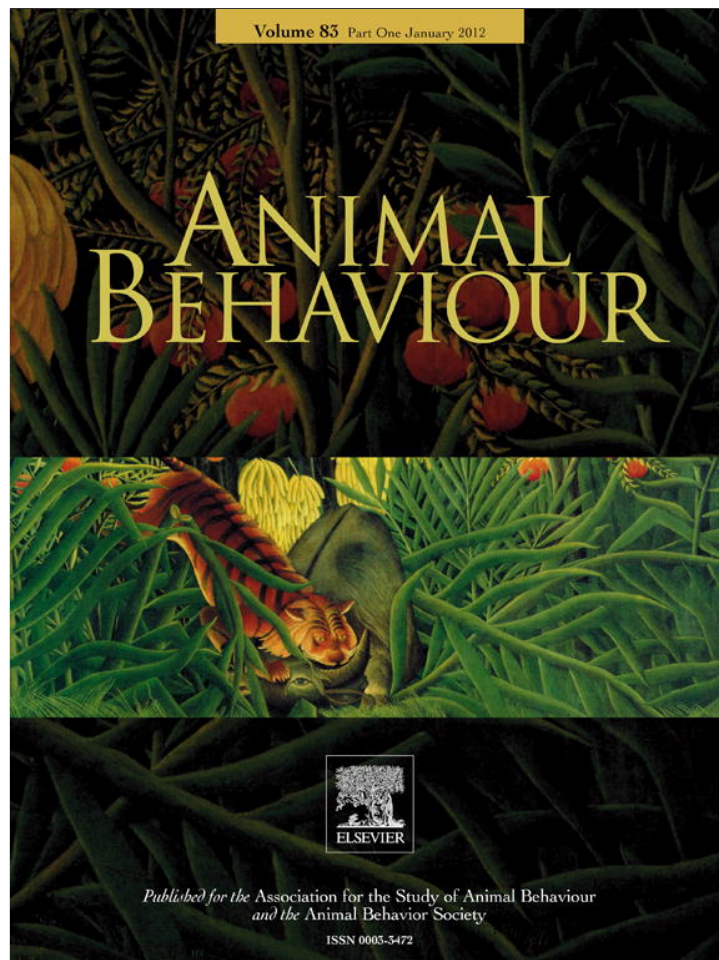


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Facing multiple information sources while foraging on successive patches: how does a parasitoid deal with experience?

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Animals adjust their behaviour in response to changing environmental conditions. This form of plasticity can result from animals' experience and their capacity to update information about their habitat. In the context of optimal foraging in patchy environments, animals may estimate profitability of patches from different cues to update their estimate of the profitability of the whole habitat. Updating may be achieved by weighting pieces of information obtained at different times. We studied how female parasitoids, *Venturia canescens*, weight different cues about each host patch profitability they successively encounter to adjust their foraging decisions accordingly. Our results show that parasitoids clearly perceived the profitability of the patches and that their foraging decisions were equally influenced by older and more recent foraging experience. We designed a second experiment to unravel, from three interdependent cues of patch profitability, which information source was mainly used to update the estimate of environmental profitability. The number of eggs laid in previously visited host patches seems to be an integrative cue of environmental profitability. We discuss the adaptive value of the weighting of successive pieces of information and the use of the different information sources in regard to the ecological context in which the wasps thrive.

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To adjust their behaviour to environmental conditions, animals should gather and use information to reduce uncertainty caused by environmental variations (Dall et al. 2005). Processing current information, derived from the individual's immediate perception of its environment, and past information, stemming from individual evolutionary history (innate behavioural response) and/or experience (McNamara et al. 2006; Mery & Burns 2010), are intimately related, yet not fully overlapping processes. Here we focused on two questions raised by the use of past information. (1) How does an individual manage older pieces of information together with more recent ones? (2) Within a set of same-aged information, which information is used?

The modification of behaviour produced by individual experience (a definition of learning: Papaj & Prokopy 1989; Dukas 1998) can be a response to a weighted average of older and more recent information. From an adaptive perspective, giving more weight to more recent information, older pieces of information eventually being forgotten, is expected when organisms face spatial and/or

temporal heterogeneity over their lifetime. Tadpoles exposed to temporal changes in predation pressure exhibit such a behavioural plasticity: their activity levels increase when predators are removed from their environments (van Buskirk 2002). Giving more weight to older information (e.g. imprinting, Lorenz 1965/1970) should be selected for when heterogeneity occurs between generations (Stephens 1991; Moran 1992). The relative weighting of more recent versus older information depends also on the balance between the costs of acquiring new information and managing past information (Dukas 1998).

In addition to the issue of 'how' to weight past information, animals have to choose 'which' source of past information to use. In natural conditions, animals face various information sources that can be partially redundant. For instance, in the context of mate choice, male condition can be correlated with several physical features (Birkhead et al. 1998). Using redundant information can enhance parameter estimation or make target detection easier. Female *Scaphiopus couchii* toads choose their mates according to their call and brightness, and both parameters are correlated with male size and condition (Pfennig & Tinsley 2002; Vásquez & Pfennig 2007). But, as a consequence of redundancy, some cues of weaker detectability or reliability should also be ignored (Stephens 1989; Vet et al. 1991; Gould 1993). Costs of information processing, in terms of time and energy, may also limit repeatedly gathering the same information. Furthermore, at least in *Drosophila*, information

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storage incurs a cost in terms of fecundity and longevity because of the protein synthesis required for memory formation (Mery & Kawecki 2005). Consequently, not all current pieces of information gathered should be remembered: only the information that improves an animal's fitness should be stored for subsequent use (Mangel 1993; Stephens 1993; Potting et al. 1997; Vos et al. 1998).

Parasitoid insects represent a good opportunity to understand past information use in the context of host foraging (Papaj & Lewis 1993; Hoedjes et al. 2011). Indeed, to maximize the number of offspring produced, parasitoid females have to allocate their time and eggs between host patches, but the density and profitability of patches may vary in time and space. Parasitoid females thus have to collect information to match the current environmental conditions. Numerous studies have described the use of different sources of current and past information during patch exploitation (reviewed in van Alphen et al. 2003; Wajnberg 2006). But, to our knowledge, only one experimental study, on the aphid parasitoid *Lysiphlebus testaceipes*, has aimed to investigate how past information is weighted (Tentelier et al. 2009), despite the evolutionary implications. Likewise, in parasitoids, although the relative value of multiple sources of information has been evaluated in several studies (Wäckers & Lewis 1999; Thiel & Hoffmeister 2006; Muratori et al. 2008), we failed to find any attempt at untangling the hierarchy of correlated, redundant cues.

In this study, we first sought to identify how past information is weighted in the parasitoid wasp *Venturia canescens* (Hymenoptera: Ichneumonidae). To this aim, we investigated how an individual adjusts its current patch exploitation behaviour according to the past environmental profitability it experienced. Wasps were given three successive host patches of different host density. If *V. canescens* gives more weight to the first gathered information, cues indicating low host density in the first patch should favour more intense patch exploitation on the last patch, regardless of the host density of the intermediate one. If older and more recent pieces of information are given the same weight, information collected on both the first and second patches should influence third-patch behaviour. Consequently, the mean profitability of the series of patches should influence behaviour on the last patch. Furthermore, if older information does not weigh as much as more recent information, a difference in behaviour should arise from series of patches with the same average environmental profitability but different orders of host density.

In a second experiment, we took advantage of the knowledge of the different sources of information used for patch exploitation in *V. canescens* (see Methods) to identify the main source(s) of past information used by the wasps within a set of correlated cues.

METHODS

Biological Model

Venturia canescens is a solitary (i.e. at most, one adult emerges from a parasitized host) synovigenic (i.e. produces eggs throughout adult life) endoparasitoid of lepidopteran larvae, mainly Pyralidae (Salt 1976; Harvey & Thompson 1995). Its lifetime expectancy is 2 or 3 days under water and food deprivation and can reach 2–3 weeks in favourable laboratory conditions (Desouhant et al. 2005). The maximum egg load varies from 110 to 160 eggs (Harvey et al. 2001; Roberts & Schmidt 2004). Thelytokous (i.e. they produce only daughters by obligate parthenogenesis) *V. canescens* lives mainly in bakeries, mills and granaries (Salt 1976), where it finds hosts aggregated in patches (Athanasidou & Saitanis 2006), the abundance of which can vary enormously (Skovgard et al. 1999). Host larvae that are concealed in the substrate are localized via a kairomone, a mandibular gland secretion released while

they eat (Corbet 1971; Castelo et al. 2003). *Venturia canescens* probes the host-contaminated substrate with its ovipositor. Egg laying occurs when the ovipositor reaches a suitable host. It is followed by a characteristic movement of the abdomen called 'cocking' (Rogers 1972; Amat et al. 2003). *Venturia canescens* avoids superparasitism, that is, laying eggs in already parasitized hosts (Sirot et al. 1997; Amat et al. 2009). As a consequence, the density of suitable hosts decreases with the time spent exploiting a patch.

Females use current information to adjust their host patch exploitation behaviour. Host kairomones, whose amount secreted is proportional to the density of larvae (Corbet 1971), allow the parasitoids to estimate host density in the patch and influence the time allocated to search for hosts on a patch (i.e. patch residence time; Waage 1979; Driessen et al. 1995; Driessen & Bernstein 1999). Ovipositions are also a source of information and result in an increase or a decrease, according to the ecological context, in the wasp's tendency to leave the patch (Waage 1979; Driessen et al. 1995; Lucchetta et al. 2007; Amat et al. 2009). Lastly, the patch-leaving tendency increases with the time spent on the patch (Driessen & Bernstein 1999). Host kairomone concentration, number of eggs laid by the parasitoid and time spent so far on a patch are three nonindependent sources of information that are positively correlated with host density and that constitute redundant cues for this variable.

Females also use past information: they are able to learn to associate a chemical or visual cue with a reward in host- and food-searching contexts (Thorpe & Jones 1937; Lucchetta et al. 2008; Desouhant et al. 2010). Their behaviour on a current patch is also influenced by travel time between the two host patches (Thiel et al. 2006; Liu et al. 2009).

We used a strain of thelytokous wasps that originated from individuals captured in the field near Valence, France (GPS coordinates: 44°58.344'N, 4°55.659'E, 180 m; INRA station Gotheron) in summer 2006, during a large field sampling. The wasps were reared on *Ephestia kuehniella* (Lepidoptera: Pyralidae) larvae. Host larvae were obtained from a mass-rearing facility in Antibes (Biotop, France) and grew on wheat semolina. Parasitoids and hosts were kept in a controlled environment (rearing conditions: 25 ± 1 °C, 75 ± 5% relative humidity and 12:12 h light:dark).

For the experiments, the wasps were isolated, immediately after their emergence, in a plastic tube (30 mm diameter, 70 mm height) with a droplet of 50% water–diluted honey for 1 h, to avoid starvation. All of the wasps were kept in rearing conditions, in a room without any host odour, for approximately 24 h, until the experiment began. At the end of each experimental day, the wasps were frozen (–20 °C) to allow for later measurements and dissection (see below). Each wasp was used only once. Experiments were conducted in rearing conditions, between 1030 and 1700 hours.

Experiment 1: Influence of Previous Foraging Experience

To determine how past information is weighted in *V. canescens*, we compared the behaviour of wasps that had experienced environments of different profitability. The wasps' host patch exploitation behaviour is described by the number of ovipositions and the patch residence time (van Alphen et al. 2003).

The environment consisted of series of three host patches, each being either of high (R, for 'rich') or low (P, for 'poor') host density. Five different arrangements (hereafter called series) of the two kinds of patches were used (Table 1). We designed four series of patches to determine the influence of experience on the first two patches on the host exploitation behaviour of *V. canescens* on the third patch. These series represent a set of environmental profitabilities from a low (series PPR) to a high level (RRR). Two types of medium profitability environment (PRR and RPR) were created to

Table 1
Host density, mean number of ovipositions + SE and sample sizes for the different host patch series (experiment 1)

Series name	First patch		Second patch		Third patch		Number of wasps
	Host density	Ovipositions (+SE)	Host density	Ovipositions (+SE)	Host density	Ovipositions (+SE)	
PPR	5	1.84+0.29	5	1.16+0.18	15	3.24+0.48	25
PRR	5		15	3.21+0.51	15	2.93+0.50	24
RPR	15	3.72+0.30	5	0.88+0.23	15	2.96+0.57	25
RRR	15		15	3.06+0.37	15	3.00+0.49	25
RRP	15		15		5	1.28+0.27	25

'P' in the series name refers to a 'poor' patch (low host density: five hosts), 'R' in the series name to a 'rich' patch (high host density: 15 hosts).

detect a differential weight given to information sources (i.e. kairomone concentration, number of eggs laid and patch residence time) depending on time.

Host patches were obtained by filling plastic petri dishes (5 mm deep, 55 mm diameter) with clean wheat semolina together with five (P patches) or 15 (R patches) third-instar, healthy host larvae. These densities should be discriminated by *V. canescens* on the basis of kairomone concentration (Driessen & Bernstein 1999); we hereafter call kairomone concentration 'kairomone level', as we did not measure the exact kairomone amount in the patches. To test whether *V. canescens*' discrimination ability between rich and poor patches persisted beyond the exploitation of two patches, we compared the wasps' exploitation behaviour on the third patch of a fifth series RRP versus the series RRR. The patches were kept for 8 days in rearing conditions, allowing the semolina to be soaked by the larvae's kairomone. To prevent the larvae from escaping, the patches were covered with a tight thin veil. For the trials, the patches were placed at the centre of an 'arena', a larger dish (140 mm diameter) filled to the rim with clean semolina (e.g. Driessen et al. 1995; Amat et al. 2006). The patch was embedded such that its surface was flush with the surrounding semolina. Each host patch and each arena were used once ($N = 372$).

Each tested wasp was allowed to exploit and to leave freely the three host patches. Each trial was ended when the wasp left the arena for the surrounding area or stayed for more than 3 min on the arena ($N = 2$ of 124 tested wasps), and then the foraging wasp was caught in a plastic tube (30 mm diameter, 70 mm height), without food. To avoid an effect of travel time on subsequent host patch exploitation (Thiel et al. 2006; Liu et al. 2009), we fixed the resting time between two successive trials to 450 s. This duration was chosen because in natural conditions females find host populations in less than 600 s (Desouhant et al. 2003) and in flight mills, the median flight duration is about 180 s (Lukas et al. 2010). So that we could easily catch each tested wasp, experiments were performed under a glass cover (30 cm diameter, 13 cm height).

Each experimental day, we sequentially tested the five series of three patches (i.e. five wasps), except for 1 day (see Table 1 for sample sizes). The order was randomized to control for a potential effect of the hour of the day.

On each patch, the behaviour of the wasps was recorded with the event-recorder program Jwatcher 1.0 (Blumstein & Daniel

2007). We recorded the time the wasp stayed in different locations (the patch, the arena or the area surrounding the arena), the timing of its activities (cleaning, resting, drumming the substrate with the antennae, probing the substrate with the ovipositor) and the occurrences of cocking. We defined patch residence time as the time between the first and the last contact of the wasps with the patch. This means that all but the last excursion of the wasps on the arena were included in this measure (Driessen et al. 1995).

To test the effects of size and egg load on the exploitation behaviour of the wasps, after the experiment we measured the length of the third left leg's tibia, a good estimator of individual size (Pelosse et al. 2007), and we recorded the number of chorionic eggs in the frozen wasps.

Experiment 2: Sources of Past Information

The correlation between the three potential sources of information, that is, kairomone level, number of eggs laid and patch residence time, prevented us from identifying the informational role of each cue. The aim of experiment 2 was to make the number of eggs laid become independent of kairomone level to determine which information sources the wasp uses while foraging on successive patches.

Wasps were tested on two successive host patches. Only the first patch was manipulated to set the opportunities to lay eggs at the same level, irrespective of the kairomone level (Table 2, Fig. 1). In this way, the wasps were 'tricked', by making them perceive a patch of a given host density through kairomone level, but with mismatching oviposition opportunities. This process allowed us to study separately the informational role of kairomone level and number of ovipositions performed on the previous patch.

The first patch of the series had either a low or a high kairomone level, but the number of larvae available was fixed to 10. Because the wasps tend to exploit patches with higher kairomone level for a longer time, we also manipulated the temporal accessibility of larvae for oviposition: the higher the level of kairomones was, the less time the larvae were accessible. A manipulated patch was obtained as follows (Fig. 1a). First, a plastic petri dish was prepared as in experiment 1, except that gauze was added inside the semolina. Then, after 8 days and just before the experiment began, the larvae were extricated. The gauze, which was holding most of the silk, and as a consequence the host kairomones

Table 2
Mean number of ovipositions + SE and sample sizes for the different host patch series (experiment 2)

Series name	First patch (manipulated)				Second patch		Number of wasps
	Kairomone level	Actual host density	Host time availability (s/min)	Ovipositions (+SE)	Host density	Ovipositions (+SE)	
Fake poor	Low	10	50	2.50+0.34	10	2.55+0.36	33
Fake rich	High	10	30	2.66+0.28	10	3.00+0.40	32

In the 'fake poor' series, a low kairomone level was produced by five hosts during 8 days; in the 'fake rich' series, a high kairomone level was produced by 15 hosts during the same time. The first patch of each series was manipulated according to the protocol described in Fig. 1.

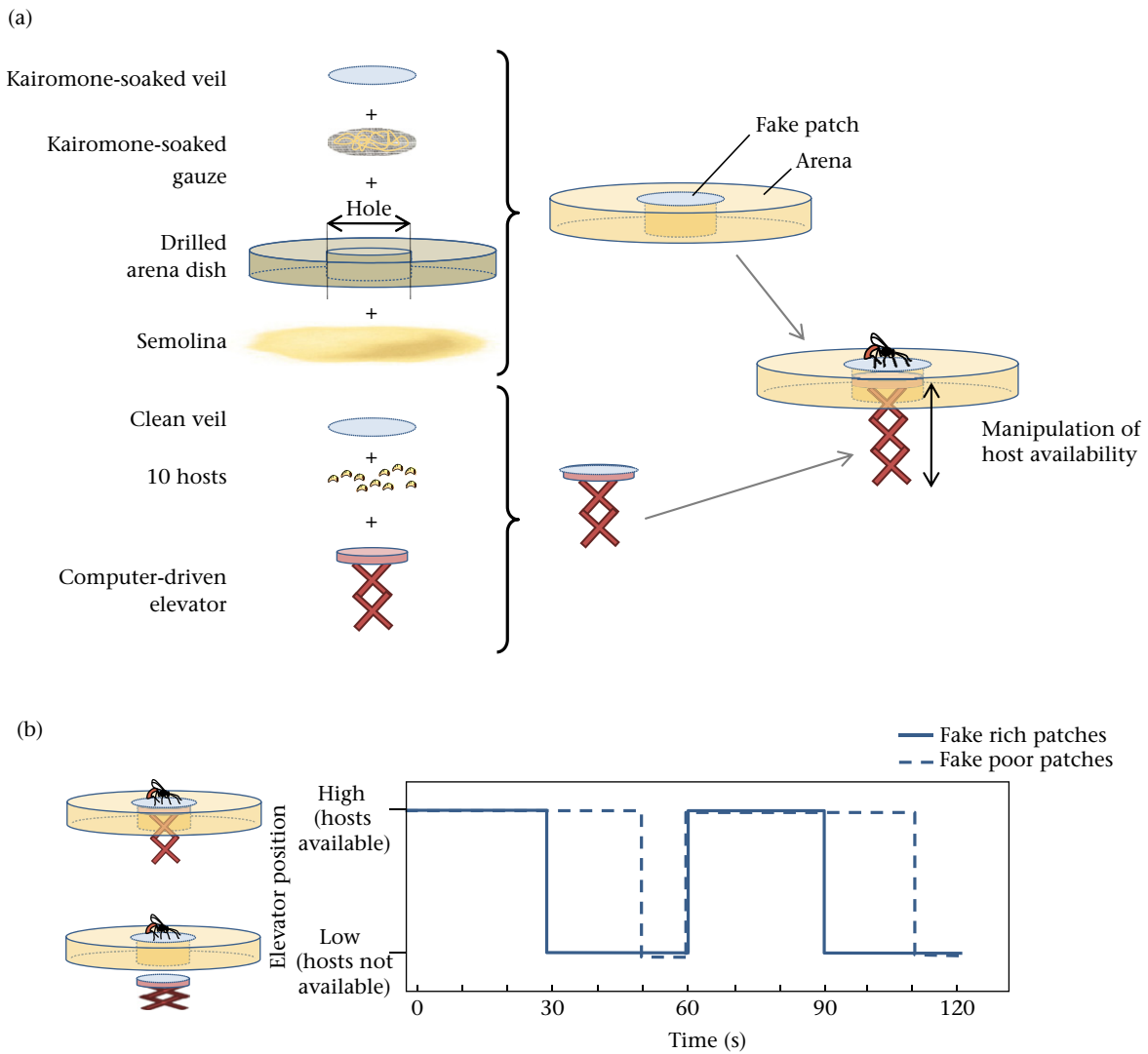


Figure 1. Experiment 2 first-patch manipulation. (a) Fake patch assembly. (b) Manipulation of time availability of hosts. Fake rich patches present a high kairomone level produced by 15 hosts during 8 days; fake poor patches present a low kairomone level produced by five hosts during 8 days. Since females stay a longer time on high kairomone level patches, the manipulation of time availability of hosts, via changes in elevator position, makes the wasps lay as much eggs on both types of fake patches.

(Corbet 1971; Waage 1979), and the veil covering the patch were tightened one on the other at the end of a tube 57 mm in diameter sitting in the centre of a dish 140 mm in diameter, which had a hole 57 mm in diameter drilled in its centre. The rest of the dish, the 'arena', was filled to the rim with clean semolina. The surface of the manipulated patch was not different from the surface of an unmanipulated one. Finally, 10 fifth-instar larvae were put on a cylindrical base 55 mm in diameter, which was covered by a thin veil to prevent them from escaping. This cylindrical base could easily slide inside the 57 mm-diameter tube: it was placed on a computer-driven elevator that allowed us to position the larvae just below and in contact with the gauze and veil (elevator in the 'high' position), or a few centimetres below (elevator in the 'low' position). In the high position, larvae were accessible for oviposition. In the low position, larvae were not accessible, but the wasps still probed the gauze with silk. The time the host larvae were accessible was empirically adjusted to make the wasps lay on the high and low kairomone level patches lay on average the same number of eggs (30 s/min in the high kairomone level and 50 s/min in the low kairomone level, Fig. 1b). In low kairomone level patches, initially prepared with five larvae (called 'fake poor'

patches), we manipulated the duration of accessibility of larvae to control for a potential influence of the functioning of the elevator engine. High kairomone level patches, initially prepared with 15 larvae, were called 'fake rich' patches.

The second patch of the series was not manipulated and was prepared as in experiment 1, with 10 larvae, independently of the series.

Trials were conducted by alternating the two kinds of series ('fake rich' or 'poor' series with a fake rich or a fake poor patch as the first patch, respectively). Sample sizes are shown in Table 2. One wasp in a fake rich series was discarded because it died before the end of the trial.

Patch exploitation by the wasp was allowed in the same conditions as in experiment 1. The variables measured were the same as in experiment 1. In addition, we recorded the position of the elevator (high or low) with Jwatcher.

Data Analysis

Before performing the main analyses, we calculated an 'oviposition score', to evaluate each wasp's ability to lay eggs. This score

was taken to be equal to the intercept estimated for each individual by the following mixed model (generalized linear model, Poisson distribution of errors, 'log' link):

number of ovipositions ~ patch rank x (kairomone level + series type) + wasp identity.

Patch rank, kairomone level (high or low in experiment 1; high, low or medium in experiment 2) and series type (five modalities, only in experiment 1) were fixed effects, and wasp identity was a random effect.

In the main analyses, the wasps' host foraging behaviour was studied through the number of eggs laid and the patch residence time (van Alphen et al. 2003). These variables were analysed by means of generalized linear models (number of ovipositions: Poisson distribution of errors, 'log' link; patch residence time: gamma distribution of errors, 'inverse' link). Distinct analyses were conducted for each patch rank in the series. The explanatory variables were tested sequentially (Tables 3, 4).

To remove the potential effects of the intrinsic differences between individuals (size and ability to oviposit) on the response variables, we systematically included the wasps' initial egg load on the patch (number of eggs in the abdomen at the beginning of a given patch exploitation), tibia length and oviposition score as explanatory variables in all of the statistical models.

The current host density (experiment 1) or kairomone level (experiment 2) was then introduced as an explanatory variable (Driessen et al. 1995). Lastly, the effect of past information was

studied through the previous patch(es) host density or kairomone level, number of ovipositions and patch residence time. Host density or kairomone level was introduced first because neither can be shaped by the other variables. The number of ovipositions and the patch residence time are interdependent: it is not possible to argue a priori for one order or the other. We performed an Akaike information criterion (AIC)-based model selection to select the final model. While analysing the wasps' behaviour on the third patch in experiment 1, we introduced past information variables from the first patch before those from the second patch. Indeed, while the first piece of information can influence the second, the reverse influence is not possible.

In all of the analyses, nonsignificant two-way interactions were deleted through a backward procedure. The statistical analyses were performed with the software R (R 2.7.0, R Core Development Team, Vienna, Austria; libraries: MASS, nlme, lattice and effects).

RESULTS

Experiment 1: Influence of Previous Foraging Experience

Influence of host density on first-patch behaviour

Females discriminated between R and P patches, laying significantly more eggs and spending significantly more time on R than on P first patches (Tables 1, 3).

Table 3

Analysis of the number of ovipositions and patch residence time in experiment 1, according to the patch rank in the different host patch series

	df	Number of ovipositions		Patch residence time	
		Deviance	$P > \chi^2 $	Deviance	$P > \chi^2 $
First patch					
Individual effect					
Egg load	1	0.03	0.87	0.78	0.18
Tibia length	1	4.46	0.04	1.67	0.05
Oviposition score	1	101.89	<0.001	13.42	<0.001
Current patch					
Host density	1	40.61	<0.001	6.16	<0.001
Second patch					
Individual effect					
Egg load	1	0.00	0.97	0.05	0.70
Tibia length	1	4.61	0.03	0.28	0.34
Oviposition score	1	106.19	<0.001	19.03	<0.001
Current patch					
Host density	1	59.51	<0.001	9.14	<0.001
Previous patch					
Host density	1	1.45	0.23	0.25	0.37
Number of ovipositions	1	22.21	<0.001	3.98	<0.001
Patch residence time	1	0.11	0.74	2.54	<0.01
Third patch: series RRR vs RRP					
Individual effect					
Egg load	1	5.38	0.02	1.56	0.11
Tibia length	1	0.63	0.43	0.09	0.71
Oviposition score	1	43.83	<0.001	7.37	<0.001
Current patch					
Host density	1	18.15	<0.001	0.82	0.25
Third patch: series RRR, PRR, RPR and PPR					
Individual effect					
Egg load	1	0.25	0.62	1.23	0.08
Tibia length	1	0.08	0.78	0.16	0.52
Oviposition score	1	121.67	<0.001	14.73	<0.001
Antepenultimate patch					
Host density	1	0.21	0.65	0.01	0.90
Number of ovipositions	1	25.99	<0.001	5.38	<0.001
Patch residence time	1	0.30	0.59	0.1	0.61
Previous patch					
Host density	1	0.39	0.53	0.43	0.30
Number of ovipositions	1	24.35	<0.001	1.09	0.09
Patch residence time	1	0.02	0.88	0.21	0.46

For the third patch, results of series RRR and RRP were analysed in a separate model from the results of series RRR, PRR, RPR and PPR. Note the importance of individual effect (oviposition score).

Table 4
Analysis of the number of ovipositions and patch residence time in experiment 2, according to the patch rank in the different host patch series

	<i>df</i>	Number of ovipositions		Patch residence time	
		Deviance	$P > \chi^2 $	Deviance	$P > \chi^2 $
First patch					
Individual effect					
Egg load	1	0.56	0.46	0.24	0.35
Tibia length	1	0.20	0.66	0.4	0.23
Oviposition score	1	33.94	<0.001	2.19	<0.01
Current patch					
Second patch					
Individual effect					
Kairomone level	1	0.04	0.84	8.38	<0.001
Egg load	1	0.00	0.98	0.3	0.25
Tibia length	1	0.12	0.73	0.62	0.10
Oviposition score	1	63.78	<0.001	3.65	<0.001
Previous patch					
Kairomone level	1	0.38	0.54	0.17	0.38
Number of ovipositions	1	22.29	<0.001	0.81	0.06
Patch residence time	1	0.06	0.81	0.08	0.55

Note the importance of individual effect (oviposition score).

Influence of current host density and first-patch experience on second-patch behaviour

On the second patch, we tested whether (1) females used current information (discrimination between R and P patches) on the patch, and (2) they were influenced by their experience on the first patch.

Females laid significantly more eggs and spent significantly more time on R than on P second patches (Table 3, Fig. 2). The number of ovipositions in the second patch declined with the number laid on the first one (Fig. 2). We did not find any influence of kairomone levels or of residence time on the first patch on the number of eggs laid on the second patch (Table 3).

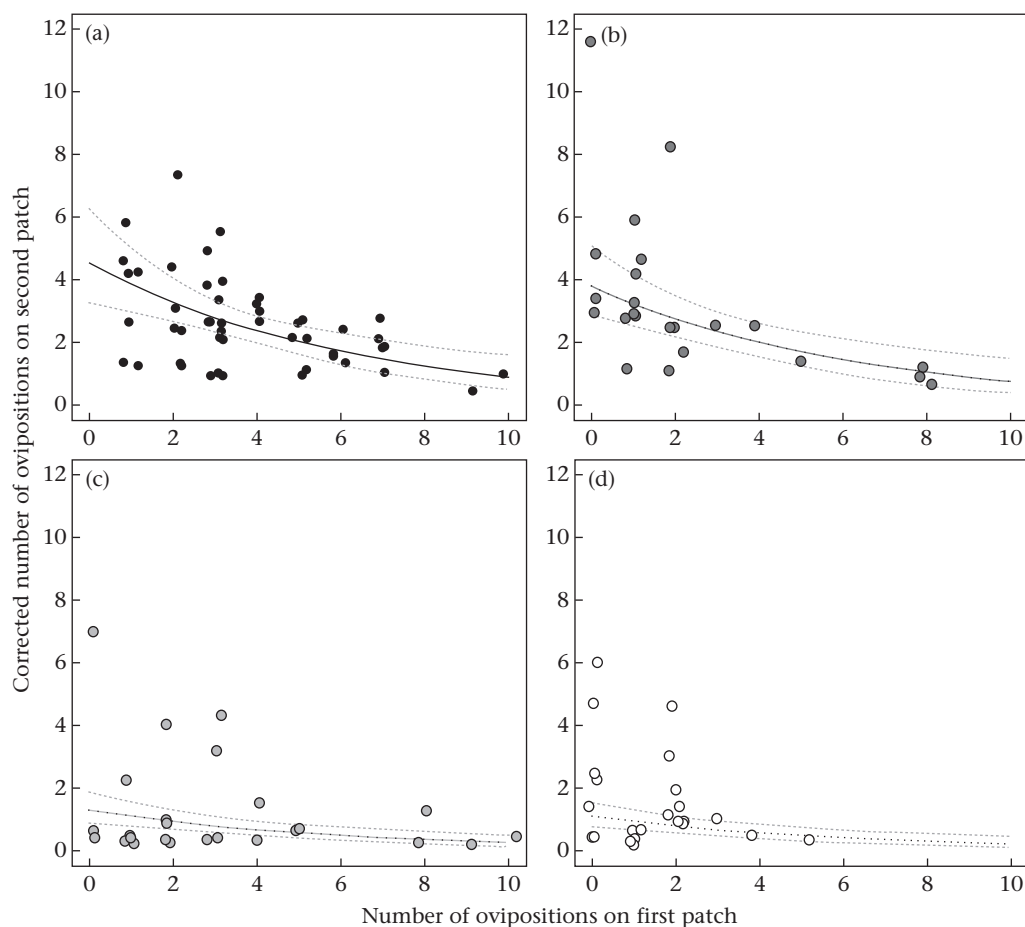


Figure 2. Relationship between the corrected number of ovipositions performed on the second patch and the number of ovipositions performed on the first patch (experiment 1), according to the host density succession that the wasp met. (a) RR, (b) PR, (c) RP and (d) PP. P: poor patch (low host density: five hosts); R: rich patch (high host density: 15 hosts). Because of the (positive) effect of oviposition score (see Data Analysis section for a definition) on the number of ovipositions on the second patch, hiding the effect of first-patch ovipositions, here the corrected number of ovipositions is shown. It represents the number of ovipositions that would have been observed if all of the wasps had had the same egg load, tibia length, oviposition score and previous patch residence time. Curves show the predictions of the GLM for the corresponding data. A 95% pointwise confidence interval is drawn around each curve. Points were jittered to avoid overlapping.

Similarly, patch residence time in the second patch declined with the number of eggs laid in the first one, but was positively correlated with first-patch residence time (Table 3).

Influence of current host density on third-patch behaviour

From the data obtained with the third patch of the series RRR and RRP, we tested whether females discriminated between R and P patches while visiting the third patch. Females laid significantly more eggs on R than on P third patches (Table 3). They spent an equivalent time on R and P third patches (Table 3).

Influence of experience of first two patches on third-patch behaviour

An analysis of data from the third patch of the series RRR, PPR, RPR and PRR allowed us to test the relative influence of experience on each of the first two patches. The more eggs the wasp laid on the first and second patches, the fewer eggs it laid on the third one (Fig. 3). No effects of kairomone levels or patch residence time on the first and second patches were detected (Table 3). The effect of the number of ovipositions in the first and second patches on the number of ovipositions in the third patch was similar, as shown by the deviance score of the model (Table 3) and the value of the GLM estimated coefficients (in first patch: coefficient + SE = $-0.249 + 0.048$; second patch: coefficient + SE = $-0.182 + 0.047$; Fig. 3b).

The higher the number of ovipositions on the first patch, the shorter the time spent on the third one. The number of eggs laid on the second patch had only a marginal influence on the residence time on the third patch. No effects of first- and second-patch kairomone levels or patch residence time were detected (Table 3).

Experiment 2: Sources of Past Information

To check whether the elevator disturbed the wasps' behaviour, we compared the probing rates in the first patch (i.e. the time invested in probing divided by the total time spent on the patch) when the elevator was in the high or low position (paired Wilcoxon test). We performed one analysis for fake poor patches and another one for fake rich patches.

The elevator did not disturb the wasps during first-patch exploitation: independently of the kairomone level, no significant difference was found between probing rates in the high and low positions of the platform (paired Wilcoxon test: fake rich patches: $V = 353$, $P = 0.20$, median, first and third quartiles (high position/low position) = 0.41/0.40, 0.36/0.35, 0.44/0.43; fake poor patches: $V = 313$, $P = 0.36$, median, first and third quartiles (high position/low position) = 0.29/0.29, 0.23/0.26, 0.34/0.35).

The analysis of patch residence time on the first patch allowed us to check whether females differentiated between manipulated rich and poor patches on the basis of kairomone level. Patch residence times on fake rich patches were significantly longer than on fake poor patches (Table 4).

An analysis of the number of eggs laid on the first patch allowed us to test whether the wasps laid as many eggs on manipulated poor as on manipulated rich patches. The number of ovipositions performed by the wasps was not different between the two kinds of first patches (high and low kairomone level, Tables 2, 4).

Identification of the source(s) of past information used

The analysis of the data obtained on the second patch aimed at identifying the source(s) of past information used by *V. canescens*. The number of ovipositions on the second patch was significantly lower when the number of eggs laid on the first patch was higher. No effect of the kairomone level or patch residence time on that patch was found (Table 4, Fig. 4).

The patch residence time on the second patch was not influenced by the kairomone level or patch residence time of the first patch. The influence of the number of ovipositions on the first patch was only marginally significant (Table 4).

DISCUSSION

When foraging on three successive host patches, the parasitoid wasp *V. canescens* adjusted its current patch exploitation according to its previous experience on both the first and second host patches,

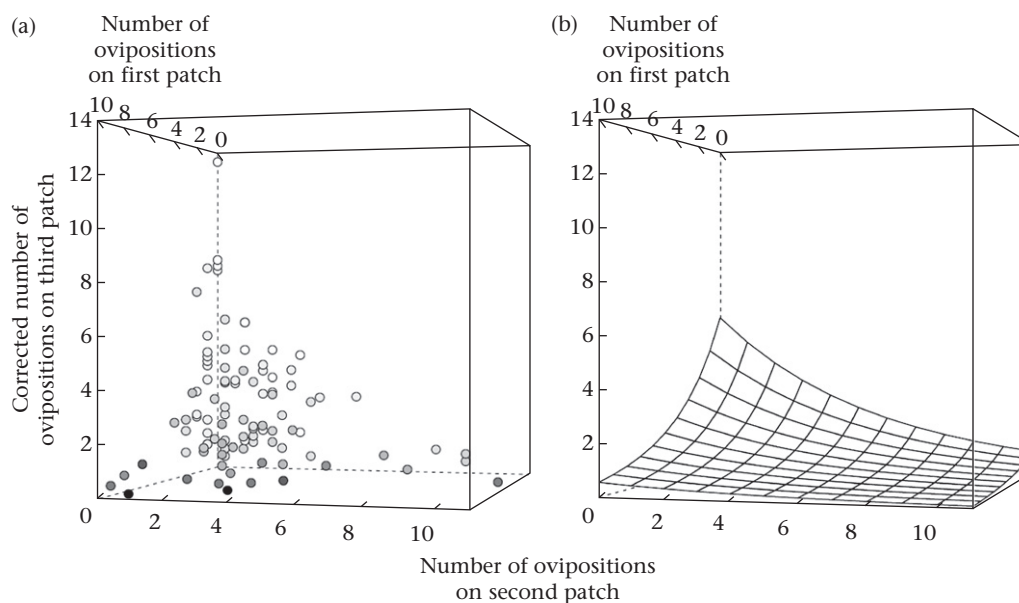


Figure 3. Relationship between the corrected number of ovipositions performed on the third patch and the number of ovipositions performed on the first and second patches (experiment 1). (a) Raw data. To enhance the depth perception, the points corresponding to a higher number of ovipositions in the first patch are filled with a darker grey. Points were jittered to avoid overlapping. (b) Predictions of the GLM for the corresponding data (see Data Analysis section). Because of the (positive) effect of oviposition score (see Data Analysis section for a definition) on the number of ovipositions on the third patch, hiding the effect of the first and second patch ovipositions, here the corrected number of ovipositions is shown. It represents the number of ovipositions that would have been observed if all of the wasps had had the same egg load, tibia length, oviposition score and previous patch residence time.

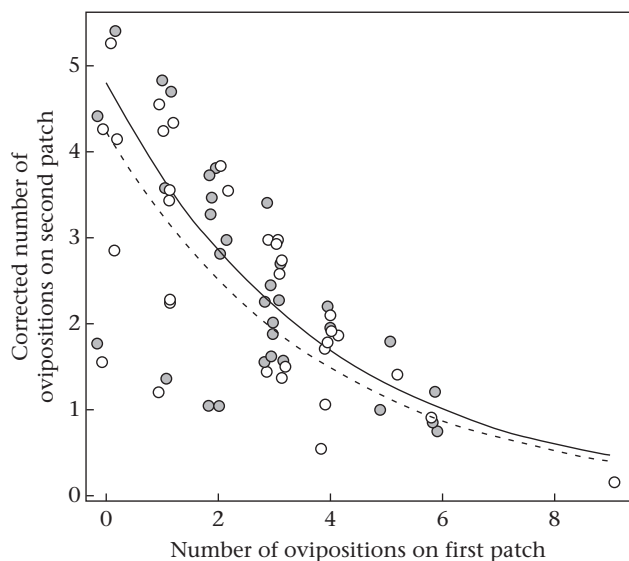


Figure 4. Relationship between the corrected number of ovipositions performed on the second patch and the number of ovipositions performed on the first patch (experiment 2), according to the first-patch kairomone level. Because of the (positive) effect of oviposition score (see Data Analysis section for a definition) on the number of ovipositions on the second patch, hiding the effect of first-patch ovipositions, here the corrected number of ovipositions is shown. It represents the number of ovipositions that would have been observed if all of the wasps had had the same egg load, tibia length, oviposition score and previous patch residence time. Curves show the predictions of the GLM for the corresponding data. Points were offset to avoid overlapping. Grey dots and full line: high kairomone level first patch; white dots and dashed line: low kairomone level first patch.

older and more recent information being weighted equally at the timescale tested. Of host kairomone level, number of eggs laid and patch residence time, three cues that are known to be used as current information, only the number of eggs laid on the previously visited patches seemed to be a past information source.

In accordance with the results of previous studies (Waage 1979; Driessen et al. 1995), the wasps invested more time and eggs on patches with higher host density, that is, the wasps had available the information about current host density. This result is important because it allows us to consider that they can store this source of information, which may enable them to adjust adaptively their current behaviour to the environmental profitability they experienced. This discrimination ability persisted until the third patch.

Influence of Previous Foraging Experience

Use of past information raises the question of information weighting according to the time elapsed since it was gathered and stored. In our results and given the timescale we worked with in experiment 1 (mean patch residence time + SE = 9.14 + 0.37 min, and interpatch time of 7 min 30 s), older experience (from the first patch) has as much weight as more recent experience (from the second patch). This kind of continuous updating process has been demonstrated to take place in bumblebees. On a short timescale (3 h), they adaptively adjust their patch-leaving rules to the distribution of rewards experienced in a Bayesian-like manner, that is behaving as if they updated prior knowledge of the resource distribution to estimate the patch quality (Biernaskie et al. 2009).

In our experiments, the females laying more eggs on the previous patches oviposited less and spent less time searching for hosts on the current patch. Under the hypothesis that the number of eggs laid is a reliable cue of patch host density for females (Driessen et al. 1995) and then of environmental profitability, our

results are concordant with Charnov's (1976) predictions: for a given travel time between patches, foragers invest less time and eggs in each patch in profitable environments than in less profitable ones. Female wasps thus behave as if they were using adaptively an estimate of the whole environmental profitability experienced so far. Here, experiments were conducted on a short timescale relative to the animal's lifetime expectancy (2–3 weeks in laboratory conditions: Desouhant et al. 2005). The display of this behavioural plasticity on this timescale appears to be in phase with the pace of variation in host density (McNamara & Houston 1987). Indeed, significant variations in environmental host density are expected to occur within a time range of more than 1 day but less than the individual's lifetime (Skovgard et al. 1999; Athanassiou & Saitanis 2006). This plasticity could be compared with that obtained by Tentelier et al. (2009), who hypothesized that in *L. testaceipes*, a parasitoid experiencing a relatively stable habitat during its short life (2.56 days at 25 °C in the laboratory; van Steenis 1994), only the very first piece of information to be gathered is used. Of course, we are not in a position to predict how *V. canescens* balances consecutive pieces of past information on a larger timescale: further experiments with longer series of patches or longer resting times are needed. Nevertheless, because significant variations are expected to happen within an individual's lifetime, we hypothesize that giving more weight to more recent than to older information, that is, forgetting potentially obsolete older information, may be adaptive.

An alternative explanation for the observed decrease in investment (eggs laid and time spent) with the rank of the exploited patch could be that the wasps cannot perceive the transitions and exploit the patch series as if they were on a single large patch. In that case, oviposition rate should decrease with time spent on a patch and tendency to leave the patch should increase with time because females avoid laying in already parasitized hosts. Several points suggest that this explanation is unlikely. First, females left the patch on their own, as in experiments with single patches (as in Driessen et al. 1995). Second, during the resting time, the wasps did not have accessible any host odour: their olfactory landscape should then give them a cue of patch desertion. Last, they could not find any of their own chemical traces on a patch they began to exploit (Bernstein & Driessen 1996): this absence should indicate to them that they were exploiting a new patch. Nevertheless, one could argue that resting times were too short to allow the wasp's antennae to become resensitized to kairomones. Such a sensitization/desensitization mechanism was hypothesized in previous studies to explain the effect of travel time on patch residence time (Waage 1979; Thiel & Hoffmeister 2004). Our results give little support to this hypothesis. Indeed, if the wasps entered the patch with kairomone-saturated antennae, no behavioural disparity should have been found between high and low kairomone level in current patches. Furthermore, if the wasps entered the patch with partially saturated antennae, for those coming from rich patches with a higher saturation level, we should have found an effect of the kairomone level of the previously visited patch on the current behaviour.

Sources of Past Information

In the second experiment, among the set of available sources of information known to be used as current information, the number of eggs laid on the previous patch clearly influenced the wasp's behaviour on the current patch. In contrast with this result, the kairomone level of the previous patch and the previous patch residence time seem not to be used as main past information sources. This result raises questions about the nature of the process involved. Is it a cognitive process? It also raises the issue of the

informational value of each of these three cues in the ecological context of host patch exploitation.

While kairomone level is positively correlated with the initial motivation to stay on and exploit a host patch (Iwasa et al. 1981; Driessen et al. 1995), kairomone levels of patches visited previously had no effect on the wasp's current behaviour. This result contradicts the involvement of olfactory information and thus sheds doubt on the involvement of any cognitive process. Other mechanisms could explain the negative correlation between the number of eggs laid in previous patches and ovipositions on the current one. First, the effect of the previous number of ovipositions could be caused by a decrease in egg load pressure. In three *Drosophila* species, an increase in ovarian pressure is associated with an increase in oviposition rate (Horton & Krysan 1991; Takahashi 2007). Second, after exploiting several patches, females could be egg limited, which has been shown to be related to diminishing oviposition rates (Casas et al. 2000). Both explanatory hypotheses seem implausible. Indeed, the number of eggs laid on the successive patches ($2.58 + 0.22$ eggs on average \pm SE, see also Tables 1 and 2) seems insufficient to generate a decrease in egg load pressure or an egg limitation condition: at the end of the trials in experiments 1 and 2, wasps had on average (mean \pm SE) $99.8 + 2.16$ and $117.3 + 3.48$ mature eggs in their ovaries, respectively. Moreover, potential effects of these two mechanisms are not consistent with the lack of statistical effect of egg load on patch exploitation behaviours (Tables 3, 4). We are not able to conclude at this stage whether in *V. canescens* the use of past information relies on a cognitive process or not. We can only state that females behave as if they use an estimate of environmental profitability based on the egg-laying performance they experienced so far. In the same vein, some animals seem to use Bayesian estimation of environmental parameters even if they do not calculate any probability (McNamara & Houston 1980; McNamara et al. 2006).

The results of experiment 2 provide information on the reliability of the cues we tested in the context of host foraging. Driessen et al. (1995) clearly showed that kairomone level is related to the motivation to continue searching for hosts on a patch. But this cue does not indicate the accessibility of host larvae (more or less deeply concealed in their food substrate) nor their quality (e.g. parasitism status). Kairomone level may also fluctuate with variables other than host density such as the amount of time the host larvae were feeding at the same place in the substrate. Moreover, each female also suffers from runs of good or bad luck, leading to discrepancies in its oviposition performance. Thus, kairomone level predicts the expected number of larvae to be parasitized, but does not necessarily match the wasp's performance. Unlike kairomone level, the number of ovipositions integrates all of these variables. Moreover the number of eggs laid depends on the wasp's physiological state and environmental variables (Amat et al. 2006). Consequently it appears to depict the environmental profitability experienced by the wasp far better than kairomone level. Even if the wasp is not able to count the eggs laid, several mechanisms such as hormonal change (Casas et al. 2009) may provide information to the wasps about egg-laying events. This lack of previous kairomone level effect could be paralleled with one result of Driessen & Bernstein (1999), who found that each oviposition affected the patch-leaving tendency independently from the kairomone concentration.

One could also interpret the effect of previously laid eggs as the wasps avoiding future egg limitation. High oviposition rate in early life could indicate to the wasp that such a situation may occur in forthcoming days. But this explanation is unlikely here, given the synovigenic nature of *V. canescens* and the number of eggs it can produce during its lifetime (up to 560: Roberts & Schmidt 2004), even under unfavourable conditions (e.g. starvation or low host density, Pelosse et al. 2011).

Despite the fact that patch residence time is a major determinant of lifetime reproductive success in parasitoids (van Alphen et al. 2003), *V. canescens* did not use previous patch residence times as past information. This result is all the more surprising as (1) numerous insect species, including bees and parasitoids, can sense the passage of time elapsed (Schmidt & Smiths 1987; Boisvert & Sherry 2006; Skorupski & Chittka 2006; Tentelier et al. 2006; Thiel 2011), (2) as a 'rate maximizer', *V. canescens* is expected to be under selection to maximize the number of offspring produced per unit of time (Wajnberg 2006) and (3) previous studies on *V. canescens* are consistent with the assumption of sensitivity to time: thelytokous *V. canescens* modulate their behaviour according to the time already spent on the current patch (Driessen et al. 1995) and to the time elapsed between patches, even in the absence of energetic expenditure (Thiel et al. 2006; Liu et al. 2009). We suspect that this result may be linked to our experimental set-up: time spent foraging for hosts may play an informational role on larger timescales and/or for longer previous patch residence times, possibly encountered in anthropic conditions (C. Bernstein, personal observation). Moreover, the lack of effect of previous patch residence times on current patch exploitation may be caused by strong effects of current ovipositions (Driessen & Bernstein 1999) and short resting times between two successive patches on the wasp's tendency to leave the patch (Thiel 2011).

The lack of effect of previous patch residence times, together with the fact that the more eggs a wasp laid in a previous patch the fewer it laid on a subsequent one, may also lead to a conceptual framework other than rate maximizing. The short resting times experienced by the wasps in relation to their lifetime expectancy could indicate a short distance between neighbouring patches (Liu et al. 2009). The negative correlation between previous and subsequent number of ovipositions could then be interpreted as the wasps avoiding laying too many eggs in a small area as a risk-spreading strategy. From this point of view, patch residence time does not appear to be a crucial variable, a lack of effect being potentially expected.

Our results show that *V. canescens* is able to update continuously the information it gathers, at least on a short timescale. This finding confirms that parasitoid insects are good biological models to investigate Bayesian use of information with the distinctive feature that they also have available external cues (e.g. kairomone concentration) to estimate patch resource quality (Pierre & Green 2008). Finally, our results show that, contrary to what is usually expected, patch residence time in previously visited patches is not relevant for deciding how to exploit a patch of resources.

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