Original Article

Information gleaned and former patch quality determine foraging behavior of parasitic wasps

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A good estimate of patch quality is of prime importance for a randomly searching forager with limited longevity or fecundity. The forager can perceive cues related to the presence of resource on arrival in a patch and estimates its quality relatively to previous patches. This prior estimate can then be updated through sampling in the patch. However, these 3 sources of information have never been manipulated independently in the same experiment to quantify the effect of each one on foraging behavior. Here, we report experiments highlighting the mechanism by which the braconid *Asobara tabida*, a parasitoid wasp laying eggs in *Drosophila* larvae, uses information both gleaned from the previous patch visited and obtained on arrival in the next one, to estimate the quality of the latter and to behave accordingly. We disentangled the effects of the prior estimate of patch quality made on arrival in the patch and the effect of sampling in the patch on the foraging behavior of the parasitoid. We show that information gleaned by *A. tabida* from a previously visited patch plays a strong role in the response to both chemical cues and oviposition events by parasitoid when exploiting a patch. The information process highlighted in the present study is consistent with the Bayesian-like decision-making, which is suspected in parasitoids, bumblebees, and humans. Moreover, motivation to stay in the patch is likely to be tuned to the forager's experience. *Key words:* Bayesian updating, decision, making, optimal foraging behavior, patch quality estimate. *[Behav Ecol]*

INTRODUCTION

When a depletable resource is patchily distributed in the environment, a forager has to decide to what level it should exploit each patch to maximize its intake rate during its lifetime (Stephens and Krebs 1986; Krebs and Davies 1997; Danchin et al. 2008). Charnov's (1976) marginal value theorem predicts that each visited patch should be harvested to the same quitting harvest rate, which corresponds to the average energy gain in the whole environment. However, the forager is not omniscient, and gleaning information is a way to adjust foraging strategies to the environment. This is quite relevant when resource is hidden in a patch (i.e., food or hosts under the ground or inside plant structures) or when information about the patch quality is inaccurate because the forager is uncertain about the gain it could achieve by exploiting it. To estimate the patch quality actively could thus be decisive to adjust the foraging behavior.

The ability to estimate patch quality has been investigated in a wide range of taxa, such as mammals (Valone and Brown 1989), birds (Valone 1992; Templeton and Giraldeau 1996; van Gils et al. 2003), and insects (Tentelier et al. 2006; Biernaskie and Gegear 2007). It plays an important role in determining patch residence time. We can identify at least 4 ways for a solitary forager to estimate the current patch quality (Figure 1): (i) with an innate knowledge before foraging, (ii) from information gleaned from previous patches, (iii) from information perceived on arrival in the patch, and (iv) through sampling in the current patch. We point out that the way a for-

ager estimates patch quality influences its foraging strategy, as was shown in birds, mammals, and insects parasitoids (Valone and Brown 1989, van Alphen et al. 2003) and that the use of information depends on the costs of gleaning, retaining, and retrieving it (Dukas 1999; Olsson and Brown 2006).

The forager can use information it already has before having any foraging experience (Figure 1, i). When organisms have evolved in a stable habitat, innate behavioral responses resulting from natural selection are adaptive for a forager without any experience or when the forager is unable to accurately estimate patch quality with cues of the environment (McNamara et al. 2006; Mery and Burns 2010). In this case, the forager has an innate estimate of both the average quality of the environment and of patch quality on arrival, as it was shown in parasitoids (Wajnberg et al. 2000; Boivin et al. 2004). Such a forager will be inclined to use a fixed time rule (to stay a fixed time in each patch whatever the patch quality, see Olsson and Brown 2010) or a giving-up density rule (to leave the patch after harvesting a given number of resource, see Brown 1988) in order to decide when to leave the patch.

In many cases, a forager gleans information from patch to patch and learns the distribution of resource items among the patches (Figure 1, ii). Then, it can estimate the probability of encountering a given patch type and adjust its foraging strategy accordingly, such behavior being viewed as Bayesian (McNamara et al. 2006). For example, birds, mammals, and insects are known to use preharvest information and adjust their foraging strategy in a patch through previous experience (see, respectively, Valone 1991; van Baaren et al. 2005; Vásquez et al. 2006). This informs a forager both on the average quality of the environment and on the estimate of patch quality relatively to that of others. The patch residence time should increase when the subsequent patch is richer than the previous one. However, the use of information requiring memory could be costly (Eliassen et al. 2009). On the
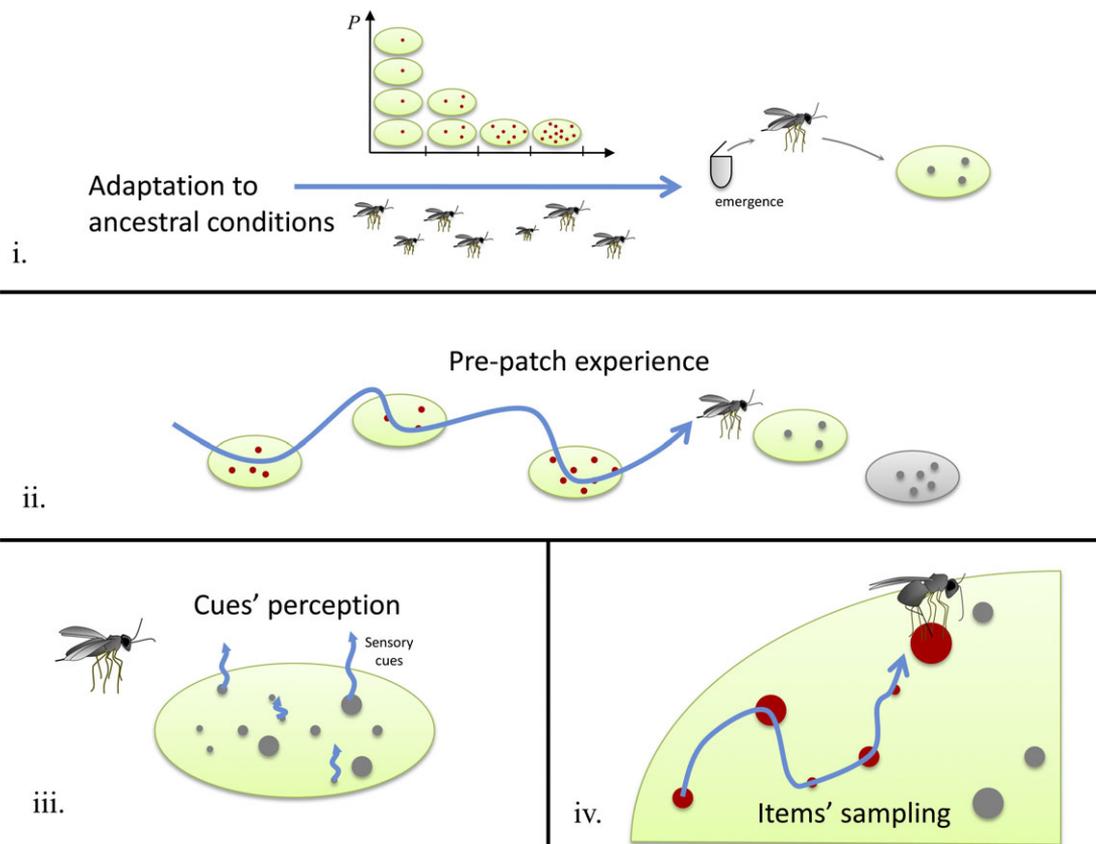
Figure 1
The different sources of information used by a solitary forager to estimate either the average quality of the environment (i, ii) or the visited patch quality (i, ii, iii, and iv). (i) From an innate knowledge before foraging (at emergence, the forager is assumed to know P, the prior probability of encountering each patch type). (ii) From information gleaned before entering the patch (the forager gleans and retains information from patch to patch). (iii) From information perceived on arrival in the patch (the forager perceives sensory cues of plausible presence of resource). (iv) Through sampling on the current patch (to inspect resource items gives the forager more accurate information of the estimate of patch quality). The case of a parasitic wasp is illustrated, but it can be extended to a wide range of taxa. Circles represent resource items and ellipses represent patches. In green and red: what is assumed to be known or estimated through information used. In gray: what is not yet estimated or known by the forager. A color version of this image is available online.

opposite, a forager which is insensitive to prepatch experience estimates the patch quality absolutely, only based on cues from the current patch, and the residence time should be independent of that of the one in the previous patch.

On arrival on a patch, a forager could perceive sensory cues of plausible presence of resource (i.e., vibration, visual, and chemical cues, Figure 1, iii), as it is the case in spiders (Persons and Uetz 1996). According to Brown (1988), Valone and Brown (1989), and Driessen and Bernstein (1999), a forager capable of making an accurate estimate of patch quality on arrival is inclined to use the giving-up density rule to leave the patch because the residual quality of the patch is directly related to the initial estimate.

To refine the prior estimate of patch quality, a forager can also sample the resource in the patch (Figure 1, iv), thus obtaining more accurate information about the patch quality and about the density of resource items (Persons and Uetz 1996; Olsson and Brown 2006). Pierre et al. (2003) showed that a parasitic wasp behaves as if it updates its prior patch estimate at each host encounter in the patch and then decides to stay or leave the patch using the updated information on patch profitability. According to the authors, this behavior is in agreement with a Bayesian updating of patch quality. Different authors have shown that both the spatial distribution of patches and the accuracy with which a forager can estimate prior patch quality influence the way the estimate of patch profitability is updated by using information from resource sampling

(Iwasa et al. 1981; Driessen and Bernstein 1999; van Alphen et al. 2003; Outreman et al. 2005; van Baaren et al. 2005). For example, Iwasa et al. (1981) assumed that encountering a resource item increases a forager's responsiveness in the patch when the resource is aggregated among patches. However, encountering a host in a poor patch should have a weaker incremental effect on the tendency to stay than encountering a host in a rich patch because more remaining hosts are expected in a rich patch than in a poor patch (Muratori et al. 2008).

Patch quality can be estimated in several ways and may be influenced by many factors. In published empirical studies, the effect of a prior estimate of patch quality (either by a relative or by an absolute estimate) and its updating during foraging have never been disentangled. Indeed the effect of the information obtained on arrival in a patch has generally been confounded with the effects of all the intrapatch events because of the exact correspondence between the strength of such cues and resource density in the patch. As a consequence, a measure of the residence time cannot reveal if the forager has the ability to estimate the patch quality on arrival, how it updates the patch profitability by sampling and if it modifies its behavior accordingly. Here, we study this problem using a novel experimental design in which we quantify the effect of a prior estimate of patch quality on arrival, taking into account both prepatch experience and cues perceived in the current patch. We independently study the potential modification of the estimate of patch quality in response to

intrapatch events and look at the interaction between prior estimate and the effects of intrapatch events.

Females of the *Drosophila* parasitoid wasp *Asobara tabida* (Hymenoptera: Braconidae) were used to study the effect of different sources of information on the decision to leave the patch. It has previously been shown that *A. tabida* female responds to chemical cues providing information on the presence of host larvae (i.e., kaimones, see Galis and van Alphen 1981; van Alphen and Galis 1983), increases its residence time with oviposition (van Alphen and Galis 1983) and responds to prepatch experience (Thiel and Hoffmeister 2006), even though, until now, the effects of the estimate of patch quality on arrival and during sampling have never been disentangled. In this study, we tested the hypothesis that the parasitoid estimates the patch quality either in an absolute or in a relative way by disentangling the effect of the prior estimate on arrival in the patch and the effect of encountering the resource item. Then, we quantified the effect of prepatch experience on the modification of the response to kairomones regardless of what the forager encounters inside the patch. By manipulating the cues used by the parasitoid to estimate its quality on arrival, we quantified the incremental effect of an oviposition on the residence time. An oviposition in a patch having a high apparent quality should increase the residence time more than one in a poorer patch because a high estimate indicates a high expectation of finding subsequent hosts in the patch.

MATERIALS AND METHODS

Biological material

The strain of the solitary parasitoid *A. tabida* used in our experiments was collected in Chasse-sur-Rhône (lat 45°34′N, long 4°48′E) in September 2008 and reared in the laboratory on *Drosophila subobscura* hosts, collected in The Netherlands in 1980. Wasps and their hosts were reared in a climate room (20 °C, 60% relative humidity, and 16:8 h Light:Dark). Emerged females were allowed to mate with males from the rearing during 4 h and then were stored at 12 °C with sugar water as source of carbohydrate and moisture until required for the experiments. For all experiments, tested females were 4–10 days old, and the second instar host larvae were 4–5 days old, the preferred host stage for *A. tabida* (van Alphen and Drijver 1981). One day prior to an experiment, wasps were allowed to oviposit in 15 hosts during 2 h at 20 °C. We then selected only females that lay eggs (Samson-Boshuizen et al. 1973) and kept them at 20 °C with sugar and water until the beginning of the experiment (Table 1).

Experimental design

We performed 2 experiments in which 120 *A. tabida* females have visited 2 successive patches (60 females per experi-

ment). In the first experiment, the first patch contained 1, 4, or 16 *Drosophila* larvae and the corresponding amount of kairomones. The second patch contained only kairomones emitted by 4 larvae. In the second experiment, the first patch was the same as in the first experiment, but the second patch contained kairomones emitted by 4 larvae and 1 host larva.

Patches were made by placing 200 μl of fresh water containing 80 mg baker's yeast on a Petri dish (Ø = 5 cm) containing a thin agar layer. The viscous yeast suspension was enclosed in a perspex ring (h = 3 mm, Ø = 2 cm) placed on the center of the Petri dish. The excess water was evaporated to provide a suitable substrate for moving host larvae and searching parasitoids. To prepare the first patch, 1, 4, or 16 larvae were allowed to crawl and feed during 1 day prior to the experiment. Although the larvae are present in the patch, they leave a substance, used as kairomones by *A. tabida* females. The concentration of this substance is proportional to the number of hosts present (Galis and van Alphen 1981). The perspex ring was then removed. The first patch contained host larvae, and the corresponding amount of kairomones produced by them (van Alphen and Galis 1983). To prepare the second patch of the first experiment, only 4 larvae were allowed to crawl and feed during 24 h. Then, both the perspex ring and the larvae were removed. For the second experiment, one larva was left in the yeast. By this procedure, it is possible to manipulate the amount of kairomones emitted by the hosts (the apparent quality of the patch, corresponding to 4 larvae in the experiment), and the number of hosts present in the patch independently (i.e., the true quality of the patch, 0 or 1 larva).

The experiments

The first patch was offered to a single female (Table 1). The female was introduced into the covered Petri dish. The exploitation of the first patch was terminated when the female left the patch for more than 60 s or when she attempted to migrate. The female was then isolated in a clean Petri dish with sugar water for 10 min. After this fixed time interval, a second patch was offered to the female, and patch residence time was measured in the same manner. During the experiment, we observed and recorded behavior continuously, using the event recording program "The Observer" (Noldus 3.0, 2000). The occurrence of ovipositions and the total duration of a patch visit were noted. Eighteen to 21 females were tested per treatment. The combinations of the first and second patches used in the 2 experiments are summarized in Table 1. Each treatment was randomly assigned to a female regardless to her age.

Table 1
The experimental setup

Experiment	Series	Number of females tested	Quality of the conditioning patch		Quality of the testing patch	
			Kairomone level[a]	Host density	Kairomone level[a]	Host density
1	A	21	1	1	4	0
	B	20	4	4	4	0
	C	18	16	16	4	0
2	D	22	1	1	4	1
	E	20	4	4	4	1
	F	19	16	16	4	1

In the conditioning patch, the kairomones were emitted by the hosts effectively contained in the patch. In the testing patch, the amount of kairomones differs from the number of hosts.

[a] Given by the number of host larvae that produced kairomones during 24 h.

Statistical analyses

For each treatment, the patch residence time was analyzed using Cox's proportional hazard model (Cox 1972; Collett 1994). This model estimates the hazard rate at time t, which can be interpreted biologically as a tendency to leave the patch. We estimated the effect of the different cues (concentration of kairomones from the current and the previous patch, number of encountered hosts, and age of the females) on the tendency to leave the current patch. The hazard rate $h(t)$ at time t in the patch is given by:

$$h\left(t, z_1, \ldots, z_i, \ldots, z_n\right) = h_0\left(t\right)\exp\left\{\sum_{i=1}^{n}\beta_i z_i\right\}, \quad (1)$$

where $h_0(t)$ is the baseline hazard function to leave the patch depending only on the time spent on it (all covariates are set to zero), z_i, the covariates which influence the tendency to leave the patch with β_i contributions. If the expression $\exp\{\Sigma\beta_i z_i\}$ is lower than one, the patch-leaving tendency is reduced, resulting in an increase of the residence time, whereas a hazard ratio greater than one increases this tendency, resulting in a decrease of the residence time (Cox 1975). The mean residence times are given with standard error. All the analyses were carried out using R 2.11 software.

RESULTS

The residence time in the first patch

Patch residence time increased as a function of patch density in the first visited patch. The mean residence time was, respectively, 221 s ± 17 s (series A and D), 1054 s ± 53 s (B and E), and 2518 s ± 73 s (C and F) in the first patches. During the patch exploitation, the kairomone level and the number of ovipositions significantly decreased the patch-leaving tendency of A. tabida females (Table 2—first visited patch). The higher the kairomones level, the lower was the patch-leaving tendency ($\exp(\beta) = 0.42123$, $z = -6.973$, $P < 0.0001$). Each oviposition decreased female's patch-leaving tendency by a factor of 0.491, but this incremental effect was dependent on the current patch density ($\exp(\beta) = 1.05179$, $z = 4.816$, $P < 0.0001$). An oviposition in a rich patch decreased the patch-leaving tendency less than an oviposition in a poor patch. In the first patch as in the second patch, the age of the females did not influence her tendency to leave it (Table 2).
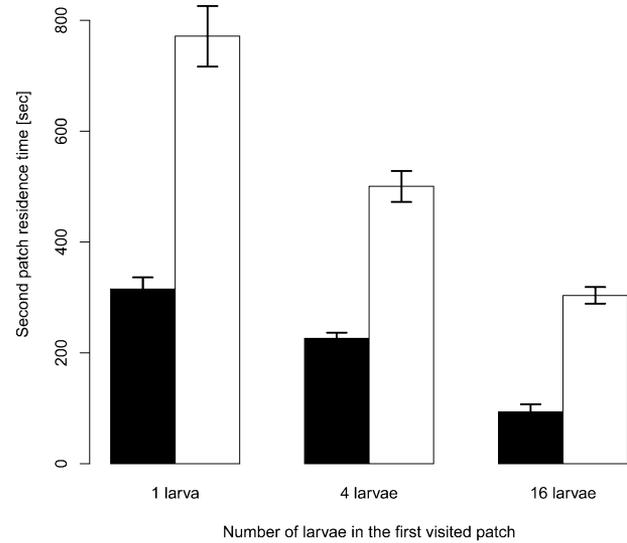

Figure 2
Mean (± standard error) residence time in the second patch as a function of the quality of the first patch visited. In black: patches without larva, in white: patches with one larva.

The patch residence time in the second patch containing only kairomones

The residence time in the second patch containing only kairomones (experiment 1, series A, B, and C) was strongly influenced by the previous patch density (Figure 2). During the second patch exploitation, the previous patch density significantly influenced the patch-leaving tendency of A. tabida (Table 2): The higher the previous patch density, the higher the patch-leaving tendency ($\exp(\beta) = 1.15816$, $z = 6.680$, $P < 0.0001$).

The patch residence time in the second patch containing kairomones plus one larva

In this second patch, each female attacked the host larva. The oviposition decreased female's patch-leaving tendency by a factor of 0.121 (Table 2). The residence time in the second patch that contained one larva is longer than in the one that contained only kairomones (Figure 2). However, the effect of an oviposition on the second patch-leaving tendency was dependent on the density of the previously visited patch (Table 2).

Table 2

Estimated regression coefficient (β) of a Cox proportional hazard model for tested covariates on the patch-leaving tendency of *Asobara tabida* foraging in conditioning patches and testing patches

	Covariates	β	SE(β)	exp(β)	z	P value	Effect on the patch-leaving tendency
First visited patch	Patch density	−0.86457	0.12399	0.42123	−6.973	3.10×10^{-12}	↓
	Oviposition	−0.71087	0.15666	0.49122	−4.538	5.69×10^{-6}	↓
	Interaction between oviposition and patch density	0.05049	0.01049	1.05179	4.816	1.47×10^{-6}	↑
	Age of the females	0.03802	0.05318	1.03875	0.715	0.475	
Second visited patch	Previous patch density	0.14683	0.02198	1.15816	6.680	2.38×10^{-11}	↑
	Oviposition	−2.11216	0.32665	0.12098	−6.466	1.01×10^{-11}	↓
	Interaction between oviposition and previous patch density	0.06787	0.02924	1.07023	2.312	0.0203	↑
	Age of the females	−0.04388	0.06118	0.95706	−0.717	0.4732	

SE, standard error.

The increase in residence time on the second patch containing a single host was more important when wasps experienced a patch containing 1 larva before (series D) than when it contained 4 or 16 hosts larvae (series E and F, respectively).

DISCUSSION

The aim of the present study was to determine the different sources of information used to estimate the patch quality and to measure the possible interactions among them on the decision to leave the patch. In our study, we were able to manipulate 2 sources of information leading to an estimate of the patch quality, both effects being reported separately: The information gleaned in the previously visited patch (case of Figure 1, ii) and the information obtained during sampling on the current patch (case of Figure 1, iv). We were able to show that the parasitoid estimates the patch quality relative to that of the previous patch in addition to perceiving the chemical cues on arrival (case of Figure 1, iii) because we observed the foraging behavior in a patch containing the same level of kairomones (regardless of the previous patch and the presence of one larva in the subsequent patch). We showed that prepatch experience strongly influences the responsiveness of *A. tabida* females in a patch containing only kairomones. This variable persistence of a parasitoid to search for hosts in a patch containing only kairomones is evidence of the relative estimate of patch quality on arrival because in our experiment, the effect of this chemical cue is not linked to the sampling in the patch. We also showed that prepatch experience modified the effect of encountering a host on the patch residence time: The poorer the patch seemed, the weaker was the incremental effect. This second result indicated that *A. tabida* females updated their estimate of patch quality during foraging in accordance to their prior estimate.

In a recent study, Thiel and Hoffmeister (2006) showed that host density of the previous patch weakly influences future patch-leaving decision of *A. tabida*, the species used in the present study. In their study, the foraging behavior was observed on patches containing a given number of hosts and the corresponding level of kairomones. The effect of the information obtained on arrival in a patch is confounded with the effects of all the intrapatch events because of the exact correspondence between the strength of the chemical cue and host density in the patch. Our experimental setup demonstrates unsuspected abilities of parasitic wasps to estimate patch quality by integrating different sources of information.

Our results showed that parasitic wasps are able to both accurately estimate the patch quality at arrival and update this estimate by sampling the resource, something so far not demonstrated in other taxa, such as rodents and birds (Valone and Brown 1989). In the case of *A. tabida*, the distribution of *Drosophila* larvae is the result of an aggregation response of *Drosophila* females (Bartelt et al. 1985; Takahashi 2006; Lof et al. 2008). Patches closer to each other are thus more likely to be infested by fruit flies than those further away. As a consequence, we expect *A. tabida* and other *Drosophila* parasitoids to be sensitive to the density of the previous patch (see Outreman et al. 2005) because the expectation to find a patch of a quality similar to that of the previous one is higher than that of finding one that differs considerably in density. Thus, the ability of estimating the initial quality of a given patch, taking previous experience into account, is consistent with the ecology of *A. tabida*. Moreover, the fact that *A. tabida* females linked oviposition to the relative estimate of patch quality is also consistent with its ecological conditions. To corroborate the value of the chemical cue perceived on arrival to the number of hosts in the patch is relevant when cues value vary in space and time. Hilker and McNeil (2008) pointed out that parasi-

toids cope with an "unstable infochemical environment" and need to gain information about the strength of chemical cues.

The information processing demonstrated in our study might require calculation. For example, Iwasa et al. (1981) proposed a Bayesian estimating function of the remaining number of resource items in a patch, which is based on the number of prey encountered at time t in the patch. This model is widely cited in the case of foraging parasitic wasps (for a review, see van Alphen et al. 2003). However, to estimate patch quality in such way is unrealistic and cannot be achieved by cognitive processes of any organism. Pierre (2011) recently demonstrated that a simple mechanism of motivation depending both on the perception of patch quality at arrival and on the number of encounters with resource items (initially proposed by Waage 1979) mimics precisely the theoretical Bayesian solution. This proximate solution implies that the responsiveness of the forager—which is fixed at arrival according to perceived cues of the patch quality—decreases with time and suddenly increases (Waage 1979) at each resource encounter. Such variation in motivation level was demonstrated for many parasitoid species (van Alphen et al. 2003; Wajnberg 2006) and bumblebees (Lefebvre et al. 2007; Biernaskie et al. 2009). Even humans have been shown to use such mechanism in a foraging task (Louâpre et al. 2010). However, this motivation model is simplistic and cannot explain the results of our study. Indeed, in Waage's model, the responsiveness of the forager at arrival in a patch is linearly linked to cues from this patch and is not modified by prepatch experience. Moreover, both the rate of decay in motivation and the responsiveness arousal at each resource encountering are unrelated to prepatch experience. Even if some of our results are in accordance with this proximate mechanism (the residence time in the first patch related to its quality and the incremental effect of the oviposition), we also demonstrated that the motivation function could be modified by prepatch experience. We specifically showed that the increment is tuned by the experience, and we pointed out that further investigations are required to show which other motivation parameters are modified by the experience, taking into account the fact that all the motivation parameters cannot be identified separately (Pierre 2011). It is plausible that memory affects these parameters in foraging parasitic wasps and other organisms and allows them to estimate relative patch quality. Learning and memory are known to be adaptive when a forager needs to retain information from previous patches and retrieves it at arrival in a new patch (Eliassen et al. 2009). However, to be adaptive, the cost of collecting information must be lower than the cost of an inappropriate patch-leaving decision (Dukas 1999; Olsson and Brown 2006). Further research is required to highlight the link between motivation to forage and memory.

All experiments conducted in this study comply with the current laws of France.

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