Parasitoids update the habitat profitability by adjusting the kairomone responsiveness to their oviposition experience

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Abstract. 1. Coping with unpredictability is crucial for insect parasitoids whose fitness depends on their ability to find hosts. One way to optimise their foraging behaviour is to glean information and to update the estimation of the habitat profitability through experience. Kairomone responsiveness (also called 'motivation to stay') is usually seen as a biological variable that reflects the initial estimate of patch quality.

2. In the present study, an experiment was performed to test if the kairomone responsiveness of *Asobara tabida* Nees females (Hymenoptera: Braconidae) at arrival in a patch is specifically influenced by the number of hosts previously encountered in a series of patches of different qualities, thus highlighting their ability to estimate habitat profitability.

3. *Asobara tabida* females keep trace of the number of hosts previously encountered in prior patches and adjust their foraging behaviour in the next, regardless of the kairomone level perceived in these patches. First, these results demonstrate the ability of parasitoids to estimate the relative patch quality on the basis of the number of hosts previously encountered. Second, they provide new insight into how parasitoids handle information from patch to patch. This ability is discussed in an evolutionary context.

Key words. *Asobara tabida*, foraging behaviour, habitat profitability, kairomones, parasitoid, responsiveness.

Introduction

Insect parasitoids face a major challenge to ensure their fitness: hosts are generally hidden in patches and they have to locate and to select hosts before ovipositing. To maximise their oviposition rate during their life time involves optimising the time spent in each of the visited patches according to the environment profitability (Charnov, 1976). Parasitoids behave as if they update patch assessment relative to the previously visited ones, and adjust their residence time on subsequent patches accordingly, thus showing a consistency between optimal predictions and the observed behaviour (Thiel & Hoffmeister, 2004, 2006; Tentelier *et al.*, 2009; Louâpre *et al.*, 2011). They are obviously not able to have a quantitative estimation of a patch quality, even less so, its value relative to the other patches. One main current

challenge for researchers is thus to highlight how parasitoids perceive, store, and use information from their environment in order to behave efficiently (Louâpre *et al.*, 2011; Goubert *et al.*, 2013).

Kairomones (infochemicals emitted by the hosts) (see Rutledge, 1996 for a review of the chemical composition of kairomones) and the number of hosts encountered in the patch are known to be used by parasitoids to behave as if they estimate the environment profitability (reviewed Wajnberg, 2006). For example, *Asobara tabida* Nees females (Hymenoptera: Braconidae) react to water-soluble kairomones produced by *Drosophila* larvae by increasing their searching time with the kairomones concentration (Galis & van Alphen, 1981, van Alphen & Galis, 1983). The aerial concentration of kairomones is thus one main environment indicator on which parasitoids may base their estimation-like process of environment profitability (Louâpre *et al.*, 2011). They also respond to the number of larvae encountered in a patch by decreasing their tendency to

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Table 1. The experimental design.

	Patch rank	Control series		Test series	
		Kairomones' level[*]	Number of larvae in the patch	Kairomones' level[*]	Number of larvae in the patch
Initial conditioning	1	10	10	10	10
Confirmation or modification of the cue's reliability	2	10	10	10	4
	3	10	10	10	4
Response in a patch with kairomones only	4	10	0	10	0

[*]Relative to the number of larvae kept in the patch during 24 h.

leave it at each oviposition. The estimation-like process of environment profitability is thus updated at each larva encountered (Louâpre *et al.*, 2011).

The confounding effects of kairomones and host encounters make it difficult to test if the number of hosts previously encountered in the last patches is information that modulated the kairomone responsiveness regardless of other cues. Only Louâpre *et al.* (2011) and Froissart *et al.* (2012) recently disentangled the effect of several cues and identified which of them influence the decision to leave the patch. The specific purpose of the present study was to test whether the kairomone responsiveness of *A. tabida* females is influenced by the number of hosts previously encountered in a series of patches. Such information is indeed sufficient to influence the decision to leave the subsequent patch, regardless of the plausible effect of kairomones emitted from these patches. Here, the patch time duration was observed in a four-patch series containing a constant amount of kairomones and a various number of hosts. The fourth patch contained only kairomones in order to test whether the number of hosts laid in prior patches modifies the kairomone responsiveness at arrival in it. With this procedure, the variations of the last patch residence time can be attributed separately either to influence egg-laying in previous patches or to the kairomone level perceived in previous patches.

Materials and methods

The biological material

Asobara tabida females were mated at emergence and kept at 12 °C with 20% diluted honey during 4–5 days (see Louâpre & Pierre, 2012 for a complete description of the rearing). One day before the experiment, females were allowed to oviposit in a patch containing 15 *Drosophila subobscura* second instar larvae during 2 h at 20 °C to select only females that actually lay eggs (van Alphen & Drijver, 1982). Responsive females were then kept at 20 °C during 1 day with 20% diluted honey until the experiment.

The experiment

We observed the foraging behaviour of females in a series of four artificial patches in the lab containing the same level of kairomones and a different number of larvae. The preparation of the patches containing baker's yeast in Petri dishes was the one used by Louâpre *et al.* (2011). A patch of baker's yeast (Ø = 2 cm) was deposited at the centre of a clean Petri dish (Ø = 5 cm) covered by a thin agar layer. Ten second instar larvae were allowed to feed and crawl in this medium. After 24 h, some of the larvae were removed or not in order to prepare patches with a given level of kairomones and a different number of larvae.

Two batches of 15 females each were first introduced in patches containing 10 larvae. One batch was assigned to the control series with two patches containing 10 larvae and the other batch was assigned to the test series, with two patches containing only four larvae. All the females were then introduced in a fourth patch containing only kairomones emitted by 10 larvae (Table 1).

Each female was introduced in the first patch of one of the two series and was considered to exit the patch when she tried to migrate by the lid or when she left the yeast' patch for more than 60 s. The female was then isolated in a clean Petri dish for 10 min with sugar water before being introduced in the subsequent patch. For each visited patch of the two series, we recorded in real time the patch residence time and oviposition with the event recording program The Observer (Noldus 3.0, 2000). Patch residence time, number of ovipositions, and time to find hosts were analysed using Wilcoxon's rank sum tests (noted W) at a critical level of $\alpha = 0.05$. Wilcoxon's signed rank tests were applied to compare individuals from the same series in two different patches (noted V). Statistical analyses were performed using R 2.14.0 software.

Results and Discussion

The environment profitability updating

Females that experienced poor patches reduced their residence time in the third patch in comparison to the second one (V = 119, $P < 0.001$) (Fig. 1a). They reduced their residence time in the last patch in comparison with the control females (W = 16, *P*-value < 0.001). These data are consistent with a Bayesian updating process of habitat profitability using the number of hosts previously encountered (Waage, 1979; Iwasa *et al.*, 1981; Louâpre *et al.*, 2011; Pierre, 2011). Having experienced a series of poor patches, the relative estimate of the mean patch quality
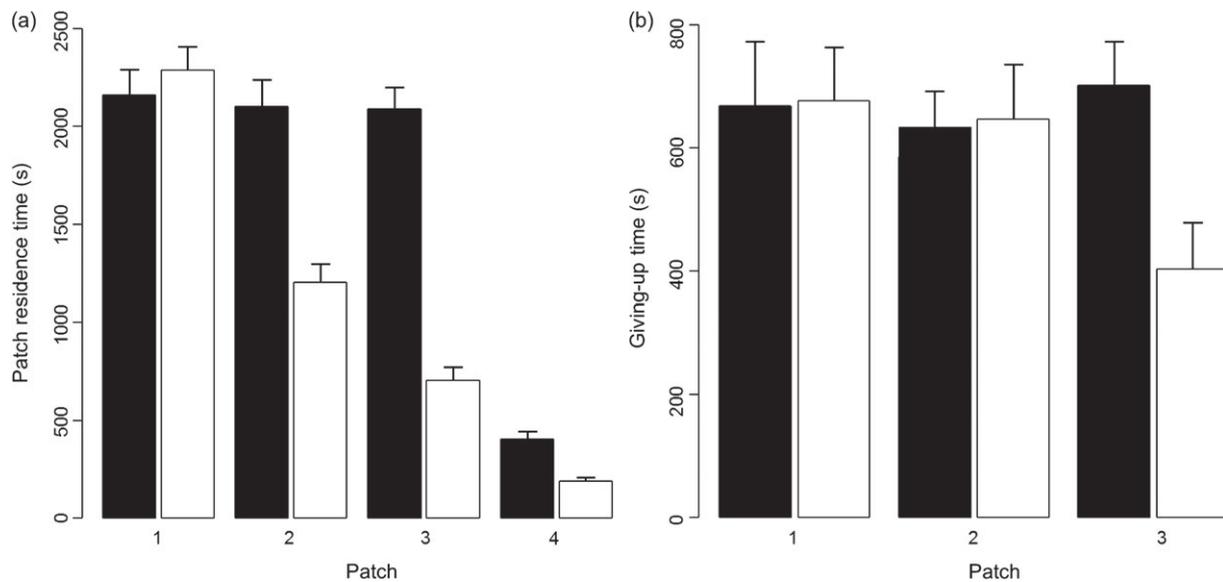
Fig. 1. (a) Residence time and (b) giving-up time of *Asobara tabida* females in the four patches of the control series (black) and the test series (white). See Table 1 for the content of the patches. $N = 15$ for each series. Error bars: standard errors.

is low on arrival to the last patch in comparison to females that visited rich patches. In contrast, females of the control series stayed a constant time in the two intermediate patches after having laid the same number of eggs ($V = 61$, $P = 0.978$) (Fig. 1a). Such an inflexible behaviour was already observed on another species, when the habitat profitability is unchanged among patches (Tentelier *et al.*, 2009).

The foraging theory predicts an increase in foraging effort inside patches when the average patch quality decreases (Charnov, 1976; Stephens & Krebs, 1986). In our experiment, the foraging effort in patches containing hosts may be given by the giving-up time (i.e. the time between the last oviposition and the patch departure) (Fig. 1b). The giving-up time of females did not differ between the two series in the second patch ($W = 133$, $P = 0.412$) whereas it was reduced in the third one for the test series ($W = 48$, $P < 0.01$). The decrease in environment quality in the two intermediate poor patches could be responsible for the decrease of the giving-up time: females decide to leave patches quickly after having perceived a decrease in environment profitability. We note that such adaptive behaviour is observed not directly in the second patch but in the third, thus showing that the environment profitability updating is performed after leaving the second patch.

The underlying mechanism of information handling

Egg depletion, kairomone habituation or learning may be involved in the environment profitability updating observed here. Thiel and Hoffmeister (2004) proposed that *A. tabida* females use an 'egg-load timer mechanism' that mimics the environment profitability updating. Here, the mean number of ovipositions did not differ significantly between patches 2 and 3 for control females: each female laid 9.5 ± 1.5 eggs on average in each patch ($V = 11$, *P*-value $= 0.354$). Similarly,

the mean number of ovipositions did not differ significantly between these patches for the females of the test series: each female laid 3.8 ± 1.3 eggs on average in each patch ($V = 40$, *P*-value $= 0.554$). Moreover, the total number of eggs laid by females of the control and the test series at the end of the experiment (respectively, 28.13 ± 3.89 eggs and 17.87 ± 2.59 eggs) is small compared with the lifetime potential fecundity of *A. tabida*, estimated at more than 400 eggs (Vayssade *et al.*, 2012). We thus exclude the hypothesis of an egg load effect in our experimental condition. A mechanism based on kairomone habituation was also proposed to explain the adaptive behaviour of parasitoids during foraging: Tentelier *et al.* (2006) suggest that the motivation to stay in a subsequent patch after having visited a rich patch is reduced because parasitoids are desensitised to kairomones. This does not fit our data: the females who stayed longer in the last fourth patch containing only kairomones (the more responsive females) are those who were longer exposed to kairomones in the rich patches. The patch quality assessment could thus imply different mechanisms of kairomone habituation and memory in parasitoids. We showed recently (Louâpre & Pierre, 2012) that foraging in a given patch influences the behaviour of *A. tabida* in the next one and that such an effect involves the short-term memory. The present data suggest that the specific information stored by *A. tabida* females consists of the number of hosts encountered in previous patches.

An adaptive behaviour using selective information

Our data demonstrate a progressive tuning of the quantitative meaning of infochemical according to the quality of the previous visited patches. Such ability appears to be adaptive in the environment in which parasitoids evolve. Indeed, modification of kairomone responsiveness is viewed as an adaptation to the variable reliability of available information

(Schurmann *et al.*, 2009). A fixed behavioural response to kairomones is not optimal in an environment in which patch quality vary in time and space, and therefore the cognitive ability to update cues' reliability, arising from information integration, seems to be more adaptive. Natural selection could thus have shaped cue preference to the most relevant ones but has also tailored abilities of updating the quantitative meaning of these cues in the presence of a variable infochemical environment. This is a clear case of cognitive flexibility.

Acknowledgements

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