Carbon dioxide narcosis modifies the patch leaving decision of foraging parasitoids
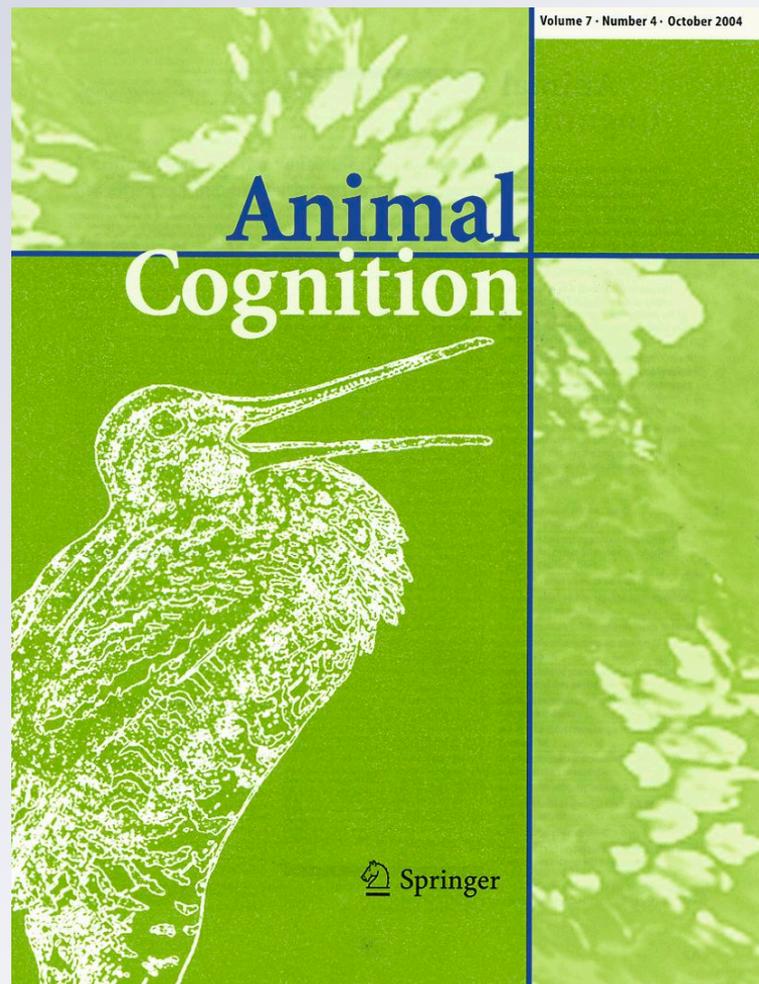
Philippe Louâpre & Jean-Sébastien Pierre

Volume 7 · Number 4 · October 2004

Animal Cognition

Springer

Springer

Springer

SHORT COMMUNICATION

Carbon dioxide narcosis modifies the patch leaving decision of foraging parasitoids

Philippe Louâpre · Jean-Sébastien Pierre

Abstract Gleaning information is a way for foragers to adjust their behavior in order to maximize their fitness. Information decreases the uncertainty about the environment and could help foragers to accurately estimate environmental characteristics. In a patchy resource, information sampled during previous patch visits is efficient only if it is retained in the memory and retrieved upon arrival in a new patch. In this study, we tested whether the braconid *Asobara tabida*, a parasitoid of *Drosophila* larvae, retains information gleaned on patch quality in the memory and adjusts its foraging behavior accordingly. Females were anesthetized with CO_2 after leaving a first patch containing a different number of hosts and were allowed to visit a second patch containing only kairomones. CO_2 is known to erase unconsolidated information from the memory. We show that in the absence of a short CO_2 narcosis, females responded according to their previous experience, whereas anesthetized females did not. The anesthetized females stayed a given time in the second patch irrespective of what they encountered before. CO_2 narcosis had no effect on the residence time of the non-experienced females in a patch containing hosts or only kairomones in comparison with the non-anesthetized females that had a previous foraging experience. We conclude that CO_2 narcosis erases the effect of the previous patch quality, perhaps due to a memory disruption. Direct information processing is likely to be involved in parasitoid decision making through retention of the information on the previous patch quality into a CO_2 sensitive memory.

P. Louâpre (✉) · J.-S. Pierre
UMR CNRS no. 6553 "Ecologie—Biodiversité—Evolution",
Université de Rennes 1, Campus de Beaulieu, Bâtiment 14A,
Avenue du Général Leclerc, 35042 Rennes Cedex, France
e-mail: philippe.louapre@mail-univscience.com

Introduction

Faced with a patchily distributed resource, foragers may optimize their resource intake rate by adjusting residence time on patch quality (Charnov 1976). A forager should leave a patch when the instantaneous resource intake falls below the average gain in the environment in order to maximize its yield (Marginal Value Theorem, Charnov 1976). Naïve foragers should initially use genetically fixed knowledge about the environment as this "marginal threshold". McNamara and Houston (1985, 1987) showed that foragers could also use experience to reach the optimal decision without being omniscient. More generally, information helps the forager to estimate both local parameters, patch quality (Iwasa et al. 1981; Green 1980; Olsson and Brown 2006) and large-scale modifications of the habitat conditions (Mangel 1990). For example, only two key pieces of information are needed to estimate the average rate of gain in the habitat: interpatch travel time and the quality of the previous patches (Tentelier et al. 2006). This information is gleaned during the forager's experience.

In order to accurately estimate habitat features, information learned from patch to patch should be stored in the memory and retrieved upon arrival in a new patch (Dunlap et al. 2009). Learning consists of three distinct stages: the acquisition of information, its storage in the memory and its retrieval, leading to behavioral alteration (Kawecki 2010). Both learning and memory decrease the uncertainty about the habitat at different scales and allow adaptive phenotypic plasticity (Oaten 1977; McNamara and Houston 1985; Stephens and Krebs 1986; Real 1992; Agrawal 2001;

Dukas 2004; Dall et al. 2005; Vásquez et al. 2006). The memory dynamic is related to the spatial and temporal variability of the environment, depending on the reliability of the perceived information (Kerr and Feldman 2003; Eliassen et al. 2009). A short-term retention of information is favored in rapid temporal and/or spatial changes in the environment and when information about the patch is accurate at a certain moment but unstable over a long period of time. Conversely, stable but heterogeneous environments make the long-term retention of information more useful for foragers (Eliassen et al. 2009). Such cognitive abilities are widespread in the animal kingdom (Shettleworth 1993, 2001; Dukas 2004, 2008) and have been extensively studied in insects such as fruitflies, honeybees, bumblebees or parasitoid species (Vet et al. 1995; Menzel and Müller 1996; Menzel 1999; Margulies et al. 2005; Barron 2009; Hoedjes et al. 2011). In insects, the retention of information could last from minutes to days or even longer depending on the situation in which the memory is implied. In bumblebees for example, short-term memory involves during intrapatch and interpatch foraging, whereas interbout travel involves the long-term retention of information (Menzel 1999; Raine and Chittka 2007).

Here, we studied whether information acquisition in a patch is retained during its exploitation and is retrieved in a subsequent patch by a hymenopteran parasitoid that lays eggs in hosts. In such foragers, both learning and memory are likely to be decisive because their foraging success is directly linked to fitness (Godfray 1994). Parasitoids have to cope with a variable patchy host resource. Thus, remembering what was encountered in previous patches could help them to more accurately estimate both the subsequent patch quality and the average patch quality in the environment. Many parasitoid species have been shown to modify their decision to leave a patch according to their off-patch experience, such as interpatch travel time and previous patch quality (Visser et al. 1992; Wajnberg et al. 2006; Outreman et al. 2005; van Baaren et al. 2005a, b; Tentelier et al. 2006; Thiel and Hoffmeister 2006; Muratori et al. 2008; Thiel 2011). Taking this into consideration, it is expected that parasitoids could use memory to retain quantitative information about the previous visited patch in order to assess the subsequent patch quality relatively.

One way to highlight the dynamic cognitive process of memorization in insects is to disrupt it by carbon dioxide narcosis (Kohler et al. 1999). CO_2 is known to have various effects on the behavioral, physiological and metabolic characteristics of insects (Nicolas and Sillans 1989), as already shown in fruitflies (Barron 2000; Brade et al. 2005) and parasitoid rove beetles (Lizé et al. 2009). Focusing on memory, CO_2 narcosis specifically erases some forms of unconsolidated memory and often impairs the memorization of recent events (Lovell and Eisenstein 1973; Breed

1981). We used this property to test whether a foraging parasitoid retains information gleaned from patch to patch in an anesthesia-sensitive memory. All of the retained information at least passes into an anesthesia-sensitive short-term memory; however, we must point out that the CO_2 narcosis does not allow to test whether this information eventually passes into a long-lasting memory such as a protein-synthesis-dependent memory.

We carried out experiments on *Asobara tabida* females (Hymenoptera: Braconidae), which lay their eggs in *Drosophila* larvae aggregated over fermenting substrates such as fruit or sap fluxes (Ellers et al. 2001). *Asobara tabida* females are attracted by so-called kairomones which are any product emitted by hosts during their life and used by parasitoids to their advantage (e.g., feces and molting). In a recent study, Louâpre et al. (2011) observed that the density of the previous patch modified the decision to leave the subsequent patch containing only kairomones: the richer the previous patch, the shorter the residence time in the subsequent one. Behavior on empty patches can nicely mirror changes in parasitoid search motivation (Thiel and Hoffmeister 2009) because the motivation to stay in such patch is only linked to the responsiveness to kairomones, not to host encounter or oviposition. We tested the effect of CO_2 narcosis on experienced females foraging on a patch containing only kairomones. We first tested whether the narcosis procedure alters the foraging behavior of *A. tabida* females without any recent foraging experience. Then, we tested whether the CO_2 anesthesia affects the decision of the experienced females to leave the patch according to the quality of the previously visited patch.

Materials and methods

Biological material

The *Asobara tabida* strain used in this study was collected in Chasse-Sur-Rhône (France, 45°34′N, 4°48′E) in September 2008 and reared in the laboratory on *Drosophila subobscura* hosts that were collected in the Netherlands in 1980. Every female was mated just after emergence and stored at 12°C until the experiment to erase age effect by decreasing metabolic rate. Low temperature exposure induces changes in the foraging behavior of insects (van Baaren et al. 2005a, b; Wilson et al. 2006), but each female was subjected to the same stored condition in our experiment. One day prior to the experiment, the naive 3–5-day-old females were allowed to search and oviposit in a pre-experimental patch containing 20-s-instar *Drosophila* larvae. This procedure ensured that each wasp used responded to the kairomones emitted by the hosts and exhibited an ovipositing behavior. The females that laid

Table 1 The experimental setup

Experiment	Series	CO$_2$ narcosis before the first patch	Patch 1		CO$_2$ narcosis before the second patch	Patch 2	
			Kairomone level*	Host density		Kairomone level*	Host density
1	A	–	4	0			
	B	✔	4	0			
	C	–	4	4			
	D	✔	4	4			
2	E	–	1	1	–	4	0
	F	–	1	1	✔	4	0
	G	–	4	4	–	4	0
	H	–	4	4	✔	4	0
	I	–	16	16	–	4	0
	J	–	16	16	✔	4	0

* Given by the number of host larvae that produced kairomones during 24 h

eggs were then kept at 20°C with sugar water until the experiment. The combinations of treatments for the two experiments are summarized in Table 1.

Experiment 1 (control): CO$_2$ narcosis effect on the females without recent foraging experience

We first tested whether CO$_2$ narcosis affected the decision to leave a patch in foraging females that had not experienced any patches since their emergence except the pre-conditioning patch. The patches used in the experiment consisted of a viscous suspension of baker's yeast (200 µl of fresh water containing 80 mg of yeast) laid on a Petri dish (Ø = 5 cm) containing a thin agar layer. This viscous suspension was enclosed in a Perspex ring (Ø = 2 cm) placed in the center of the Petri dish, thus preventing larvae from escaping. Four second-instar *D. subobscura* larvae (4 days old, length ≈ 2 mm) were introduced in a similar patch 24 ± 1 h before the experiment to ensure the presence of kairomones. The Perspex ring surrounding the patch was then removed just before the beginning of the experiment. This patch thus contained both the larvae and the corresponding amount of kairomones (van Alphen and Galis 1983). Before visiting the patch, half of the females were individually placed in a glass tube (Ø = 2 cm, *h* = 5 cm) that was covered with a foam cork. A constant 100% CO$_2$ flow was introduced in the tube for 5 s. The anesthetized females were then isolated in a clean Petri dish with sugar water for 10 min in order to recover before being introduced into the patch. The other half of the females was used as a control (they were not anesthetized) and subjected to exactly the same sequence, except for the CO$_2$ treatment.

We also tested whether the CO$_2$ narcosis specifically affected the ability of the naive females to evaluate the patch quality through the kairomone level perceived upon arrival in the patch, regardless of what they encounter during its exploitation. In this second control, both the Perspex ring and the four larvae were removed just before the experiment. Thus, the patch only contained a kairomone level corresponding to the four larvae but did not contain any larvae. Half of the females that visited this patch were also anesthetized before, as detailed above.

Experiment 2: CO$_2$ narcosis effect on the memory of the previous patch quality

We tested the ability of the females subjected to the CO$_2$ treatment to assess patch quality upon arrival in a patch, relatively to a previously visited patch. The females visited two successive patches with a constant interpatch delay of 10 min. The first patch contained either 1, 4 or 16 larvae and the second patch only contained a kairomone level corresponding to four larvae, but did not contain any larvae. With these three levels, the second patch was either less, equally or more profitable than the first patch. Half of the females were individually anesthetized immediately after leaving the first patch. The females were isolated in a clean Petri dish with sugar water for 10 min before being introduced into the second patch.

Data collection and statistical analyses

For each of the visited patches in the two experiments, we continuously observed the foraging behavior of the females. We recorded the time spent in a patch, the number of ovipositions and the frequency of oviposition when the patch contained larvae, with the event recorder The Observer® (Noldus 3.0). The exploitation of the patch was considered to be finished when the female left the patch for more than 60 s or when she attempted to migrate by the lid. Fourteen to 16 females were tested per treatment. Our data
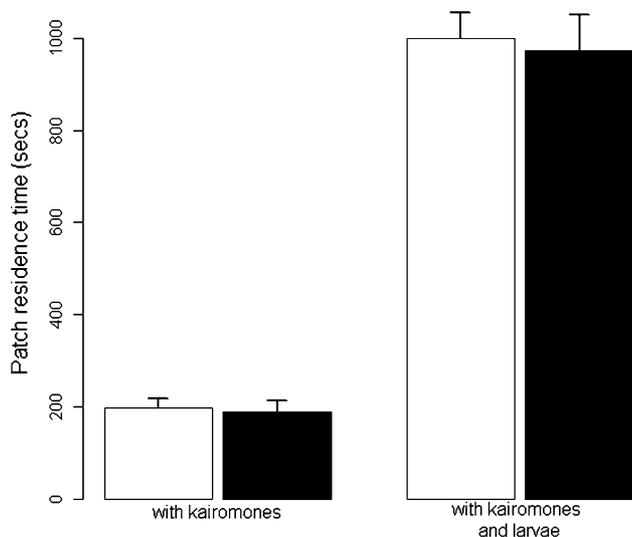
Fig. 1 Patch residence time of naive *A. tabida* females after CO_2 narcosis (*black bars*) or not (*white bars*). The visited patch either contained kairomones only, corresponding to four larvae, or kairomones plus four larvae. $N = 15$ for each treatment. *Error bars*: standard errors
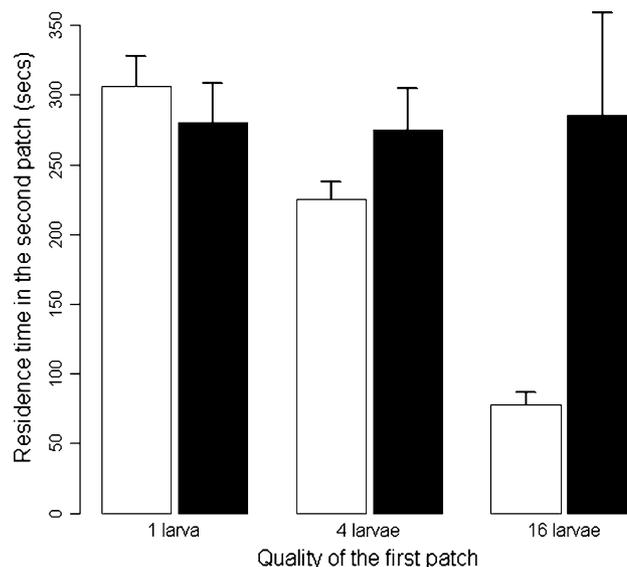

Fig. 2 Residence time in the second patch containing only kairomones emitted by four larvae as a function of the quality of the previous patch visited by *A. tabida* females. These females were either anesthetized (*black bars*) or not (*white bars*) after leaving the first patch. $N = 14$–16 for each treatment. *Error bars*: *standard errors*

did not follow a normal distribution, and therefore, we used Generalized Linear Models (GLM) for the analysis. A gamma distribution with an inverse link function was used to analyze the patch residence times and the frequency of oviposition, whereas a Poisson distribution with a log link function was used to analyze the oviposition occurrences. The combination of factors included in the models is given for each result. The mean residence times are given with the standard errors in Figs. 1, 2. All of the analyses were carried out using the R 2.11 software.

Results

Experiment 1 (control): CO_2 narcosis effect on foraging behavior of females without recent foraging experience

The residence time in a patch that contained four larvae was higher than in a patch that contained only the related amount of kairomones, whereas CO_2 narcosis did not have any significant effect on the residence time in both patches (presence of larvae: $F_{1,57} = 242.18$, $P < 0.001$; anesthesia: $F_{1,58} = 0.09$, $P = 0.76$; presence of larvae × anesthesia: $F_{1,56} = 0.08$, $P = 0.77$) (Fig. 1).

In patches that contained both larvae and the related amount of kairomones, CO_2 narcosis did not have any significant effect on the number of ovipositions (anesthesia: $F_{1,28} = 6.3016$, $P = 0.70$), nor on the number of hosts parasitized per time unit (anesthesia: $F_{1,28} = 0.8572$, $P = 0.3624$). Both anesthetized and control females laid on average 3.66 ± 0.16 eggs in the patch containing four larvae at a rate of 0.236 ± 0.014 eggs per minute.

Experiment 2: CO_2 narcosis effect on the memory of the previous patch quality

The effect of the previous patch quality on the residence time depends on the CO_2 treatment (interaction between the previous patch quality and the CO_2 treatment: $F_{5,83} = 21.108$, $P < 0.001$). The quality of the previously visited patch strongly influenced the residence time of the non-anesthetized females in the second patch containing kairomones emitted by four larvae (previous patch quality: $F_{2,42} = 5.1289$, $P < 0.001$) (Fig. 2). After CO_2 narcosis, the quality of the previous patch did not influence the second patch residence time (previous patch quality after anesthesia: $F_{2,41} = 9.1768$, $P = 0.9717$) (Fig. 2). The residence time of CO_2-anesthetized females in patches containing only kairomones in experiment 2 was longer than in the similar patch used in experiment 1 ($t = -2.81$, $P < 0.01$): on average, the experienced females stayed 279.91 ± 28.62 s, while the naive females stayed 187.35 ± 25.56 s.

Discussion

Our results show that *A. tabida* females do not respond to previous patch density in a subsequent patch containing only kairomones after a short CO_2 narcosis. They stay a given time in the second patch regardless of what they encountered before. In contrast, non-anesthetized females adjust their residence time in the second patch according to

what they encountered before. The more hosts they encountered in the previous patch, the less time they stay in the subsequent patch.

Our results highlight some aspects of the use of information by *A. tabida* females estimating patch quality upon arrival on the patch. In parasitoid wasps and other insects, foragers are assumed to enter a patch with an initial attractiveness to resource cues (reviewed in van Alphen et al. 2003; Wajnberg 2006). Because the initial level of attractiveness for kairomones is related to the number of hosts potentially present in the patch, this level has been viewed as a prior estimate of the patch quality (Waage 1979; Iwasa et al. 1981). It was recently shown that the previous patch density strongly influences the responsiveness to kairomones of *A. tabida* females, which estimate the patch quality relatively to their pre-patch experience (Louâpre et al. 2011). We show here that after being anesthetized, females do not respond to the previous patch density and stay a given time in the second patch containing only kairomones. The residence time thus is related only to host-associated cues, providing information on the apparent quality of the patch. CO_2 may alter the ability of the wasp to take past experience into account in order to evaluate the patch quality. Under this hypothesis, information on the previous patch quality could be erased by the narcosis treatment, and the wasps thus behave as if they have forgotten this information. In habitats favorable for *A. tabida*, fermenting fruit contains different numbers of host larvae (Ellers and van Alphen 1997). According to Thiel and Hoffmeister (2004), the travel time between fermenting fruit containing hosts only lasts a few minutes. Thus, the patch quality varies in space and time, and rapid modifications of resource distribution occur at the scale of a parasitoid lifetime. Eliassen et al. (2009) showed that the gain achieved by a learning forager depends on stochasticity in resource encounters, variability in patch distribution and trends in the habitat. To base the decision to leave a patch according to recent experience may be adaptive in the case where latest foraging events provide reliable information about the state of the habitat (Real 1991, 1992), as is the case in the favorable end of the range of habitats in which *A. tabida* evolved. However, in other *A. tabida* habitats, with lower patch density than in fermenting fruit, such as sap trees, a larger temporal retention of information could be more adaptive than a short-term one (Eliassen et al. 2009). Whether *A. tabida* females are capable of long-term retention of their previous experience remains unknown, but our results clearly give insights on their ability to retain and use their previous experience on the short term. It could be plausible that information about the previous patch passes into a long-term memory requiring protein synthesis, but further investigation is required to test the hypothesis of a larger temporal memory.

In our experiment, CO_2 narcosis affects the decision of experienced *A. tabida* females to leave the patch and has no observable effect on the foraging behavior of the naive parasitoids. However, when only kairomones were offered to CO_2 treated females, either experienced or not, the experienced females stayed longer in a patch containing only kairomones than the naive females. The difference in the patch residence time is observed between two independent experiments, many experimental artifacts could be responsible for such observation, and no definitive conclusion can be drawn from this comparison. We hypothesize that CO_2 did not completely erase the effect of previous patch experience on the decision of experienced females to leave the subsequent one. Another mechanism, not based on CO_2-sensitive memory, is likely to be involved in our experiment. Both habituation to kairomones or fatigue have been mentioned to explain an early pre-patch response of *A. tabida* (van Alphen and Galis 1983) by reducing the residence time in the subsequent patch. In our case, the opposite effect is found, and such mechanisms are unlikely to explain our results. Driessen and Hemerik (1992) and Casas et al. (2000) showed that egg load also influences the foraging behavior of parasitoids. In our experiment, anesthetized females that had laid a different number of eggs in the previous patch stayed a constant amount of time in the subsequent one. It seems unlikely that the lack of previous patch response after CO_2 narcosis is due to egg depletion; however, our results tend to show that ovipositing in a previous patch—regardless of the number of times—affects the decision to leave the subsequent patch by a CO_2-resistant process other than the ones mentioned above. To have a recent ovipositing experience could induce physiological changes not linked to memory. This physiological modification could explain the behavioral response observed in *A. tabida* females.

To conclude, a short CO_2 treatment modified the decision to leave the patch for female *A. tabida* in our experiment, erasing the quantitative effect of the previous patch quality. This suggests that CO_2-sensitive memory mechanism is involved in the decision-making process that determines when to leave a patch. Further empirical investigations are necessary to completely define the memorization processes occurring during foraging in parasitoid.

References

Agrawal AA (2001) Phenotypic plasticity in the interactions and evolution of species. Science 294:321–326

Barron AB (2000) Anaesthetising Drosophila for behavioural studies. J Insect Physiol 46:439–442

Barron AB (2009) Learned host preferences. In: Whitman DW, Ananthakrishnan TN (eds) Phenotypic plasticity of insects: mechanisms and consequences. Science Publishers, Plymouth, p 894

Brade NH, Martin ME, Cooper RL (2005) The physiological and behavioral effects of carbon dioxide on *Drosophila melanogaster* larvae. Comp Biochem Physiol 140:363–376

Breed MD (1981) Individual recognition and learning of queen odors by worker honeybees. Proc Natl Acad Sci USA 78:2635–2637

Casas J, Nisbet RM, Swarbrick S, Murdoch W (2000) Eggload dynamics and oviposition rate in a wild population of a parasitic wasp. J Anim Ecol 69:185–193

Charnov E (1976) Optimal foraging, the marginal value theorem. Theor Popul Biol 9:129–136

Dall SRX, Giradleau LA, Olsson O, McNamara JM, Stephens DW (2005) Information and its use by animals in evolutionary ecology. Trends Ecol Evol 20:187–193

Driessen G, Hemerik L (1992) The time and egg budget of *Leptopilina clavipes*, a parasitoid of larval *Drosophila*. Ecol Entomol 17:17–27

Dukas R (2004) Evolutionary biology of animal cognition. Annu Rev Ecol Evol Syst 35:347–374

Dukas R (2008) Evolutionary biology of insect learning. Annu Rev Entomol 53:145–160

Dunlap AI, McLinnb CM, MacCormicke HA, Scottd ME, Kerre B (2009) Why some memories do not last a lifetime: dynamic long-term retrieval in changing environments. Behav Ecol 20:1096–1105

Eliassen S, Jørgensen C, Mangel M, Giske J (2009) Quantifying the adaptive value of learning in foraging behavior. Am Nat 174:478–489

Ellers J, van Alphen JJM (1997) Life history evolution in *Asobara tabida*: plasticity in allocation of fat reserves to survival and reproduction. J Evol Biol 10:771–785

Ellers J, Bax M, van Alphen JJM (2001) Seasonal changes in female size and its relation to reproduction in the parasitoid *Asobara tabida*. Oikos 92:309–314

Godfray HCJ (1994) Parasitoids: behavioral and evolutionary ecology. Princeton Univ Press, Princeton

Green RF (1980) Bayesian birds: A simple example of Oaten's stochastic model of optimal foraging. Theor Popul Biol 18:244–256

Hoedjes KM, Martinus MK, Huigens ME, Dicke M, Vet EM, Smid HM (2011) Natural variation in learning rate and memory dynamics in parasitoid wasps: opportunities for converging ecology and neuroscience. Proc Royal Society B 278:889–897

Iwasa Y, Higashi M, Yamamura N (1981) Prey distribution as a factor determining the choice of optimal foraging strategy. Am Nat 117:710–723

Kawecki TJ (2010) Evolutionary ecology of learning: insights from fruit flies. Pop Ecol 52:15–25

Kerr B, Feldman MW (2003) Carving the cognitive niche: optimal learning strategies in homogeneous and heterogeneous environments. J Theor Biol 220:169–188

Kohler I, Meier R, Busato A, Neiger-Aeschbacher G, Schatzmann U (1999) Is carbon dioxide (CO_2) a useful short acting anaesthetic for small laboratory animals? Lab Anim 33:155–161

Lizé A, Clément J, Cortesero AM, Poinsot D (2009) Kin recognition loss following anesthesia in beetle larvae (*Aleochara bilineata*, Coleoptera, Staphylinidae). Anim Cog 13:189–194

Louâpre P, van Baaren J, Pierre JS, van Alphen JJM (2011) Information gleaned and former patch quality determine foraging behavior of parasitic wasps. Behav Ecol. doi:10.1093/beheco/arr090

Lovell KL, Eisenstein E (1973) Dark avoidance learning and memory disruption by carbon dioxide in cockroaches. Physio and Behav 10:835–840

Mangel M (1990) Dynamic information in uncertain and changing worlds. J Theor Biol 146:317–332

Margulies C, Tully T, Dubnau J (2005) Deconstructing memory in *Drosophila*. Current Biol 15:700–713

McNamara JM, Houston AI (1985) Optimal foraging and learning. J Theor Biol 117:231–249

McNamara JM, Houston AI (1987) Memory and the efficient use of information. J Theor Biol 125:385–395

Menzel R (1999) Memory dynamics in the honeybee. J Comp Physiol A 185:323–340

Menzel R, Müller U (1996) Learning and memory in honeybees: from behavior to neural substrates. Ann Rev Neuro 19:379–404

Muratori F, Boivin G, Hance T (2008) The impact of patch encounter rate on patch residence time of female parasitoids increases with patch quality. Ecol Entom 33:422–427

Nicolas G, Sillans D (1989) Immediate and latent effects of carbon dioxide on insects. Ann Rev Entom 34:97–116

Oaten A (1977) Optimal foraging in patches: case for stochasticity. Theor Pop Biol 12:263–285

Olsson O, Brown JS (2006) The foraging benefits of information and the penalty of ignorance. Oikos 112:260–273

Outreman Y, Le Ralec A, Wajnberg E, Pierre JP (2005) Effects of within- and among-patch experiences on the patch-leaving decision rules in an insect parasitoid. Behav Ecol Sociobiol 58:208–217

Raine NE, Chittka L (2007) Pollen foraging: learning a complex motor skill by bumblebees (*Bombus terrestris*). Naturwissenschaften 94:459–464

Real LA (1991) Animal choice behavior and the evolution of cognitive architecture. Science 253:980–986

Real LA (1992) Information processing and the evolutionary ecology of cognitive architecture. Am Nat 140:108–145

Shettleworth SJ (1993) Varieties of learning and memory in animals. J Exp Psychol Anim Behav Proc 19:5–14

Shettleworth SJ (2001) Animal cognition and animal behaviour. Anim Behav 61:277–286

Stephens DW, Krebs JR (1986) Foraging theory. Princeton University Press, Princeton

Tentelier C, Desouhant E, Fauvergue X (2006) Habitat assessment by parasitoids: mechanisms for patch use behavior. Behav Ecol 17:515–521

Thiel A (2011) How to measure patch encounter rate: decision-making mechanisms in the parasitic wasp *Asobara tabida*. Anim Cog 14:73–82

Thiel A, Hoffmeister TS (2004) Knowing your habitat: linking patch-encounter rate and patch exploitation in parasitoids. Behav Ecol 15:419–425

Thiel A, Hoffmeister TS (2006) Selective information use in parasitoid wasps. Anim Biol 56:233–245

Thiel A, Hoffmeister TS (2009) Decision-making dynamics in parasitoids of *Drosophila*. Adv Parasitol 70:45–66

van Alphen JJM, Galis F (1983) Patch time allocation and parasitization efficiency of *Asobara tabida*, a larva parasitoid of Drosophila. J Anim Ecol 52:937–952

van Alphen JJM, Bernstein C, Driessen G (2003) Information acquisition and time allocation in insect parasitoids. Trends Ecol Evol 18:81–87

van Baaren J, Boivin G, Outreman Y (2005a) Patch exploitation strategy by an egg parasitoid in constant or variable environment. Ecol Entomol 30:502–509

van Baaren J, Outreman Y, Boivin G (2005b) Effect of low temperature exposure on oviposition behaviour and patch exploitation strategy in parasitic wasps. Anim Behav 70:153–163

Vásquez RA, Grossi B, Márquez IB (2006) On the value of information: studying changes in patch assessment abilities through learning. Oikos 112:298–310

Vet LEM, Lewis WJ, Cardé RT (1995) Parasitoid foraging and learning. In: Cardé RT, Bell WJ (eds) Chemical ecology of insects 2. Chapman and Hall, NY, pp 65–101

Visser ME, van Alphen JJM, Nell HW (1992) Adaptive superparasitism and patch time allocation in insect parasitoids. Behav Ecol Sociobiol 31:163–171

Waage JK (1979) Foraging for patchily-distributed hosts by the parasitoid *Nemeritis canescens*. J Anim Ecol 48:353–371

Wajnberg E (2006) Time allocation strategies in insect parasitoids: from ultimate predictions to proximate behavioral mechanisms. Behav Ecol Sociobiol 60:589–611

Wajnberg E, Bernhard P, Hamelin F, Boivin G (2006) Optimal patch time allocation for time-limited foragers. Behav Ecol Sociobiol 60:1–10

Wilson EE, Holway D, Nieh JC (2006) Cold anaesthesia decreases foraging recruitment in the New World bumblebee, *Bombus occidentalis*. J Apic Res 45:169–172