

ORIGINAL ARTICLE

When parasitoids deal with the spatial distribution of their hosts: consequences for both partners

Philippe Louâpre^{1,2} , Cécile Le Lann³ and Thierry Hance¹

¹Earth and Life Institute, Université Catholique de Louvain, Louvain-la-Neuve, Belgium; ²CNRS, Biogéosciences UMR 6282, Université Bourgogne Franche-Comté, Dijon, France and ³UMR CNRS 6553 Ecobio, University of Rennes 1, Rennes Cedex, France

Abstract Insect parasitoids developing inside hosts face a true challenge: hosts are scattered in the field and their localization and selection require the use of complex and sometime confusing information. It was assumed for a long time that small-brained organisms like parasitoids have evolved simple and efficient behavioral mechanisms, leading them to be adapted to a given ecological situation, for example, the spatial distribution of hosts in the habitat. However, hosts are not static and their distribution may also vary through generations and within the life of parasitoid individuals. We investigated if and how parasitoids deal with such a spatial complexity in a mesocosm experiment. We used the *Aphidius rhopalosiphi*/*Sitobion avenae* parasitoid/host system to investigate if parasitoid females experiencing different host aggregation levels exhibit different foraging behaviors independently of the number of hosts in the environment. We showed that *A. rhopalosiphi* females exploited hosts more intensively both within and among patches at higher host aggregation levels. We discussed the adaptiveness of such behaviors in the light of evolution and biological control.

Key words *Aphidius rhopalosiphi*; foraging behavior; parasitoid; sequential adjustment; *Sitobion avenae*; spatial distribution

Introduction

Information and decision processes are key components of female parasitoid fitness because they allow them to maximize the number of hosts parasitized during their life (van Alphen *et al.*, 2003). In order to optimize their fitness, female parasitoids need to locate and access host patches, select available hosts in the patches, and leave them at the appropriate depletion level (Charnov, 1976; Stephens & Krebs, 1986; Godfray, 1994). As a consequence, the spatial distribution of hosts among patches and how this patchiness is perceived are of fundamental importance for maximizing the host exploitation rate (Iwasa *et al.*, 1981; Rodrigues-Girones & Vasquez, 1997; Pierre & Green, 2008; Pierre, 2011).

Correspondence: Philippe Louâpre, UMR 6282 Biogéosciences, Université Bourgogne Franche-Comté, 6 Boulevard Gabriel, Dijon 21000, France. Tel: +33 3 80 39 62 27; email: philippe.louapre@u-bourgogne.fr

The host distribution (also later called field infestation distribution) is highly dynamic and can drastically complicate the foraging task for parasitoids, during their lifetime and/or from generation to generation. For example, the spatial distribution of herbivore hosts varies in space and time and it may be disrupted by many ecological factors, such as climate (Andrade *et al.*, 2013), local variation of the plant structure and quality (Rincon *et al.*, 2015; Riolo *et al.*, 2015), or the agricultural landscape complexity and the degree of fragmentation (Al Hassan *et al.*, 2012; Banks & Gagic, 2016). One key model of such host dynamic distribution is aphid feeding on plant sap: colonies can rapidly grow since females reproduced parthenogenetically during the main part of the year. In this system, the spatial distribution of individuals depends on both the rate at which winged forms are produced and leave the native colony to disperse in a new habitat (Ben-Ari *et al.*, 2015) and the movement of apterous forms that can be induced by the presence of natural enemies such as predators/parasitoids disturbing the colony

(Sloggett & Weisser, 2002), as well as abiotic factors acting at a local scale such as wind or rain (Mann *et al.*, 1995). The spatial distribution of aphids also varies at a larger temporal scale, as aphids are scarce and distributed among few patches in winter, while in spring they are abundant and aggregated in large patches (Legrand *et al.*, 2004; Stilmant *et al.*, 2008; Andrade *et al.*, 2013; Honek *et al.*, 2016).

The variability of hosts in space and time may drastically modify the optimal decisions parasitoids should make in order to maximize their long-term fitness gain (Spataro & Bernstein, 2007; Calcagno *et al.*, 2014). For example, Visser *et al.* (1999) demonstrated by using an experimental arena with five host patches that the habitat exploitation by the parasitoid *Trybliographa rapae* (Hymenoptera: Figitidae) depends in part on the host distribution. Such response to the host distribution that varies in space and time may involve spatial orientation and spatial memory (Collett & Collett, 2002; Dukas, 2008; Collett, 2009), perception of the quality of patches previously visited (Outreman *et al.*, 2005; Le Lann *et al.*, 2008; Louâpre *et al.*, 2011), and measurement of time linked to oviposition rate or patch encounter rate (Charnov, 1976; Marshall *et al.*, 1989; Adler & Kotar, 1999; Hills & Adler, 2002; Thiel & Hoffmeister, 2004; Vásquez *et al.*, 2006; Collett, 2009; Thiel, 2011). Such a variability represents a selection pressure that probably determines the proximate mechanisms and the behaviors leading to the optimal choice selection for parasitoids (van Alphen *et al.*, 2003; van Alphen & Bernstein, 2008).

In this study, we compared the foraging behavior of *Aphidius* parasitoid females experiencing different host aggregation levels by manipulating both the number of patches (plant with at least one host) and the host patch density in mesocosms with the same number of hosts and the same number of plants. To date, the effect of the host distribution (simulated by the patch encounter rate or the quality of the visited patches) was often confounded with the whole quality of the explored environment (i.e. the total number of hosts within the set-up) in studies investigating the foraging behaviour of *Aphidius* species in complex environments (see for example, Outreman *et al.*, 2005; Muratori *et al.*, 2008; Lanteigne *et al.*, 2015). However, the number of hosts in an environment and their distribution among patches are two different parameters characterizing the habitat for parasitoids. We thus monitored the foraging behavior of the aphid parasitoid *Aphidius rhopalosiphi* De Stefani-Perez (Hymenoptera: Aphidiinae) in a multipatch environment consisting of different aggregation levels of its main host, the grain aphid *Sitobion avenae* Fabricius (Hemiptera: Aphididae). In their natural environment, *A. rhopalosiphi*

females encounter very contrasted aphid aggregation levels during their life or through generations, as detailed above. Given that aphids move and develop rapidly, *A. rhopalosiphi* females must be able to respond to a highly ephemeral distribution of aphids (Winder *et al.*, 2014). *Aphidius rhopalosiphi* females perceive host patch density within the environment through interpatch travel time, and modify their response according to their previous acquired experience (Outreman *et al.*, 2005; Muratori *et al.*, 2008). In consequence, we hypothesized that the foraging strategy of different *A. rhopalosiphi* females depends on the aggregation level of their hosts even if the environments contain the same number of hosts: The foraging effort (estimated, among others, by the patch residence time and the number of ovipositor contacts) in each visited patch should be high for females exposed to a high level of host aggregation while it should be lower for females exploring a more uniform distribution of these hosts. Moreover, as leaving a patch is risky when the hosts are highly aggregated in the environment (the lower the number of patches, the lower the probability to encounter another patch after leaving the current one), we also expected that parasitoids would sample more intensively the neighboring environment at a high host aggregation level in comparison with a low one, even if both environments contain the same number of hosts. Finally, the expected adaptive behavior expressed by *A. rhopalosiphi* should impact the aphid population of a given size depending on their aggregation among the wheat plants. We expected that the aphid population should suffer more importantly when individuals are clumped among some patches in comparison with a more uniform distribution.

Materials and methods

Parasitoids and hosts

The *A. rhopalosiphi* females used in the study originated from mummies collected from a mass rearing at the Plant Protection and Ecotoxicology Unit of the Walloon Agricultural Research Centre (Belgium). The parasitoid was maintained on a *Sitobion avenae* colony established in 2013 from individuals collected in corn crops at the Marbaix (UCL) experimental farm (50°06 N, 4°63 W). The parasitoids and their hosts were reared in nylon boxes (50 cm × 50 cm × 50 cm) on fresh winter wheat (*Triticum aestivum*) under controlled climatic conditions (21 ± 1°C, 60% ± 10% RH and 16 L : 8 D photoperiod). All experiments were conducted under the same conditions used for rearing, and involved only 2- to 4-d-old, mated, and fed *A. rhopalosiphi* females. To eliminate females that

were unable to oviposit, females were offered five healthy hosts for parasitism for 60 min prior to the commencement of experiments (Le Lann *et al.*, 2008). Only second instar aphid nymphs were used, as this is the preferred instar of *A. rhopalosiphi* (Outreman *et al.*, 2001a).

Experimental design

In order to analyze the influence of aphid spatial distribution on neighboring plants on the foraging behavior of parasitoids, each female was exposed in mesocosms to one host aggregation level (low, medium, or high) while the number of hosts and plants remain the same among treatments. For this purpose, mesocosms were constituted by 16 wheat plants infested by 16 second instars *S. avenae* according to three levels of host aggregation: (i) low: one aphid per plant on all 16 plants; (ii) medium: 4 aphids per plant on the 4 central plants; and (iii) high: 8 aphids on each of the 2 central plants (Fig. 1). Each plant with at least one aphid was considered to be a patch, by contrast with plants without aphids. Wheat plants ($h = 15$ cm) planted 10 cm apart in a tray containing a 5 cm sand layer and covered by a thin layer of water to prevent aphid escapes were placed inside a Plexiglas cage (50 cm \times 50 cm \times 50 cm) having ventilation holes on each side. To prevent the accumulation of chemicals emitted by the plants or aphids, a fan located on the top of the cage removed the air from the cage at a rate of 20 cm³/s. One hour after the aphid infestation, a single 2- to 4-d-old, mated, and fed (with a drop of honey) *A. rhopalosiphi* female

was deposited on the bottom of the wheat plants on which at least one aphid had been placed, and the cage was closed. The female parasitoid was observed continuously, and the following behaviors were noted: arrival to and departure from a plant, walking, resting, cleaning, host attack (antennal contact with an aphid, followed by ovipositor contact) or rejection (antennal contact with an aphid, not followed by ovipositor contact), departure behaviors (female standing still on the border of a leaf and rotating its antennae circularly in many directions) (Outreman *et al.*, 2005). To identify if parasitoids visited several times the same patches, the number of wheat plants visited by a female and their position in the mesocosm were noted. The experiment was stopped after 1 h or when the female rested or cleaned continuously for more than 15 min. A total of 31 females was tested in the experiment (11, 10, and 10 females experienced the low, medium, and high levels of host aggregation, respectively), for a total of 496 aphids (176, 120, and 120 aphids in the low, medium, and high levels of host aggregation, respectively).

Statistical analyses

The number of hosts encountered in a mesocosm could be considered as a proxy of its quality and thus may inform about the optimal aphid density and distribution. In consequence, we analyzed the relationships between that number and factors such as the number of aphids on wheat plants, the rank of visit of the wheat plant, and the exploitation state of the wheat plant (never exploited

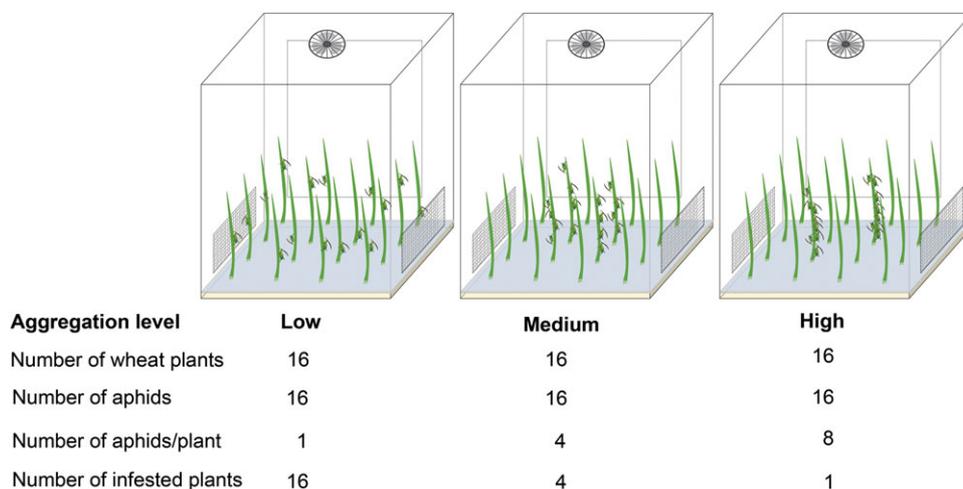


Fig. 1 Experimental design, showing the three levels of aphid aggregation (low, medium, and high) tested. In each case, the cage contained 16 wheat plants planted in a sand layer, covered by a thin water layer to avoid aphid escape for their patch. Only the aggregation level (not the whole habitat quality) varied between the modalities. Ventilation holes on each side and a top-fan mimicked a weak air-flow avoiding air saturation.

Table 1 Estimated regression coefficients (β) and hazard ratios [$\exp(\beta)$] for covariates included in the Cox proportional hazard model. The model described the patch-leaving tendency of *Aphidius rhopalosiphi* foraging in a multipatch environment containing 16 wheat plants and 16 *Sitobion avenae* aphids distributed according to different levels of aggregation. χ^2 corresponds to the likelihood ratio tests. The overall significance of the fitting model: $\chi^2 = 308$, $df = 17.77$, P value < 0.001 .

Factors/covariates	β	$\exp(\beta)$	χ^2	df	P value	Tendency to leave the patch
Level of hosts aggregation	-0.062	0.939	8.38	1	0.004	↓
Number of aphids on the wheat plant (1)	-0.518	0.595	32.79	1	>0.001	↓
Number of wheat plants previously visited	0.184	1.202	16.20	1	>0.001	↑
Revisit of the wheat plant (2)	1.225	3.406	7.07	1	0.008	↑
First wheat plant visited	0.634	1.886	3.60	1	0.058	—
Ovipositor contact	0.160	1.174	6.77	1	0.009	↑
Leaving posture	0.642	1.900	125.57	1	>0.001	↑
Cleaning	-0.401	0.670	25.10	1	>0.001	↓
Interaction between (1) and (2)	0.454	1.575	7.26	1	0.007	↑
Identity of the female (frailty term)			19.75	10.06	0.033	—

or previously exploited) as explanatory fixed factors using a generalized linear mixed model with clustered data (Poisson distribution). The identity of each female was included in the model as random effect, enabling data concerning the same female to be correlated. In the same way, patch residence time (censored data for parasitoids still foraging inside a patch at the end of the experiment) was analyzed using a Cox's proportional hazard model (Cox, 1972). This model determines a patch-leaving tendency associated with different fixed factors and time dependent covariates (Table 1), in terms of a hazard ratio. Thus, the tendency of a female to leave the current patch can decrease (hazard ratio < 1) or increase (hazard ratio > 1) depending on events occurring during the experiment or fixed by the experimenter. The duration of the departure behavior was analyzed by a linear mixed model including the number of aphids on the wheat plant and the exploitation state of these plants as fixed factors and the identity of the females as a random effect. The effect of host aggregation on the proportion of attacked hosts was analyzed with a generalized linear model with (Poisson distribution as error family). All analyses were carried out using R 3.4.0 software (R Development Core Team, 2017), with glmmML (Broström, 2013), nlme (Pinheiro et al., 2015), and survival (Therneau, 2014) packages.

Results

Oviposition behavior

The number of ovipositor contacts observed increased with the number of aphids on wheat plants ($\beta = 0.29$,

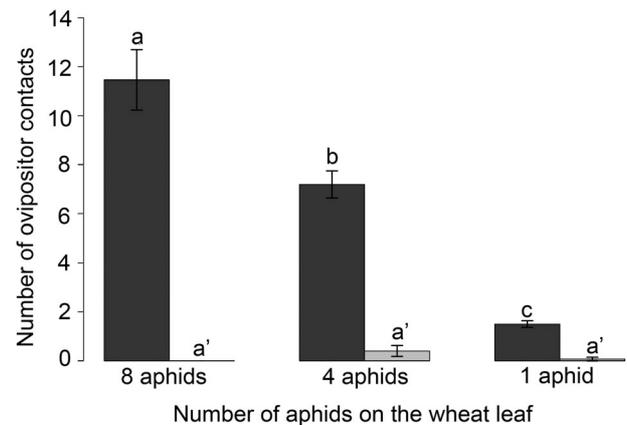


Fig. 2 The number of ovipositor contacts by the parasitoid in patches as a function of the number of aphids on the wheat plant and revisits to the patches (black: first visit; gray: subsequent visit). Different letters above bars indicate a significant difference, according to the Tukey's HSD test.

$z = 0.032$, $P < 0.001$) but this effect was modulated by the patch exploitation state (never or already visited) (interaction terms; $\beta = -0.843$, $z = -5.432$, $P < 0.001$), and the rank of the visited patch (interaction term; $\beta = -0.023$, $z = -2.1428$, $P = 0.032$): The number of aphids on a patch had an effect only on wheat plants never visited previously and was close to zero on plants that had been visited at least twice (Fig. 2). In addition, the number of ovipositor contacts decreased on the second and subsequent wheat plants visited in comparison with the first visited wheat plant; this phenomenon occurred at all three host aggregation levels (Fig. 3).

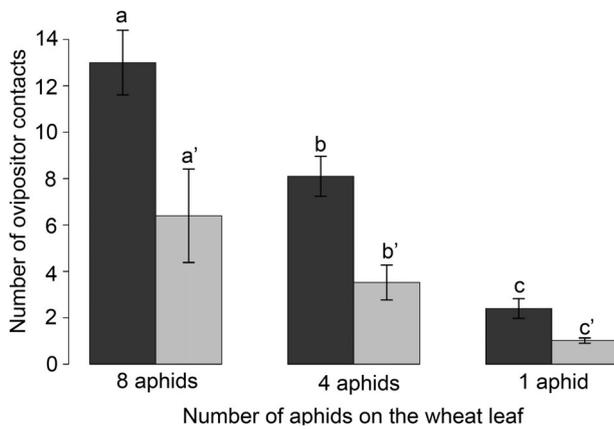


Fig. 3 The number of ovipositor contacts in patches as a function of the number of aphids on the wheat plant and the rank of the patch visit (black: first patch visited; gray: second or subsequent patch visited).

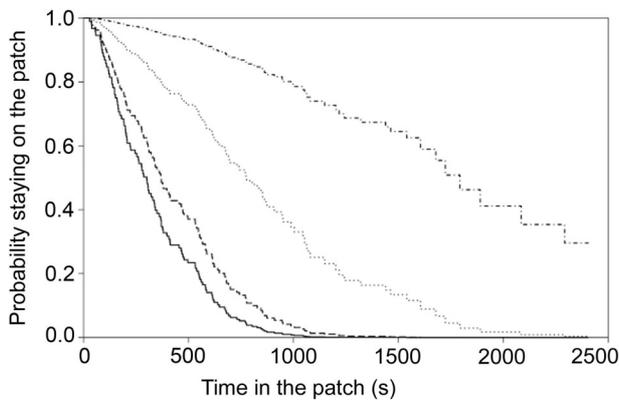


Fig. 4 Probability of the parasitoid of staying on the patch (Kaplan–Meyer survival curves) during the course of patch exploitation (in seconds) as a function of the number of aphids (solid: zero aphids; dashed: one aphid; dotted: four aphids; dot-dashed: eight aphids).

The allocation of time in patches

Data fitted with a Cox proportional hazard model pointed out that several parameters significantly influenced the tendency of the parasitoids to leave the wheat plants they visited (Table 1). First, as expected, the patch-leaving tendency decreased as the host aggregation level increased (including wheat plants without aphids). In the same way, the number of aphids on the visited wheat plants (from 0 to 8) influenced the tendency of the parasitoids to stay on wheat plants: the higher the number of aphids on a wheat plant, the lesser the tendency of the parasitoid to leave it (Fig. 4). The tendency of parasitoids to leave a

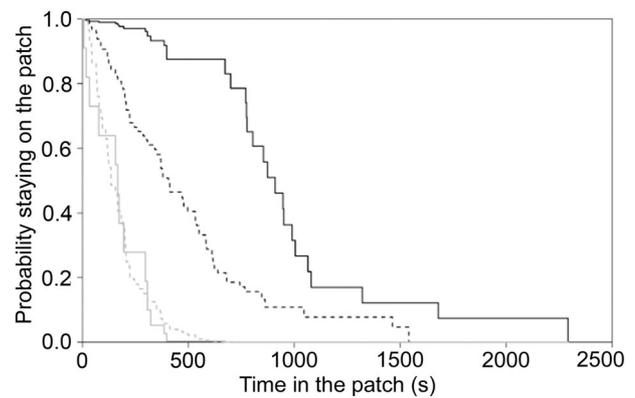


Fig. 5 Probability of the parasitoid of staying on wheat plants having one (gray) and four aphids (black) for the first (solid) and subsequent visits to the same patch (dashed).

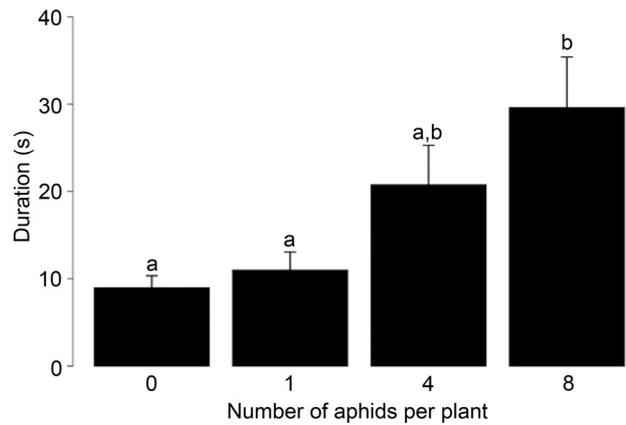


Fig. 6 The duration of the patch-leaving posture displayed by parasitoid females on wheat plants having varying numbers of aphids (0, 1, 4, or 8).

patch previously exploited did not depend on the numbers of aphids in it (Fig. 5).

The patch departure behavior

The duration of the patch departure behavior was longer when more aphids were present on the patch ($F_{3,213} = 5.318$, $P = 0.001$), but did not depend on previous visits of the same patch ($F_{1,213} = 1.572$, $P = 0.211$). Indeed, this duration was longer on wheat plants having eight aphids ($z = 3.371$, $P = 0.004$) than on plants having zero or one aphid ($z = 1.436$, $P = 0.006$) (Fig. 6).

The proportion of attacked hosts

The proportion of aphids attacked by *A. rhopalosiphi* increased with the host aggregation level (GLMM: $df =$

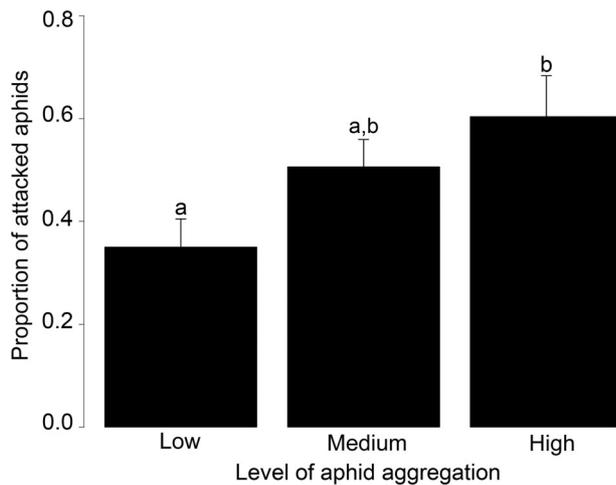


Fig. 7 The proportion of aphids attacked (on a total of 16) during the course of the experiment depending of their aggregation level among the wheat plants.

2, $\chi^2 = 5.016$, $P < 0.017$; Fig. 7): aphids were attacked in larger proportions in the environment with the high host aggregation level than in the medium and low ones.

Discussion

The aim of this study was to test the effect of the host aggregation level on the foraging strategies of aphid parasitoids. We showed that the tendency to leave a wheat plant as well as the number of ovipositor contacts in each of the visited patches differed between the treatments: the foraging intensity seems to be stronger for females experiencing a high host aggregation level than lower ones. Moreover, the spatial distribution of hosts in mesocosms influenced the way parasitoids acquired information about the host availability as they spend more time to explore environments characterized with more aggregated hosts than with more uniformly distributed ones. We also demonstrated that the host attack rate by parasitoids increased when hosts were aggregated on few patches. Therefore, the way aphids are distributed among wheat plants influences their own survival as well as the foraging behavior of their parasitoids.

Parasitoids showed a low patch-leaving tendency when the host aggregation level was high compared to lower aggregation levels. Such response is consistent with the theoretical model of optimal patch departure: the higher the host aggregation level, the lower the patch-leaving tendency (Iwasa *et al.*, 1981). Linked to the proximate mechanisms of foraging, parasitoids tend to concentrate their foraging effort in few patches when foraging on a highly

aggregated resource probably through a higher incremental mechanism (Pierre & Green, 2008; Pierre, 2011). This study provides the first empirical evidence that the host aggregation level is a key feature of the environment perceived by parasitoids, regardless of the average quality, although this may not be a general rule. Indeed, it was recently reported that the parasitoid *Meteorus pulchricornis* foraging on soybean plants does not respond to host aggregation level within a patch (Sheng *et al.*, 2014). It is possible that patches are perceived in different ways by parasitoids when foraging on plants varying in architectural complexity (e.g., wheat plants vs. soybean plants), and that the potential adaptive mechanism we observed on wheat plants in the present study occurs at a larger scale on soybeans. It is also possible that at the spatial scale of the mesocosm used in our study, parasitoid perceived the patchiness of their hosts while at the plant scale used in other studies, such distribution is not perceived. Based on the unambiguous definition of a patch (Waage, 1979), the patchiness of the host distribution in the mesocosm we used here is likely to be perceived by the parasitoids, as *A. rhopalosiphi* expressed different arresting behaviors before leaving each wheat plants containing aphids, even once.

Different sources of information can be used by parasitoids in order to express their adaptive response to the host aggregation. They do not only perceive the average quality of their habitat, but also the way aphids are distributed among the patches. As previously shown, we showed that *A. rhopalosiphi* responds to cues acquired in the current patch and the neighboring ones (even when they were not visited) and combines this information with its previous patch exploitation experience to adjust its foraging behavior sequentially (Outreman *et al.*, 2005). It was generally assumed that parasitoids expressed such an adaptive behavior by an intrapatch information perception. Here we also showed that *A. rhopalosiphi* seems to perceive cues about the host aggregation level, such as the presence of neighboring wheat plants containing aphids, at a distance, as observed in other parasitoid species (Corley *et al.*, 2010; Fischbein *et al.*, 2012). In *Aphidius* species such as *A. ervi*, patches of aphids are located thorough the perception of the alarm pheromones (*E*)- β -farnesene emitted in large quantities when attacked (Micha & Wyss, 1996; Hatano *et al.*, 2008; Vandermoten *et al.*, 2012). As first mentioned by Outreman *et al.* (2005), *A. rhopalosiphi* females circles their antennae in the air at the leaf border before leaving the visited plants. We interpret this patch-leaving behavior as the need for the females to analyze cues coming from the neighboring patches and probably to compare them with previous experience or other cues to make a take-off decision. The

patch departure behavior probably enables the parasitoids to detect such aphid kairomones derived from neighboring patches, or alarm pheromones emitted by parasitized aphids, and so to detect the presence and/or the quality of other nearby patches. Here we showed that the richer the visited patch, the longer the patch departure behavior. It is thus plausible that the high number of aphids in patches and therefore the quantity of alarm pheromones emitted in the current visited patch might disrupt the ability of parasitoids to detect cues from other patches in the environment (Shaltiel & Ayal, 1998). An alternative hypothesis is that kairomones emitted by attacked hosts are attractive for *A. rhopalosiphi* at a distance of the patch entrance (Micha & Wyss, 1996), and repellent once upon the patch entrance (Outreman *et al.*, 2001b). To specifically determine the effect of kairomones perceived at a distance or inside a patch is a key point requiring further investigations as field observations reported that alarm pheromone emitted at natural levels did not attract predators and parasitoids under field conditions (Joachim & Weisser, 2015).

We demonstrated that the host aggregation levels influenced the foraging behavior of parasitoids regardless of the total number of hosts in the environment. Winder *et al.* (2013) showed that the spatial distribution of *S. avenae* and *Metopolophium dirhodum*, two main targets of the parasitoid *A. rhopalosiphi*, may be highly variable, even in winter, but depends on the scale at which the spatial process is considered. For example, aphid colonies are extremely ephemeral at the host plant scale, continuously redistributed through local dispersal, while aphid populations seem to be more stable at the field scale. At this scale, variation of the spatial pattern emerges from the season considered (Langer *et al.*, 1997; Legrand *et al.*, 2004; Honek *et al.*, 2016). As pointed out by several authors, optimization of biological control programs requires an understanding of the response of parasitoids to the distribution of their hosts at the relevant scales (i.e., spatial scale: from the host plant to the field, temporal scale: from the individual lifespan to the season) (Raymond *et al.*, 2015; Boses Baillod *et al.*, 2017; Morgan *et al.*, 2017). In our study, we showed that both the ovipositor contact rate was higher when aphids were aggregated on some wheat plants than homogeneously distributed among many wheat plants, and that *A. rhopalosiphi* disperse more and visit more wheat plants at a low aphid aggregation level. Aphid populations are thus likely to suffer more from a parasitoid attack when aggregated among a few number of patches, than when they are more uniformly distributed among the plants. While the host density is known to have a strong impact on the density, the distribution and the behavior of natural enemies (Morgan *et al.*, 2017), the host aggregation is not taken

into account itself. For instance, in the beginning of the season when aphids are sparse and dispersed among the wheat plants, the ability of *A. rhopalosiphi* to perceive such a uniform distribution of cereal aphids may result on a high parasitism rate by dispersing parasitoids among the infested wheat plants (Legrand *et al.*, 2004). Early releases of parasitoids in the season may thus slow down the initial growth rate of aphid populations by using natural enemies that adjust their foraging strategy to the aggregation of their hosts (Chambers *et al.*, 1986; Sigsgaard, 2002; Legrand *et al.*, 2004).

Acknowledgments

This research was supported by the OPTIFIELD program cofunded by the Académie Universitaire Louvain (AUL) and the Marie Curie Actions of the European Commission. We thank J.P. Jansen (Centre Wallon de Recherches Agronomiques) and G. Collignon (Ferme expérimentale de Marbaix—UCL) for providing the parasitoid and aphid strains, and O. Lebbe and M. Pirnay for their technical support. All applicable institutional and national guidelines for the care and use of animals were followed.

Author contributions

PL, TH, and CLL conceived and designed the experiments. PL performed the experiments. PL, TH, and CLL analyzed the data and wrote the manuscript.

Disclosure

The authors declare that they have no conflict of interest.

References

- Adler, F.R. and Kotar, M. (1999) Departure time versus departure rate: how to forage optimally when you are stupid. *Evolutionary Ecology Research*, 1, 411–421.
- Andrade, T.O., Hervé, M., Outreman, Y., Krespi, L. and van Baaren, J. (2013) Winter host exploitation influences fitness traits in a parasitoid. *Entomologia Experimentalis et Applicata*, 147, 167–174.
- Banks, J.E. and Gagic, V. (2016) Aphid parasitoids respond to vegetation heterogeneity but not to fragmentation scale: An experimental field study. *Basic & Applied Ecology*, 17, 438–446.
- Ben-Ari, M., Gish, M. and Inbar, M. (2015) Walking aphids can partake in within-field dispersal to distant plants. *Basic & Applied Ecology*, 16, 162–171.

- Bosem Baillood, A., Tschartke, T., Clough, Y. and Batáry, P. (2017) Landscape-scale interactions of spatial and temporal cropland heterogeneity drive biological control of cereal aphids. *Journal of Applied Ecology*, 54, 1804–1813.
- Broström, G. (2013) R Package. glmmML: generalized linear models with clustering.
- Calcagno, V., Mailleret, L., Wajnberg, E. and Grogard, F. (2014) How optimal foragers should respond to habitat changes: a reanalysis of the Marginal Value Theorem. *Journal of Mathematical Biology*, 69, 1237–1265.
- Chambers, R.J., Sunderland, K.D., Stacey, D.L. and Wyatt, I.J. (1986) Control of cereal aphids in winter wheat by natural enemies: aphid specific predators, parasitoids and pathogenic fungi. *Annals of Applied Biology*, 108, 219–231.
- Charnov, E.L. (1976) Optimal foraging, the marginal value theorem. *Theoretical Population Biology*, 9, 129–136.
- Collett, T.S. and Collett, M. (2002) Memory use in insect visual navigation. *Nature Reviews Neuroscience*, 3, 542–552.
- Collett, M. (2009) Spatial memories in insects. *Current Biology*, 19, 1103–1108.
- Corley, J.C., Villacide, J.M. and van Nouhuys, S. (2010) Patch time allocation by a parasitoid: the influence of con-specifics, host abundance and distance to the patch. *Journal of Insect Behavior*, 23, 431–440.
- Cox, D.R. (1972) Regression models and life-tables. *Journal of the Royal Statistical Society*, 34, 187–220.
- Dukas, R. (2008) Evolutionary biology of insect learning. *Annual Review of Entomology*, 53, 145–160.
- Fischbein, D., Bettinelli, J., Bernstein, C. and Corley, J.C. (2012) Patch choice from a distance and use of habitat information during foraging by the parasitoid *Ibalia leucospoides*. *Ecological Entomology*, 37, 161–168.
- Godfray, H.C.J. (1994) *Parasitoids: Behavioral and Evolutionary Ecology*. Princeton University Press, Princeton.
- Al Hassan, D., Burel, F., Plantegenest, M., Kindlmann, P., Butet, A. and Parisey, N. (2012) Relationship between landscape composition and the abundance of aphids and their natural enemies in crop fields. *European Journal of Environmental Sciences*, 2, 89–101.
- Hatano, E., Kunert, G., Bartram, S., Boland, W., Gershenson, J. and Weisser, W.W. (2008) Do aphid colonies amplify their emission of alarm pheromone? *Journal of Chemical Ecology*, 34, 1149–1152.
- Hills, T.T. and Adler, F.R. (2002) Time's crooked arrow: optimal foraging and rate-biased time perception. *Animal Behaviour*, 64, 589–597.
- Honek, A., Martinkova, Z., Dixon, A.F.G. and Saska, P. (2016) Annual predictions of the peak numbers of *Sitobion avenae* infesting winter wheat. *Journal of Applied Ecology*, 141, 352–362.
- Iwasa, Y., Higashi, M. and Yamamura, N. (1981) Prey distribution as a factor determining the choice of optimal foraging strategy. *American Naturalist*, 117, 710–723.
- Joachim, C. and Weisser, W.W. (2015) Does the aphid alarm pheromone (*E*)- β -farnesene act as a kairomone under field conditions? *Journal of Chemical Ecology*, 41, 267–275.
- Langer, A., Stilmant, D., Verbois, D. and Hance, T. (1997) Seasonal activity and distribution of cereal aphid parasitoids in Belgium. *Entomophaga*, 42, 185–191.
- Lanteigne, M.E., Brodeur, J., Jenni, S. and Boivin, G. (2015) Patch experience changes host acceptance of the aphid parasitoid *Aphidius ervi*. *Journal of Insect Behavior*, 28, 436–446.
- Legrand, M.A., Colinet, H., Vernon, P. and Hance, T. (2004) Autumn, winter and spring dynamics of aphid *Sitobion avenae* and parasitoid *Aphidius rhopalosiphii* interactions. *Annals of Applied Biology*, 145, 139–144.
- Le Lann, C., Outreman, Y., Van Alphen, J.J.M., Krespi, L., Pierre, J.S. and van Baaren, J. (2008) Do past experience and competitive ability influence foraging strategies of parasitoids under interspecific competition? *Ecological Entomology*, 33, 691–700.
- Louâpre, P., van Baaren, J., Pierre, J.S. and van Alphen, J.J.M. (2011) Information gleaned and former patch quality determine foraging behavior of parasitic wasps. *Behavioral Ecology*, 22, 1064–1069.
- Mann, J.A., Tatchell, G.M., Dupuch, M.J., Harrington, R., Clark, S.J. and McCartney, H.A. (1995) Movement of apterous *Sitobion avenae* (Homoptera: Aphididae) in response to leaf disturbances caused by wind and rain. *Annals of Applied Biology*, 126, 417–427.
- Marschall, E.A., Chesson, P.L. and Stein, R.A. (1989) Foraging in a patchy environment: prey-encounter rate and residence time distributions. *Animal Behaviour*, 37, 444–454.
- Micha, S.G. and Wyss, U. (1996) Aphid alarm pheromone (*E*)- β -farnesene: a host finding kairomone for the aphid primary parasitoid *Aphidius uzbekistanicus* (Hymenoptera: Aphidinae). *Chemoecology*, 7, 132–139.
- Morgan, W.H., Thébault, E., Seymour, C.L. and van Veen, F.J.F. (2017) Density dependence and environmental factors affect population stability of an agricultural pest and its specialist parasitoid. *BioControl*, 62, 175–184.
- Muratori, F., Boivin, G. and Hance, T. (2008) The impact of patch encounter rate on patch residence time of female parasitoids increases with patch quality. *Ecological Entomology*, 33, 422–427.
- Outreman, Y., Le Ralec, A., Wajnberg, E. and Pierre, J.S. (2001a) Can imperfect host discrimination explain partial patch exploitation in parasitoids? *Ecological Entomology*, 26, 271–280.
- Outreman, Y., Le Ralec, A., Plantegenest, M., Chaubet, B. and Pierre, J.S. (2001b) Superparasitism limitation in an aphid

- parasitoid: cornicle secretion avoidance and host discrimination ability. *Journal of Insect Physiology*, 47, 339–348.
- Outreman, Y., Le Ralec, A., Wajnberg, E. and Pierre, J.S. (2005) Effects of within- and among-patch experiences on the patch-leaving decision rules in an insect parasitoid. *Behavioral Ecology & Sociobiology*, 58, 208–217.
- Pierre, J.S. and Green, R.F. (2008) A Bayesian approach to optimal foraging in parasitoids. *Behavioral Ecology of Insect Parasitoids: From Theoretical Approaches to Field Applications* (eds. E. Wajnberg, C. Bernstein, J.J.M. van Alphen), pp. 357–383. Blackwell Publishing Ltd, Oxford.
- Pierre, J. (2011) Neuroeconomics in parasitoids: computing accurately with a minute brain. *Oikos*, 120, 77–83.
- Pinheiro, J., Bates, D., DedRoy, S. and Sarkar, D. (2015) R package. nlme.
- Raymond, L., Ortiz-Martinez, S.A. and Lavandero, B. (2015) Temporal variability of aphid biological control in contrasting landscape contexts. *BioControl*, 90, 148–156.
- Riolo, M.A., Rohani, P. and Hunter, M.D. (2015) Local variation in plant quality influences large-scale population dynamics. *Oikos*, 124, 1160–1170.
- Rincon, D.F., Hoy, C.W. and Cañas, L.A. (2015) Generating within-plant spatial distributions of an insect herbivore based on aggregation patterns and per-node infestation probabilities. *Environmental Entomology*, 44, 194–209.
- Rodrigues-Girones, M. and Vasquez, R.A. (1997) Density-dependent patch exploitation and acquisition of environmental information. *Theoretical Population Biology*, 52, 32–42.
- Shaltiel, L. and Ayal, Y. (1998) The use of kairomones for foraging decisions by an aphid parasitoid in small host aggregations. *Ecological Entomology*, 23, 319–329.
- Sheng, S., Feng, S.F., Meng, L. and Li, B.P. (2014) Departure mechanisms for host search on high-density patches by the *Meteorus pulchricornis*. *Journal of Insect Science*, 14, article number 205.
- Sigsgaard, L. (2002) A survey of aphids and aphid parasitoids in cereal fields in Denmark, and the parasitoids' role in biological control. *Journal of Applied Entomology*, 126, 101–107.
- Sloggett, J.J. and Weisser, W.W. (2002) Parasitoids induce production of the dispersal morph of the pea aphid, *Acyrtosiphon pisum*. *Oikos*, 98, 323–333.
- Spataro, T. and Bernstein, C. (2007) Influence of environmental conditions on patch exploitation strategies of parasitoids. *Behavioral Ecology*, 18, 742–749.
- Stephens, D.W. and Krebs, J.R. (1986) *Foraging Theory*. Princeton University Press, New Jersey, Princeton.
- Stilmant, D., Bellinghen, C., Hance, T. and Boivin, G. (2008) Host specialization in habitat specialists and generalists. *Oecologia*, 156, 905–912.
- Therneau, T.M. (2014) R package. Survival.
- Thiel, A. (2011) How to measure patch encounter rate: decision-making mechanisms in the parasitic wasp *Asobara tabida*. *Animal Cognition*, 14, 73–82.
- Thiel, A. and Hoffmeister, T.S. (2004) Knowing your habitat: linking patch-encounter rate and patch exploitation in parasitoids. *Behavioral Ecology*, 15, 419–425.
- van Alphen, J.J.M., Bernstein, C. and Driessen, G. (2003) Information acquisition and time allocation in insect parasitoids. *Trends in Ecology & Evolution*, 18, 81–87.
- van Alphen, J.J.M. and Bernstein, C. (2008) Information acquisition, information processing, and patch time allocation in insect parasitoids. *Behavioural Ecology of Insect Parasitoids: From Theoretical Approaches to Field Applications* (eds. E. Wajnberg, C. Bernstein, J.J.M. van Alphen), pp. 172–192. Blackwell Publishing Ltd, Oxford.
- Vandermoten, S., Mescher, M.C., Francis, F., Haubruge, E. and Verheggen, F.J. (2012) Aphid alarm pheromone: an overview of current knowledge on biosynthesis and functions. *Insect Biochemistry & Molecular Biology*, 42, 155–163.
- Vásquez, R.A., Grossi, B. and Natalia Márquez, I. (2006) On the value of information: studying changes in patch assessment abilities through learning. *Oikos*, 112, 298–310.
- Visser, M.E., Jones, T.H. and Driessen, G. (1999) Interference among insect parasitoids: a multi-patch experiment. *Journal of Animal Ecology*, 68, 108–120.
- Waage, J.K. (1979) Foraging for patchily-distributed hosts by the parasitoid, *Nemeritis canescens*. *Journal of Animal Ecology*, 48, 353–371.
- Winder, L., Alexander, C.J., Woolley, C., Perry, J.N. and Holland, J.M. (2014) Cereal aphid colony turnover and persistence in winter wheat. *PLoS ONE*, 9, e106822.
- Winder, L., Alexander, C.J., Woolley, C., Perry, J.N. and Holland, J.M. (2013) The spatial distribution of canopy-resident and ground-resident cereal aphids (*Sitobion avenae* and *Metopolophium dirhodum*) in winter wheat. *Arthropod-Plant Interactions*, 7, 21–32.

Manuscript received November 28, 2017

Final version received January 30, 2018

Accepted February 22, 2018