

Light Environments Differently Affect Parasitoid Wasps and their Hosts' Locomotor Activity

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Abstract In natural environments, organisms must adapt to changing light conditions. Significant research has been done on diurnal pollinating insects' vision. However, little is known on parasitoid insects. Here, we studied how locomotor activity of the parasitoid wasp *Aphidius ervi* and its main host, the pea aphid *Acyrtosiphon pisum*, is affected under controlled artificial illumination. Using LEDs of 5 different wavelengths (361, 450, 500–600, 626 and 660 nm), we created different artificial light spectra that parasitoids and host aphids can encounter in natural environment including leaf-shade and direct sunlight. We found that pea aphid probability of walking depended on interactions between illumination, developmental stage and genotype as expressed in clonal variation. Artificial light intensity did not affect the parasitoid's probability of walking as opposed to wavelength, and activity depended on the sex of individuals. Males were more active than females under all monochromatic wavelength spectra tested. Virgin females were much less active under the artificial leaf-shade illumination and artificial sunlight, as compared to males and mated females. Delay before flight for females was favored by sunlight illumination whereas the light environment did not affect flight delay for males. We demonstrated that locomotor activity of *A. pisum* (walking) and of *A. ervi* (walking and flight) vary according to the light environment.

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This study should help develop better understanding of the effects of illumination on host-parasitoid interactions, which in turn may help control insect pest populations.

Keywords Light · *Aphidius ervi* · aphids · *Acyrtosiphon pisum* · locomotor activity · flight

Introduction

Much research has been done on diurnal insect vision, especially on insect pollinators such as honeybees and bumble bees (Lotto and Chittka 2005; Dyer 2006; Arnold and Chittka 2012). These studies focused on the ability of these insects to discriminate colors under controlled luminous environments. However, there is a lack of knowledge regarding the impact of light environment on other insects that also use plants as their habitat and resources, such as aphids and their natural enemies. Yet the study of wavelength-dependent behavior of herbivore hosts and their specialist parasitoid wasps, could improve our knowledge on the control of insect pest populations through natural enemies (reviewed in Antignus 2000).

At the scale of aphids and their parasitoids, the light environment varies greatly in terms of spectral composition and intensity, according to the time of day, cloud cover, habitat, and whether the solar spectrum is direct or diffuse (i.e. the blue of the sky) (Endler 1993; Johnsen et al. 2006; Thorne et al. 2009). Many of the wavelengths to which these insects are sensitive are blocked by their natural habitat, i.e. the foliage of their host plants. In studying effects of illumination on their interactions, we must distinguish between effects on locomotor activity (walking and flight), and on the other hand, the effects related to vision, that is their ability to distinguish and recognize "objects", i.e. especially potential hosts for the wasps, and approaching wasps as natural enemies for the aphids.

In many parasitoids, males emerge before females, from a few hours to a few days (protandria), and benefit by mating with females, possibly including their full siblings, before they disperse (reviewed in Boulton et al. 2015). This is the case in *Aphidius ervi* (Hymenoptera, Braconidae), a quasi-gregarious parasitoid, where peak male emergence appears hours earlier than females after the beginning of the photophase (He 2008). In the study of He (2008), light intensity remained constant and thus only the time since the beginning of the photophase determined emergence time of individuals for this braconid.

Some recent studies considered that the light environment, both intensity and wavelength, may impact the locomotor activity of herbivorous insects or their natural enemies. For example, for *Orius sauteri* (Hemiptera, Anthocoridae), Wang et al. (2013) showed that the speed of movement of adult females was reduced at low intensity (1000 lux vs 5000 lux) and for short wavelengths (blue LED = 478nm vs red LED = 678nm). Locomotor activity is a key aspect of host-searching behavior. As locomotor activity is higher at high intensity for the hyperparasitoid *Aphelinus asychis*, a greater number of hosts could be killed or parasitized in a well-lit environment (Schirmer et al. 2008). Chen et al. (2012) showed that orange and red lights did not elicit a significant phototactic response from *Aphidius gifuensis* (Hymenoptera, Braconidae), but they speculated that heat produced by wavelengths superior to 628 nm could be a factor affecting this parasitoid movement.

There are two types of locomotion highlighting two phases of host and/or habitat location for plant-dwelling insects: long distance search by flight and short distance search by walking (Prokopy and Owens 1983; Vinson 1976, 1998). Wavelengths may affect the locomotion of several insects. Mound (1962) hypothesized that flight activity of the herbivore *Bemisia tabaci* (Hemiptera, Aleyrodidae) depends on a tradeoff between emigration triggered by UV sensitivity and the landing reaction controlled by yellow sensitivity. This hypothesis has been supported by studies investigating the effects of UV-blocking plastics on greenhouse pests. For example, the flight activity of winged aphids *Myzus persicae* (Hemiptera, Aphididae), and the whitefly *Trialeurodes vaporariorum* (Hemiptera, Aleyrodidae) is reduced when UV radiations are absorbed by plastic sheets, thereby decreasing infestation of new plants (Chyzik et al. 2003; Doukas and Payne 2007a). Interestingly parasitoids foraging on plants may differ from their hosts in their response to the light environment. When *T. vaporariorum* was present on greenhouse plants, its specialized parasitoid wasp *Encarsia formosa* (Hymenoptera, Aphelinidae) were active on plants even in UV-blocked light environment (Doukas and Payne 2007b), suggesting that the parasitoid was less affected by the absence of UV than its hosts. In addition to wavelengths, light intensity may also affect flight behavior of parasitoids. High light intensity increased the use of flight by *Cotesia glomerata* (Hymenoptera, Braconidae) to access plants with hosts (11.3% at 600 lux and 26.7% at 1600 lux) (Gu and Dorn 2001).

Most insects possess three types of photoreceptors : UV ($\lambda_{\max} = 350$ nm), blue ($\lambda_{\max} = 440$ nm) and green ($\lambda_{\max} = 530$ nm) (Peitsch et al. 1992; Briscoe and Chittka 2001). Accordingly, Kirchner et al. (2005) reported the presence of the three types of photoreceptors for the aphid *M. persicae*. Intraspecific variation of phototactic responses were found in aphids. A recent study of the phototactic behavior of winged and wingless morphs of the pea aphid *Acyrtosiphon pisum* (Zhang et al. 2016) showed that winged adults of a pink clone presented different phototactic reactions to different wavelengths related to age. For example, one-day old winged adults showed no reaction to green light, whereas 8-day old winged adults showed a negative phototaxis to this wavelength. The authors suggested that these behaviors may help aphids to disperse and/or assist them in locating their host plant.

For parasitoids, it has been shown that the perception and attraction or repulsion for a particular wavelength may be different between males and females of *Pachyneuron aphidis* (Hymenoptera, Pteromalidae), a common hyperparasitoid of *A. gifuensis* mummies (Chen et al. 2014). Surprisingly, Chen et al. (2012) who studied the phototactic response of *A. gifuensis*, did not distinguish the response of males from that of females.

Studies concerning the impact of the light environment (composition of spectrum and intensity) on the locomotor activity of hymenopteran parasitoids are still too scarce. Moreover, there appears to be no detailed studies of the locomotor activity of parasitoids while searching for hosts, neither as a function of the wavelengths in their natural environment nor of the response of their hosts to being approached and attacked by their natural enemies.

Many aphid species are considered as pests of cereal and forage crops, causing losses through phloem feeding, plant pathogen transmission, and foliage contamination with honeydew (Vilcinskis 2016). Reproducing asexually as viviparous clones, many are polymorphic for traits including body color and are symbiotically associated with bacteria. There is a general obligate aphid endosymbiont, *Buchnera aphidicola*, and

often one or more facultative endosymbionts (Gauthier et al. 2015). Thus, within the same population, it is possible to find several clones that differ in color and composition of their endosymbiotic community. Facultative symbionts may confer several advantages to aphids under specific conditions, such as resistance to specialized parasitoids (Guay et al. 2009; Oliver et al. 2010; Cayetano and Vorburger 2015). To our knowledge, responses of different aphid clones to the light environment in terms of locomotor and defensive behavior have not been investigated.

In an attempt to add new knowledge on host-parasitoid interactions, which could improve the control of insect pest populations, we studied the influence of the immediate light environment on the activity of insects belonging to a model host-parasitoid system, starting with locomotor activity, which is critical in host parasitoid interactions. Our study system is composed of the parasitoid wasp *Aphidius ervi* and its main host, the pea aphid *Acyrtosiphon pisum*. We developed an electronic device composed of 5 types of LEDs to manipulate the light environment in terms of intensity and wavelength composition.

To determine whether pea aphid locomotor activity depends on the light environment, we recorded the walking activity of immatures and adults of two green and two pink clones of the pea aphid, under four light environments exploring the entire light spectrum. We predicted that there was clonal variation of the locomotor behavior for pea aphid, which might be associated to color variation as part of their defense syndrome. We also expected that adult aphids would be more active than immatures since they usually choose their distribution on the plants to feed and reproduce, whereas young nymphs remain generally motionless behind the mother (Legrand and Barbosa 2000). Due to the lack of evidence for red photoreceptors in our studied insects (Briscoe and Chittka 2001; Döring et al. 2011; Chen et al. 2012), we hypothesized that the long wavelengths (red) will lead to a reduction in the locomotor activity of parasitoids and aphids.

For the parasitoid *A. ervi*, we predicted that since males emerge a few hours before females as mentioned above, they were expected to be more active than females under low light intensity and in the presence of long wavelengths. We also distinguished walking and flight behaviors for the parasitoid. We found useful to separate walking activity related to close range host or mate-searching, and flight that is a key factor for dispersal and new host and mate finding. We predicted that the time delay before takeoff for flight would be longer in the absence of short wavelengths (< 400 nm), corresponding to a leaf-shade illumination (Döring and Röhrig 2016 ; P.C. personal observations). On the contrary, in the presence of UV radiation, we expected that time delay before flight would be shorter, meaning that the parasitoids would disperse probably to find hosts or mates.

Materials and Methods

Light Environment

To create our different light environment (Fig. 1), we first measured sunlight and leaf-shade of broad bean (*Vicia faba*) spectra in the field (Fig. 1a) in the region of Quebec City (46.911625, -71.051129) in mid-July at noon, by using a mobile experimental set-

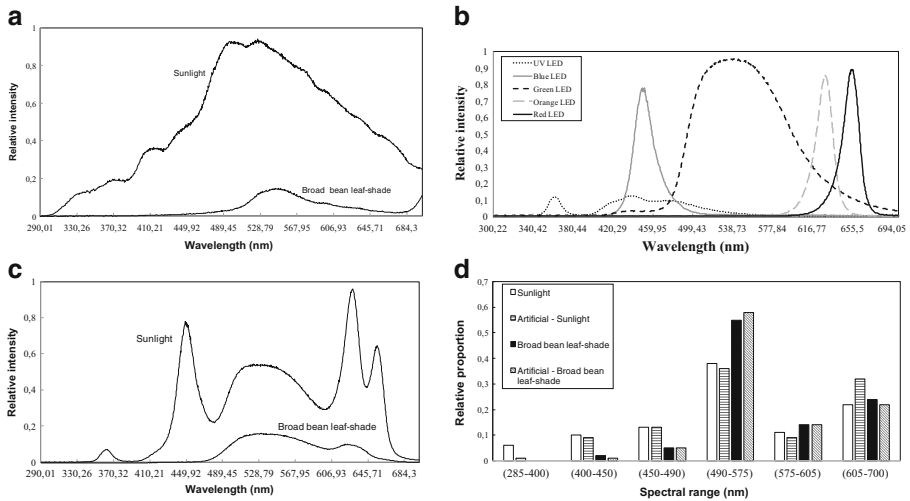


Fig. 1 Spectrum of sunlight and broad bean leaf-shade between 290 and 700nm. **a** Natural spectrum taken near Quebec City (46.911625, -71.051129) in mid-July at noon. **b** Spectrum of the five LEDs used to create artificial illuminations. **c** Artificial spectrum created with an electronic system composed of LEDs of 5 different wavelengths. **d** Comparison between natural and artificial spectrum of the relative proportion of each spectral range

up (spectrometer: HR4000CG-UV-NIR, Ocean Optics, Dunedin, USA). We measured these two lighting conditions because they are the most met by aphids and parasitoids in nature. Then, we constructed a light environment box (L: 50 cm, W: 30 cm, H: 40 cm) fitted with five types of LEDs (peak wavelength - products code): UV (361 nm - L5-1-U5TH15-1), blue (450 nm - 720-LDCQARVOAQ241), green (500-600 nm - LCG H9RM-LXLZ-1), orange (626 nm - LR CP7P-JRJT-1-0-350-R18) and red (660 nm - SSL-LX5093SRC/F) (Fig. 1b). The UV, blue and green LEDs were chosen to match as much as possible the spectral sensitivity peaks of the three types of photoreceptors assumed to be possessed by the insects studied here (see below). We used a microcontroller ARDUINO Leonardo (© 2017 ARDUINO) connected to LEDs and to a laptop to dynamically control the spectral content (wavelengths) and quantity of illumination (light intensity). We used neutral diffusers to scatter light rays and thus limit spots of light created by individual LEDs. With this simple base, we were able to replicate largely the sunlight and leaf-shade illumination that we had previously measured. As infrared radiations are probably not involved in the studied insects' vision, and because we needed to avoid heat effects on locomotor activity, they were removed from all spectra and only spectral composition between 300 and 700nm were replicated (Fig. 1c). The comparison of the spectral composition for each spectrum is shown in Fig. 1d. For values of light intensities used in each experiment, see Table 1.

Study Organisms

Green and pink adult morphs of pea aphids *Acyrtosiphon pisum* were collected on Alfalfa (*Medicago sativa*) and red clover (*Trifolium pratense*) in early summer at Université Laval experimental farm, Saint-Augustin de Desmaures (Québec, Canada). They were separated and reared clonally on broad bean *Vicia faba* plants at 20°C ± 1°C, 65% RH and under a

Table 1 Light intensities ($\mu\text{W}/\text{cm}^2$) used for each experiment

Experiments	Illumination	Light intensities ($\mu\text{W}/\text{cm}^2$)
Aphids walking activity	UV / medium	20
	Leaf-shade / dim	43
	Sunlight UV+ / dim	95
	Red / medium	9
Parasitoids walking Activity	<u>Monochromatics</u>	(dim; medium; bright)
	UV	4; 20; 40
	Blue	25; 112; 224
	Green	18; 88; 176
	Orange	17; 87; 173
	Red	2; 9; 19
	<u>Polychromatics</u>	
	Leaf-shade / dim	43
	Leaf-shade / bright	86
	Sunlight UV- / dim	83
	Sunlight UV+ / dim	95
	Sunlight UV+ / bright	209
Parasitoids flight activity	Leaf-shade / bright	86
	Sunlight UV+ / dim	95

16L: 8D photoperiod. We randomly selected 2 green and 2 pink clones for our experiments (see Table 2 for characteristics), and used only wingless individuals.

Parasitoid wasp colonies were established from *Aphidius ervi* from Biobest (Canada Ltd. Leamington, ON). They were reared on a green clone of pea aphid, not involved in the experiment and maintained at $20^\circ\text{C} \pm 1^\circ\text{C}$, 65% RH and under a 16L: 8D photoperiod. The experimental wasps were isolated at the mummy stage. At emergence, two experimental groups were obtained: 1) virgin group: males and females were kept isolated to prevent mating and, 2) mated group: males and females were mated under direct observation. At the time of the experiment, adult wasps were aged 24–30h. One male and one female of each experimental group were observed at the same time in an individual Petri dish, the two dishes being placed side by side in the experimental box.

Table 2 Characteristics of the *Acyrtosiphon pisum* clones used in experiments

Clone	Color	Host-plant – origin	Facultative symbiont(s)
ECH18V (clone 1)	Green	Alfalfa – Québec (QC, Canada)	<i>H. defensa</i> + PAXS + <i>R. insecticola</i> + <i>S. symbiotica</i>
TR29V (clone 2)	Green	Red clover – Québec (QC, Canada)	<i>H. defensa</i> + <i>S. symbiotica</i>
LU14R (clone 1)	Pink	Alfalfa – Québec (QC, Canada)	None
TR18R (clone 2)	Pink	Red clover – Québec (QC, Canada)	<i>R. insecticola</i>

Experiments were conducted in a dark room at $20^{\circ}\text{C} \pm 1^{\circ}\text{C}$ between 8:30 and 12:00 am. Aphids and parasitoids were kept in the dark during at least 30 min before the beginning of the experiment. They continuously had access to food until they were used for the experiment. All observations were made on insects kept in a cleaned (Sparkleen™ 1 detergent from Fisherbrand™), transparent Petri dish (D: 5 cm, H: 1 cm), to remove any potential chemical traces.

Aphid Locomotor Activity (Walking)

To test whether light environment could affect the walking activity of aphids, we simultaneously recorded with chronometers the time spent walking by adults and immature (3rd instar nymphs) aphids of the 4 experimental clones. Each aphid was submitted to one of the four different light environments, during a 5-min test, which were: 1) UV/medium light, 2) Leaf-shade/dim light, 3) Sunlight/dim light and 4) Red/medium light. We chose these four light environments to explore the entire light spectrum. UV and red lights acted as positive and negative controls respectively. The sunlight condition was composed of the UV light, red light, and the green part of the leaf-shade condition. Ten complete blocks were obtained by having 10 aphids of each clone x age interactions (N = 8 groups) tested under each light condition (N = 4 lights). We thus tested 320 aphids.

Parasitoid Locomotor Activity (Walking and Flight)

The effects of light environments on the walking activity of *A. ervi* were tested on 4 experimental groups of wasps: virgin females, mated females, virgin males and mated males. We placed one parasitoid of each group in a Petri dish and recorded walking duration of parasitoids under 20 different light environments. There were 5 monochromatic environments (UV, blue, green, orange and red) x 3 light intensities (dim, medium and bright; see Table 1 for details) and 5 polychromatic environments corresponding to 1) Leaf-shade/dim light, 2) Leaf-shade/bright light, 3) Sunlight without UV/dim light, 4) Sunlight with UV/dim light, 5) Sunlight with UV/ bright light. Monochromatic environments were studied to see the potential specific effect of wavelengths spread over the entire spectrum, on locomotor activity. Polychromatic environments were chosen assuming that they match the illumination most commonly met in the field by parasitoids, including intensity variation. They can be considered as: leaf-shade illumination near the soil, leaf-shade illumination at the top of a plant, sunlight illumination on a cloudy day, sunlight illumination in the mid-morning and sunlight illumination at midday, respectively. All light environments were provided randomly to each individual for a 1-min test separated by 2 min in the dark, to minimize the possibility that previous light environment influenced locomotor activity in the following light environment. In preliminary tests, we noted that if a wasp responded to the stimulus, it walked almost immediately after its release, otherwise it remained motionless during (almost) all the test. We thus decided to do 1-min tests since the preliminary experiments with longer time (5 min) would produce the same results. Twelve complete blocks were obtained by having 12 wasps of each experimental group (N = 4 groups) submitted to all lighting conditions. We thus tested 48 wasps (the maximum that could be handled) for a total of 720 walking activity measurements from

the 15 monochromatic light environments provided and 240 from the 5 polychromatic light environments.

For delay before flight, only 1) Leaf-shade/bright light and 2) Sunlight with UV/dim light were tested. In this experiment, a similar light intensity in both leaf-shade and sunlight conditions was used to focus on the impact of spectral composition (especially presence or absence of UV) and not intensity. The light intensity under leaf-shade condition actually was 90.5% of our sunlight condition (see Table 1 for values). We measured time delay between the removal of the top of the Petri dish and the first flight of each wasp. We stopped the test when the parasitoid flew away (maximum observed = 2 min). We used 15 mated females and 15 mated males in each light condition ($N = 2$ light conditions) and each wasp was tested only once, to avoid any past-experience effects. Only mated wasps were used here because the previous experiment showed that there was no difference between mated and virgin males and because virgin females were motionless (see the Results section).

Statistical Analysis

Aphids We graphically assessed the distribution of walking activity and we chose to analyze the probability that aphids would be active using the GLIMMIX procedure from SAS software, because most individuals were either totally active or totally inactive. A split-plot binomial model has been used to compare the probability of aphids being active with Light as the main plot and Color, Instar and their double interactions as subplots fixed effects. We set Clone (nested in Color) as subplot random effect.

Parasitoids For walking activity, we analyzed the probability of being active under each light environment because there were a lot of zeros in the binary data. Based on the distribution of walking activity, all individuals walking from 0 to 33,3% (excluded) of the total test duration were considered as inactive and those walking from 33,3 to 100% of the total test duration were considered as active. Analysis was performed using a variance comparison test with randomized complete block and repeated measures design, using the “glmmPQL” function from MASS package on R software (version 3.2.3). For delay before flight, we used a negative binomial regression that corrected for the overdispersed Poisson distribution of the data. We used the “lsmeans” function from lsmeans package to contrast levels of specified factors (Least Squares Means method).

Results

Aphids Walking Activity

The probability of aphids being active (walking) varied markedly between light environments (light; $F_{3,27} = 9.58$, $p < 0.001$; Table 3). The red light environment stood apart, significantly reducing activity (Table 4). There was a significant interaction between aphid color and instar (age) (color*instar; $F_{1,252} = 10.3$, $p = 0.0015$). For green aphids, adults were significantly less active than 3rd instars (Table 4), but there was no significant difference between adults and immatures for pink aphids (Table 4).

Table 3 Statistical modeling of probability of *Acyrtosiphon pisum* being active (walking) under controlled light environments. A split-plot binomial model was fitted to data including Light (UV, Leaves, Sun and Red) as main plot effect, Color morph (Green, Pink), Instar (Adult, Nymph) and their interactions as subplot effects, and Clone within color morph as a random effect

Effects	Numerator df	Denominator df	F	P ²
Main Plot				
Light (F) ¹	3	27	9.58	< 0.001*
Subplot				
Color (F)	1	252	0.13	0.7162
Instar (F)	1	252	1.88	0.1715
Light*Color (F)	3	252	1.24	0.2953
Light*Instar (F)	3	252	1.75	0.1577
Color*Instar (F)	1	252	10.30	0.0015*
Clone (green) (R)	1	269	36.64	< 0.001*
Clone (pink) (R)	1	269	35.77	< 0.001*

¹ Fixed effects (F) and Random effects (R)

² Asterisks indicate significant value at $\alpha=0.05$

Table 4 Post-hoc comparisons for fixed (Light and Color*Instar) and random factors (Clone(Color)) significantly affecting ($p < 0.05$) probability of *Acyrtosiphon pisum* walking under controlled light environments, using least squares means method (LSM)

Fixed Effects	df	t	Mean ¹	S. E
Light environment				
UV	27	0.12	0.56 a	0.51
Leaf-shade	27	-0.20	0.40 a	0.49
Sunlight	27	-0.42	0.29 a	0.43
Red	27	-1.40	0.05 b	0.10
Color*Instar				
Green Adult	252	-0.94	0.06 A	0.17
Green Young	252	-0.24	0.33 B	0.64
Pink Adult	252	0.06	0.54 A	0.70
Pink Young	252	-0.23	0.34 A	0.64
Random Effects				
Clone (green)				
Green Clone1	252	-5.12	0.00 *	0.00
Green Clone2	252	3.81	0.88	0.06
Clone (pink)				
Pink Clone1	252	2.92	0.76 *	0.07
Pink Clone2	252	-3.96	0.16	0.06

¹ Different lowercase letters indicate significant differences between light conditions at $\alpha=0.05$. Different capital letters indicate significant differences between instars within a Color morph at $\alpha=0.05$. Asterisks indicate significant differences between Clone within a Color morph at $\alpha=0.05$

Contrasts on the random effect (i.e clones' identity) showed that there was large variation among clones of the same color morph (pink; $F_{1,269} = 35.77$, $p < 0.0001$; green; $F_{1,269} = 35.77$, $p < 0.0001$; Table 3, Table 4).

Parasitoids Walking Activity

For monochromatic environments, intensity did not significantly affect the parasitoids' probability of being active (intensity; $F_{2,616} = 2.46$, $p = 0.09$, Table 5). However, activity was significantly affected by light quality (wavelength; $F_{4,616} = 18.4$, $p < 0.001$; Fig. 2) and sex (sex; $F_{1,33} = 9.17$, $p < 0.01$), but not reproductive status (repro; $F_{1,33} = 0.22$, $p = 0.64$). The averaged probability of males being active was over four times greater than that of females (68.2% vs 16.5%, $t = -5.19$, $df = 11$, $p < 0.001$). No significant interaction was found between the factors.

For polychromatic spectra (Fig. 3), light environment had a marginally non-significant effect on the parasitoids' probability of walking (light; $F_{4,176} = 3.98$, $p = 0.054$; Table 6). Sex significantly affected the probability of walking (sex; $F_{1,33} = 3.15$, $p = 0.016$), but not reproductive status (repro; $F_{1,33} = 0.18$, $p = 0.674$). The probability of walking was again greater for males than females (89.9% vs 57.1%, $t = -2.424$, $df = 11$, $p = 0.033$), mostly due to virgin females, but differences between virgin females and other groups were not significant except under "leaf-shade/ bright" condition (V. females vs M. females, $df = 11$, $t = 4.652$, $p = 0.038$; V. females vs V. males, $df = 11$, $t = -6.459$, $p = 0.003$; V. females vs M. males, $df = 11$, $t = 4.791$, $p = 0.032$).

Table 5 Variance analysis using a binomial model on randomized complete blocs and repeated measures for monochromatic light environments on the probability of *Aphidius ervi* wasps walking. The factors decomposing inter-wasp variability are Sex (male, female) and Reproductive status (virgin, mated). Measures were repeated on a same wasp individual through Wavelengths conditions (UV, blue, green, orange, red) and Intensity (low, medium, high)

Effects	Numerator df	Denominator df	F	p^1
Sex (S)	1	33	9.172	0.005*
Reproductive status (R)	1	33	0.218	0.644
S*R	1	33	0.015	0.905
Wavelength (W)	4	616	18.43	< 0.001*
W*S	4	616	1.695	0.149
W*R	4	616	0.322	0.863
W*S*R	4	616	1.941	0.102
Intensity (I)	2	616	2.464	0.086
I*S	2	616	0.678	0.508
I*R	2	616	0.619	0.539
I*W	8	616	0.851	0.558
I*W*S	8	616	0.913	0.505
I*W*R	8	616	0.514	0.847
I*S*R	2	616	0.062	0.939
I*W*S*R	8	616	0.236	0.984

¹ Asterisks indicate significant value at $\alpha=0.05$

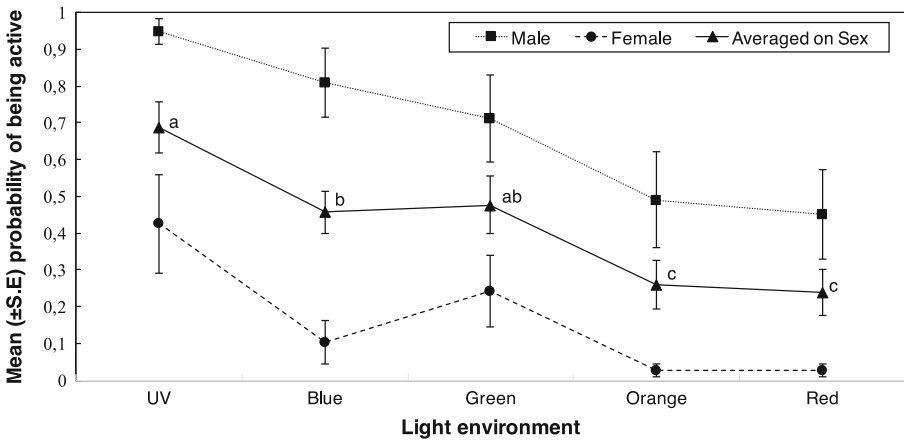


Fig. 2 Probability (Mean ± S.E) of being active (walking) for males and females *Aphidius ervi*, under different monochromatic light environments. Since intensity did not affect probability of being active ($F_{2,616} = 2.46$, $p = 0.09$), the mean probability of being active averaged on intensity for each wavelength is shown. Significant differences were found between wavelengths ($F_{4,616} = 18.43$, $p < 0.001$). Different lowercase letters indicate significant differences between light environments on probability averaged on sex ($p < 0.05$ with Tukey method p value adjustment). A significant difference was found between males and females ($F_{1,33} = 9.172$, $p = 0.005$). $N = 24$ males and $N = 24$ females in each wavelength group, males being the most active

Parasitoids Flight Activity

Results in Fig. 4 show that there was a significant interaction between light and sex on delay before takeoff (interaction; $z = 3.096$, $p = 0.002$). Females took off nearly instantaneously when exposed to sunlight illumination, whereas they took off after a longer delay under leaf-shade condition (10.5s vs 31.3s, z ratio = 2.67, $p = 0.03$). For

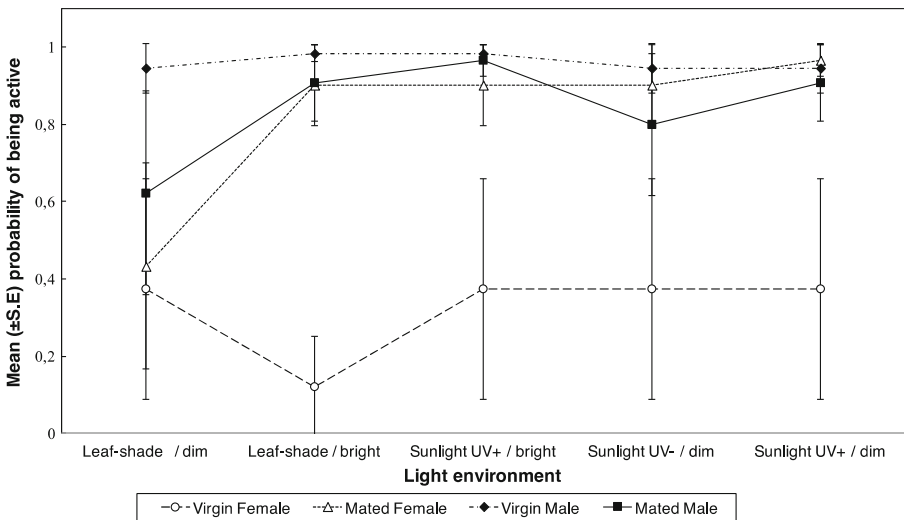


Fig. 3 Probability (Mean ± S.E) of walking for males and females *Aphidius ervi* under the five different polychromatic light environments. Light environment did not affect the probability of being active ($F_{4,176} = 3.98$, $p = 0.054$) whereas sex did ($F_{1,33} = 3.15$, $p = 0.016$), mostly due to virgin females (see text for details). $N = 12$ wasps/ group in each light environment

Table 6 Variance analysis using a binomial model on randomized complete blocks and repeated measures for polychromatic light environments (artificial sunlight or leaf shade) on the probability of *Aphidius ervi* wasps walking. The factors decomposing inter-wasp variability are Sex (male, female) and Reproductive status (virgin, mated). Measures were repeated on a same individual wasp through Light environments (leaf-shade/dim light, leaf-shade/bright light, sunlight without UV/dim light, sunlight with UV/dim light, sunlight with UV/ bright light)

Effects	Numerator df	Denominator df	F	p ¹
Sex (S)	1	33	3.147	0.016*
Reproductive status (R)	1	33	0.180	0.674
S*R	1	33	3.48	0.071
Light environment (L)	4	176	3.981	0.054
L*S	4	176	1.289	0.276
L*R	4	176	2.097	0.083
L*S*R	4	176	0.792	0.532

¹ Asterisks indicate significant value at $\alpha=0.05$

males, the light environment had no effect on flight delay (25.3s vs 36.8s, z ratio = -1.09, $p = 0.69$). The flight delay was not significantly different between males and females under leaf-shade condition (25.3s vs 31.3s, z ratio = 0.63, $p = 0.92$) but the difference between females and males was significant under sunlight condition (36.8s vs 10.5s, z ratio = -2.93, $p < 0.02$).

Discussion

The main objective of this study was to understand how the immediate light environment can affect the locomotor activity of the parasitoid wasp *A. ervi* and different phenotypes of its main host the pea aphid, *A. pisum*. Being sap sucking insects, aphids are relatively inactive compared to parasitoid wasps using them as hosts. Nevertheless, we observed significant variation in aphid walking activity under the different light conditions.

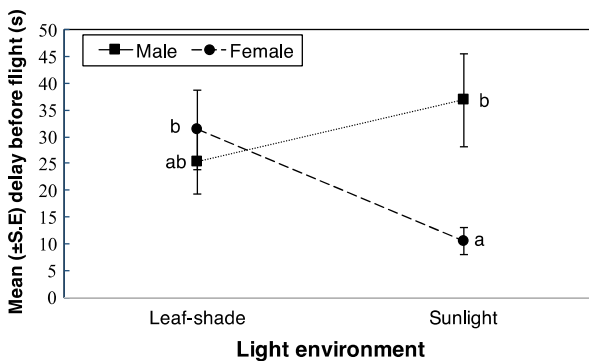


Fig. 4 Mean delay (\pm S.E.) before flight (s) of males and females *Aphidius ervi* under leaf-shade and sunlight illumination. Different lowercase letters indicate significant differences between groups ($p < 0.05$ with Tukey method p value adjustment). $N=15$ males and females in each light environment

Wingless pea aphids showed large variations in walking activity under controlled light environments, which depended on clone's identity and developmental stage (adult or 3rd instars). Overall, the aphids were much less active than parasitoids as expected. We found that 56% of aphids were active under UV, both color morphs and instars combined. It appeared that red light specifically inhibited aphid activity, significantly reducing the probability of being active to only about 5%. These results are in agreement with a recent study (Zhang et al. 2016) analyzing the phototaxy of different instars of the pea aphid. However, their results are difficult to compare to ours, as they observed a single (pink) pea aphid clone.

Color preference of adult winged aphids was previously studied in order to develop color traps in the field (reviewed in Döring and Chittka 2007). Here, we studied wingless aphids because parasitoid wasps preferentially attack young wingless instars (Ives et al. 1999; He et al. 2011). We could expect wingless adults to be more active than 3rd instars under UV light, hypothetically because they are larger and better able to search for a shelter and a suitable feeding site on host plants when exposed to potentially damaging UV wavelengths (Burdick et al. 2015). However, it was the clone within color morph that had the most significant effect on pea aphid activity. Aphids of some clones remained motionless, while others were very active (Table 4). It is well-known that aphids present interclonal variation in escape (Braendle and Weisser 2001) and aggregation behaviors (Muratori et al. 2014). Pea aphid color morph and tendency to move in the presence of a wasp are both important factors involved in the success of parasitism by *A. ervi* (e.g. Bilodeau et al. 2013). We show here that there is clonal variation of aphid walking activity that can also vary according to aphid instar. In combination with clonal variation, locomotor variations could contribute to the success or failure of parasitism. It will be interesting to study in future works the effect of clonal variations on probability of being attacked under different light conditions.

Turning to the parasitoid, a surprising result was that light intensity did not affect the locomotor activity of *A. ervi*. Intensity was the main obstacle in our experiments. LEDs are spot light sources, and even though we used neutral diffusers, the number of LEDs we could install without creating spots of light was limited. We thus could not achieve intensities similar to those in the field. Even though dim intensities were about 10 times weaker than bright intensities for our monochromatic environments, we can suppose that the differences were not perceived by parasitoids or that they did not respond to them. However, even under relatively low intensity, the males were active during almost all test duration (about 80% of the time, all light environments combined), meaning that intensity was high enough to trigger locomotor activity of these diurnal insects. We were also able to demonstrate a difference in behavioral response to the light environment between male, which were more active than female wasps.

Insects must adapt to daily variations of spectral composition of sunlight and habitat illumination (Endler 1993; Thorne et al. 2009). The monochromatic lights were especially studied here in order to detect the potential effect of wavelength on *A. ervi* locomotor activity. UV was the wavelength that most elicited its locomotor activity (around 94% of males were active and 43% of females, Fig. 2). Based on the results, it is likely that *A. ervi* wasps are the most responsive to UV, followed by blue and green light. It is well known that Hymenopteran wasps possess three types of photoreceptors: UV, blue and green (Peitsch et al. 1992), however the relative sensitivity of each photoreceptor has not been measured. As we observed for the aphids, the red-light

environment most reduced *A. ervi* locomotion, even if it remained high for males (around 45% of males). *Aphidius gifuensis* cannot perceive red light like most insects, (Chen et al. 2012), thus we assume that the same applies for the closely related *A. ervi*.

For a given wavelength, we found that male *A. ervi* were generally more active than females as mentioned. Sexual phototactic differences have also been found in the pteromalid *P. aphidis*, where females were attracted by 380 nm (UV), but no response was observed in males (Chen et al. 2014). Their results also indicated that females were the most sensitive to wavelengths corresponding to the green color (550 nm to 590 nm). The authors suggested that sexual behavioral differentiation in response to visual stimuli can be explained by the fact that in parasitoids it is the female who undertakes the search for hosts, whereas the males search for sexual partners. The female would therefore be more sensitive to wavelengths allowing it to localize the hosts in their immediate habitat. With *A. ervi*, we can assume the same sex specific roles, meaning that females should search for hosts and males for virgin females. Since no hosts was present in the test, female *A. ervi* remained only moderately active (maximum 43% of females were active under UV). No male was seen in courtship behavior, which is evident to characteristic wing vibration (McClure et al. 2007; Villagra et al. 2011), suggesting that males did not detect the presence of the females, even though they were present in individual Petri dish nearby those of females. We can suppose that in the natural context, males remain very active whatever is the wavelength, to maximize their chances to meet unmated females, who are also mobile.

Under polychromatic artificial illuminations simulating sunlight or leaf-shade, the difference between males and females was also significant overall. However, only the activity of virgin females stands out, as they were generally less active than all other groups (Fig. 3); we could not bring out significant differences using contrasts between the other groups compared. In other studies, virgin female *Lysiphlebus testaceipes* (Hymenoptera: Braconidae) and *Nasonia vitripennis* (Hymenoptera: Pteromalidae) stayed inactive more often and longer than mated females (Fauvergue et al. 2008; King et al. 2000), which likely increases probability of being localized by a searching male. In our experiments, the tested wasps were 24–30h aged, so they had already spent about 15% of their lifespan as virgins (1 day, out of about 1 week, P.C. personal observations). Males search for mates by responding to the females' sex pheromone in many parasitoids species (Fauvergue et al. 1999; Villagra et al. 2008), but the attractiveness of old virgin females of *A. ervi* is reduced compared to younger ones (McClure et al. 2007). He and Wang (2008) also showed that the proportion of daughters produced by *A. ervi* decreased with parental age at mating, suggesting reduced insemination or sperm use to fertilize eggs. In our situation (virgin females and absence of hosts) and under artificial sunlight and leaf-shade illuminations, we can suppose that the trade-off between searching for hosts and mating later, or mating early and then searching for hosts was biased toward waiting for mating.

Our working hypothesis was that wasp walking behavior would be favored in the absence of short wavelengths < 400 nm (simulated leaf-shade illumination), as opposed to flight being favored in presence of UV radiation (simulated sunlight illumination) (Mound 1962). Interestingly enough, we showed a difference in delay before takeoff between males and females. Indeed, our hypothesis is supported for females as they flew away almost instantaneously when they were exposed to a sunlight environment while they kept walking longer under the leaf-shade lighting condition. This result can

be explained by the fact that hosts of *A. ervi* (such as pea aphids) are found naturally beneath leaves (Lagos et al. 2001). Leaf-shade conditions would indicate to females that the possibility of finding hosts nearby is high under such conditions. However, the delay before flight for females remained short under both light conditions (min = 8 sec under leaf-shade, max = 45 sec under sunlight, Fig. 4), supposedly due to absence or insufficient olfactory cues indicating the presence of hosts in this experiment (Weinbrenner and Volkl 2002). Unlike females, the effect of illumination on flight takeoff delay for males (average 25–35 sec) was not significant. For males, the hypothesis must be rejected. This may suggest that walking is the first component of male mate-searching behavior, in absence of females' sex-pheromones. Males could be equally adapted to find females under both illumination conditions in natural environments, first by walking for some time to potentially detect a female, eventually finally flying away in absence of stimulation.

We have also shown that the delay before flight between males and females did not differ significantly under leaf-shade condition, whereas it was 3.5 time shorter for females than for males under sunlight condition. Thus, the sunlight illumination seems to stimulate flight more strongly for females than males. Flight thus seems to be a significant component of female host-searching behavior under sunlight illumination. This would be advantageous because females could thus easily disperse to adjacent plants to search for other host patches.

Results of this study demonstrate that the light environment can differentially affect the locomotor activity of both pea aphids and their parasitoids. Since locomotor activity and host-searching and parasitism are strongly connected, it will be interesting to study the capacities of parasitoids' host-location and recognition in close encounters according to the light environment, with special attention to the critical role of aphid inter clonal phenotypic variation, including color morph and tendency to move.

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