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# Light dependency of life trails, reproduction, locomotion, and predation in the polyphagous ladybird *Hippodamia variegata*

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**Abstract**

Light is regarded a key environmental cue influencing biological, physiological, and behavioral characteristics in insects. We compared the development, reproduction, locomotion, and predation ability of the predatory ladybird *Hippodamia variegata* (Goeze) (Coleoptera: Coccinellidae) under various photoperiods, light intensities, and light wavelengths. The results indicated long daylight, high light intensity, and particular colors light (blue, green, and yellow) could benefit *H. variegata* especially in shortening the period of immature development, increasing mating frequency (shorter mating and pre-oviposition periods), higher fecundity, and a higher proportion of eggs hatched. Average locomotion speed and prey consumption rate of *H. variegata* increased with prolonged day length and increased light intensity. However, very high intensity of light could inhibit predation rates. Furthermore, green and yellow wavelength conditions increased locomotion speed of *H. variegata*, and the number of prey consumed increased with increased wavelength. The present study not only revealed significant influences of light conditions on the development and fertility of *H. variegata*, it also provided sufficient empirical data to improve the efficiency of mass rearing and field releases of this predatory ladybird by regulation of light conditions during biological control applications.

## Introduction

Light is among the most fundamental of environmental factors and has been widely studied via life-history traits in its influence on the physiology of arthropods (Jander & Waterman, 1960; Tobe & Pratt, 1974; Dudt & Shure, 1994). Variation in characteristics of natural light primarily accompany seasonal change (Walker & Steffen, 1996). Routine variation in photoperiod, intensity, and wavelength has been shown to affect insects in development, reproduction, activity level, foraging, and consumption (Bishop, 1969; Tauber & Tauber, 1976; Wyatt & Brown, 1977; Zaslavski, 1988). Prolonged daylight is known to accelerate the development of many coleopteran species (Aksit et al., 2007), whereas the lepidopteran species *Heliothis virescens* (Fabricius) prefers to emerge from pupae under prolonged dark conditions (Henneberry & Clayton, 1984). Study of the aphidophagous ladybird *Coelophora saucia* (Mulsant) has shown a higher mating frequency with shorter mating periods when they are exposed to a long day length of white light (Pathak, 2006). Our previous work has shown that high intensity of light with long wavelengths (red end of the spectrum) increases the locomotory activities of the predatory flower bug *Orius sauteri* (Poppius) (Wang et al., 2013c). In terms of light regulation in assisting greenhouse vegetable plant production, it is advantageous to investigate the effects of light on insects within agricultural systems (Ehret et al., 1989; Hao & Papadopoulos, 1999). Research on the influence of light on the performance of arthropod insects not only reveals mechanisms of environmental adaptation but provides information necessary for utilizing insects for assisting agriculture, in particular, the mass rearing and release of natural enemies for biological control of arthropod pests.

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The predatory ladybird native to Asia, *Hippodamia variegata* (Goeze) (Coleoptera: Coccinellidae), is well known as an efficacious biological control agent particularly in China. This coccinellid species preys on various herbivorous pests including aphids, whiteflies, thrips, and larvae of some lepidopteran species in crop land, greenhouse vegetables, and orchards (Obrycki & Orr, 1990; Franzmann, 2002; Kontodimas & Stathas, 2005). A series of studies has shown high capture success rate of *H. variegata* to different prey. Under a constant temperature, *H. variegata* has been shown to be consistent in development, prey consumption, and oviposition when preying on two aphid species (Michels & Flanders, 1992). Unfortunately, few details have been available in previously published documents on the influence of environmental and physical conditions on life-history traits of ladybirds, especially the impact of light (Hodek et al., 1996). Our previous work showed clearly that photoperiod variation influences development, oviposition, and prey consumption of the predatory ladybird *Cheilomenes sexmaculata* (Fabricius) (Wang et al., 2013b). This has been supported by other research on the influence of light on predatory coccinellids (Omkar et al., 2005; Aksit et al., 2007). Such evaluations of light condition on the development and reproductive performance of predatory biological control agents are necessary both for biological control regulation and quality control in mass rearing.

Here, we report on work focusing on the influences of a number of primary light factors—photoperiod, light intensity, and light wavelength—on development, mating and reproduction, locomotion speed, and predation of the ladybird *H. variegata*. Our work contributes to determining the optimal light conditions for the rearing of *H. variegata* and evaluating its environmental adaptability. Furthermore, the results could help to create optimal environmental conditions for the release of *H. variegata* in vegetable greenhouses as biological control agents.

## Materials and methods

### Insects

Over 300 *H. variegata* adults were collected from experimental cotton fields (116°28′E, 39°95′N) of the Beijing Academy of Agriculture and Forestry Sciences (BAAFS), Beijing, China, during May 2013. The ladybirds were transported and reared in the Laboratory of Natural Enemies Research, Institute of Plant and Environment Protection, BAAFS, on the aphid *Aphis craccivora* Koch (Hemiptera: Aphididae) to establish an experimental population under 25 °C, 65% relative humidity, L12:D12 h, and 800 lux white light intensity (regulated by an automatic environmental condition management system, L-100; Suntech, Beijing, China). The ladybirds were maintained in culturing cages (45 × 50 × 60 cm, 40 pairs per cage) with daily supplied food aphids with several fresh broad bean [*Vicia faba* L. (Fabaceae) cv. LinCan-5] seedlings. After three generations of culturing, newly hatched adults were selected for further experiments.

### Light condition settings

We varied three primary light factors: photoperiod (L:D = 0:24, 8:16, 12:12, 16:8, and 24:0; light intensity = 1.2 W $m^{-2}$ and white light), light intensity (0.6, 0.9, 1.2, 1.5, and 1.8 W $m^{-2}$; L12:D12 photoperiod and white light), and light color [wavelength = 640 (red), 570 (yellow), 520 (green), 465 (blue), and 390 nm (purple); L12:D12 photoperiod and light intensity = 1.2 W $m^{-2}$). The white light in all tests was provided by white LED lights (XF101; Unihero, Guangdong, China). The remaining environmental conditions were regulated as per ladybird culturing above. The light environment was set using LED lamps (XF201; Unihero). The exact light wavelength of each colored LED resource has been measured by LED colored wavelength detector (HDR, Otsuka, Japan).

### Development and reproduction

Newly laid eggs of *H. variegata* were collected on broad bean leaves and placed in plastic Petri dishes (9 cm diameter, two clusters per dish). The Petri dishes were placed under the variable environmental conditions as mentioned earlier. The hatched first instars were kept individually with food aphids in Petri dishes as above. We supplemented the aphids daily until adults emerged. We recorded the period of development of each instar until eclosion.

Pairs of 10-day-old *A. variegata* adults were reared in Petri dishes with *Myzus persicae* (Sulzer) (Hemiptera: Aphididae) food aphids and maintained under environmental conditions with varying photoperiod, for developmental observation (one pair per dish). Then we continuously observed the mating process and recorded the mating duration of the ladybirds. When the ladybirds finished copulation and separated, we eliminated the male and individually reared the female with a daily food supply of aphids. Afterward, we calculated the pre-oviposition and oviposition duration, total fecundity, and the proportion of offspring that hatched, until the death of the female. The tests were repeated under different wavelengths and levels of light intensity, respectively. The observations were replicated 30× for each treatment and new individuals were used in each replication.

### Locomotion and predation

We examined the locomotion of *H. variegata* using an animal/insect behavior analysis device (CASO-L;

Camsonar, London, UK). A randomly selected 10-day-old *H. variegata* virgin adult (0.014–0.018 g body weight) was placed on the central sample plate and sealed in with a transparent cover (40 cm diameter, 2.5 cm high). The environment was set at different photoperiods for developmental observation. We adjusted the focus of the monitoring camera, ensured the scope was cleaned, and then mounted. Meanwhile, analysis software (Imagine A/S – 1.3; Camsonar) was linked with the monitoring camera to analyze the locomotion of ladybirds. Ladybirds were observed for 30 min. The software calculated and recorded the average speed of *H. variegata* adults in 5-min intervals. LEDs emitting light of different wavelengths were set around the sample plate at 25 cm from the center. The tests were repeated under different wavelengths and levels of light intensity. The observations were replicated 30× for each treatment and new individuals were used in each replication.

For comparing the predation ability of *H. variegata* adults among light environments, an adult after 12 h starvation was placed with 200 third-instar nymphs of a *M. persicae* in a large glass Petri dish (30 cm diameter) covered by a 40-mesh fabric net for ventilation. The number of prey aphid consumed was recorded 24 h later. We repeated the tests 30× and under the same wavelengths and levels of light intensity as the locomotory experiments.

#### Statistical analysis

All data were checked for normality and heterogeneity of variance following Kolmogorov–Smirnov's and Bartletts' test and found to be distributed normally with homogeneous variances. The influences of different light conditions on the developmental period, mating, reproduction, locomotion, and prey consumption of *H. variegata* were analyzed using one-way analyses of variance (ANOVA) with either photoperiod, light intensity, or wavelength as independent factors. Variation in egg hatching among photoperiods, light intensities, and light wavelengths was examined by logistic analysis. The post-hoc comparisons were conducted using Tukey's test if significant differences were detected by one-way ANOVA. Statistical analyses were carried out using SPSS 18.0 software (Allen & Bennett, 2010).

## Results

#### Development under various light conditions

As shown in Table 1, variation of photoperiod influences the development of *H. variegata* ladybirds in the egg stage, instar 1–4 stages, pupal stage, and total immature stage. Similarly, developmental periods of *H. variegata* were significantly different across light intensities (Table 2) and wavelengths (Table 3).

#### Mating and reproduction under various light conditions

Like development, photoperiod can significantly affect reproductive performance of *H. variegata* in terms of mating duration, pre-oviposition duration, oviposition duration, and total fecundity, although the proportion of offspring hatching did not vary significantly (Table 4; Figure 1). The results showed variation in light intensity could significantly influence all reproductive characteristics (Table 5), as did light wavelength (Table 6). Furthermore, both light intensity and light wavelength could significantly influence offspring hatchability (Figures 2 and 3).

#### Locomotion and predation under various light conditions

The average speed of adult *H. variegata* locomotion and their prey consumption rate were significantly influenced by photoperiod (Figure 4), light intensity (Figure 5), and wavelength (Figure 6).

**Table 1** Mean (± SE) duration of development of each immature stage of *Hippodamia variegata* at various photoperiods

| Photoperiod (L:D) | Development duration (days) | | | | | | |
|---|---|---|---|---|---|---|---|
| | Egg | Instar 1 | Instar 2 | Instar 3 | Instar 4 | Pupa | Total immature |
| 0:24 | 3.5 ± 0.1a | 3.4 ± 0.2a | 2.4 ± 0.1a | 2.3 ± 0.2a | 3.7 ± 0.1a | 3.5 ± 0.1a | 18.8 ± 0.2a |
| 8:16 | 3.2 ± 0.1b | 3.3 ± 0.1a | 2.5 ± 0.1a | 2.4 ± 0.1a | 3.3 ± 0.1b | 3.5 ± 0.2a | 18.1 ± 0.3a |
| 12:12 | 3.1 ± 0.2b | 3.0 ± 0.1b | 1.9 ± 0.1b | 2.1 ± 0.1b | 2.9 ± 0.2c | 3.2 ± 0.1b | 16.2 ± 0.3b |
| 16:8 | 2.8 ± 0.1c | 2.7 ± 0.1c | 1.8 ± 0.2b | 1.8 ± 0.1c | 2.7 ± 0.1d | 3.2 ± 0.2b | 15.0 ± 0.3b |
| 24:0 | 2.6 ± 0.2d | 2.4 ± 0.2d | 1.6 ± 0.1c | 1.6 ± 0.2d | 2.6 ± 0.1d | 3.1 ± 0.2b | 13.9 ± 0.4c |
| F | 102.18 | 345.74 | 375.62 | 217.94 | 293.37 | 293.17 | 739.49 |
| d.f. | 4,113 | 4,111 | 4,111 | 4,111 | 4,111 | 4,106 | 4,106 |
| P | <0.01 | <0.01 | <0.01 | <0.01 | <0.01 | <0.01 | <0.01 |

Means within a column followed by different letters are significantly different (one-way ANOVA followed by Tukey's post-hoc test: P<0.05).

**Table 2** Mean (± SE) duration of development of each immature stage of *Hippodamia variegata* at various light intensities

| Intensity ($W\ m^{-2}$) | Development duration (days) | | | | | | |
|---|---|---|---|---|---|---|---|
| | Egg | Instar 1 | Instar 2 | Instar 3 | Instar 4 | Pupa | Total immature |
| 0.6 | 3.7 ± 0.3a | 3.6 ± 0.2a | 2.7 ± 0.1a | 2.5 ± 0.2a | 3.4 ± 0.1a | 3.4 ± 0.1a | 19.3 ± 0.4a |
| 0.9 | 3.3 ± 0.2b | 3.2 ± 0.3b | 2.6 ± 0.2a | 2.5 ± 0.1a | 3.1 ± 0.1b | 3.5 ± 0.2a | 18.2 ± 0.3b |
| 1.2 | 3.2 ± 0.2b | 3.1 ± 0.2b | 2.1 ± 0.1b | 2.0 ± 0.1b | 3.0 ± 0.2b | 3.1 ± 0.1b | 16.5 ± 0.2c |
| 1.5 | 2.6 ± 0.1c | 2.6 ± 0.1c | 1.7 ± 0.2c | 1.7 ± 0.1c | 2.5 ± 0.3c | 2.9 ± 0.2b | 14.0 ± 0.3d |
| 1.8 | 2.5 ± 0.2c | 2.4 ± 0.1d | 1.7 ± 0.2c | 1.5 ± 0.1c | 2.4 ± 0.2c | 3.1 ± 0.3b | 13.6 ± 0.3d |
| F | 98.76 | 316.82 | 346.95 | 197.61 | 287.72 | 301.05 | 713.97 |
| d.f. | 4,106 | 4,106 | 4,105 | 4,105 | 4,105 | 4,101 | 4,101 |
| P | <0.01 | <0.01 | <0.01 | <0.01 | <0.01 | <0.01 | <0.01 |

Means within a column followed by different letters are significantly different (one-way ANOVA followed by Tukey's post-hoc test: $P<0.05$).

**Table 3** Mean (± SE) duration of development of each immature stage of *Hippodamia variegata* at various light wavelengths

| Wavelength (nm) | Development duration (days) | | | | | | |
|---|---|---|---|---|---|---|---|
| | Egg | Instar 1 | Instar 2 | Instar 3 | Instar 4 | Pupa | Total immature |
| 390 (purple) | 2.8 ± 0.2c | 3.1 ± 0.1b | 1.9 ± 0.1c | 2.1 ± 0.2b | 2.8 ± 0.1b | 3.3 ± 0.1b | 16.0 ± 0.2b |
| 465 (blue) | 2.5 ± 0.1c | 2.5 ± 0.1c | 1.6 ± 0.1d | 1.7 ± 0.2c | 2.5 ± 0.1c | 3.0 ± 0.1c | 13.8 ± 0.2c |
| 520 (green) | 2.7 ± 0.1c | 2.6 ± 0.1c | 1.7 ± 0.1d | 1.6 ± 0.2c | 2.4 ± 0.1c | 3.1 ± 0.1c | 14.1 ± 0.5c |
| 570 (yellow) | 3.1 ± 0.2b | 3.2 ± 0.1v | 2.3 ± 0.1b | 2.4 ± 0.1a | 3.5 ± 0.3a | 3.6 ± 0.2a | 18.1 ± 0.2a |
| 640 (red) | 3.3 ± 0.1a | 3.5 ± 0.2a | 2.6 ± 0.1a | 2.5 ± 0.2a | 3.4 ± 0.1a | 3.5 ± 0.1a | 18.8 ± 0.3a |
| F | 67.12 | 205.67 | 154.13 | 164.31 | 187.64 | 198.11 | 688.43 |
| d.f. | 4,103 | 4,102 | 4,102 | 4,102 | 4,102 | 4,98 | 4,98 |
| P | <0.01 | <0.01 | <0.01 | <0.01 | <0.01 | <0.01 | <0.01 |

Means within a column followed by different letters are significantly different (one-way ANOVA followed by Tukey's post-hoc test: $P<0.05$).

**Table 4** Mean (± SE) reproductive characteristics of *Hippodamia variegata* at various photoperiods

| Photoperiod (L:D) | Mating duration (min) | Pre-oviposition duration (days) | Oviposition duration (days) | Total fecundity |
|---|---|---|---|---|
| 0:24 | 203.5 ± 8.7a | 12.1 ± 2.4a | 15.4 ± 1.9b | 96.2 ± 3.5d |
| 8:16 | 146.8 ± 9.8b | 11.3 ± 3.1a | 17.8 ± 3.5b | 95.4 ± 7.8d |
| 12:12 | 132.7 ± 6.3b | 9.5 ± 2.1b | 17.6 ± 2.7b | 100.6 ± 6.6c |
| 16:8 | 115.7 ± 5.5c | 8.3 ± 1.1b | 23.5 ± 5.5a | 134.7 ± 9.5b |
| 24:0 | 65.8 ± 4.8d | 6.9 ± 0.9c | 22.7 ± 3.4a | 149.6 ± 8.7a |
| F | 169.75 | 144.71 | 198.5 | 213.75 |
| d.f. | 4,145 | 4,145 | 4,144 | 4,144 |
| P | <0.01 | <0.01 | <0.01 | <0.01 |

Means within a column followed by different letters are significantly different (one-way ANOVA followed by Tukey's post-hoc test: $P<0.05$).

## Discussion

Predatory ladybirds have been widely investigated and evaluated for their potential in biological control (Aalbersberg et al., 1988; Obrycki & Orr, 1990; Franzmann, 2002). Nevertheless, little is known of the impact of light on *H. variegata*, even though this environmental variable strongly affects insects in a variety of biological, physiological, and behavioral aspects. As we demonstrated here, photoperiod, light intensity, and wavelength significantly affect the development, mating, oviposition, and fertility of *H. variegata*. Almost all ladybirds completed the life cycle irrespective of the light environment. Long light period and high light intensity had a positive influence in terms of shortening the development period and increasing reproduction, locomotion, and predation. An environment colored as the natural habitat (primarily green and yellow) may benefit *H. variegata* life-history traits and could improve the efficiency of mass rearing.

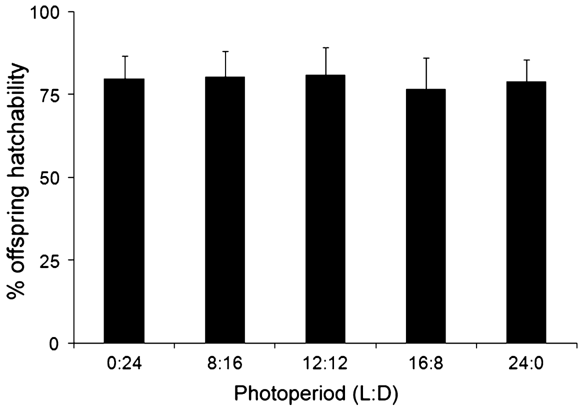


**Figure 1** Mean (+ SE) offspring hatchability (%) of *Hippodamia variegata* at various photoperiods (Wald = 2.98, d.f. = 4,144, P = 0.21).

Our results clearly showed that long daylight period with high light intensity are beneficial to the life history of *H. variegata*, as with many other Coleoptera species (Aksit et al., 2007). As a common coccinellid species living in cold temperate zones (northern China and the far east of Asia), *H. variegata* showed generation cycles in rhythm with season (four generations per year). Our previous work showed that mating preference and copulatory behavior varied according to seasonal environment could be observed in another temperate-zone predatory ladybird, *Harmonia axyridis* (Pallas) (Wang et al., 2009, 2013a). Thus, the photoperiod and intensity of light should be regarded as signals used in insects for seasonal adaptations of a biological, physiological, or behavioral nature, such as diapause and hibernation (Teetes et al., 1969; Hodkova & Hodek, 2004). Previous work with *H. axyridis* and *C. sexmaculata* showed a similar tendency in variation in life-history traits: the period of development would decrease with increasing light period (Berkvens et al., 2008; Wang et al., 2013b). As with our results, the predatory flower bug *O. sauteri* demonstrated a decrease in immature development with increased light

**Table 5** Mean (± SE) reproductive characteristics of *Hippodamia variegata* at various light intensities

| Intensity (W $m^{-2}$) | Mating duration (min) | Pre-oviposition duration (days) | Oviposition duration (days) | Total fecundity |
|---|---|---|---|---|
| 0.6 | 217.6 ± 11.3a | 14.7 ± 3.3a | 15.4 ± 1.3d | 64.5 ± 3.6d |
| 0.9 | 197.6 ± 6.9a | 10.9 ± 2.7b | 19.4 ± 2.4c | 86.2 ± 4.4d |
| 1.2 | 113.6 ± 9.7b | 10.7 ± 2.3b | 20.6 ± 3.1c | 124.6 ± 7.6c |
| 1.5 | 98.4 ± 9.5c | 6.4 ± 1.9c | 25.7 ± 2.7b | 149.8 ± 5.7b |
| 1.8 | 56.9 ± 8.3d | 5.9 ± 1.2c | 28.6 ± 3.9a | 151.2 ± 5.2a |
| $F_{4,145}$ | 216.54 | 167.74 | 303.12 | 364.71 |
| P | <0.01 | <0.01 | <0.01 | <0.01 |

Means within a column followed by different letters are significantly different (one-way ANOVA followed by Tukey's post-hoc test: P<0.05).

**Table 6** Mean (± SE) reproductive characteristics of *Hippodamia variegata* at various light wavelengths

| Wavelength (nm) | Mating duration (min) | Pre-oviposition duration (days) | Oviposition duration (days) | Total fecundity |
|---|---|---|---|---|
| 390 (purple) | 84.6 ± 10.4c | 11.3 ± 0.9b | 16.4 ± 1.3d | 147.5 ± 10.3c |
| 465 (blue) | 156.4 ± 11.2a | 12.4 ± 1.7b | 20.3 ± 2.4c | 146.4 ± 11.4c |
| 520 (green) | 172.3 ± 13.5a | 9.8 ± 1.6c | 26.7 ± 3.1a | 187.5 ± 12.4a |
| 570 (yellow) | 114.6 ± 10b | 10.4 ± 2.4c | 23.5 ± 2.7b | 166.4 ± 10.5b |
| 640 (red) | 64.5 ± 9.8d | 15.4 ± 1.8a | 17.9 ± 3.9d | 133.5 ± 15.6d |
| $F_{4,145}$ | 384.56 | 103.17 | 258.94 | 121.73 |
| P | <0.01 | <0.01 | <0.01 | <0.01 |

Means within a column followed by different letters are significantly different (one-way ANOVA followed by Tukey's post-hoc test: P<0.05).

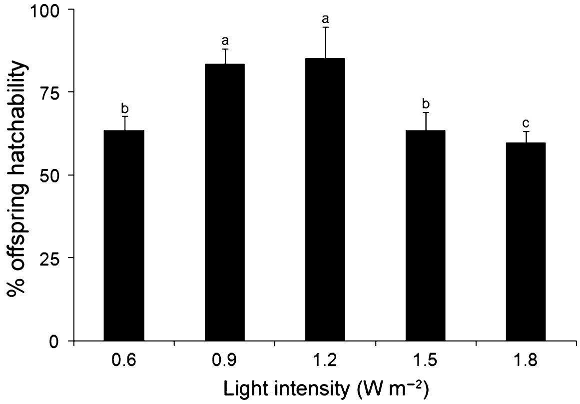


**Figure 2** Mean (+ SE) offspring hatchability (%) of *Hippodamia variegata* at various light intensities (Wald = 103.5, d.f. = 4,145, P<0.01). Means with different letters are significantly different (Tukey's post-hoc test: P<0.05).

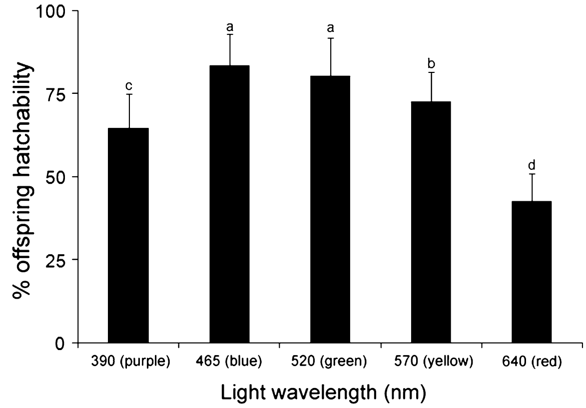


**Figure 3** Mean (+ SE) offspring hatchability (%) of *Hippodamia variegata* at various light wavelengths (Wald = 193.2, d.f. = 4,145, P<0.01). Means with different letters are significantly different (Tukey's post-hoc test: P<0.05).

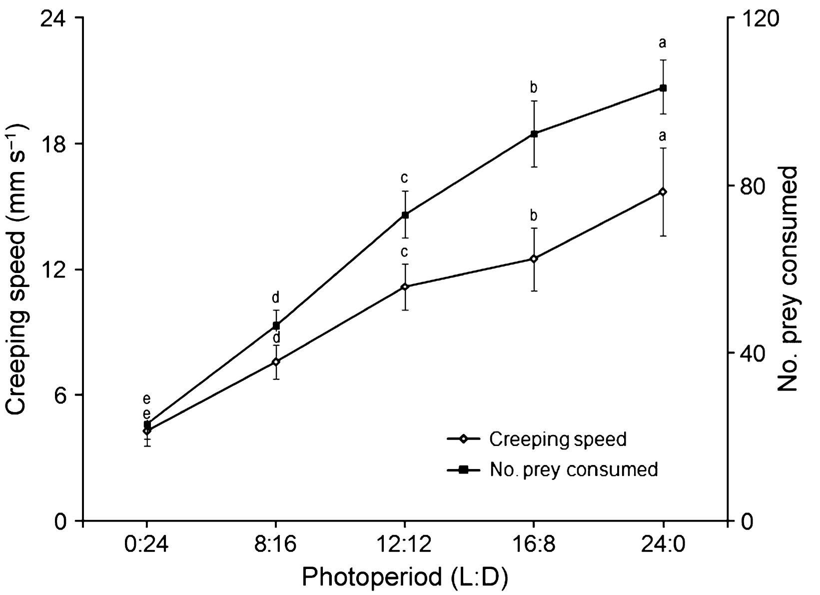


**Figure 4** Mean (± SE) *Hippodamia variegata* locomotive speed within 5 min ($F_{4,145}$ = 168.46, P<0.01) and number of *Myzus persicae* consumed within 24 h ($F_{4,145}$ = 284.7, P<0.01) at various photoperiods. Means within a variable capped with different letters are significantly different (Tukey's post-hoc test: P<0.05).

intensity (Wang et al., 2013c). However, the increase of light intensity was shown to negatively impact the fertility of *O. sauteri* by inhibiting fertility of the eggs. Similarly, a long daylight and high light intensity increases most characteristics in reproductive efficiency apart from egg hatching. In contrast to *O. sauteri*, the fecundity of *H. variegata* was doubled in high light intensity compared to dark conditions, with the greatest degree of egg hatching under a mid-level of light intensity (0.8 and 1.2 W $m^{-2}$). Many previous studies indicate that the high fertility of ladybirds may be linked with high sperm load or large seminal vesicle transited to females (Majerus, 1994). So at present, our observations may indicate that light intensity might influence the efficiency of sperm transmission during copulation. Females receiving insufficient sperm may lay more eggs to counteract the losses caused by high light intensity. Further research is needed to evaluate this possibility.

*Hippodamia variegata* were more active when exposed to a long photoperiod with high light intensity. Based on our results, the high speed of movement under these conditions could be an adaptation for more effective prey consumption. We observed a similar reaction in *C. sexmaculata* and *O. saueri* (Wang et al., 2013b,c). In the limited range available, the predatory insects depend on a visual search when seeking prey (Majerus, 1994), as opposed to parasitoids, for example, which locate food

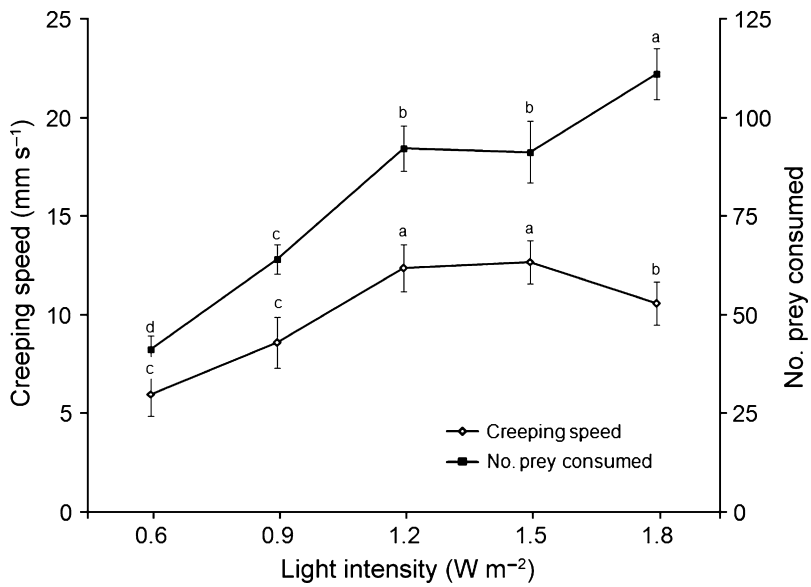


**Figure 5** Mean (± SE) *Hippodamia variegata* locomotive speed within 5 min ($F_{4,145}$ = 211.3, P<0.01) and number of *Myzus persicae* consumed within 24 h ($F_{4,145}$ = 198.78, P<0.01) at various light intensities. Means within a variable capped with different letters are significantly different (Tukey's post-hoc test: P<0.05).

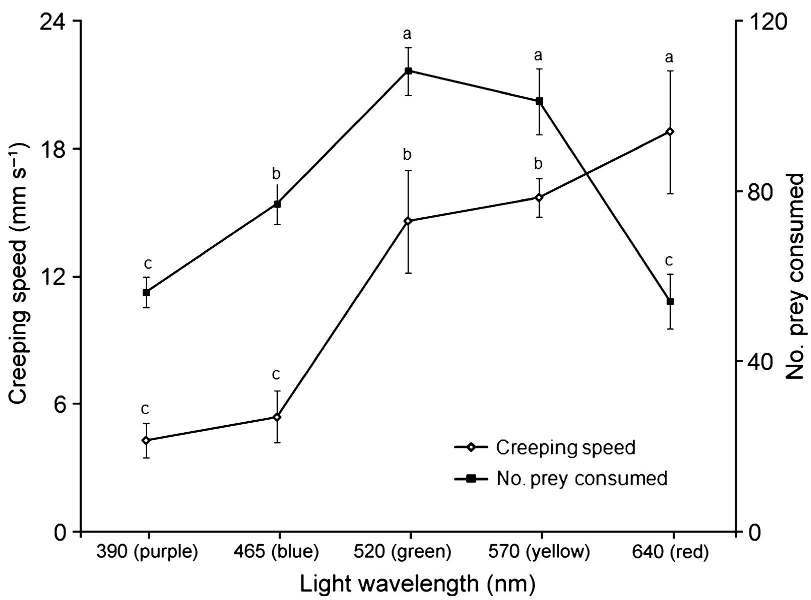


**Figure 6** Mean (± SE) *Hippodamia variegata* locomotive speed within 5 min ($F_{4,145}$ = 197.33, P<0.01) and number of *Myzus persicae* consumed within 24 h ($F_{4,145}$ = 277.46, P<0.01) at various light wavelengths. Means within a variable capped with different letters are significantly different (Tukey's post-hoc test: P<0.05).

mainly by detection of volatile signals (Bell, 1990; Wäckers, 1994). Thus, the bright environment with long periods of light could help predators to find and capture their targets and it seems that increasing the light supplement does not negatively influence the predation ability. Long wavelengths (the red and yellow part of the visible spectrum) had a negative effect on development compared to short wavelengths (purple light). Wavelengths around green (similar to the natural plant canopy) appeared most suitable for *H. variegata*. This differed from previous studies on *O. sauteri*, in which we observed contrasting results on the influence of blue and yellow light (Wang et al., 2013c). Moreover, white light has been determined as the most fitting for the development and reproduction of the ladybirds *Propylea dissecta* (Mulsant) and *C. sexmaculata* (Omkar et al., 2005). Furthermore, the poorest reproductive performance was observed in tests using red and purple light, the best in green lighting. *Hippodamia variegata* may prey on more aphids when they are under green light conditions, even though the ladybird may move faster under longer wavelength conditions. These results indicate that the adaptation to wavelength conditions is (polyphagous) species specific, although green light appears the most generally applicable. Nevertheless, previous work has also reported longer wavelengths might impede the development and feeding behavior in fruit flies, moths, and coccinellids (White et al., 1994; Saika et al., 2002; Omkar et al., 2005).

Our results provide data of potentially direct value in light management for increasing mass rearing efficiency, field release, and the colonizing effectiveness of a predatory ladybird. Until now, the commercial application of plant-culturing illumination systems (Massa et al., 2008) has been widely popularized for greenhouse vegetables (Manicad & McGuire, 2000; Külheim et al., 2002; Massa et al., 2008). Systematic research into photoperiod, light intensity, and wavelength influence to *H. variegata* such as reported here should help to evaluate the impact of culturing light conditions on the practical effectiveness of predatory ladybirds. Consequently, the effect of light on the plant, as well as indirect effects of light on pests, via plant feeding or volatile cues, should be investigated, and how they influence the performance (i.e., behavior, life-history traits, and population dynamics) of natural enemies. Furthermore, tailored adjustment of environmental conditions is necessary in commercial mass rearing of natural enemies. Increasing adoption of LED illumination management technology may benefit rearing biological control agents. Revealing and confirming the exact characteristics of light required to meet the demands of artificial natural enemy production in commercial biological control application is certainly needed in future.

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