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Humans influence shrimp movement: a conservation behavior case study with "Shrimp Watching" ecotourism

Watcharapong Hongjamrassilp* and Daniel T. Blumstein

Department of Ecology and Evolutionary Biology, University of California Los Angeles, Los Angeles, CA 90095-1606, USA

*Address correspondence to Watcharapong Hongjamrassilp. E-mail: watcharapong.hg@gmail.com, winbiologist@ucla.edu.

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Abstract

An increase in ecotourism adversely impacts many animals and contributes to biodiversity loss. To mitigate these impacts, we illustrate the application of a conservation behavior framework toward the development of a sustainable ecotourism management plan. In Ubon Ratchathani, Thailand, thousands of tourists annually come to see a unique mass migration of shrimps on land (referred to as "shrimp parading"). Preliminary work suggests that this tourism has negatively impacted the shrimps. To reduce tourism-related impacts we studied: 1) the decisions shrimps make when parading and 2) how shrimps respond to different light intensities and colors. We created an artificial stream and tested the conditions that influence parading by experimentally varying the presence of light and systematically manipulating water velocity (10, 60, and 100 cm/s). Additionally, we conducted an in situ experiment to study how shrimps respond to tourists' lights under three intensities (50,400, and 9,000 lux) and five colors (white, blue, green, orange, and red). We found most shrimps prefer to leave the river when it is dark and there is low water flow. Shrimps responded the least to red (λmax = 630 nm) and orange (λmax = 625 nm) light at 50 lux. These findings were used to develop a management plan by creating three different tourist zones, which maximize tourist needs and minimize the anthropogenic impacts on the shrimps. This work could be used as an example of the application of conservation behavior framework in developing management plan for sustainable ecotourism for other invertebrate taxa.

Key words: anthropogenic light, caridean shrimps, collective behavior, freshwater prawn, migration, nature-based tourism

In this Anthropocene epoch, human activities have negatively affected the global environment at multiple scales that range from the individual to the ecosystem. Tourism has created a number of deleterious impacts on organisms and the environment (Haysmith and Hunt 1995; Green and Giese 2004; Tablado and D' Amico 2017). According to the United Nations World Tourism Organization, the number of tourists has increased annually (UNWTO 2018), which has been associated with economic benefits but also with associated environmental costs.

Without effective management, an increase in the number of tourists in natural habitats results in ecosystem damage and species loss (Hall 2010; Gil et al. 2015). For example, the Great Barrier Reef, one of the world's largest coral reefs, is being damaged by many factors, including overuse by tourism (De'ath et al. 2012). The loss of coral reef habitat has changed the species composition of coral reef fishes (Richardson et al. 2018) and might ultimately lead to ecosystem collapse. Another example can be seen in the decline of the firefly population at Amphawa floating market, Samut Songkhram, Thailand (Nurancha et al. 2013). Fireflies are well known for being an indicator of a healthy environment, especially for aquatic ecosystems (Kazama et al. 2007) because more than half of their lifecycle strictly relies on the aquatic environment. After the promotion of this as an ecotourist site, the number of tourists has dramatically increased, which resulted in increased urbanization in the area, resulting in the loss of many aquatic habitats that the fireflies inhabited. In addition, the overuse of pesticides from urban areas has led to the contamination of associated aquatic habitats. These anthropogenic pollution and disturbance have resulted in habitat degradation which reduced firefly survival and population size (Sartsanga et al. 2018). Despite attempts by the government and state to reduce impacts, the firefly population has not recovered.

Conservation behavior is an interdisciplinary discipline that integrates basic insights of animal behavior through the lens of behavioral ecology, genetics, physiology, and evolution with conservation biology and wildlife management (Blumstein and Fernández-Juricic 2010; Berger-Tal and Saltz 2016). The ultimate goal is to sustainably and effectively conserve and manage focal animal species. Therefore, a deep understanding of how animals perceive and respond to anthropogenic threats will allow us to mitigate disturbances.

Much research has shown that animals respond to humans as stressors in that human activities can alter wildlife behavior resulting in population declines (Geffroy et al. 2017). For example, the study of effects of visitors on breeding Adélie penguins *Pygoscelis adeliae* found that, if a single visitor approaches a penguin nest within 5 m, it can interrupt the incubation activity resulting in decreased hatching success (Green and Giese 2004). Even merely taking photographs with a digital single-lens reflex (SLR) camera can be disturbing as shown by Huang et al. (2011) where they found that shutter noise decreased display behavior of an Anolis lizard *Anolis cristatellus*. Reductions in this display could have reproductive consequences and the results suggest that anthropogenic stimuli may distract animals and enhance their vulnerability to predators. Thus, an understanding of how animals respond to stressors, including humans, offers a chance to create sustainable management plans.

When animals move together (i.e., collective or group movement), they attract public attention and, in some cases, are the focus of nature-based tourism. For instance, the annual mass migration of monarch butterflies *Danaus plexippusin* in Mexico (Geiling 2015) attracts >100,000 tourists annually. According to a survey of 118 million U.S. households, this has an economic value of as much as $6 billion (Diffendorfer et al. 2014). Because of the economic impacts of tourism, there are concerns of overexploitation and climate change that affect migratory animals, which could result in population declines, population extinction, and associated phenomena. These include the potential extinction of wildebeest (*Connochaetes* spp.), that migrate through the Serengeti ecosystem (Harris et al. 2009), and the decline of mass migration and overwintering of monarch butterflies in Mexico (Barve et al. 2012; Brower et al. 2012). To prevent such losses, it is essential to have a fundamental understanding of the basic biology of group movement. Although we know something about group movement in birds, fishes, and mammals, the biology of group movement in invertebrates, a group that is quite important for ecosystem function, remains more of a mystery and its study could lead to novel insights for other groups as well.

Parading shrimps *Macrobrachium dienbienphuense* Đăng and Nguyên, 1972, an Asian endemic species of freshwater shrimps, perform a unique type of group movement known as "Parading Behavior" (Figure 1 a,b; Video 1). This behavior is unique in that the freshwater shrimps, which have an obligate aquatic lifestyle, climb out of a river at night and walk en masse upstream on land along a river bank within a splash zone for 5–20 m before heading back to the river before sunrise (Hongjamrassilp et al. 2020). This natural phenomenon occurs annually during the rainy season (mid-August to early October) at the Lamduan rapids, in Ubon Ratchathani province, Thailand. Little is known about this extraordinary behavior. Previous research found that the shrimps, especially juveniles, collectively move on land to escape strong water currents that otherwise would wash them downstream. The main environmental factors associated with parading include high water velocity, low light, and low air temperature (Hongjamrassilp et al. 2020). These shrimps are strictly aquatic, and by leaving the water to move on land, they experience several costs such as desiccation and predation from terrestrial animals (W.H. unpublished observations). Therefore, an understanding of the decision to leave the water collectively is an interesting and important question for movement ecology, and one that has implications for effective management.

Every year, thousands of tourists witness this group movement as part of "Shrimp Watching" ecotourism (Hongjamrassilp et al. 2021) (Figure 1C; Video 2). Yet, despite national and international attention, and a growing number of tourists annually, there is no tourism management plan because of the lack of fundamental knowledge about this shrimp species. Observations from rangers in the Nature and Wildlife Education Center at Ubon Ratchathani province suggest that the shrimp population has decreased during the past 5 years. Indeed, our preliminary observations showed that fewer shrimps were present when tourists were present suggesting that tourists might negatively affect parading behavior (Figure 2). From our observations, two possible anthropogenic threats for the shrimps include being trampled by tourists (a relatively rare occurrence) and light from tourist's flashlights which drives shrimps off the land and back to the rapids where they get washed downstream. This disturbance potentially increases the energetic cost of movement for the shrimps. However, crustaceans may perceive light differently from humans (Cronin and Porter 2008), and if so, to mitigate the effect of anthropogenic light on the shrimps, it is essential to determine the effect of different light intensities and colors on the shrimps.

Freshwater *Macrobrachium* shrimps contribute tremendously in many ways to freshwater ecosystems and human societies worldwide. They serve as a food source for humans in many cultures, especially in Southeast Asia (Motoh 1980). At the same time, they also play crucial roles in maintaining the stability of stream ecosystems by recycling nutrients for primary producers (e.g., phytoplankton) or being a predator (Mantel and Dudgeon 2004a, 2004b; Hein et al. 2011), which are essential to their food web (Covich et al. 1999). Many freshwater aquatic species feed on juvenile *Macrobrachium* shrimps (Zimmerman and Covich 2003; Covich et al. 2006). Therefore, local extinction of these shrimps by an increase in tourism might affect the security of stream ecosystems and, in the long term, might cause extinction cascades of other species, resulting in ecological collapse.

To prevent this loss, we 1) studied the decisions that shrimps make about initiating parading, and 2) investigated the effect of anthropogenic light intensity and color on parading. For the first study, we hypothesized that shrimps will decide to leave the water when they encounter high water velocity and only under dark conditions. For the second study, we postulated that red light, which shrimps could not perceive well, has less effect on shrimps while

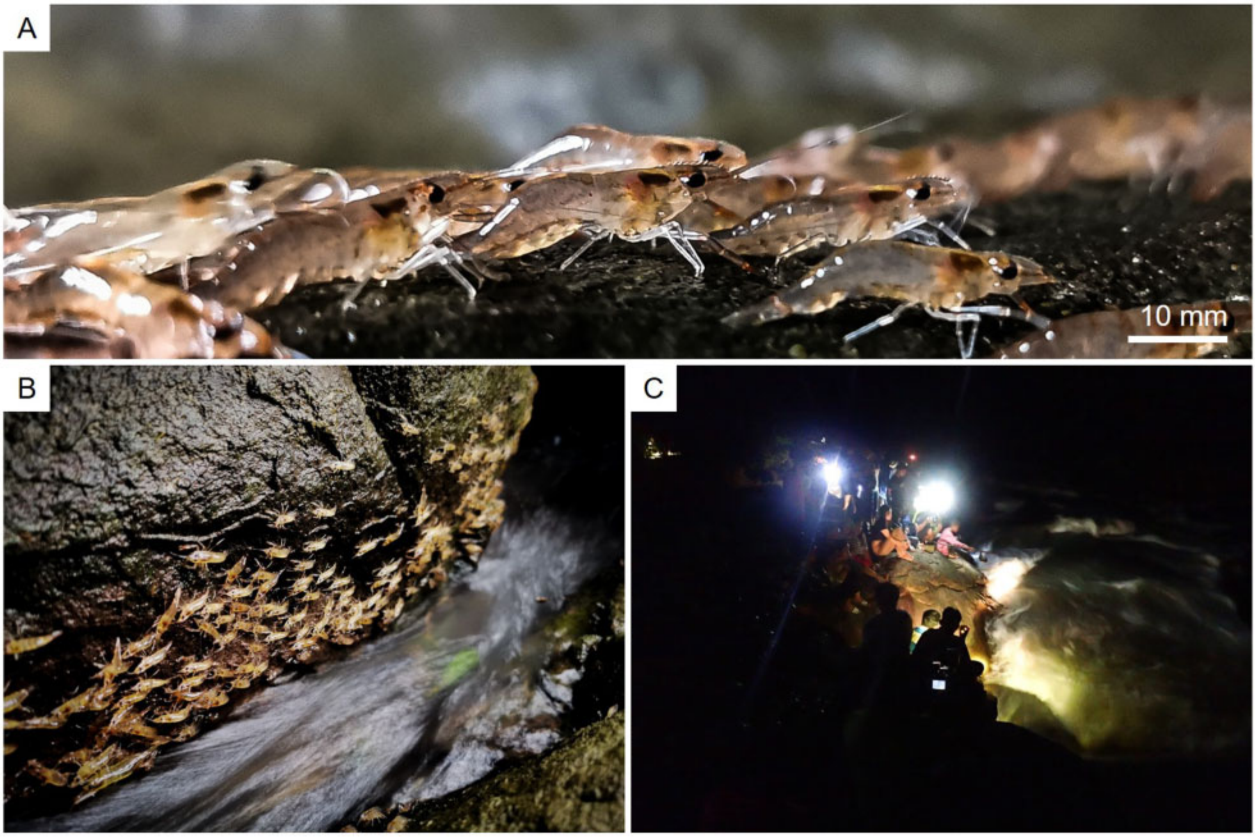

Figure 1. (A) A close-up photo of juvenile parading shrimps (*M. dienbienphuense*). (B) Shrimp parading is seen when they collectively climb out of a river and walk upstream along the riverbank. (C) Tourists with their flashlights waiting to watch the shrimp parade. Photos by W. Hongjamrassilp.

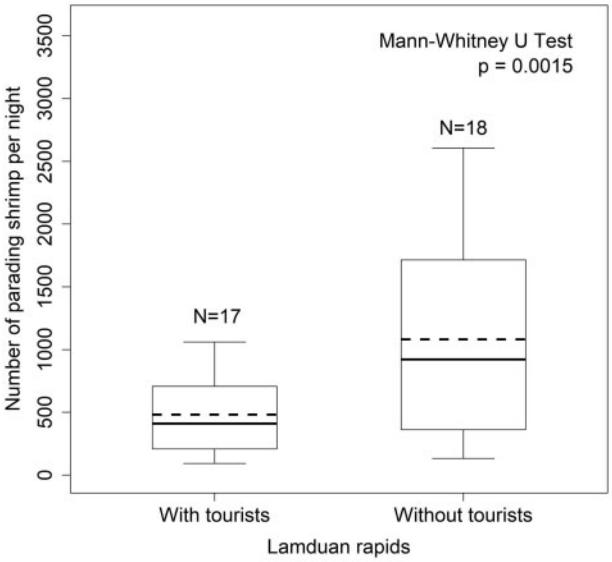

Figure 2. Preliminary observations show the difference between the number of shrimps that leave the river at Lamduan rapids when tourists were present and absent. We used night camera traps to take photos of shrimps that passed a $20 \times 20\,\text{cm}^2$ plot every 5 min between 18:00 and 07:00 h. We counted the number of shrimps from photos and calculated an average number of shrimps under each condition. The bold lines in the boxplot are the median and the dashed lines are the means. Whiskers above and below the box represent maximum and minimum value, respectively. *N* is the number of days we observed the shrimp.

parading on land compared with other light colors. An understanding of the decisions shrimps make to collectively move on land together with how they respond to anthropogenic light during collective movement permits us to make biologically informed suggestions for a sustainable management plan so as to mitigate anthropogenic disturbances on shrimps.

Materials and Methods

Study site

We divided this research into two parts. We first conducted an experiment on captive shrimps at the Ubon Ratchathani Wildlife and Nature Education Center (14°26′19.3″N 105°06′08.0″E), ~1 km away from the parading site in Lamduan Rapids (14°26′05.5″N 105°06′19.3″E) in Ubon Ratchathani, Thailand. Then we conducted an in situ experiment at the parading site where tourists come to watch the shrimps. We conducted the second study after 22.00 h when all tourists had left the parading site.

Study 1: How does light and water velocity influence the decision to parade?

Previous studies revealed that water velocity and light are two main factors that play a vital role in triggering shrimp parading (Lee and Fielder 1979; Fievet 1999; Torkkola and Hemsley 2019; Hongjamrassilp et al. 2020). To explore how shrimps integrate these two factors in their decision to climb out of the river, we conducted an experiment in an artificial stream which was adapted

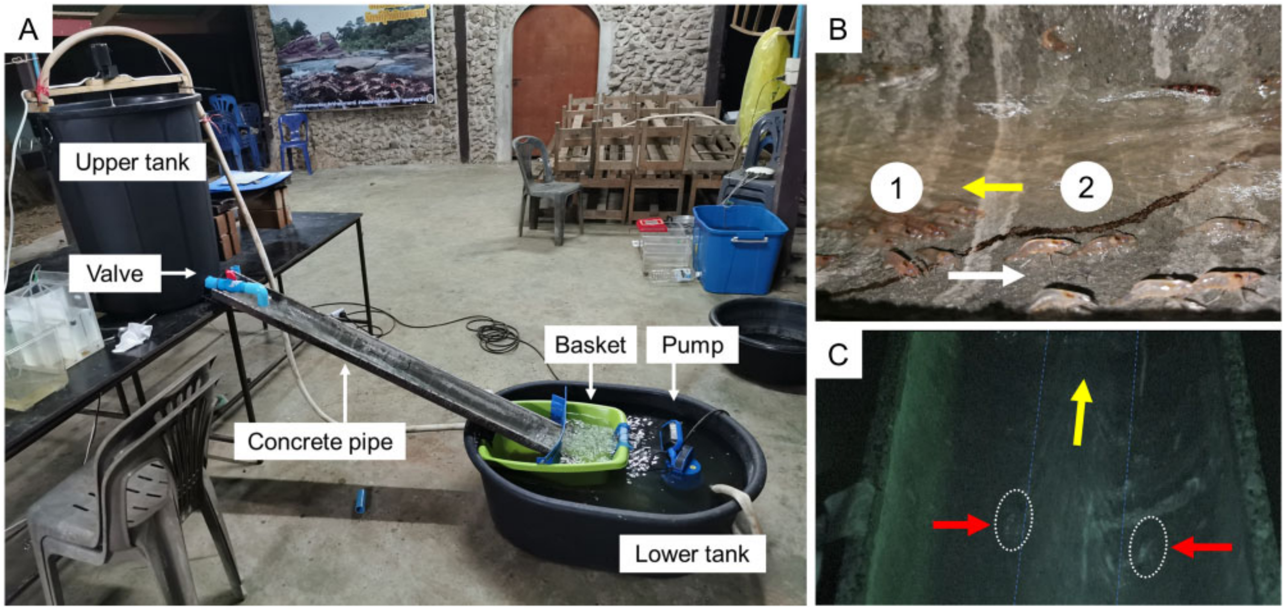

Figure 3. (A) The artificial stream used in this study. Shrimps were put in the basket in the lower tank. (B) A photo during the experiment. Point 1 shows the shrimps that began to walk out of the water. Point 2 shows the shrimps that walked out of the water; we counted the number of shrimps that walked out of the river as in number 2. (C) A still captured from the night camcorder. White-circles show shrimps that were walking out of the water. The yellow arrows in (B) and (C) indicate the flow direction, and the white arrow in (B) indicates the shrimp walking direction.

from Hamano et al. (1995) and Olivier et al. (2013). The artificial stream consisted of an upper and a lower tank bridged by a 2 m of semicircular concrete pipe (Figure 3). We installed a valve at upper tank which was used to adjust water velocity for the water that flowed to the lower tank. At the lower tank, we installed a pump to move the water back to the upper tank, making this a closed system. At the end of the concrete pipe in the lower tank, we attached a small basket ($32 \times 28 \times 15\,\text{cm}^3$; Length × Width × Height) to hold the shrimps during our experiment.

We systematically varied water velocity at three levels (10, 60, and 100 cm/s) in combination with light at two levels (no light and 500 lux light). We used 500 lux because this was close to light intensity at sunrise and sunset (Nielson 1963; Nelson et al. 1997; Goymann et al. 2012). We measured water velocity at the end of the concrete pipe with a digital flow meter fitted with 60 mm impellers (Flowatch, JDC Electronic, Switzerland). We measured and calibrated light intensity with an Extech EA33 EasyView Light Meter (Extech Instruments, Nashua, NH). We created six experimental conditions (light paired with each water velocity and no light paired with each velocity). To start the experiment, we put 300 juvenile shrimps in the basket in the lower tank and established a treatment. Then, for each condition, we filmed (with a Sony FDR-AX33 camcorder using night shot mode) the shrimps that moved out of the artificial river and walked along the concrete pipe for ten minutes. After the manipulation, all shrimps were released back into the river. We used a new group of shrimps in each condition. We repeated each condition 10 times. We counted, from the video, the number of shrimps that paraded.

To account for the count data, and to determine whether and how velocity and light influenced parading, we fitted a generalized linear model and set family parameter as “quasi-Poisson” using the function *glm* in package stats version 3.6.2 (R Core Team 2020) and compared the difference in the number of shrimps between each condition using the function *Anova* in package car version 3.0–8 (Fox and Weisberg 2019). Specifically, we tested for the main effects of light, the main effects of water velocity, and the interaction between light and velocity. Models were fitted in R 4.0.2 (R Core Team 2020). We calculated pairwise differences and tested their significance with Tukey’s range test.

Study 2: Does light intensity and color influence parading?

Based on our observations, we found that the main anthropogenic threat to the shrimps is light from tourists’ flashlights. To mitigate the anthropogenic disturbance on parading, we designed an experiment to understand how shrimps responded to different light intensities and colors.

Study 2.1: Light intensity

We conducted an experiment to determine if certain light intensities could reduce the impact of illumination on parading. We varied white light in three different intensities (9,000, 400, and 50 lux) with a control group under no light. These intensities mimicked the light intensity from a spotlight that rangers used to guide tourists 0.5 m from the light source, 2 m from light source, and smartphone flashlights 50 cm from light source, respectively. To do so we set up a spotlight BENEX ET-0815 (Taichung City, Taiwan) 50 cm from the parading area (splash zone on the riverbank) (Supplementary Figure S1) and measured light intensity prior to start the experiment with a light meter. We then filmed shrimps that walked past the observation zone with the camcorder using night mode. We counted the shrimps that completed the walk under the observation zone and the shrimps that walked out of the observation zone and/or back to the river ($N = 30$ at each light intensity treatment). We compared the number of shrimps that walked back to the river under different light intensities with a chi-square test of independence setting our alpha to 0.05. We implemented the pairwise chi-square test with Bonferroni’s correction to compare the difference between significant groups.

Study 2.2: Light colors

Decapod eyes contain different types and proportions of pigments in their eyes compared with human eyes (Goldsmith and Fernandez 1968; Cronin and Feller 2014). Therefore, they should perceive light differently compared with humans and might respond differently to different wavelengths. We conducted an experiment to determine if certain light wavelengths could reduce the impact of illumination on parading (Supplementary Figure S1). To do so, we set up a 50 lux light using BENEX ET-0815 (Taichung City, Taiwan) at the parading area. We manipulated light color by covering the light source with no filter, or adding a red, green, blue, or orange cellophane filter to the light source (Supplementary Figure S1). We used a cellophane filter to change the light color because it is an inexpensive way that tourists could manipulate the color of their personal lights. We quantified wavelengths with a spectrophotometer (UV–vis spectrophotometry model 722, Yucheng Technologies Ltd, Beijing, China) to find the maximum wavelength (λmax) (Supplementary Figure S2). When the shrimps began to parade, we turned on the light and recorded them with the camcorder.

We counted the number of shrimps that walked back to the river under different light colors ($N = 30$ in each light color treatment) and compared them with a chi-square test of independence setting our alpha to 0.05. Since we hypothesized that shrimps which spend more time moving on land will have a high risk for desiccation and predation, we quantified the walking speed of the shrimps under different colors by dividing the distance the shrimps paraded by time. Because our data were not normally distributed, and the variances were not homogenous, we implemented Kruskal–Wallis *H* test to test the differences in walking speeds under different light colors ($N = 30$ individuals per light color treatment) and used Dunn's multiple comparison test to test for differences in behavioral responses to the different light colors.

Results

Study 1: How light and water velocity influence the decision to parade?

We found no interaction between light and water velocity on the shrimps' decision to parade (Likelihood ratio [LR] $\chi^2 = 0.277$, degrees of freedom [df] = 2, $P = 0.87$). We found that most shrimps decided to parade at the 10 cm/s flow velocity (FV) compared with the faster 60 and 100 cm/s (LR $\chi^2 = 148.84$, $df = 2$, $P < 0.001$) (Figure 4A). In addition, more shrimps paraded under the no light condition compared with the light condition (LR $\chi^2 = 23.81$, $df = 1$, $P < 0.001$) (Figure 4B). From this, we conclude that shrimps use both light and FV as factors to decide when they will leave the water and parade; they are more likely to leave the water when it is dark and there is low water flow.

Study 2: Does light intensity and color influence parading?

Study 2.1: Light intensity

We found that light intensity affected the shrimps while parading ($\chi^2 = 60.15$, $df = 3$, $P < 0.001$). More shrimps walked back to the river under high light intensity (9,000 lux) and intermediate intensity (400 lux) compared with the shrimps under low intensity (50 lux), and no light condition (Supplementary Table S1). Moreover, we found that the number of shrimps that walked back to the river under low light was not statistically different from the number that walked back under no light ($P = 1.00$; Supplementary Table S1) indicating that light sources less than ~50 lux have less effect on shrimps compared with higher light intensities.

Study 2.2: Light colors

We found no difference in the number of shrimps that walked back to the river under different light colors at 50 lux light intensity ($\chi^2 = 7.5$, $df = 5$, $P = 0.186$). However, walking speeds of shrimps illuminated by white light (40.10 ± 37.43 cm/min, mean ± Standard Deviation (SD)), blue light (λmax = 380 nm) (30.95 ± 26.18 cm/min), and green light (λmax = 520 nm) (61.91 ± 51.17 cm/min) were significantly slower than those illuminated with red light (λmax = 630 nm) (66.93 ± 44.71 cm/min), orange light (λmax = 625 nm) (67.28 ± 43.78 cm/min), and no light (81.27 ± 43.82 cm/min) ($\chi^2 = 48.538$, $df = 5$, $P \leq 0.001$) (Figure 5). Therefore, if tourists used red or orange filters with <50 lux while watching the shrimps, this could mitigate anthropogenic disturbance.

Discussion

Our results show that parading shrimps collectively walked out of the river when water flow was low enough for them to climb out. They preferred to collectively walk in the dark. Moreover, we found that high (9,000 lux) and intermediate (400 lux) light intensities modified parading behavior by forcing them back to the river. We also found that light color influenced shrimp walking speed; shrimp walked more slowly when illuminated with white, blue, and green light than with orange and red light.

Shrimps in the genus *Macrobrachium* engage in group movements for two purposes: 1) to spawn downstream during the adult stage and 2) to disperse upstream during the juvenile stage. Both occur at night; *Macrobrachium* are nocturnal. This nocturnal habit may reduce predation from diurnal predators (Kikkert et al. 2009; Bauer 2013). Moreover, collective movement can saturate nocturnal predators (known as "Dilution effect") (Duncan and Vigne 1979; Foster and Treherne 1981; Lehtonen and Jaatinen 2016). In the case of *M. dienbienphuense*, our results show that more shrimps climbed out of the artificial stream in the dark. However, lack of illumination was not an absolute requirement for movement. Fievet (1999) reported daylight group movement of *M. faustinum* on Guadeloupe Island, French West Indies whereby that species moved out of a river and climbed along a dam during the daytime when the dam had exceptionally high-water flow. This suggests that the shrimps might be able to trade-off the costs of being washed downstream with the risk from predation (e.g., by herons) (Fievet 1999).

Previous work found positive correlations between the number of shrimps that paraded out of a river and water velocity (Torkkola and Hemsley 2019; Hongjamrassilp et al. 2020). However, our experiment extends the previous studies by confirming the causation and demonstrating that shrimps decide to parade at the low flow zone rather than the high flow zone. Hongjamrassilp et al. (2020) proposed four zones associated with parading: 1) downstream zone (FV of laminar flow = 5–10 cm/s), 2) turbulent zone (FV = 10–20 cm/s), 3) high-velocity zone (FV = 120–200 cm/s), and 4) upstream zone (FV = 60–100 cm/s). They found that shrimps started to move out of a river in the turbulent zone, which precedes the high-velocity zone, and walked, in a splash zone, past the high-velocity zone for around 5–20 m before heading back into the river at the upstream zone. Our experiment confirms that the shrimps decide to move out of a river when the flow velocity was not too strong so the shrimps were able to cling to rocks along the riverbank and climb

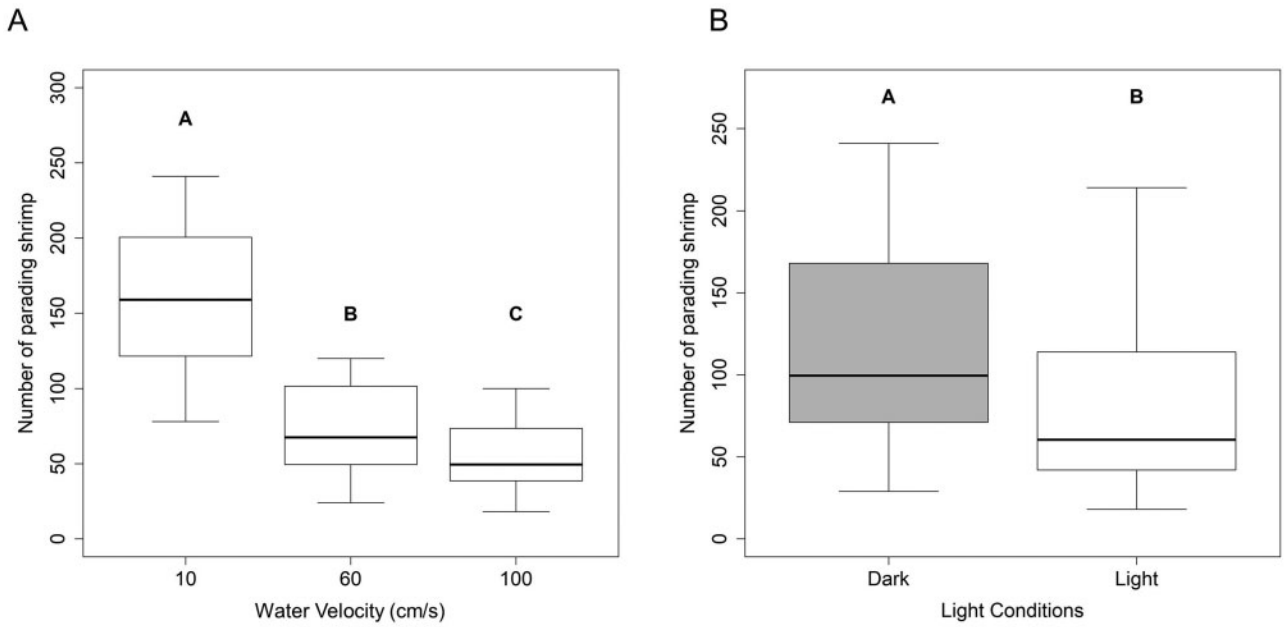

Figure 4. (A) The number of shrimps that leave the water as a function of 3 different water velocities. (B) The number of shrimps that leave the water as a function of 2 different light conditions. Letters above boxplots' whisker indicate significantly different responses (Dunn's test, $P < 0.05$). The bold lines in the boxplots are the median. Whiskers above and below the box represent maximum and minimum value, respectively.

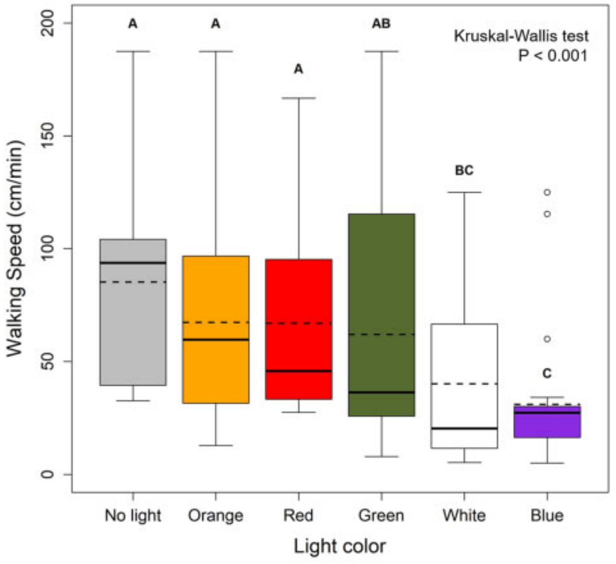

Figure 5. Shrimp walking speed as a function of different light treatments. Similar letters above boxplot's whisker indicate no significant difference between speeds as a function of light color. The bold lines in the boxplot are the median and the dashed lines are the means. Whiskers above and below the box represent maximum and minimum value, respectively. White circles represent outliers.

out at that area. Moreover, personal observations at the Lamduan rapids reveal that illuminating shrimps at the starting point (turbulent zone) before they moved out of the river delayed the time the shrimps initiated their nocturnal terrestrial walks.

Adult nocturnal decapod crustaceans have a special type of compound eye called a "reflecting superposition eye" which is very sensitive to light intensity (brightness) compared with another type of compound eye called an "apposition eye," which usually can be found in diurnal arthropods (Gaten 1998; Greiner 2006; Warrant 2017; Palmer et al. 2018). In decapod crustaceans, including shrimps in the genus *Macrobrachium*, the reflecting superposition eye is a primitive (plesiomorphic) trait (Gaten 1998) which permits sensitivity to dim light while maintaining image resolution (Matsuda and Wilder 2014; Palmer et al. 2018). This special type of eye could help the shrimp avoid predators under dim light. Our study showed that juvenile *M. dienbienphuense* responded negatively to high light intensity by returning to the river and being washed downstream. We hypothesize that this increases energetic costs to the shrimps which must still move upstream. Therefore, exposing shrimps to high light intensities will negatively affect juvenile shrimps by increasing energetic and predatory costs, assuming that there are more predators downstream (McDowall 2007; Covich et al. 2009).

Several studies on color sensitivity in Macrobrachium *rosenbergii*, a popular commercial species of *Macrobracium* shrimps, revealed that their larvae are sensitive to wavelength 460–550 nm which falls between blue to green light (Kawamura et al. 2016; Kawamura et al. 2018). Moreover, the larvae show positive phototaxis to white and blue light. This could help the larvae find food (Kawamura et al. 2016; Kawamura et al. 2020). In contrast, post-larval stages, which include juveniles and adults, show negative phototaxis to this light wavelength (Kawamura et al. 2020). Our results show a similar pattern in which juvenile shrimps are distracted by the different light wavelengths while parading. The juveniles decreased walking speed under white, blue (λmax = 380 nm), and green (λmax = 520 nm) light. This indicates that *M. dienbienphuense* have a negative response to the same wavelength as *M. rosenbergii*. Therefore, to mitigate the effect of anthropogenic light on parading behavior, tourists should use the dim red (λmax = 630 nm) and orange (λmax = 625 nm) light to observe shrimp parading.

Research on the effect of light on amphidromous shrimp upstream migration reveals that light intensity at 70 lux from mercury vapor lamps could inhibit the upstream migration of the shrimps

(Hamano and Honke 1997). However, that research was conducted to test the response of shrimps toward light underwater. Our work tested the similar response of the shrimps while they were moving on land. Both Hamano and Honke (1997) and our study shows the same pattern of negative-phototaxis in shrimps. Moreover, Bernardi (1990) and our study indicate that red light affects shrimp movement less than other light wavelengths. Therefore, based on our understandings of how parading shrimps respond to light, we suggest the scientific evidence-based management recommendations for this "Shrimp Watching" ecotourism (read more in Supplementary document).

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Authors' Contributions

W.H. and D.T.B designed the study. W.H. collected and analyzed the data. W.H. and D.T.B wrote and edited the manuscript.

Supplementary Material

Supplementary material can be found at https://academic.oup.com/cz.

Conflict of Interest Statement

We have no conflict of interest to declare.

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