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Bridging ethology and ecotourism: A case study of Shrimp Watching tourism in Thailand

A dissertation submitted in partial satisfaction of the requirements

for the degree Doctor of Philosophy in Biology

by

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ABSTRACT OF THE DISSERTATION

Bridging ethology and ecotourism: A case study of Shrimp Watching tourism in Thailand

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Doctor of Philosophy in Biology

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Professor Daniel T. Blumstein, Chair

Ethological studies not only provide insights on how and why animals perform extraordinary behaviors, but they also provide an opportunity to understand how animals are disturbed by human activities in the Anthropocene. Ecotourism, a popular recreational activity, is a worldwide growing business that can be used as a tool for biodiversity conservation. However, a lack of fundamental knowledge and effective management plans for an ecotourism site may lead to an increase in anthropogenic disturbances and ultimately degrade a site's biodiversity. In Ubon Ratchathani, Thailand, locals discovered a unique migration of freshwater shrimp known as "Parading Behavior", an unusual type of upstream migration in which hundreds of thousands of shrimp climb out of water and walk on land to the headwater. This behavior has captured public attention and Shrimp Watching tourism has been promoted as a must-see event at Ubon Ratchathani. While striking, this behavior is poorly understood. Preliminary evidence suggests that tourists might disturb the shrimp population during migrating. Unfortunately, we know very

little about the biology of, and anthropogenic threats to, the shrimp. Therefore, my dissertation aims to: (1) understand proximate and ultimate causes of the parading behavior, (2) investigate the effect of light from tourists on parading shrimp, and (3) evaluate perceptions toward the parading shrimp from locals, stakeholders, and tourists. I use the results from these behavioral studies together with an understanding of tourists, locals, and stakeholders' attitudes toward the parading shrimp to mitigate the anthropogenic disturbances and design an effective sustainable ecotourism management plan.

The dissertation of Watcharapong Hongjamrassilp is approved.

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2021

DEDICATION PAGE

I dedicate my dissertation to my family members who have always supported me since I started my dream of being a biologist, and all my teachers who brought me to the biology world.

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All chapters are the result of collaborations and all co-authors contributed considerably. All co-authors have given their permission to use publications in this dissertation.

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CHAPTER 1

INTRODUCTION

Introduction

Since the rise of humans, our activities have caused numerous environmental problems at various levels ranging from a local to a global scale. The intensity of these problems has increased together with our ability to move across the continents (Science for Environment Policy, 2015). One of the anthropogenic activities that has created a number of deleterious impacts on organisms and ecosystems is "Tourism".

The tourism industry is one of the world's largest industries contributing, before the COVID-19 pandemic, over US$ 7.6 trillion of world income per year (The World Travel & Tourism Council, 2016). According to The World Tourism Organization, the number of tourists has been increasing annually resulting in huge economic benefits in many countries (UNWTO, 2018). Nevertheless, an increase in tourists with ineffective tourism management plans for each tourist site may create novel environmental problems, especially for the type of tourism called "Ecotourism".

Ecotourism, a type of nature-based tourism, is defined as responsible travel to natural areas, which aims to conserve the environment and sustain the well-being of local people (Ceballos-Lascurain, 1996; The International Ecotourism Society, 2015). Even though ecotourism has positive intentions to conserve the environment and may have potential socioeconomic benefits, many case studies show the failure of using ecotourism as a conservation tool. One of the examples that explicitly demonstrates the impacts of ecotourism on the environment is a case study of the over-tourism in the Great Barrier Reef (GBR), Australia (Harriott, 2004; De'ath et al., 2012). GBR is known as one of the world's largest coral reef systems in the world, which hosts more than 1,500 species of marine life (CRC Reef Research Centre, 2006). Every year, over 1.6 million visitors travel to the GBR for tourism purposes. Because of the rapid growth of tourism, the development of tourism infrastructure around the GBR has increased since the 1980s. However, this increased development, and the tourists it supported, had a large anthropogenic footprint that caused problems to the GBR. These include increased sewage discharge to the reef along with a variety of inappropriate tourism activities (e.g., fish feeding, littering, and anchoring from cruises) that resulted in the gradual decline of coral reefs (Harriott, 2004). 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 in the near future. To mitigate these problems, it is necessary to understand how our activities affect the ecosystem especially at the smallest level (i.e., species).

Much research has shown that tourists can negatively impact wildlife. Because wildlife perceives tourists as stressors, tourist activities could cause adverse physiological and behavioral changes in wildlife, which ultimately might result in the decline of their population (Geffroy et al., 2017). For instance, research from Green and Giese (2004) reveals that if a tourist approaches an Adélie penguin (*Pygoscelis adeliae*) within 5 m while the penguin is incubating its eggs, the incubating process can be interrupted leading to the decrease in the percent of hatching. Another example can be seen in the study by Huang et al. (2011) about the effect of photography on West Indian anoles (*Anolis cristatellus*). The researchers found that shutter noise from tourist cameras decreased the display behavior of the anoles, which not only plays a role in reproduction but also increases an individual's conspicuousness. 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, understanding how animals respond to tourist's activities could provide opportunities to create environmentally sustainable management plans to mitigate the anthropogenic impacts on animals.

In addition to understanding the impact of tourist activities on animals, it is also necessary to understand the stakeholders' perceptions of the ecotourism system (e.g., how they value their resources, how they aware about the effect of anthropogenic threats on animals, and their willingness to participate in any management plan that government decided) (Murphy & Murphy, 2004; Sánchez Cañizares et al., 2016). Two successful sea turtle ecotourism case studies in Brazil and Peru demonstrate that different in perceptions from ecotourism participants might result in different conservation outcomes. In Brazil, the economic benefits of locals are associated with the success of conservation outcomes. On the other hand, in Peru, both local willingness to participate in ecotourism management and the economic benefits of locals drive the success of conservation (Stronza & Pegas, 2008). Accordingly, it is important to understand the socioeconomic situation and perception of ecotourism by stakeholders at each ecotourism site to create practical and effective management plans.

Mass migration in animals is one of the behaviors that attract public attention and, in some cases, is the focus of nature-based tourism. For instance, the annual mass migration of monarch butterflies (*Danaus plexippusin*) in Mexico (Geiling, 2015) attracts more than a hundred thousand tourists annually. According to a survey from 118 million U.S households regarding the value of the monarch butterflies as a total one-time payment, the monarch butterflies are worth as much as $6 billion (Diffendorfer et al. 2014). Because of the economic impacts of ecotourism, concerns regarding overexploitation and climate change that affect migratory animals has created concerns over losing migratory species and phenomena, such as the extinction of wildebeest (*Connochaetes* spp.) that perform migration in southeast Kenya (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 protect and prevent this loss, it is essential to have a fundamental understanding of the basic biology of migration. Even though most animals such as birds, fishes, and mammals have been studied in the past, the biology of migration in invertebrates remains more of a mystery and could lead to insights into mass movement in other groups.

Macrobrachium (Crustacean: Decapoda: Palaemonidae) — a genus of 'freshwater' shrimp — has been reported to engage in mass migrations (Lee & Fielder, 1979; Bauer, 2013). Its species are found throughout the world in every type of aquatic habitat (Horton et al., 2018). Even though some species can be found in estuaries or marine habitats (amphidromous species), most of their life cycle occurs in freshwater habitats. Thus, carcinologists categorize this group as a freshwater species. Many amphidromous *Macrobrachium* engage in round-trip migration in which the adults migrate downstream from a river to the ocean to spawn. After the newly hatched shrimp larvae develop to the juvenile stage in the marine environment, the juveniles will migrate upstream to a freshwater habitat (Bauer, 2013). In some cases, when migration routes are blocked by man-made constructions such as dams or weirs, shrimp will climb and walk out of the water to cross the obstacle and return to the river to continue to migrate upstream (Lee & Fielder, 1979). According to Bauer (2013), this upstream and downstream migratory behavior appears to relate to the developmental strategies of the amphidromous shrimp. However, basic biological questions about proximate mechanisms involved in migration, such as factors triggering the migration or how individuals navigate to their destination, are lacking.

A long time ago, a group of native people in northeastern Thailand discovered synchronous mass migration of freshwater shrimp in the genus *Macrobrachium*. This migratory behavior is known as “parading behavior”. It occurs annually during the wet season which falls between late August and the end of September at Lamduan rapids in Nam Yuen district, Ubon Ratchathani province, Thailand. This migratory behavior is distinct from mass migrations in other crustaceans (Hick, 1985) and insects (Buhl et al., 2006) as it occurs both on land and in the water. Here the shrimp leave their primary (aquatic) habitat by climbing out a stream and walking on land for about 5 – 20 meters before moving back to the water. Local people believe that these shrimp migrate upstream to the headwater Dângrêk Mountains, the mountain range of Thailand-Cambodia that contains the headwater of the Lamduan rapids, for mating and reproduction. However, this assumption and putative function has not been verified. To date, only two notes from Lee & Fielder (1979) and Torkkola & Hemsley (2019) reported a similar migratory behavior in *M. australiense* in Queensland, Australia. However, basic information regarding the biology of this extraordinary migration, including its proximate and ultimate causes, is unknown.

Since 1999, the “Shrimp Parading” phenomenon at Lamduan rapids has been promoted as an ecotourist destination. It brings over hundred thousand of tourists to visit Ubon Ratchathani each year. Moreover, the parading shrimp has become part of the local culture. Over the past 20 years, locals have developed novel cultural practices around the shrimp (e.g., food and folk dances). Lacking the fundamental knowledge of the parading behavior, in concert with the increasing number of visitors and anthropogenic disturbance during the tourist season, it is very likely that shrimp populations will decline. Indeed, informal observations from the ranger in Nature and Wildlife Education Center, Ubon Ratchathani suggest that the population of parading shrimp seems to have decreased during the past 5 years. Furthermore, my preliminary work shows that the shrimp trend to parade more when tourists were absent indicating that tourists might influence the parading behavior. Therefore, if no effective plan for tourism management is established, it is possible that the local extinction of the parading shrimp might occur. The decline of parading shrimp will affect both the tourism business, the locals' culture, and tradition that is emerging. In addition, seeing that shrimp play essential roles in ecological services and maintaining the freshwater ecosystem, this loss will inevitably affect the balance of the local freshwater ecosystem.

Therefore, my dissertation aims to (1) describe the natural history of the parading shrimp, (2) study proximate and ultimate causes of the parading behavior, (3) study how the shrimp decide to parade out of the water, (4) identify potential threats of the parading shrimp from tourists and study its effect on the parading shrimp, and (5) understand attitudes toward the parading shrimp from tourists, locals, and stakeholders. In the end, I integrated all results to develop a sustainable management plan for this ecotourism site.

First, I studied the natural history of the parading shrimp by *in situ* observation at Lamduan rapids and Yang weir in Nam Yuen district, Ubon Ratchathani province, Thailand from August to September of 2018 – 2019. I collected fresh tissue samples of the parading shrimp and identified to species using 16S rRNA and COI genetic markers. To document the parading shrimp behavior, I used night camera traps to take photos of the shrimp that perform the parading behavior from 17:00 h. to 8:00 h. I counted the number of shrimp that paraded each night and described any behavior found from the camera traps. Moreover, I surveyed the river topology that might associate with parading behavior.

Based on a genetic study, I found that most of the shrimp that perform the parading behavior are *Macrobrachium dienbienphuense* Đăng & B.Y.Nguyên, 1972 (99%), and a few are *M. lanchesteri* De Man, 1911 (1%). The shrimp started to leave the river and paraded on land after sunset which was around 19:00 h. Most of the shrimp paraded inside the splash zone along the riverbank. The parade stopped about 30 minutes before sunrise which was around 6:00 – 7:00 h. The average walking speed of the shrimp on land was around 85.2± 43.82 (Mean±SD) cm/ min (N = 30). Finally, I found that river topology that associated with the behavior must consist of four main zones: (1) downstream zone (flow velocity = 5–10 cm/s), (2) turbulent zone (flow velocity = 10–20 cm/s), (3) running water zone (flow velocity = 120–200 cm/s), and (4) upstream zone (flow velocity = 60–100cm/s). The shrimp started to walk out of the river at a turbulent zone and paraded on land past the running water zone. They moved back to the river at the upstream zone.

Second, I tested proximate and ultimate causation of parading behavior. For the proximate causation study, I measured environmental parameters, which included (1) water velocity, (2) cloud cover, (3) humidity, (4) water temperature, (5) air temperature, (6) moonlight intensity, and counted the number of parading shrimp that paraded each night from the camera trap data. I fitted negative binomial regressions between the number of parading shrimp (as a dependent variable) and environmental parameters (as independent variables) to explain which environmental factors were associated with the shrimp leaving the water. To study the adaptive significance of parading (i.e., ultimate causation), I tested two things: (1) Do the shrimp parade for reproduction? and (2) Do the shrimp parade to escape the strong current? To test whether the shrimp parade for reproduction, I quantitatively described the population demography of parading shrimp. To test whether the shrimp parade to escape the strong current, I designed a laboratory experiment to measure whether the ability to tolerate the strong water current associated with the size of the shrimp or not (please see chapter 2 for more description of methods).

The results revealed that shrimp prefer to parade more under low light, high water velocity, and low air temperature. Based on the population demography study, I found that 93% of the parading shrimp were juveniles and 7% were adults. Moreover, year-round investigation indicated that most ovigerous females were found underwater (and not parading on land) in June and September. This indicates the parading behavior was not used for reproduction. The tank experiment showed that shrimp body size was positively associated with the ability to tolerate high water velocity. This means that big shrimp can tolerate high water velocity compared to small shrimp. Based on all of these results, I conclude that the shrimp parade to escape the strong current in the river. This benefits the small shrimp in that they will not be washed downstream where several shrimp predators live.

Third, I studied how the shrimp decided to parade out of water in the tank experiment. I varied two main factors that influenced the parading behavior: (1) light intensity (no light and 500 lux light) and (2) water velocity (10, 60, and 100 cm/s) and counted the number of shrimp that paraded in each condition. I repeated each condition 10 times.

I found that most shrimp decided to parade under no light at 10 cm/s water velocity. This result seems to conflict with the second study where the most parading occurred under the high flow condition (100 cm/s). However, if take a deep look at the river topology result from the first study, I found that the shrimp started to parade in the turbulent zone where the water velocity was about 10–20 cm/s. Therefore, this experiment together with the river topology results confirm that to be able to parade out of the river, the shrimp need a low flow zone to climb out of the river. They could not climb out of the river in the high flow zone.

Fourth, I investigated whether light intensity levels and/or light colors affected parading. To test this, I set up an *in situ* experiment at Lamduan rapids. The experiment involved filming the shrimp that walked past the observation zone under different conditions. For the light intensity study, I included three levels of white light (9000, 400, and 50 lux) and for the light color study, six conditions (blue, white, green, red, orange at 50 lux and one control, dark treatment). I compared the walking speed of the shrimp and the number of shrimp that walked back to the river using the chi-square test for the light intensity study and the Kruskal-Wallis test for the light color study.

The results revealed that more shrimp under 9000 and 400 lux light intensity walked back to the river compared to at 50 lux. Moreover, I found that under the 50 lux light intensity, the shrimp decreased walking speed under white, blue, and green light compared to red and orange light. Therefore, I conclude that the condition that least affects shrimp parading is the 50 lux light intensity with red or orange color. Based on these results, and the results from river topology, factors triggering the shrimp to parade, and the decision to parading from the first three studies, I proposed management actions to regulate tourist behavior in three different zones. In each zone, tourists must use a different light color to watch the shrimp to mitigate anthropogenic impacts on the shrimp.

Finally, to effectively manage the ecotourism site, I needed to know how much locals, tourists, and stakeholders valued the shrimp, their knowledge about the shrimp, and their willingness to change their behavior for the good of the shrimp. To do so, I used a questionnaire and interviewed key people (e.g., the director of Ubon Ratchathani Wildlife and Nature Education Center) to document the development of this ecotourism site and local beliefs about the shrimp.

I found that this ecotourism site was established in 1999 by the Thai government. However, locals knew about the shrimp long before the establishment of it as an ecotourism site. Older locals believed that the shrimp parade to the headwater to worship a god. Younger locals believed that the shrimp migrated to the headwater to breed. Results from the survey pointed out that tourists, locals, and stakeholders were aware that the population status of the shrimp was vulnerable. However, I found that locals were less aware of the value of the shrimp in terms of their contribution to their ecosystem, local culture, and local business than were tourists and stakeholders involved in the ecotourism industry. This raises the issue in which the lack of awareness of locals could lead to unsustainable ecotourism. One of the possible factors based on the survey data is that the locals lack education compared to tourists and stakeholders. This issue could be solved by the improvement of the local education system in these marginalized communities. Finally, I found that even though the three participant groups were not aware of the threats to the shrimp, they had a positive attitude to change their behavior that might affect the parading shrimp.

Overall, my research illustrates how a fundamental understanding of the behavior of animals can improve conservation and management outcomes. In this case study, I used knowledge about the shrimp parading in their natural habitat, what environmental factors triggered parading, how shrimp decided to parade, and how shrimp responded to the tourist's activities to create a management plan to mitigate the anthropogenic disturbances on the shrimp. Moreover, to increase the efficiency of the management plan, I also studied how humans think about possible management and how they valued and understood the shrimp. Thus, my dissertation illustrates a holistic framework on how to apply animal behavior knowledge to conservation and management (Figure 1.).

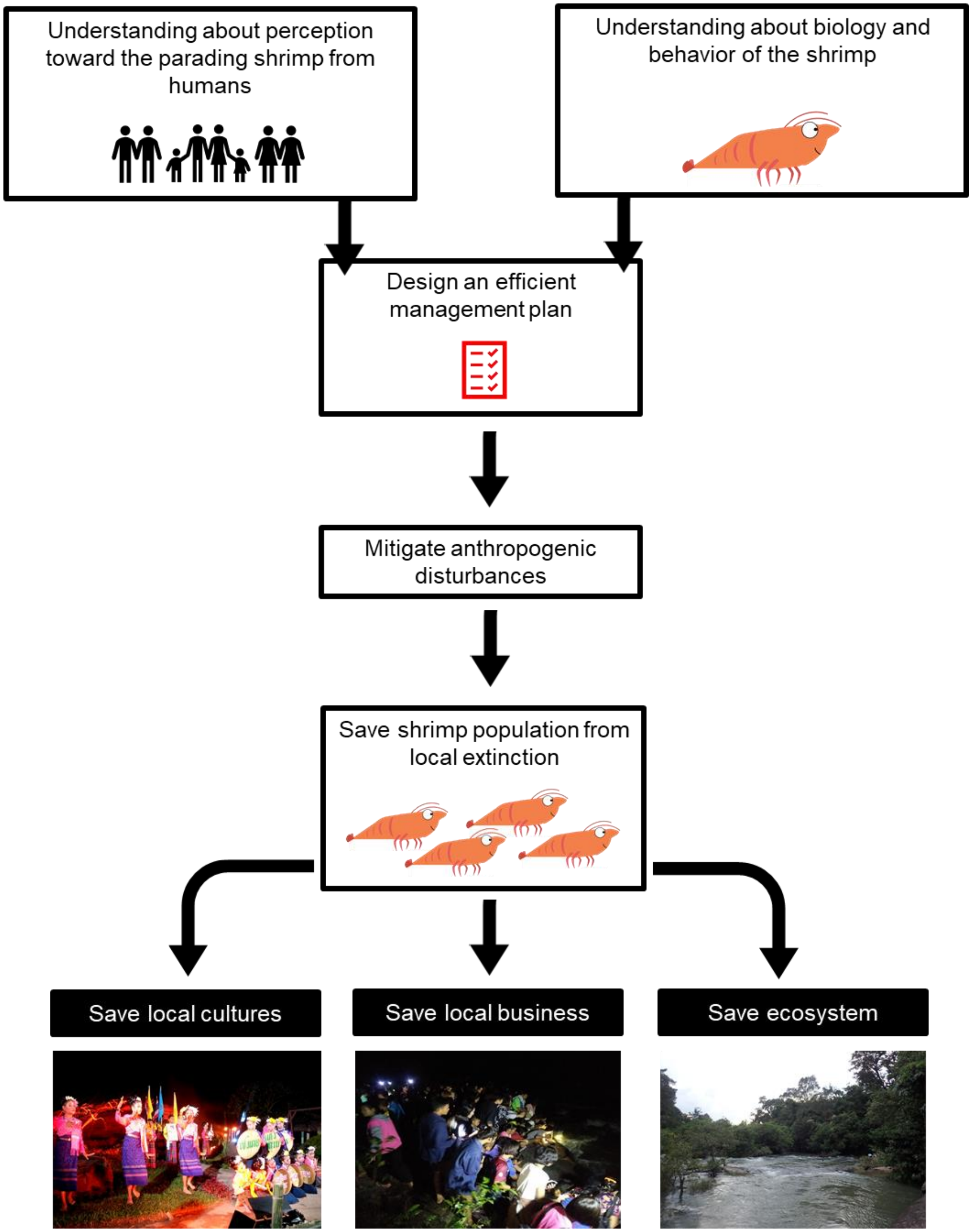

Figure 1 Summary of my dissertation on the application of animal behavior study in ecotourism management using "Shrimp Watching" ecotourism as a case study.

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CHAPTER 2

Why do shrimps leave the water? Mechanisms and functions of parading behaviour in freshwater shrimps

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Why do shrimps leave the water? Mechanisms and functions of parading behaviour in freshwater shrimps

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Keywords
collective movement; freshwater prawn; *Macrobrachium dienbienphuense*; migration; Southeast Asia.

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Abstract

An understanding of the mechanisms and functions of animal migratory behaviour may provide insights into its evolution. Furthermore, knowledge about migration may be important for conservation of rare species and may help to manage species in a rapidly changing world. Upstream migration is common in riverine animals, but little is known about proximate cues and functions of the upstream migration in aquatic macroinvertebrates. In Ubon Ratchathani, Thailand, locals have observed a synchronous mass migration of freshwater shrimps on land. This so-called 'parading behaviour' occurs annually during the rainy season and has become a large ecotourism event. Yet, we know little about the natural history, proximate causation and function of this extraordinary behaviour. Here we describe the natural history of parading behaviour and report the results from a series of experiments and observations to address its mechanisms and functions. Parading behaviour is not associated with breeding and spawning; rather, shrimps leave the water to escape strong currents. Conditions promoting shrimps to leave the water include low light, high water velocity and low air temperature. In addition, there is variation explained the specific location. River topology that creates hydrological variability and turbulence plays a role in triggering the shrimps to move out of water. Furthermore, turbidity and water chemistry were associated with shrimp activity. Finally, our results support that parading behaviour in freshwater shrimps is a mass movement upstream due to hydrological displacement. This study highlights the mechanisms that stimulate parading behaviour; a common activity in *Macrobrachium* and other decapod crustaceans.

Introduction

How animals move through their habitat plays a critical role in shaping ecosystems, and influences all levels of ecological organization from individuals to the community (Holyoak *et al*., 2008; Nathan, 2008). Investigation of movement patterns in different groups of animals may help to understand the role of movement in generating and maintaining biodiversity as well as its influence on population and species evolution (Holyoak *et al*., 2008; Duckworth, 2009). The field of movement ecology studies both proximate and ultimate causes of movement, ranging from individual to group movement, and aims to understand how movement is influenced by environmental heterogeneity (Nathan & Giuggioli, 2013). Three major areas of movement ecology research consist of: (1) investigating internal and external factors driving motion, (2) understanding mechanisms of navigation and orientation and (3) examining the physiology and motivation of movement (Holyoak *et al*., 2008). However, due to the limitation in technology and field study (Katzner & Arlettaz, 2019), we still lack the understanding of the movement ecology in many species (Nathan *et al*., 2008), especially invertebrates — organisms that play major roles in their ecosystems.

The knowledge from movement ecology studies also sheds light on conservation and management. For example, flying-fox bats (*Pteropus* spp.), a reservoir for Nipah virus, can migrate over 1000 km across Southeast Asia and Australia. An understanding of bats' spatial and temporal dynamics may inform management to control disease dispersal (Robert *et al*., 2012). Similar to flying-foxes, mass migration of locusts has destroyed food crops since the Ancient Egyptians (2470 BC) until now (Krall *et al*., 1997; Zhang *et al*., 2019). By studying the mechanisms and functions of locust migration, we may be able to better control future locust outbreaks (Buhl *et al*., 2006; Bazazi *et al*., 2008). Similarly by increasing of our knowledge about migratory behaviour in iconic species that are associated with tourism, such as monarch butterflies (*Danaus plexippus*), grey whales (*Eschrichtius robustus*) or birds provides vital information on their conservation and management (Fraser *et al*., 2018; Lemelin and Jaramillo-López, 2019).

The Crustacea is one of the subphyla in the phylum Arthropoda. Members of this subphylum can be found from deep seas (e.g. benthesicymid prawns (*Benthesicymus crenatus*) (Jamieson *et al*., 2009)) to alpine peaks (e.g. freshwater copepods (Manca *et al*., 1994)) illustrating remarkable adaptability. Many crustaceans engage in mass migrations after hatching (*Macrobrachium ohione* Bauer, 2011a, 2011b), or during mating (Christmas Island red crabs *Gecarcoidea natalis* Adamczewska & Morris, 2001). However, the mechanisms underlying crustacean aggregation, cues that trigger group formation, and how individuals navigate during migration are poorly known. Moreover, due to an extreme diversity of crustacean lifestyles (Bauer, 2004; Benvenuto *et al*., 2015), the pattern of migration and group movement of many crustaceans, traits crucial for their survival, requires substantially more study.

Macrobrachium (Crustacean: Decapoda: Palaemonidae) is a genus of freshwater shrimp comprised of more than 200 species (Zheng, Chen & Guo, 2019). Even though some species can be found in estuaries or marine habitats, most of their life cycle occurs in freshwater habitats (hereafter referred to as 'amphidromous species'). Many amphidromous *Macrobrachium* species engage in round-trip migration in which the gravid females migrate downstream from a river to the ocean to spawn at a river mouth or the gravid females spawn at the upstream area and the larvae drift downstream to the ocean. After larvae develop to the juvenile stage in the marine environment, juveniles migrate back upstream by swimming against the current to settle in freshwater habitat (Bauer, 2013). Some aspects of the proximate causation of migration, such as what environmental cues stimulate the migratory behaviour, have been studied (Bauer & Delahoussaye, 2008; Kikkert, Crowl & Covich, 2012), but much remains to be known.

A long time ago, a group of indigenous people in northeastern Thailand discovered synchronous mass terrestrial migration of 'completely freshwater shrimps' in the genus *Macrobrachium* (Fig. 1; Video S1). Called 'parading behaviour', it is a phenomenon in which freshwater shrimps collectively leave the water and walk upstream on land for a distance before returning to the river. This phenomenon occurs annually during the rainy season (the end of August to early October) and only at night.

Local lore was that parading was associated with spawning and breeding (hereafter reproduction). However, this hypothesis has never been tested. To date, only three notes from Lee & Fielder (1979), Fièvet (1999), and Torkkola & Hemsley (2019) reported a similar migratory behaviour in *M. australiense* in Queensland, Australia and *M. faustinum* on Guadeloupe Island. While the behaviour was described in previous studies, causation was not formally studied. Thus, we lack a fundamental understanding of the biology of this extraordinary phenomenon.

Since 1999, shrimp parading has been promoted as an ecotourism event in Thailand and draws >100 000 visitors annually. The lack of knowledge of the shrimps is problematic because recent evidence suggests that these shrimps may be decreasing in number and body size (W. Maiphrom, 2017, unpubl. data). Alarmingly, there are no strategies for habitat

Figure 1 Parading shrimps synchronously walking on land at night at the Lamduan Rapids, Ubon Ratchathani, Thailand. Photo: Watcharapong Hongjamrassilp.

and ecotourism management. Thus, to conserve this natural resource that can benefit local community (in terms of food, education and business), the fundamental biology of the shrimps, including life histories and movement behaviour, requires study.

Here we study the proximate causation and functions of the parading behaviour by: (1) describing the natural history of parading, (2) investigating whether parading is associated with reproduction (breeding or spawning) and (3) identifying environmental factors and habitat structure that triggers parading. Finally, we discuss whether parading is simply upstream migration of juveniles, as seen in most amphidromous *Macrobrachium* species, or whether it is a mass upstream movement triggered by hydrological displacement.

Materials and methods

Site study

Parading shrimps were studied in Nam Yuen district, Ubon Ratchathani province, Thailand from August to September of 2018 and 2019. We surveyed nine sites along the Lamdom river where parading was observed in the past (Fig. S1). However, we only found two locations with active parading behaviour: (1) the Lamduan rapids and (2) the Yang weir.

The Lamduan rapids (14°26'07.0''N; 105°06'17.0''E) are located on the Lamdom River (Fig. 2a); a river that flows down from a headwater located in the Dângrêk Mountains between Thailand and Cambodia. The distance from the headwater to the Lamduan rapids is about 25 km and the distance from the Lamduan rapids to the river's mouth, in the Mekong Delta in Vietnam, is about 900 km. During the summer (late March–May), the Lamduan rapids are dry, disconnecting the headwater and downstream portions. The upstream and downstream join back again during the rainy season (July–October).

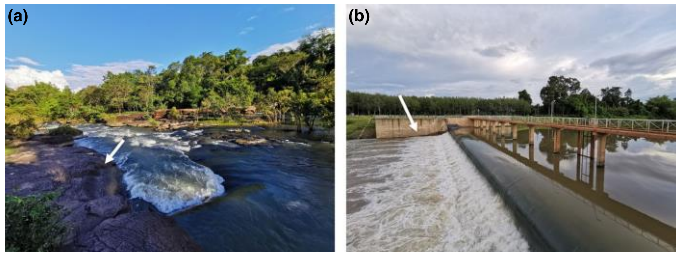

Figure 2 (a) Lamduan rapids. (b) Yang weir. White arrows indicate the area where the shrimps perform parading behaviour during the nighttime. Photos: Watcharapong Hongjamrassilp.

The highest precipitation in this area occurs in August and September (Fig. S2). The second site is Yang weir which is an inflatable rubber dam (14°29’35.5’’N; 105°08’06.5’’E) (Fig. 2b). This site is located 14 km downstream from the Lamduan rapids.

Species identification

We collected 30 shrimps from Lamduan rapids and Yang Weir (almost all parading shrimps were juveniles) while they were walking on land and identified them to genus using a morphological key (Cai, Naiyanetr & Ng, 2004), and to species with molecular identification techniques. We collected abdominal muscle tissues from ten shrimps (five from each site) and extracted total genomic DNA with a PureLink Genomic DNA Mini Kit (Carlsbad, CA, USA). We sequenced 16S ribosomal RNA (16S rRNA) and Cytochrome c oxidase I (COX1) for species identification (detailed methods regarding gene amplification and sequencing are in Supplementary Material S1).

We blasted all sequences in the National Center for Biotechnology Information (NCBI) database to search for species and confirmed the results by conducting a phylogenetic analysis with eight species of *Macrobrachium*, which are found in the Lamdom river and other places in Thailand, as an outgroup (Accession numbers in Table S1). We reconstructed the phylogeny using a maximum likelihood method with rapid bootstrap algorithm using 1000 replicates under Generalized Time Reversible (GTR) model (Yang, 2006).

Study 1 Behavioural observations

We observed parading behaviour using time-lapse night cameras (Victure trail camera HC200) and *in situ* observations. The night cameras use infrared LEDs, which should minimize shrimp disturbance. To determine when shrimps moved out of the river, we set up time-lapse night cameras *c*. 30 cm from the river to take photos every five minutes within a 20 x 20 cm quadrat between 17:00 to 08:00 h the next day. We quantified (1) the time that the shrimps started and stopped parading; (2) the distance over which shrimps travelled on land; and (3) the density of shrimps every hour during which they paraded. Moreover, we observed river structure that might be associated with parading in the two study sites by documenting hydrological variability that is a consequence of variation in river topology.

Study 2 Do the shrimps perform parading behaviour for reproduction?

Population demography and reproductive cycle of parading shrimps

Our hypothesis was that if parading behaviour was associated with reproduction (breeding or spawning), we would find more adults than juveniles. To test this hypothesis, we studied the population demography of the shrimps by collecting 30 actively parading shrimps, weekly, from the first week of August to the last week of October of 2018–2019 using a hand net (i.e. 12 collections/year; $N = 24$ collections). We measured carapace length, a proxy of body size, and plotted a frequency histogram of carapace length. In addition, to study the reproductive cycle of the adult shrimps, we used an underwater trap to collect female adults at the Lamduan rapids from 2018–2019. We aimed to collect 30 individuals each month. However, we caught fewer shrimps during the summer dry season. We counted the number of ovigerous females and compared them over months.

Study 3 Environmental factors associated with parading behaviour

Prior studies suggested that underwater migration in amphidromous shrimps was triggered by several environmental factors including water velocity, moonlight intensity, salinity and cloud cover (Kikkert *et al*., 2009). Therefore, we collected six environmental variables: (1) water velocity, (2) moonlight intensity, (3) air temperature, (4) water temperature, (5) humidity and (6) cloud cover (in okta units) in the vicinity of the parading site from the end of August to early October in 2018 and 2019. We measured all environmental variables at 20:00 h which is about one hour after the shrimps start to migrate from both the Lamduan rapids and the Yang weir site. We measured water velocity using a digital flow metre fitted with 60 mm impellers (Flowatch, JDC Electronic, Switzerland). We used a hygrometer and thermometer to measure humidity and temperature, respectively. To quantify cloud cover, we estimated it using eight sector square grids following Llusia *et al*. (2013). We obtained the moonlight illumination data from an online source (https://www.mooncalc.org). To estimate a number of shrimps that paraded each night, we counted shrimps in 180 photographs per day collected at each location using the time-lapse cameras as described above.

We conducted all statistical analyses using R 3.5.3 (R Core Team, 2019). We regressed environmental variables (including water velocity, moonlight intensity, air temperature, water temperature, humidity, cloud cover and site study) against the number of parading shrimps to explain variation in a number of shrimps per night. Prior to fitting the model, we calculated correlation coefficients among all environmental variables; only humidity and the air temperature were highly correlated ($r = -0.694$, $N = 95$, $P < 0.001$). Therefore, we omitted humidity from our model. Since the independent variable (number of parading shrimps) is a count, we fitted a negative binomial regression model using the function *glm.nb* in package MASS (Venables & Ripley, 2002). We calculated the model's pseudo R^2 with the likelihood-ratio-based method for the generalized linear model (Maddala, 1983; Cox & Snell, 1989; Magee, 1990) using *rsq.lr* function in package rsq (Zhang, 2018). To estimate partial pseudo R^2 of each independent variable, we subtracted Pseudo R^2 of the full model from Pseudo R^2 of the full model without the specific independent variable and used this value to explain effect size of each environmental variable.

Study 3.1 Does water velocity cause the parading shrimps to leave water?

Based on results from study 3, we hypothesized that parading behaviour functions to help the shrimps escape strong water currents. To test this hypothesis, we created an artificial stream that consisted of an upper tank and a lower tank. The bottom of the upper tank contained a valve to adjust flow velocity. The upper tank and lower tank were connected by a semicircular concrete pipe (Fig. S3). We placed 106 shrimps (carapace length ranged from 4.06–16.04 mm) by putting a shrimp on the centre of the concrete pipe and turning on the water from the upper tank. To quantify the maximum water velocity that the shrimp could tolerate, we increased the water velocity by adjusting the valve until the shrimp was washed down the pipe. Following this experiment, we measured each shrimp's carapace length as a proxy of body size. Finally, we calculated the Pearson correlation between maximum water velocity the shrimps could tolerate and carapace length.

Study 3.2 Does water chemistry, turbidity or turbulence cause the parading shrimps to leave water?

Based on the results from study 1, we hypothesized that turbulence might cause the shrimps to leave the water. Moreover, Kikkert *et al*. (2009) suggested that water chemistry (e.g. plant exudates from leaf litter and sediment) and turbidity were negatively correlated with migration activities in other freshwater shrimps (genus *Atya* and *Xiphocaris*). To determine whether turbulence, water chemistry and turbidity influenced shrimps activity and ultimately potentiated parading, we conducted experiments. However, we were not able to simulate the difference between chemical compounds in the water in the same way as Kikkert *et al*. (2009). Rather, we varied the source of our water. Groundwater was clear water that we sourced from an underground fountain, and river water was turbid water that we collected from the Lamduan rapids. Water from the Lamduan rapids was murkier, and we assumed that river water contained a greater diversity of chemicals than groundwater.

We divided the experimental aquaria into four conditions (hereafter treatment): (1) turbulence with river water, (2) no turbulence with river water, (3) turbulence with groundwater and (4) no turbulence with groundwater. To generate turbulence, we created an artificial stream where water was pumped uphill with aquarium pumps and flowed down to the holding tank (Fig. S4A). We used ToxTrac software (Rodriguez *et al*., 2018) to track the shrimp movement speed as a proxy of migration activity. However, shrimps are transparent and could not be detected under normal conditions. Therefore, we fed shrimps with rice that was stained with black food colouring (Fig S4B,C).

We collected actively parading shrimps and acclimated them in the aquarium with groundwater and no turbulence for 5 days to standardize shrimp activity. On the sixth day, we moved the shrimp into one of the four experimental aquaria (30 individuals per treatment). Then, every 12 h, we took each shrimp from each treatment to an observational aquarium and filmed it with a video camera for 3 min. After that, we took the shrimps back to the experimental aquarium and waited for the next 12 h. We ran all experiments for 24 h. After finishing the experiment, we measured swimming speed of each shrimp in each treatment using ToxTrac tracking software. We analysed the difference between mean rank of swimming speed among four treatments with Kruskal–Wallis test and compared the difference among significant groups using a Mann–Whitney U test.

Results

Species identification

The morphological analysis suggests two species of parading shrimps: *Macrobrachium lanchesteri* (Decapod: Caridea: Palaemonidae) comprised 1% of the sample ($N = 709$) and another unidentified *Macrobrachium* species that comprised 99% of the samples. We resolved this unidentified species with molecular techniques. We obtained a total of 408 base pairs (bp) from 16S rRNA and 692 bp from COXI from ten parading shrimps. After examining the protein-coding COXI, we found that every sequence consisted of several stop codons inside the sequences. This means that the sequences were pseudogenes and could not be included in the phylogenetic analysis. Thus, we only used sequences from 16S rRNA for species

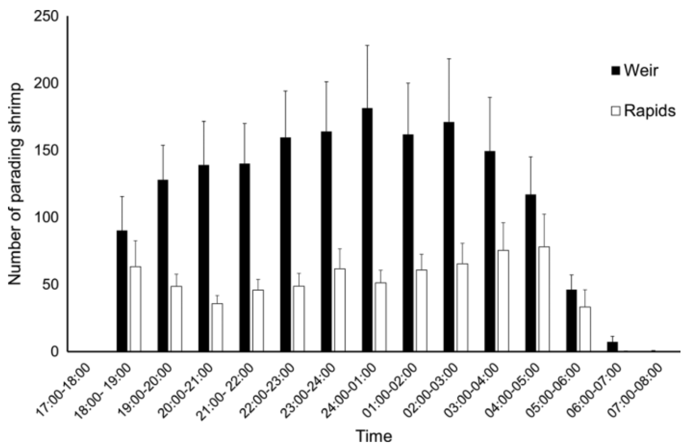

Figure 3 Estimated number (Average ± SEM) of parading shrimps from time-lapse night cameras from 2018–2019. Migrating pattern of parading shrimps at the weir (*N* = 40 days) is represented in black bars and at the Lamduan Rapids (*N* = 55 days) is represented in white bars.

identification. The result from the phylogenetic analysis reveals that all unknown specimens were clustered inside the *M. dienbienphusense* clade with *M. eriocheirum* as a sister group (Fig. S5). De Grave & Fransen (2011) synonymized *M. eriocheirum* with *M. dienbienphuense*, but Hanamura *et al*. (2011) recognized it as valid. Even though there is some difference of the opinion on the taxonomic validity of *M. eriocheirum*, 99% of the unknown *Macrobrachium* individual belonged to a single species, *M. dienbienphuense* Đặng and Nguyên, 1972.

Study 1 Behavioural observations

The time-lapse cameras revealed that the shrimps started to leave the river and paraded on land at around 19:00 h; ca. 30 min after dusk. We observed the shrimps aggregated underwater at the start point of the parading site around 18:00 until the sun completely set at around 18:45. After that, they climbed out of the river and continued to walk throughout the night (Fig. 3). While on land, they mostly walked inside the splash zone which was about 20–40 cm from the river's edge (Fig. 4). The movement ceased around 06:00–07:00 h when the sun started to rise. While moving, we found that most shrimps preferred to walk around 22:00–03:00 h at the weir and around 03:00–05:00 h at the rapids. Shrimps walked on land for 5–20 m depending on river velocity and riverbank structure. The average walking speed while moving on land was 85.2 ± 43.82 (Mean ± SD) cm/min (*N* = 30).

Observations among nine locations along the Lamdom river suggested that the Lamduan rapids and the weir had unique characteristics that could not be found elsewhere. We defined four zones based on topology and hydrology: (1) downstream zone (flow velocity = 5–10 cm/s), (2) turbulent zone (flow velocity = 10–20 cm/s), (3) running water zone (flow velocity = 120–200 cm/s) and (4) upstream zone (flow velocity = 60–100cm/s) (Fig. 5). After sunset, shrimps began to swim upstream underwater. They swam from the downstream zone to the turbulent zone. Shrimps aggregated there until the sky was dark. Once dark, the aggregated shrimps climbed out of the river and walked past the running water zone to the upstream zone. When the shrimps reached the end of the upstream zone where the flow velocity was sufficiently low (less than 60 cm/s), they returned to the river. The walking pattern varied depending on the number of migrants each night and the size of the splash zone. We observed shrimp walking in several rows when the splash zone was small. However, when the splash zone was sufficiently wide, the shrimps spread out and did not form a line.

Figure 4 Parading shrimps migrate on land mostly in the splash zone along the Lamdom river. Photo: Watcharapong Hongjamrassilp.

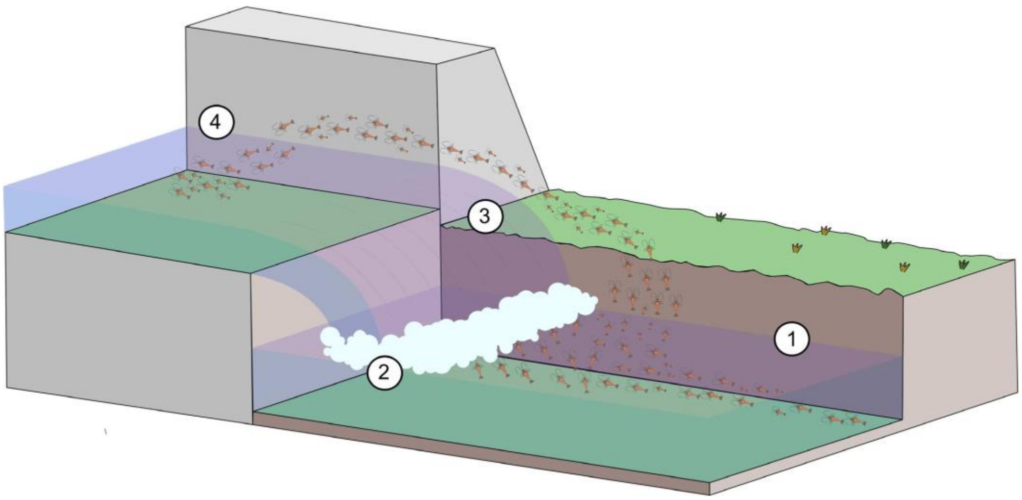

Figure 5 Four unique zones at the Yang weir, which are also found in the Lamduan rapids. Zone 1 is a downstream zone (flow velocity = 5–10 cm/s). Zone 2 is a turbulent zone (flow velocity = 10–20 cm/s). Zone 3 is a running water zone (flow velocity = 120–200 cm/s). Zone 4 is an upstream zone (flow velocity = 60–100 cm/s). Graphic credit: Boontigan Kuhasubpasin and Watcharapong Hongjamrassilp.

Study 2 Do the shrimps perform parading behaviour for reproduction?

Population demography and reproductive cycle of parading shrimps

Parading shrimps varied in their carapace length (CL) from 1.72–12.55 mm (Mean ± SD: 6.0 ± 1.439, N = 706) (Fig. 6) (relationship between CL and total length is in Fig. S6). 92% of the shrimp (CL = 1.72–7.80 mm) did not have an enlarged chela (a secondary sexual characteristic, Fig. 7a) and we did not observe eggs inside their abdomen. From this, we conclude that 92% of the parading shrimps were juveniles. Moreover, year-round data collection of adults *M. dienbienphuense* in the Lamdom River revealed that most ovigerous females were found in June to September with the peak number of ovigerous females in June (Fig. 7b). Finally, we found that within ovigerous females, eggs in their abdominal cavity were not at the same developmental stage. Some eggs already had eyes developed inside while some did not. Together, these observations suggest asynchronous spawning of *M. dienbienphuense* and suggest that parading was not associated with spawning.

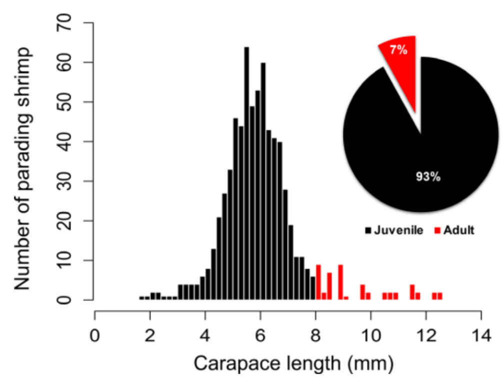

Figure 6 Histogram illustrating the frequency of parading shrimps with different carapace lengths ($N = 706$). Pie chart represents proportion of juvenile and adult *Macrobrachium dienbienphuense* which were collected while parading.

Study 3 Environmental factors associated with parading behaviour

In 2018 and 2019, we quantified data from a total of 55 days at the Lamduan rapids and 40 days at the weir. More shrimps paraded at high water velocities ($P < 0.001$) and at low air temperatures ($P = 0.006$; Table 1), and more shrimps paraded at the weir than at the Lamduan rapids ($P = 0.002$). Even though the shrimps tended to parade more with high precipitation, low moon illumination, low cloud cover and low water temperature, these independent variables were not statistically significant.

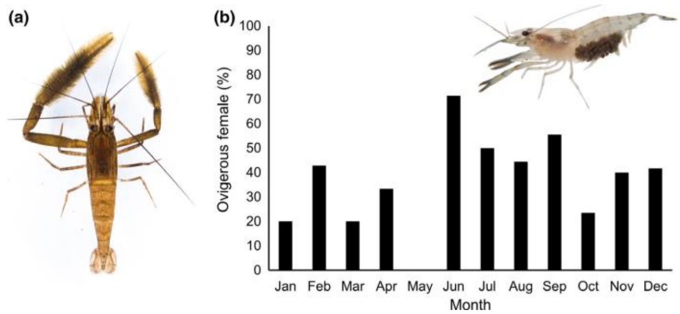

Figure 7 (a) Adult male *Macrobrachium dienbienphuense* with enlarged hairy claws. (b) The bar graph shows the percent of ovigerous females (ovigerous females in each month/ total females in each month) in different months. Top right is a female *M. dienbienphuense* with a cluster of eggs inside its abdominal cavity. Photo: Watcharapong Hongjamrassilp.

Table 1 Results from negative binomial regression describing the variation in a number of parading shrimps by environmental parameters

	Estimate	SE	Z value	*P* value	Partial Pseudo R^2	Pseudo R^2
(Intercept)	9.227	2.185	4.222	<0.000*		0.385
Precipitation	0.010	0.005	1.818	0.069	0.022	
Moon illumination	−0.003	0.003	−1.030	0.303	0.007	
Cloud cover	−0.008	0.026	−0.324	0.746	0.001	
Water temperature	−0.072	0.078	−0.923	0.356	0.003	
Air temperature	−0.082	0.030	−2.742	0.006*	0.042	
Water Velocity	0.012	0.002	5.417	<0.000*	0.130	
Location (Weir)	0.620	0.195	3.175	0.002*	0.055	

P-values with asterisk are considered significant.

Study 3.1 Does water velocity cause the parading shrimps to leave water?

Larger shrimps tolerated higher water velocity than smaller shrimps ($R = 0.856$, $N = 106$, $P < 0.001$) (Fig. 8). This result suggests that the small shrimps benefited from walking out of water because they could not tolerate the high flow at the rapids. However, the largest shrimps rarely walked out of water because they could tolerate the high flow in the rapids.

Study 3.2 Does water chemistry, turbidity or turbulence cause the parading shrimps to leave water?

At the start of the experiment (0 h), swimming speed of shrimps from the four treatments were not significantly different ($\chi^2 = 2.06$, $P = 0.56$, $N = 30$ in each treatment). However, by hour 12, shrimps started to behave differently as a function of treatment. After 12 h, shrimps in treatment 1 (with turbulence and river water) and 3 (with turbulence and groundwater) had higher swimming speeds than shrimps in treatment 2 (without turbulence and with river water) and 4 (without turbulence and with groundwater) ($\chi^2 = 26.73$, $P < 0.000$; Fig. 9, Table 2). This indicates exposure to turbulence increased the swimming speed of the shrimps during the first 12 h. After 24 h, swimming speed of shrimps in treatment 1, 2 and 3 were similar and were higher than treatment 4 ($\chi^2 = 11.25$, $P < 0.001$; Fig. 9, Table 2) suggesting that turbulence and river water increased shrimp swimming speed. However, the turbulence had a greater effect within a short period (the first 12 h)

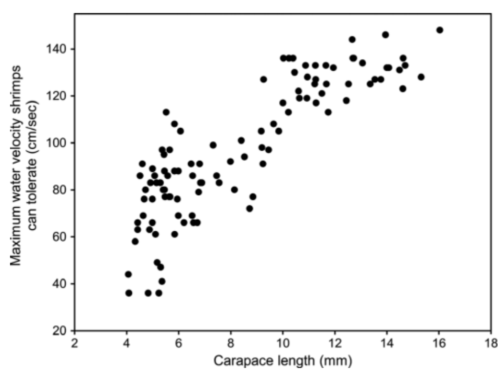

Figure 8 Relationship between carapace length and maximum water velocity that the parading shrimps can tolerate ($N = 106$).

Table 2 Results from Kruskal–Wallis test describing the difference in mean ranks of swimming speed of parading shrimps in four different treatments with Mann–Whitney U test

				Mann–Whitney U test	
Time	d.f.	Chi-square	*P*	Treatment	Group
0	3	2.06	0.56		
12	3	26.73	<0.000*	1	a
				2	b
				3	a
				4	b
24	3	11.25	<0.001*	1	a
				2	a
				3	a
				4	b

P-values with asterisks are considered significant.
Treatment 1 is turbulence and river water. Treatment 2 is non-turbulence with river water. Treatment 3 is turbulence with groundwater. Treatment 4 is non-turbulence with groundwater.

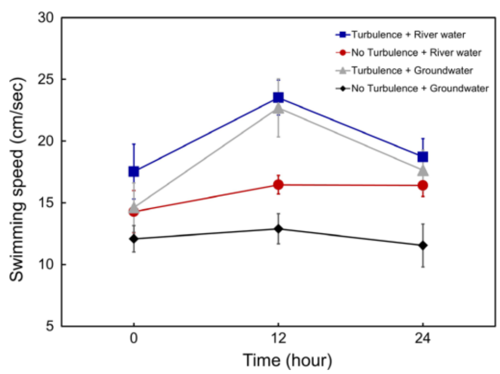

Figure 9 Temporal pattern of swimming speed (mean ± SE) of the parading shrimps in four different treatments. Hour in x-axis is number of hours after the shrimps were placed in each treatment. *N* = 30 in each treatment.

compared to the effect of the type of water, which was only important at 24 h. Based on these results, we conclude that the type of water (high turbidity and chemically complex water) and turbulence increases shrimp activity and stimulates them to walk out of the river.

Discussion

A number of species of freshwater caridean shrimps engage in what is referred to as parading behaviour. Our research shows that small shrimps leave the river and walked on land to escape strong currents. The main factors that triggered parading were low light intensity, high water velocity, low air temperature, high turbulence, high turbidity and (to date unidentified) chemicals in the water. We discuss these below.

Virtually all of the shrimps we identified performing parading behaviour in Ubon Ratchathani, Thailand were *Macrobrachium dienbienphuense*; 1% of them were *M. lanchesteri*. Both species are endemic to East and South East Asia (Chace & Bruce, 1993; Hanamura *et al*., 2011). Other studies reported parading behaviour in caridean shrimps (Decapoda, Caridea) throughout the world including in Asia (*Caridina japonica*, *Paratya compressa* and *M. japonicum* in Japan (Hamano *et al*., 1995); *M. malcomsonii* in Godvari, India (Ibrahim, 1962)), Australia (*M. australiense* in Queenland, Australia) (Lee & Fielder, 1979; Torkkola & Hemsley, 2019), and in the Americas (*Atyoida bisulcata*, *M.grandimanus* and *M. lar* in West Maui Mountain, Hawaii, USA (Benbow *et al*., 2002); *M. ohione* in the Atchafalaya River, Louisiana, USA (Olivier *et al*., 2013); *M. faustinum*, *Xiphocaris elongata* and *Atya innocous* on Guadeloupe Island, French West Indies (Fièvet, 1999)). These reports indicate that the ability to leave a river and climb over either natural barriers (e.g. waterfalls) or man-made barrier (e.g. dams or weirs) during upstream migration is widespread in amphidromous and freshwater caridean shrimps.

Ancestors of caridean shrimps are thought to have originated in marine habitats (Davis *et al*., 2018) and some species evolved to exploit freshwater habitats (Bauer, 2013). Upstream migration in concert with novel reproductive strategies (abbreviated larval development (ALD) versus extended larval development (ELD)) are two main features that allow caridean shrimp to successfully colonize freshwater habitats (Bauer, 2011a; Bauer, 2013). We suggest that parading is another behavioural adaptation that facilitates colonization of freshwater ecosystem by allowing shrimps to move past barriers to upstream areas while other organisms cannot (e.g. predatory fishes). Moreover, the ability to walk on land may facilitate overland dispersal (Torkkola & Hemsley, 2019). More observations are needed to confirm this hypothesis.

Many species of amphidromous *Macrobrachium* parade while travelling to headwaters with relatively fewer predators than downstream areas (Covich *et al*., 2009). However, until now, there have been no reports of upstream migration of the completely freshwater *Macrobrachium*. Bauer (2013) reported the upstream migration of *M. ohione*, an amphidromous species, by swimming upstream at nighttime but not at daytime. However, we did not observe *M. dienbienphuense*, which are a freshwater species (De Grave, Wowor, & Cai, 2013; WoRMS, 2020), performing upstream migration by swimming during both the day and night. We only observed them walking at night. After the parading shrimps returned to the river, we did not observe them swimming upstream. Bauer (2013) proposed that the migration between freshwater and marine system of amphidromous *Macrobrachium* was related to developmental strategy. The amphidromous species are known to have extended larval development (ELD). ELD is a type of development where adults spawn with many tiny larvae that contain a small amount of yolk (Mashiko, 1990; Walsh, 1993; Bauer, 2004). Because of less yolk, the larvae must drift downstream to the ocean where there is more food and sufficient salinity that triggers their development. In some species, gravid females migrate downstream and spawn at a river mouth (Olivier & Bauer, 2011; Bauer, 2011a). By contrast, completely freshwater species are known to exhibit a direct or abbreviated larval development (ALD), which is the type of development whereby the adult spawn with fewer larvae, but these larvae are typically in more advanced stages or, in some species, hatching out as a juvenile (post-larvae) (Hayashi & Hamano, 1984). Because completely freshwater species hatch out in an advanced developmental stage, the juveniles need not migrate.

While we do not have any direct evidence that the populations of *M. dienbienphuense* in our study sites have ALD, the distance from our study sites to the closest estuary was about 1000 km. Most of females *M. dienbienphuense* in our study sites carried eggs that were at the pigmented eye stage to pre-hatching stage indicating that they were ready to spawn. Therefore, we hypothesize that *M. dienbienphuense* in our study sites have ALD. Thus, we conclude that the function of parading behaviour in *M. dienbienphuense* is not similar to the upstream migration in amphidromous species, yet the parading behaviour helps the juvenile shrimps move past the rapids.

We observed *M. dienbienphuense* parading after sunset; light suppresses the behaviour. By contrast Fivèt (1999) observed shrimps (*M. faustinum*, *X. elongata* and *A. innocuous*) leaving the water during the day when there was a sudden strong release of water over an impoundment (water current >100 cm/s). We also observed a single event in September of 2019 where *M. dienbienphuense* continued to migrate after sunrise on a day of exceptionally heavy rain and extremely rapid flow (*c*. 220 cm/s). These anecdotes suggest that the decision to parade involves multiple drivers including at least ambient light and water velocity.

The number of parading *M. dienbienphuense* was positively correlated with water velocity and negatively correlated with shrimp size. Lee & Fielder (1979) also reported a similar pattern of smaller *M. australiense* being more likely to parade. Together, parading behaviour is a way that small shrimps can continue to move upstream where water velocity exceeds about 120 cm/s. In addition to velocity, our experiments revealed that turbulence also potentiates parading. Since most migrating shrimps make use of positive rheotaxis during the upstream migration (Lee & Fielder, 1984), turbulence might eliminate or modify flow direction (Benstead *et al*., 1999). The Lamduan rapids and the Yang weir have the turbulence zone following the running water zone (Fig. 5). Therefore, by moving on land, shrimps, especially small individuals, avoid turbulent areas. We also observed that while moving on land, shrimps often walked near the splash zone and put their legs into the river. We speculate that the shrimps sensed flow direction using setae on their legs. However, how the shrimps navigate while on land requires formal study.

Covich (1988) proposed that chemicals from leaf litter might contain toxic compounds that drive shrimps to migrate to another habitat, while Olsson *et al*. (2006) proposed that chemicals in the water could trigger the shrimps to collectively move because chemicals from leaf litter might be a food cue. Kikkert *et al*. (2009) demonstrated that *Atya* and *Xiphocaris* shrimps avoided swimming in a river with high leaf litter and high turbidity consistent with the hypothesis that they avoided toxic leaf litter. While we also found that activity was increased when shrimps were in river water compared to ground water, we cannot conclude why. Regardless, our results illustrate the potential that both chemicals and turbidity stimulate parading.

Parading behaviour was not associated with reproduction in *M. dienbienphuense* because almost all were juveniles. Several riverine species such as Atlantic salmon (*Salmo salar*) and aquatic insects migrate upstream to mate (Baglinière *et al*., 1990; Higler, 2004). Furthermore, studies in amphidromous *Macrobrachium* shows that shrimps migrate downstream to spawn in the ocean while most juveniles migrate upstream after larval development in the sea (Bauer, 2013). This suggests upstream migration in amphidromous species may not function for reproduction. Moreover, we found that the parading season was not associated with spawning because *M. dienbienphuense* has an asynchronous spawning reproductive pattern.

Information about the mechanisms and functions of parading behaviour allows us to improve conservation and management strategies for freshwater shrimps. For example, dams have been constructed throughout the world (Kaika, 2006; Zaharia *et al*., 2016), and they affect upstream migration of many riverine species including amphidromous and freshwater shrimp. Hamano *et al*. (1995), Fièvet (2000) and Olivier *et al*. (2013) demonstrated how a fundamental understanding of climbing performance in caridean shrimps could be applied to create ‘shrimp ladders’, which permit shrimp to move across dams. Furthermore, an understanding of parading behaviour can be used to limit the movement of invasive species to upstream headwaters. For instance, red swamp crayfish (*Procambarus clarkii*) (Crustacea: Astacidae), a native species in the southern United States, is an invasive predator in other parts of the world (Loureiro *et al*., 2015). By understanding crayfish climbing performance, scientists have designed a special type of roof on a dam that can prevent upstream crayfish movement (Dana *et al*., 2011). Our results could be used to create similar structures that can facilitate or limit the movement of decapod crustaceans.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Figure S1. Location of surveyed sites. Parading shrimps were only detected at sites 4 and 9. Number 4 is Lamduan rapids and number 9 is Yang weir. Table on the bottom left indicates the latitude and longitude of surveyed sites.

Figure S2. Monthly average±SEM rainfall at Phon thong village (ca. 3 km away from out study site), Nam Yuen district, Ubon Ratchathani, Thailand. Data from http://hydro-4.com/.

Figure S3. Artificial stream to study the decision to parade. Yellow arrow illustrates flow direction. Shrimps were put in the lower tank. During the experiment, the shrimp walked up from lower tank to an upper tank.

Figure S4. (a) Experimental aquarium with turbulence creating system. (b) Rice stained with black food coloring (white arrow) contrasted with a shrimp in the top right which has not eaten the rice. (c) Close-up photo of shrimp fed black rice. The white arrow points its stomach stained with black color.

Figure S5. Ultrametric phylogeny of some members of shrimps in genus *Macrobrachium* found in Thailand. S1–S5 are samples collected from the Lamduan rapids and S6–S10 are samples collected from the Yang weir. The values represented on this phylogeny are bootstrap values.

Figure S6. Relationship between total length and carapace length of *Macrobrachium dienbienphuense* with regression equation.

Table S1. Accession numbers used for phylogenetic analysis.

Video S1. Parading behaviour of parading shrimps (*M. dienbienphuense*) at Lamduan Rapids, Ubon Ratchathani, Thailand.

CHAPTER 3

Humans influence shrimp movement: A conservation behavior case study with

"Shrimp Watching" ecotourism

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

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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

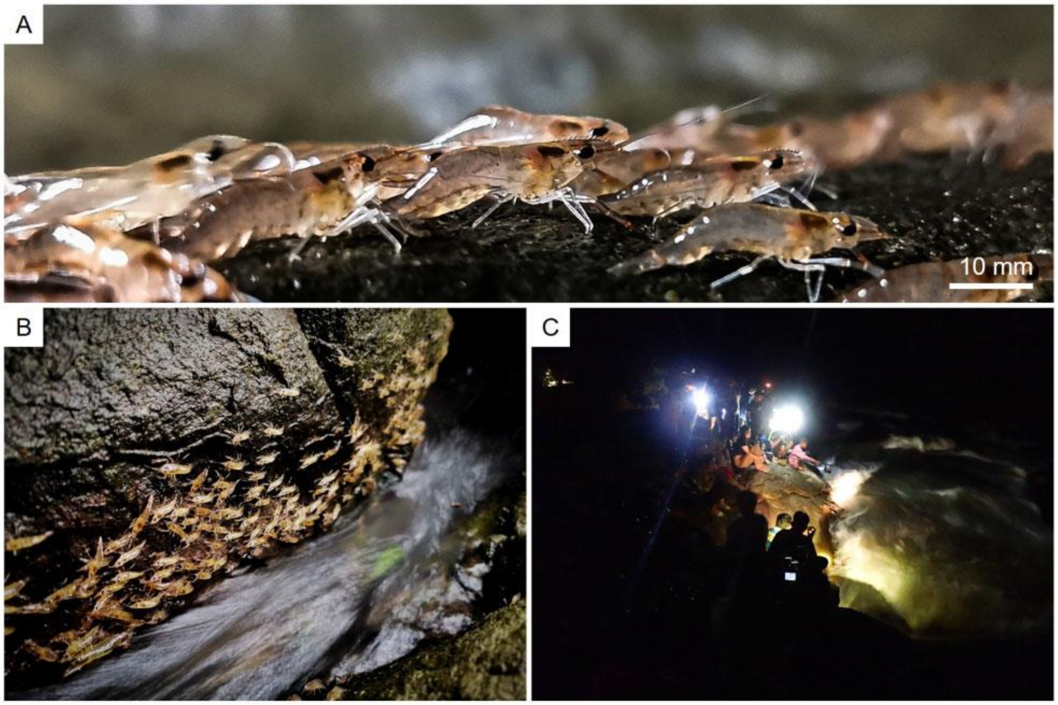

Figure 1. (A) A close-up photo of juvenile parading shrimps (*M. dienbienphuense*). (B) Shrimp parading is seen when they collectively climb out of a river and walk upstream along the riverbank. (C) Tourists with their flashlights waiting to watch the shrimp parade. Photos by W. Hongjamrassilp.

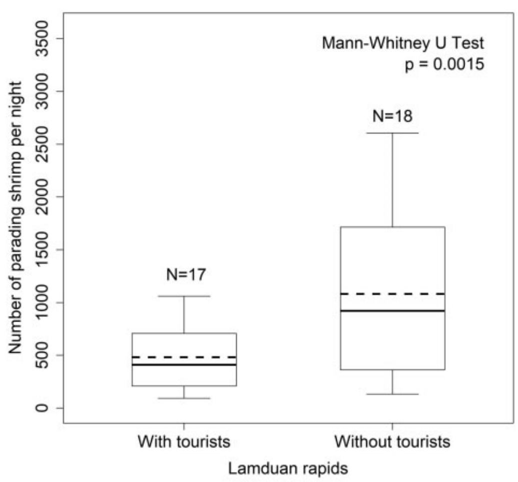

Figure 2. Preliminary observations show the difference between the number of shrimps that leave the river at Lamduan rapids when tourists were present and absent. We used night camera traps to take photos of shrimps that passed a $20 \times 20\,cm^2$ plot every 5 min between 18:00 and 07:00 h. We counted 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

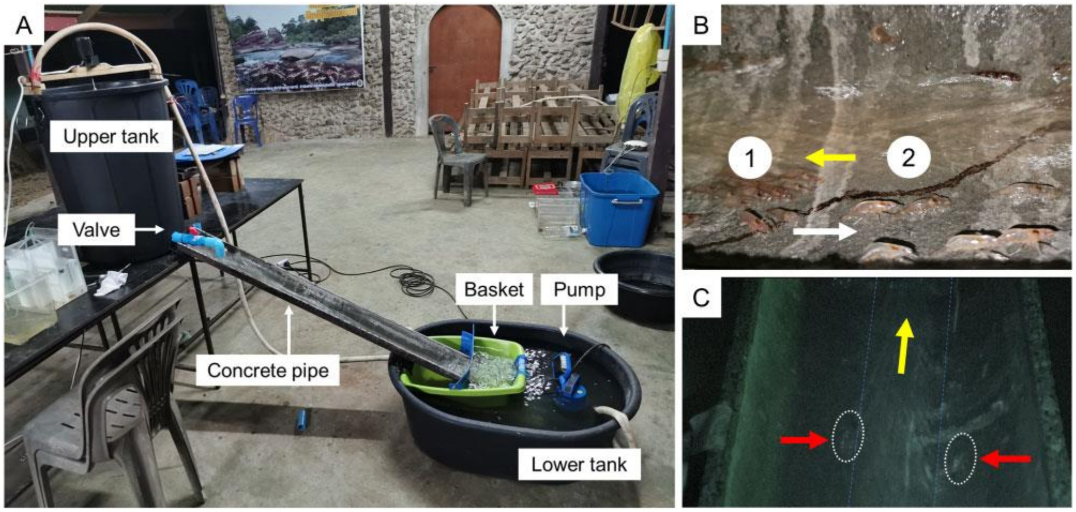

Figure 3. (A) The artificial stream used in this study. Shrimps were put in the basket in the lower tank. (B) A photo during the experiment. Point 1 shows the shrimps that began to walk out of the water. Point 2 shows the shrimps that walked out of the water; we counted the number of shrimps that walked 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 ($32 \times 28 \times 15\,cm^3$; 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

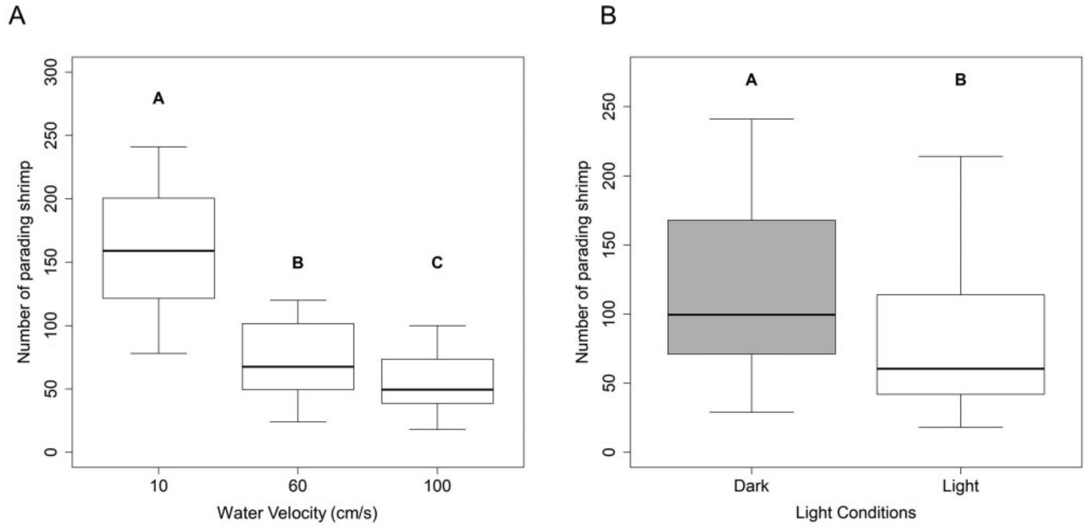

Figure 4. (A) The number of shrimps that leave the water as a function of 3 different water velocities. (B) The number of shrimps that leave the water as a function of 2 different light conditions. Letters above boxplots' whisker indicate significantly different responses (Dunn's test, $P < 0.05$). The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

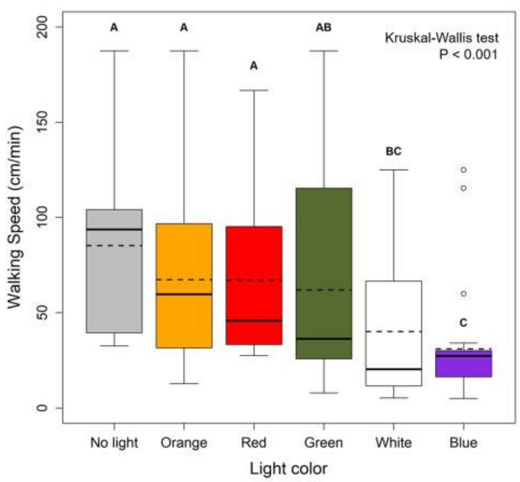

Figure 5. Shrimp walking speed as a function of different light treatments. Similar letters above boxplot's whisker indicate no significant difference between speeds as a function of light color. The bold lines in the boxplot are the median and the dashed lines are the means. Whiskers above and below 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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CHAPTER 4

"Shrimp Watching" Ecotourism in Thailand: Toward Sustainable Management Policy

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"Shrimp Watching" Ecotourism in Thailand: Toward Sustainable Management Policy

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Interest in wildlife ecotourism is increasing but many studies have identified detrimental effects making it unsustainable in the long run. We discuss a relatively new wildlife ecotourism event where tourists visit Ubon Ratchathani, Thailand to witness a mass migration of freshwater shrimp that emerge from the water and move across land known as "shrimp parading." As this has been developed into a tourist event, the number of migrating shrimp have declined, suggesting that it may be unsustainable as currently practiced. We used a questionnaire to ask how locals, tourists, and stakeholders value the shrimp and their willingness to change their behavior to mitigate anthropogenic impacts. We found that three groups of participants were not aware of potential negative impacts to the shrimp from tourism. Locals valued the tourism in terms of the economy, culture, and environment less than tourists and stakeholders. The local government applied a top-down approach to manage this tourism without a fundamental understanding of the shrimp's biology, impacts of tourists on the shrimp, or the various stakeholder perceptions. We discuss the problems and possible solutions that may be employed to help sustain this fascinating biological and cultural event and propose a framework to develop a sustainable wildlife ecotourism management plan. This case study serves as a model for others developing wildlife watching ecotourism, especially in developing countries.

Keywords: animal-based tourism, flagship species, invertebrate tourism, invertebrate conservation, sustainable ecotourism, Southeast Asia, Thailand, wildlife watching

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INTRODUCTION

The tourism industry is one of the world's largest industries, which before the COVID-19 pandemic, contributed over 8.9 trillion US dollars of world gross domestic product (The World Travel Tourism Council, 2019). Among the types of tourism, ecotourism, a type of nature-based tourism, has become increasingly popular since the late twentieth century (Buckley, 1998; Hawkins and Lamoureux, 2001).

Ecotourism is defined as responsible travel to natural areas which aims to conserve the environment as well as to sustain the well-being of local people (The International Ecotourism Society, 2015). Ecotourism may have both socioeconomic and environmental benefits through conservation. However, the success of using ecotourism as a conservation tool depends on many factors (Krüger, 2005). For example, studies of sea turtle ecotourism in Brazil and Peru revealed that different conditions might give different results. In Brazil, the economic benefits of locals are associated with the success of conservation outcomes. On the other hand, in Peru, both local participation in ecotourism management and the economic benefits of locals drive the success of conservation (Stronza and Pegas, 2008). Even though management is a key to successful conservation and sustainable ecotourism, the understanding of fundamental knowledge of each system and perceptions from three important elements of ecotourism system—tourists, ecotourism stakeholders (i.e., business owners), and locals (residents)—are essential to create positive conservation outcomes (Murphy and Murphy, 2004; Sánchez Cañizares et al., 2016).

Relatively little wildlife ecotourism has traditionally focused on invertebrates, animals that have a vital role in their ecosystem (Huntly et al., 2005). However, invertebrate ecotourism is expanding. Examples of invertebrate ecotourism (reviewed in Lemelin, 2013) includes the mass aggregation of the New Zealand glowworms (*Arachnocampa luminosa*) in a cave in New Zealand (Hall, 2012), and firefly watching tours in Amphawa, Samut Songkhram, Thailand (Nurancha et al., 2013). Moreover, when invertebrates exhibit mass migration, they could stimulate more attention from tourists (Mavhunga, 2011). This can be seen in the spectacular annual migration of monarch butterflies (*Danaus plexippus*) in the United States (Whelan, 2012), and the mass migration of red crabs (*Gecarcoidea natalis*) on Christmas Island, Australia (Back From The Brink, 2019). Several developing countries in tropical regions, where invertebrate biodiversity is high, have much potential to develop invertebrate tourism. Therefore, understanding how locals, tourists, and stakeholders in different areas think about their resources is an essential part for developing sustainable ecotourism management plans (Sánchez Cañizares et al., 2016).

"Shrimp Watching" tourism is a type of ecotourism that was promoted by the Tourism Authority of Thailand (TAT) under the "Amazing Thailand" campaign from 1998 to 1999. This event has been organized annually at Lamduan rapids, Nam Yuen district, Ubon Ratchathani, Thailand by the Nature and Wildlife Education Center Ubon Ratchathani. In September of each year, tourists from all around Thailand and other countries in Southeast Asia travel to this place to witness the unique mass migration of freshwater shrimp known as "Parading Shrimp" (**Figure 1**; **Supplementary Video 1**). This natural phenomenon occurs at night when millions of freshwater shrimp collectively climb out of the Lamduan rapids and start to parade on land toward the headwater in the Thailand-Cambodia border. Research from Hongjamrassilp et al. (2020) reveals that the shrimp leave the water to escape the strong water current in the rapids. They do not perform this unique migration for reproduction, as observed in other riverine animals, such as salmon.

Over the past 20 years, locals in Nam Yuen district have developed novel cultural practices around the shrimp (e.g., food, folk songs, and dances) indicating that the shrimp have become integrated into their culture (**Figure 2**). However, observations from rangers in the Nature and Wildlife Education Center, suggest that shrimp populations have decreased during the past 5 years (Wassana Maiphrom, pers. comm.). Indeed, (Hongjamrassilp and Blumstein, under review) report reveals that the decrease in the number of parading shrimp is associated with the presence of tourists. The decline of shrimp may ultimately influence the tourism business, the cultures that have been developed, as well as other emerging cultures and traditions.

(Hongjamrassilp and Blumstein, under review) discovered that light from tourist's flashlights is the main factor that might lead to the decrease in parading shrimp during the tourist season. They found that red and yellow lights affect the shrimp while migrating on land less than other colors. Therefore, they suggested an evidenced-based solution to mitigate the anthropogenic disturbances on the shrimp would involve creating three different zones, in which each zone allows tourists would be permitted to use different light colors while shrimp watching (**Figure 3**). However, to create and apply an effective management plan, we need to understand how participants in this tourism industry understand the problems, value their resources, and the degree to which they are willing to change their behaviors for the good of the shrimp.

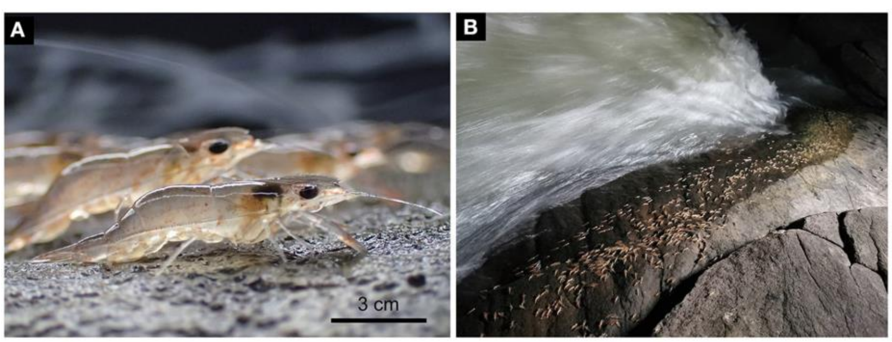

FIGURE 1 | (A) A close-up photo of the parading shrimp while parading on land. **(B)** The mass migration on land of the parading shrimp at Lamduan rapids, Ubon Ratchathani, Thailand heading toward the headwater in Dângrêk Mountains in Thai-Cambodian natural border. Photos by Watcharapong Hongjamrassilp.

FIGURE 2 | **(A)** Statue of parading shrimp at the tourism site. **(B)** Mascot design competition event for primary to high school students organized by the Nature and Wildlife Education Center at Ubon Ratchathani with the aim to increase the awareness of anthropogenic disturbances on parading shrimp. **(C)** Folk dance telling the story about the parading shrimp and how to conserve them. **(D)** A group of tourists watching the parading shrimp climb out of the river at night. Photo by **(A,B,D)** Watcharapong Hongjamrassilp and **(C)** the Nature and Wildlife Education Center at Ubon Ratchathani.

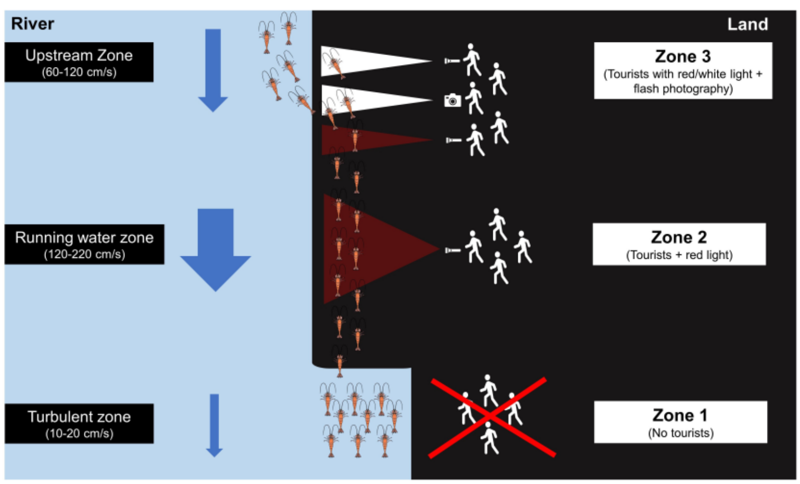

FIGURE 3 | The management plan proposed by Hongjamrassilp and Blumstein (under review). Because the shrimp respond to red light less than other light colors, they proposed to divide the tourist's site into three zones. At zone 1, tourists are not allowed to be here because light could inhibit the shrimp from emerging from the river. At zone 2, tourists can use personal flashlights. However, they need to use red light instead of white light because white light can cause the shrimp to walk back to river where they are washed downstream. Light color can be modified by covering the tourist's personal flashlight with a piece of red cellophane. Finally, at zone 3, tourists can use both red and white light and flash photography while watching the shrimp because it is safe for the shrimp to re-enter the water. The blue arrows represent water velocity.

This study had three aims. First, to understand the perceptions of locals, tourists, and stakeholders toward Shrimp Watching tourism. Second, to generate ideas about how to improve and balance the demands of users and the environment. And, third, to identify the potential factors that might negatively affect the tourism development in this area.

METHODS

Interviews About the Development of Shrimp Watching Tourism in Thailand

We interviewed the director of the Nature and Wildlife Education Center at Ubon Ratchathani who has been responsible for organizing and planning the Shrimp Parading festival since 2012 and other locals in Nam Yuen district where we conducted the survey study. The main interview questions included: (1) How was Shrimp Watching tourism developed?, (2) What is the present management plan? (3) Which locals have participated in this tourism?, and (4) What are the local beliefs and cultures related to the parading shrimp? We summarize the interviews in the results section. Because information regarding the development of Shrimp Watching tourism and the locals understanding about parading shrimp have never been documented, these interviews provide novel information.

Survey Regarding Attitudes of Locals, Tourists, and Stakeholders Toward Shrimp Watching Tourism

Questionnaire Design

Locals, tourists, and stakeholders who are directly involved with an ecotourism industry are key players in conservation and management. Understanding their thoughts about parading shrimp will allow us to develop a sustainable plan for ecotourism management. We conducted a survey using a questionnaire. We constructed the questionnaire following the suggestions from De Vaus (2013; Box 7.2). The questions were designed to mainly understand:

(1) How much do participants know and how concerned are they about parading shrimp?
(2) How much do participants understand ecological, cultural, and economic values of parading shrimp?
(3) How much do the participants know about parading shrimp's threats and their willingness to change their behavior for the shrimp?

We surveyed three main groups: (1) locals, who do not directly profit from ecotourism, (2) tourists, and (3) stakeholders (business owners), who directly profit from ecotourism, such as tourist guides, and local entrepreneurs who work at the tourist site. The questionnaire consisted of four parts. The first part was used to describe the groups and collect demographic data. The second part was used to identify the understanding and basic knowledge of the parading shrimp including concerns about the present status of the parading shrimp population. The third part was used to identify how people valued parading shrimp in terms of economics, environment, and culture. The fourth and final part was used to understand how much people knew about the threats for the parading shrimp and are willing to modify their behavior for the shrimp.

Questions were posed using a 5-point Likert-scale. We tested the reliability and internal consistency of the Likert-scale question with Cronbach's alpha coefficient (Cronbach, 1951). Responses to Likert-scale statements showed an acceptable level of internal consistency (Cronbach's $\alpha = 0.72$) meaning that the multiple Likert-scale questions were reliable. This study provides vital information to help us understand the attitudes toward parading shrimp in three key parties that will ultimately be affected by the development of a sustainable management plan.

Data Collection

We conduct the survey study in September of 2019 at the tourist site in Nam Yuen district, Ubon Ratchathani, Thailand (14° 26′ 07.0″ N; 105 ° 06′ 17.0″ E) and in nine villages nearby the tourism site (**Supplementary Document**). We spent about 3 h interviewing the director of the Nature and Wildlife Education Center at Ubon Ratchathani to learn about the development of Shrimp Watching tourism in Thailand. We spent about 40–60 min interviewing each of three old locals (>40 years) from Nhong Phoad village ($N = 1$) and Kae Don village ($N = 2$). These two villages are the two locations where the shrimp leave the water.

For the questionnaire, we collected data by interviewing each participant in person. Before the interview, we asked for permission from participants and told them about their conditions for participation which were approved by the UCLA Institutional Review Board (Protocol #18-000944). We spent no more than 15 min interviewing each participant. For tourists ($N = 133$), we haphazardly selected subjects before they went to watch the parading shrimp. For, stakeholders ($N = 35$), we interviewed local vendors, tour guides, and hotel staff in Nam Yuen district where the parading shrimp were. For locals ($N = 117$), we went to nine villages located around the tourist site in Nam Yuen district and haphazardly selected 10–13 participants per village to interview. Since most locals spoke neither Thai nor English, we hired local translators to help conduct the interviews.

Data Analysis

We used descriptive statistics to describe the participants' demographic data. For the Likert-scale questions, we used the Kruskal-Wallis test to test for differences in the mean rank of each question among three different study groups (locals, tourists, and stakeholders). We conducted multiple comparisons using a Bonferroni correction which made the new critical p-value = 0.017 (0.05/3). All data analysis were conducted in R 4.0.2 (R Core Team, 2020).

RESULTS

History of Shrimp Watching Tourism Development in Thailand

The Development of Shrimp Watching Tourism

Shrimp Watching tourism (or the Shrimp Parading festival) was first promoted as nature-based tourism under the "Amazing

Thailand" campaign in 1998–1999 when the federal government aimed to stimulate the tourism economy. The former director named the phenomenon of shrimp walking on land "Shrimp Parading" because he thought that this natural phenomenon resembles the parading activity in humans. Since 1999, the director of the Nature and Wildlife Education Center at Ubon Ratchathani has been replaced several times resulting in inconsistent management. However, from 1999 to the present, every management decision for this tourist site has been decided solely by the government staff. Locals and stakeholders have played no role in developing any ecotourism management plan.

What Is the Present Management Plan?

The present management plan (from 2012–present) includes organizing the government staff members to take care of the tourist's safety during the tourist season and educating tourists with information posters about the shrimp parading and how should tourists behave while watching the shrimp. The only management plan that focuses on the mitigation of anthropogenic threats on the shrimp is the prohibition of harvesting the parading shrimp in the tourist site.

Which Locals Have Participated in This Tourism?

From 2012–present, locals and schoolchildren from many villages around the tourist site have been invited to join the opening ceremony of the Shrimp Parading festival. Students have been involved in designing a shrimp mascot costume to represent the environmental issues in that area (**Figure 2B**). Locals who are not students are invited to sell their products (e.g., local fruits, local foods, and textiles) at the tourist site.

Local Beliefs and Cultures Related the Shrimp

Long before 1998, locals knew about the terrestrial shrimp migration. They caught the parading shrimp for food and developed several recipes. One of the most popular is Koi-Kung (Thai: ก้อยกุ้ง), the local traditional Northeastern Thai food which is made from raw shrimp marinated with lime juice (**Figure 4A**). Moreover, older residents believed that the shrimp parade to the headwater in Dângrêk Mountains to worship the Hindu god Vishu (or Phra Narai) (**Figure 4B**). Recently, locals composed a song about the present status and conservation of parading shrimp. Together, these actions illustrate the development of local culture associated with shrimp.

Survey Regarding Attitudes of Locals, Tourists, and Stakeholders Toward Shrimp Watching Tourism

Participants Socio-Demographic Characteristics

Of the 285 survey participants, 182 (63.85%) were women and 103 (36.15%) were men (**Table 1**). Within each group, the sex ratio of the locals was around 1:1 (female: male), while the tourist group was 2:1, and the stakeholder group was 3:1. Most of the participants were between 18 and

TABLE 1 | Socio-demographic characteristics of study participants.

		Tourists *N* = 133	Locals *N* = 117	Stakeholders *N* = 35
Gender	Female	88 (66.2%)	67 (57.3%)	27 (77.1%)
	Male	45 (33.8%)	50 (42.7%)	8 (22.9%)
Age	18–29	36 (27.1%)	34 (29.1%)	12 (34.2%)
	30–39	34 (25.6%)	31 (26.5%)	8 (22.9%)
	40–49	37 (27.8%)	28 (23.9%)	6 (17.1%)
	50–59	20 (15.0%)	15 (12.8%)	8 (22.9%)
	above 60	6 (4.5%)	9 (7.7%)	1 (2.9%)
Education	High school or below	54 (40.6%)	94 (80.3%)	19 (54.3%)
	Undergraduate degree	64 (48.1%)	22 (18.8%)	15 (42.9%)
	Graduate degree	15 (11.3%)	1 (0.9%)	1 (2.9%)

FIGURE 4 | (A) Koi-Kung, a local Northeastern Thai dish, made from parading shrimp. **(B)** Bas relief carving of "Reclining Vishnu Lintel on the Serpent Ananta (Phra Narai Lintel)" carved under the Lam Dom Yai river. This carving can be seen only in the dry season (March –April) when the river dries up. Photo by **(A)** Prapun Traiyasut and **(B)** the Nature and Wildlife Education Center at Ubon Ratchathani.

49 years. In the tourist and stakeholder groups, most of the respondent's highest education was high school (40.6% for tourists and 54.3% for stakeholders) and undergraduate degree (48.1% for tourists and 42.9% for stakeholders), while the majority of local's highest degree was high school (80.3%) (**Table 3**). Participants learned about the parading shrimp from their friends and family (57%), social media (23%), television news (15%), newspapers (3%), and other ways (2%).

How Much Do Participants Know About and Have Concerns for Parading Shrimp?

All three groups of participants felt neutral about their knowledge regarding the parading shrimp, but stakeholders were likely to have more confidence about their knowledge than tourists, and locals ($P < 0.01$; **Table 2** Question 1). They also would like to learn more about the parading shrimp. However, tourists would like to learn more about the parading shrimp than locals ($P < 0.001$; **Table 2** Question 2). Most participants were aware that the parading shrimp population was vulnerable. Nevertheless, tourists and stakeholders were more aware of this vulnerability than locals ($P < 0.01$; **Table 2** Question 4). Overall, locals, tourists, and stakeholders were all very concerned about local extinction (of the parading shrimp ($P > 0.05$; **Table 2** Question 3).

How Much Do Participants Understand Ecological, Cultural, and Economic Values of Parading Shrimp?

All three groups of participants have a fair level of knowledge regarding the roles of the parading shrimp in the freshwater ecosystem (**Table 3**; Questions 1–3). They all believed that the shrimp play potentially important roles in freshwater ecosystems, are part of local cultures, and important to the local economy. However, locals agreed less to this statement than tourists and stakeholders ($P < 0.01$; **Table 3**; Questions 4–6). Locals agreed that shrimp were important for tourism, but when asked about the local economy, locals felt neutral about the role of the shrimp in the local economy (**Table 3**; Questions 6–7). This may reflect the fact that locals have not been actively involved in the shrimp ecotourism, and that they do not economically benefit from this ecotourism.

How Much Do the Participants Know About Parading Shrimp's Threats and How Willing Are They to Change Their Behavior for the Shrimp?

Few interviewees knew about the threats to the parading shrimp, and almost no one knew that tourist's lights were a major threat (**Table 4**). Locals realized that human consumption can harm the shrimp population and trampling on the shrimp might be a threat; by contrast tourists and stakeholders felt neutral about these actions (**Table 4**). Moreover, most participants responded positively toward adjusting their behavior to help the shrimp by staying on the trail or designed areas and not touching the shrimp. They felt neutral about being quiet, not using a personal flashlight, and not using flash photography while watching the shrimp parade (**Table 5**).

DISCUSSION

Invertebrates play several essential roles in ecosystem; however, they are largely ignored by public especially in the ecotourism sector (Huntly et al., 2005). One of the reasons is that they are not charismatic like birds and mammals (Clark and May, 2002). Furthermore, invertebrates have been viewed as an invasive species to humans and usually are eradicated without animal welfare regulation (Clark, 2015). Several efforts have tried to promote invertebrates as flagship species for conservation or as a focus of ecotourism such as marine invertebrates (Veríssimo et al., 2012), local insects (Barua et al., 2012; Schlegel et al., 2015), Queen Alexandra's birdwing (*Ornithoptera alexandrae*) (Cranston, 2010), and fireflies (Fallon et al., 2019; Lewis et al., 2020). However, with few exceptions, the effort has rarely been

TABLE 2 | Summary of participants' knowledge about the parading shrimp, their awareness, and their willingness to learn more about the shrimp.

	Participant	Mean	*SD*	Median	K-W	*p*-value	Pairwise Comparison	*p*-value
Q1. How much do you think you know about the parading shrimp?	Tourist	3.37	1.23	4	26.94	< 0.01*	Local—Stakeholder	< 0.01*
	Local	3.15	0.78	3			Local—Tourist	< 0.01*
	Stakeholder	3.97	0.82	4			Stakeholder—Tourist	< 0.01*
Q2. How much do you want to learn more about the parading shrimp?	Tourist	4.54	0.61	5	9.52	< 0.01*	Local—Stakeholder	0.343
	Local	4.28	0.73	4			Local—Tourist	< 0.01*
	Stakeholder	4.49	0.66	5			Stakeholder—Tourist	1.000
Q3. How do you feel about extinction of parading shrimp?	Tourist	4.38	0.95	5	2.30	0.317		
	Local	4.24	0.96	5				
	Stakeholder	4.43	0.85	5				
Q4. Do you think the population of the parading shrimp is endangered, vulnerable, or least concern?	Tourist	1.64	0.64	2	26.98	< 0.01*	Local—Stakeholder	< 0.01*
	Local	2.06	0.67	2			Local—Tourist	< 0.01*
	Stakeholder	1.60	0.60	2			Stakeholder—Tourist	1.000

Questions 1–3 consisted of five Likert scales (1 = strongly disagree, 3 = neutral, and 5 = totally agree). Question 4 had three choices (1 is least concern, 2 is vulnerable, and 3 is endangered). Asterisks indicate significant (p < 0.05 for KW test and <0.01 for pairwise comparison) results.

TABLE 3 | Summary of participants understanding of the ecological roles and values of the parading shrimp (1 = strongly disagree, 3 = neutral, and 5 = totally agree).

	Participant	Mean	*SD*	Median	K-W	*p*-value	Pairwise Comparison	*p*-value
Q1 Primary food source for aquatic species	Tourist	3.77	0.99	4	20.86	< 0.01*	Local—Stakeholder	0.273
	Local	3.42	0.63	3			Local—Tourist	< 0.01*
	Stakeholder	3.6	0.91	4			Stakeholder—Tourist	0.547
Q2 Help to filter water	Tourist	3.3	0.95	3	13.13	< 0.01*	Local—Stakeholder	< 0.01*
	Local	3.15	0.65	3			Local—Tourist	0.072
	Stakeholder	3.6	0.77	4			Stakeholder—Tourist	0.141
Q3 Help in nutrient recycle	Tourist	3.64	0.99	4	21.73	< 0.01*	Local—Stakeholder	< 0.01*
	Local	3.34	0.65	3			Local—Tourist	< 0.01*
	Stakeholder	3.74	0.56	4			Stakeholder—Tourist	1
Q4 How important are freshwater shrimp for the ecosystem?	Tourist	4.26	0.77	4	47.14	< 0.01*	Local—Stakeholder	< 0.01*
	Local	3.55	0.91	4			Local—Tourist	< 0.01*
	Stakeholder	4.43	0.65	5			Stakeholder—Tourist	0.873
Q5 How important are freshwater shrimp for the local culture?	Tourist	4.07	0.76	4	17.4	< 0.01*	Local—Stakeholder	< 0.01*
	Local	3.71	0.81	4			Local—Tourist	< 0.01*
	Stakeholder	4.11	0.99	4			Stakeholder—Tourist	1
Q6 How important are freshwater shrimp for the local economy?	Tourist	3.93	0.84	4	13.92	< 0.01*	Local—Stakeholder	< 0.01*
	Local	3.67	0.73	4			Local—Tourist	< 0.01*
	Stakeholder	4.11	1.02	4			Stakeholder—Tourist	0.482
Q7 How important are freshwater shrimp for tourism?	Tourist	4.32	0.77	4	6.63	0.036	Local—Stakeholder	0.229
	Local	4.12	0.76	4			Local—Tourist	< 0.01*
	Stakeholder	4.26	0.78	4			Stakeholder—Tourist	0.556

Asterisks indicate significant (p < 0.05 for KW test and <0.01 for pairwise comparison) results.

TABLE 4 | Summary of participant's awareness of the threats to parading shrimp (1 = strongly disagree, 3 = neutral, and 5 = totally agree).

	Participant	Mean	*SD*	Median	K-W	*p*-value	Pairwise Comparison	*p*-value
Tourist's noise	Tourist	2.99	1.23	3	3.36	0.187		
	Local	3.26	0.87	3				
	Stakeholder	3.37	0.88	3				
Human consumption	Tourist	3.50	1.31	4	12.11	< 0.01*	Local—Stakeholder	< 0.01*
	Local	3.93	0.97	4			Local—Tourist	0.054
	Stakeholder	3.23	1.14	3			Stakeholder—Tourist	0.276
Trample	Tourist	3.01	1.25	3	11.16	< 0.01*	Local—Stakeholder	0.062
	Local	3.47	0.96	4			Local—Tourist	< 0.01*
	Stakeholder	3.00	1.03	3			Stakeholder—Tourist	1.000
Light from tourist's flashlight	Tourist	3.35	1.28	3	1.83	0.400		
	Local	3.24	0.90	3				
	Stakeholder	3.34	1.11	3				

Asterisks indicate significant (p < 0.05 for KW test and <0.01 for pairwise comparison) results.

successful. Our research demonstrates that tourists are interested in a small freshwater shrimp that engage in mass migration and thus this is one of few examples of an ecotourism event focused on an invertebrate.

We suggest that these freshwater shrimp in Ubon Ratchathani, Thailand could be used as a flagship species for both ecotourism and conservation. Schlegel et al. (2015) suggest that local insects have the potential to be used as flagship species for conservation in Switzerland. To increase the conservation value, information regarding local insects should be included in primary school curriculum because this is when students pay most attention to their local environment and biodiversity (Lindemann-Matthies, 2006; Jaun-Holderegger, 2012). Therefore, we suggest the educational staff in Ubon Ratchathani create curriculum that uses the parading shrimp and their unique migratory behavior to teach primary school students (Wolff and Skarstein, 2020). This should include information about shrimp biology, their ecological roles, and the roles of shrimp in their local culture and local economy (e.g., through ecotourism).

Following the first publication (in November 2020) that described the Thai parading shrimp, there were a number of high-profile international press reports such as The New

TABLE 5 | Summary of participants' willingness to change their behavior to help the parading shrimp (1 = strongly disagree, 3 = neutral, and 5 = totally agree).

	Participant	Mean	*SD*	Median	K-W	*p*-value	Pairwise Comparison	*p*-value
Q1 Don't use personal flashlight	Tourist	3.62	1.17	4	3.83	0.147		
	Local	3.44	1.03	4				
	Stakeholder	3.37	1.11	4				
Q2 Don't use flash photography	Tourist	3.53	1.16	4	6.07	0.048*	Local—Stakeholder	0.810
	Local	3.32	1.06	4			Local—Tourist	0.027*
	Stakeholder	3.06	1.11	3			Stakeholder—Tourist	0.076
Q3 Only quiet talking while watching them	Tourist	3.90	1.07	4	7.94	0.019*	Local—Stakeholder	0.151
	Local	3.61	1.02	4			Local—Tourist	< 0.01*
	Stakeholder	3.89	0.90	4			Stakeholder—Tourist	0.567
Q4 Don't catch or touch them (observations only)	Tourist	4.34	0.98	5	4.15	0.125		
	Local	4.30	0.67	4				
	Stakeholder	4.40	0.55	4				
Q5 Stay on trails or the place where the ranger staffs organize	Tourist	4.45	0.84	5	0.45	0.797		
	Local	4.47	0.69	5				
	Stakeholder	4.46	0.66	5				

Asterisks indicate significant (p < 0.05 for KW test and <0.01 for pairwise comparison) results.

York Times, National Geographic, and Smithsonian Magazine (Buehler, 2020; Fox, 2020; Preston, 2020). Hence, *Macrobrachium* shrimp might have potential to serve as a flagship species for freshwater conservation since they have relatives on every continent except Antarctica and Europe that engage in similar behavior (Holthuis and Ng, 2010; Hongjamrassilp et al., 2020). More investigation into this is warranted.

Concerns regarding adverse effects of technology on animal-based tourism have increased together with the exponential improvement of technology (Pacheco, 2018; Essen et al., 2020). In our case study, we found that light from flashlight and mobile phones that tourists use force the shrimp to walk back to the river which results in them getting washed downstream. The consequence of this action has not been well-studied but have been hypothesized that the shrimp might end up be eaten by other predators downstream (Hongjamrassilp and Blumstein, under review). (Hongjamrassilp and Blumstein, under review) suggested a solution to mitigate this problem by using red or yellow cellophane as a filter to change the light color. However, technology could also benefit the shrimp if is used properly. Our results show that technology plays role in promoting the parading shrimp. Some 38% of participants heard about the parading shrimp through electronic devices (23% from social media and 15% from news from TV). Moreover, a search using Google Trends looking up the term "กุ้งเดินขบวน (Parading shrimp in Thai)" in Thailand from January to December 2019, revealed that that people search "parading shrimp" the most during the first 2 weeks of the tourist season (i.e., in September) (Google Trends, 2020). Unfortunately, we found no websites that provide correct scientific information about the parading shrimp. Therefore, we suggest that the government should take this opportunity to create an online site that provides information about the shrimp, promotes shrimp ecotourism, and provides sustainable tourism guidelines.

Sustainable ecotourism requires collaboration between private stakeholders and government sectors (Bhuiyan et al., 2011). Moreover, locals' understandings and attitudes toward their resources are key factors to create sustainability (Vincent and Thompson, 2002). Our results indicated that all three main groups in this study (locals, stakeholders, and tourists) were concerned that the shrimp are vulnerable to declines, and that they would like to learn more about the shrimp. Even though they realized that the shrimp are part of the local culture, economy and ecosystem services, their knowledge regarding the roles of shrimp in the freshwater ecosystem was modest. Locals valued the shrimp in terms of culture, economy, and the environment less than tourists and stakeholders. Moreover, most of them did not realize that light from a flashlight is a threat to the shrimp, and they felt neutral toward the plan to reduce the use of personal flashlights to mitigate the effect of tourists on shrimp. We discuss the issues for Shrimp Watching tourism and make suggestions for further management below.

The survey results clearly show that tourists, stakeholders, and locals felt neutral about their knowledge regarding the shrimp. Moreover, they did not know that a key threat to the shrimp comes from the lights used by tourists. These results are not surprising because when the government promoted this Shrimp Watching in 1998–1999, little was known about the fundamental biology of the shrimp and nothing was known about anthropogenic threats to the shrimp. The first study studying parading shrimp biology and their responses to the anthropogenic threats came out in 2020, two decades after this ecotourism event was created (Hongjamrassilp et al., 2020). This Shrimp Watching tourism in Thailand is a case study showing the importance of developing a formal understanding of the effect of anthropogenic impacts on animals to properly manage them.

All three groups in this survey indicated that they were aware of decreasing shrimp populations, and they were willing to learn more about the shrimp. Based on this, we suggest that government managers could reduce anthropogenic disturbances on the parading shrimp by instating targeted educational programs aimed at each of the three participant groups. Tourists and stakeholders directly contact the shrimp and are unaware that light from their flashlights can harm the shrimp. This might be the reason why they felt neutral about the suggestion to do not use a personal flashlight and flash photography while watching the shrimp. However, they agreed to stay on the trail. Therefore, education must be targeted to inform these groups about the negative impacts of the personal flashlight use and flash photography. (Hongjamrassilp and Blumstein, under review) proposed creating three different zones for tourists. Tourists can use their flashlight and flash photography at one of the zones, but not the others. If successful, this plan could minimize the anthropogenic effects while maximizing tourist's desires to see the shrimp.

Sustainable ecotourism requires community members to obtain economic benefits from ecotourism (Vincent and Thompson, 2002; Li, 2006). This means they should first understand and value their natural resources. However, our results suggest that locals not otherwise involved in the ecotourism industry valued the shrimp less than the other two groups. This might be a function of differences in education or differences in economic status. Our results indicate that 80.3% of locals in this study completed their education at the high school level or below, but we do not have data regarding the participant's annual income. In other parts of the world, low education is associated with low socioeconomic status (e.g., American Psychological Association, 2017). Perhaps the neutrality of locals toward the tourism is because they do not obtain enough economic benefits from it. Other research has shown that if locals do not obtain sufficient benefits, it may lead to unsustainable ecotourism (Talsma and Molenbroek, 2012; Thanvisitthpon, 2016). We suggest that the government should support locals by educating them about the economic values of the shrimp and providing key information on how to conserve them. Importantly, however, the government has an important role in stimulating job creation around shrimp ecotourism so as to increase the number of individuals that benefit from it. Doing so may help increase the desire of locals to conserve this remarkable natural phenomenon.

While we have identified key roles for the government in helping to create more sustainable shrimp ecotourism, we recognize that this is a very top-down approach. Top-down management has been shown in other countries to be associated with unsustainable ecotourism (Garrod, 2003; Talsma and Molenbroek, 2012). In Thailand, research has shown top-down tourism development results in unsustainable outcomes and less effective (Ping, (n.d); Connell and Rugendyke, 2008; Muangasame and McKercher, 2015). One of the reasons is that locals do not get enough economic benefit from that tourism (Thanvisitthpon, 2016). On the other hand, creating a more bottom-up management, where locals and stakeholders participate in planning and development, provides an opportunity to improve the likelihood of a sustainable outcome (Middleton, 1997; Kopolratana, 2009; Talsma and Molenbroek, 2012; Theerapappisit, 2012). A case study in Jordan demonstrated that bottom-up approach can lead to sustainable cultural tourism (Jamhawi and Hajahjah, 2017). However, bottom-up approach alone could also lead to several problems. For example, locals sometimes lack of understanding regarding the concept of sustainability and knowledge about their own resources (Victurine, 2000). In our case study, we found that the locals do not really understand about the threats to the shrimp and the importance of the shrimp in environment, cultural, and economy aspects. This can result in ineffective plan development from locals who might want to only use the resource to get benefit for their own but do not aware about next generations. Another example is the issue regarding monopolization of resources. In Thailand, it has been known that the management power in community or ability to access resources is not equally distributed. Instead, it is centralized with local mafia (Shepherd, 2002; Kontogeorgopoulos, 2005) and Tambon Administrative Organization (TAO). People with good connections with the TAO can access more resources than others (Leksakundilok and Hirsch, 2008). Therefore, we suggest that the government should combine bottom-up and top-down approaches whereby the government, acting as the leader, actively involves the local community and stakeholders to plan and manage the tourist site for sustainable use (Wisansing, 2004; Kubickova and Campbell, 2020).

There are a number of issues that should be considered when applying a top-down and bottom-up approach, especially in developing countries. We will discuss two main examples. First, there is a real threat of what is referred to as "pseudo-participation" or "passive participation" (Tosun, 2000; Leksakundilok and Hirsch, 2008). Even though the top-down and bottom-up approach aims to equally involve stakeholders and locals during the process of management plan development, in many cases, stakeholders and locals actually act as consultants rather than participants and their input has not always been used during plan development. This pseudo-participation commonly occurs in many case studies from developing countries (Mowforth and Munt, 1998). Second, there is fear among locals and stakeholders of the authority power, and this impedes active collaboration. For instance, a case study from The Doi Tung Development Project in Thailand shows that when there is conflict of interest, it is difficult for locals to negotiate with authorities because they fear the authority's power (Theerapappisit, 2009). This cultural issue can be observed throughout Thailand and other developing countries such as Cambodia and Indonesia (Cole, 2006; Ellis and Sheridan, 2015; Palmer and Chuamuangphan, 2018). More discussions regarding implementation problems of top-down and bottom-up approach can be seen in Leksakundilok and Hirsch (2008) and Theerapappisit (2009). Governmental officials must be aware of these if they want to have a chance at creating truly sustainable management plans.

We have illustrated, with this case study, how an understanding of the biology of animals as well as an understanding of the people involved in ecotourism are essential for the scientific management of ecotourism and the creation of sustainable tourism. Here we propose a process to create sustainable wildlife ecotourism, which includes integrating top-down and bottom-up approaches (**Figure 5**). While we describe this process generally, it can be applied to manage parading shrimp, and it also could be applied to other targets of ecotourism (including plants and ecosystems). This process involves four steps.

First, as a fundamental step of all conservation and management, it is essential to critically study biology and ecology (e.g., ecological roles) of each focal species (National Research Council, 1992). Often, this will be funded by the government or conducted by government researchers. Combined with this, surveys must be used to develop an understanding of how locals and stakeholders, who have an essential role in sustainable management, value the focal species along three major dimensions: culture, economy, and environment. Their understanding about their resources and their engagement are essential for successful conservation and management (Boiral and Heras-Saizarbitoria, 2017; Sterling et al., 2017). With these data in hand, the government can develop educational materials to ensure all locals and stakeholders have sufficient knowledge about the biology and ecology of the species/ecosystem. Built into this process is evaluation (Treephan et al., 2019), to ensure all locals and stakeholders understand the biological, ecological, and cultural values of the focal animals.

Second, it is essential to identify potential anthropogenic threats and study how these threats affect the focal animals (Tapper, 2006; Blumstein et al., 2017). Again, this will often be funded by the government or conducted by government researchers. With these data, surveys can be used to develop an understanding of the knowledge of locals and stakeholders about these threats. And again, educational materials and evaluation will ensure that locals and stakeholders understand the threats to the species. Depending upon existing knowledge of the system being studied, this process can be combined with the above process. A certificate program, educational program, or exam can be used to screen participants who wish to participate in step 3.

Third, the government, working together with certified locals and stakeholders, can develop a management plan to mitigate the anthropogenic threats on the focal species based on the knowledge of threats generated from targeted research (Wisansing, 2004; Kubickova and Campbell, 2020). This process will likely involve several iterations to ensure that locals and stakeholders support the proposed management actions, and, if

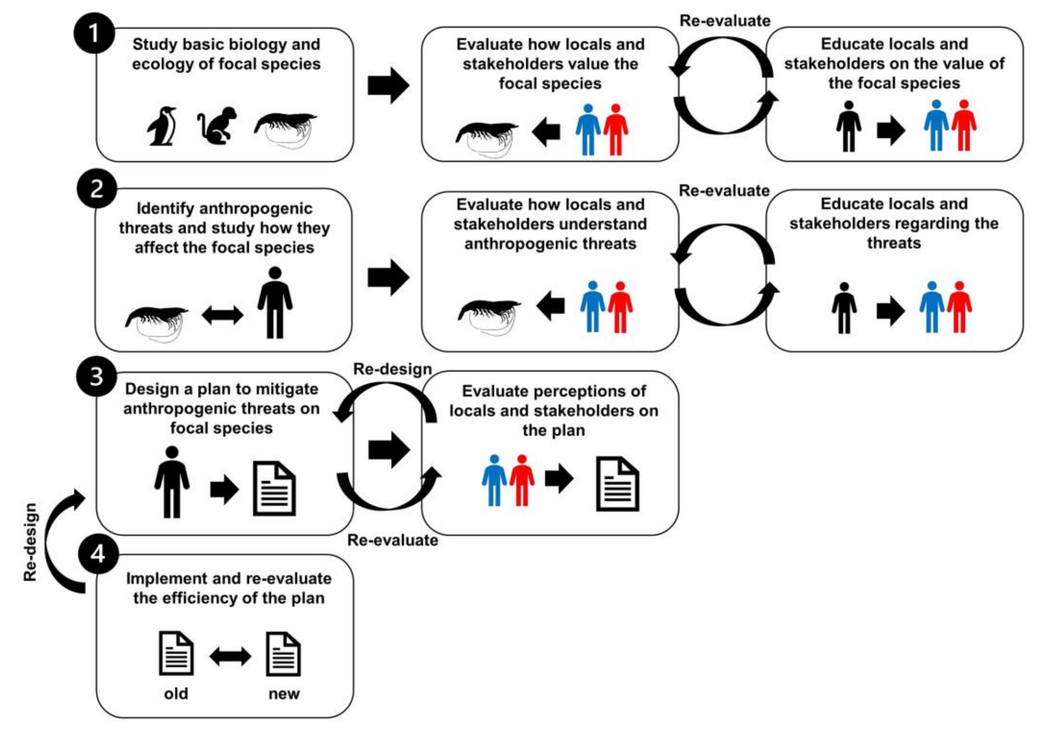

FIGURE 5 | Four-step framework to develop a sustainable wildlife ecotourism management plan. The colors of human symbols represent: (1) black = government staff, (2) red = stakeholders, and (3) blue = locals.

required, the management action have remediations built in so as to not negatively affect the local economy.

Finally, the management plan should be implemented and re-evaluated over time (Salafsky et al., 2001; Higham et al., 2008). If the management plan is not effective in maintaining the biological or ecological resource (e.g., the population of a focal species declines), it should be re-designed with locals and stakeholder input. Throughout, the government is working closely with those who will be most affected by management to generate sustainable management solutions.

By working together, and committing to adaptive management (Holling, 1978; Dreiss et al., 2017), we hope that this spectacular natural phenomenon of shrimp leaving the water is able to entertain and educates future generations of tourists and provides needed resources to this rural Thai economy. Moreover, our suggested management framework could be used to develop a management strategy during developing of a new wildlife ecotourism, especially in developing countries.

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

ETHICS STATEMENT

The studies involving human participants were reviewed and approved by UCLA Institutional Review Board. Written informed consent for participation was not required for this study in accordance with the national legislation and the institutional requirements.

AUTHOR CONTRIBUTIONS

WH and DB designed the study and wrote and edited the manuscript. WH and PT collected survey and interview data. WH analyzed the data. All authors contributed to the article and approved the submitted version.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fcosc.2020.624239/full#supplementary-material

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