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ARTICLE

Chemical cues mediate social monogamy in a marine caridean shrimp, *Lysmata debelius*

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Abstract

To better understand the social monogamy in decapod crustaceans, individual recognition in a socially monogamous shrimp, *Lysmata debelius*, was investigated. We hypothesized that chemical cues play an important role in mediating monogamy, because chemical cues is the primary form of communicaition. To test this, we first examined mate recognition and second tested the presence of chemical cues in individual recognition. The individual recognition to conspecifics of different reproductive statuses was tested in a Y-maze excluding visual cues and tactile cues. Inter-molt and pre-molt euhermaphrodite-phase shrimps served as males and females, respectively. A focal male (cue detector) was placed in the bottom chamber, and two shrimps (cue releasers) of different statuses were placed in the upper two champers, respectively. We find that the focal male spent more time in the front of the chamber holding the paired partner when the other shrimp was not female, and prefered to the female stranger rather than its male partner. Interestingly, when both stranger and partner were females, the focal male actually spent more time in the chamber holding the female stranger. The results indicate that olfactory chemical cues mediate monogamy in *L. debelius* in place of visual cues, and the chemical cues are probably individual specific (i.e. identification odor). The courtship and mating behaviors of *L. debelius* were also reported for the first time. During mating, *L. debelius* displayed no courtship behavior, differing from its sister species, *L. wurdemanni* which live in aggregation, and *L. amboinensis* which live in low denstiy. Combining the previous results in *L. wurdemanni* and *L. amboinensis*, we can conclude that *L. wurdemanni* has the most elaborate precopulatory courtship rituals, *L. amboinesis* has less, and *L. debelius* has none, i.e. the behavioral activity between male and pre- and post-molt female decreases with the population intensity. This behavioral pattern should be sexually selected in different social systems. The present study would enrich our understanding of the evolution of social-dependent behaviors in crustaceans.

Keywords Individual recognition · Chemical cue · *Lysmata debelius* · Monogamy

Introduction

Animals living in different social organizations show diverse social behaviors (Ellis and Free 1964; Cely and Tibbetts 2017). For example, for reproduction, mate recognition initiates mate-searching and mate-guarding behaviors, which are identified as two social-dependent fundamental behaviors in aquatic animals, especially in crustaceans (Seibt 1973; Rufino and Jones 2001; Correa and Thiel 2003; Bauer and Thiel 2011). In decapod crustaceans, species living in high population densities display pure searching, i. e. males frequently encounter other members of the population, checking them for sex and receptivity, and newly molted females are quickly copulated and abandoned, while species with low encounter rates with conspecifics show monogamy or mate-guarding behavior (Zhang and Lin 2004a, b; Bauer and Thiel 2011; Wong and Michiels 2011).

Social animals differentiate familiar group members from strangers depending on individual recognition, which refers to the ability to identify specific individuals (Page and Breed 1987; Meunier et al. 2011; Signorotti et al. 2015; Bagnères

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and Hanus 2015). Reproductive success is greatly depend on the ability of male in recognizing matable females (Andersson 1994; Kvarnemo 2018). Individual recognition of mates is very important for animals that maintain a long-term social bond as well, especially for socially monogamous species. When monogamous individuals encounter conspecifics, rapid discrimination of the mate from a conspecific intruder is crucial to maintaining the pair bond, especially after a period of separation from their mate. Recognition of specific individuals for social interactions (Tibbetts 2002; Mateo 2004; Wiley 2013) has been well documented in various taxa, including many decapod crustaceans (Johnson 1977; Caldwell 1985; Karavanich and Atema 1998; Rahman et al. 2001; Gherardi and Tiedemann 2004; Gherardi et al. 2012; Schoepf and Schradin 2012; Chak et al. 2015).

Individual recognition is initiated by multiple sensory stimuli such as visual, tactile, and chemical cues or through a combination of them, with chemical stimulation is essential to the recognition process in crustaceans (Díaz and Thiel 2004; Chak et al. 2015; Kenison et al. 2018). For example, in *Carcinus maenas*, male crabs recognize mature females through the release of chemical cues from mature females (Bamber and Naylor 1996; Hardege and Terschak 2010). Further the banded coral shrimp *Stenopus hispidus* behaves differently when re-paired with previous mates than with strangers of same sex, size and appearance, the shrimp distinguish strangers from mated conspecifics, indicating that chemical stimuli may be the basis for the recognition (Johnson 1977). Moreover, olfaction has been proved to be the dominant channel in the binary discrimination of a crab, *Pagurus longicarpus,* in comparison to visual sensory (Gherardi and Tiedemann 2004).

Although it has been well known that animals living in different social systems show disparate social behaviors (Cely and Tibbetts 2017), case studies of closely related species is rare (Schoepf and Schradin 2012). The social systems of *Lysmata* shrimp vary from pair-bonded-living to group-living (Bauer 2006), providing a unique opportunity to test social-related behavioral difference in closely related species, which would enrich our understanding of the evolution of social-dependent behaviors in crustaceans.

Species in the genus *Lysmata* are a group of protandric simultaneous hermaphrodites (Bauer and Holt 1998; Fiedler 1998; Bauer 2000; Lin and Zhang 2001; Rhyne and Lin 2006; Baeza 2013). This means a shrimp first matures as a male, then may become a euhermaphrodite during growth. A euhermaphrodite-phase (EP) shrimp with both male and female functions can mate as a female during the small window of the post-molt period as well as a male during inter-molt period (Bauer 2000; Zhang and Lin 2006; Zhang et al. 2012). *Lysmata* shrimp have three distinct ecological characteristics that correspond to their social behavior. In *Lysmata*, most species are group-living (e.g., *L. wurdemanni* may aggregate in large numbers of more than several hundred shrimps), two species (*L. amboinensis* and *L. graham*) live in low density in small groups or even social monogamy, and one (*L. debelius*) is a pair-living species (Fiedler 1998; Bauer 2002; Zhang et al. 2007). Males make frequent contact with females in the group living species, displaying pure searching and active courtship behavior prior to the female molting, thus males are unlikely to defend or guard a pre-molt female (Correa and Thiel 2003; Zhang and Lin 2006; Zhang et al. 2007). The low-density-living species *L. amboinensis* is inactive in the precopulatory search (Fletcher et al. 1995; Zhang et al. 2007; Wong and Michiels 2011). Chemical signals involved in mate recognition of *L. wurdemanni*, a group living species, have been demonstrated (Zhang and Lin 2006; Zhang et al. 2010a, b, 2011). Although we still do not know the mating behavior of *L. debelius*, we believe that chemical cues play a key role in mate recognition, in this socially monogamous species.

The fire shrimp *L. debelius*, native to the Indo-Pacific reefs, exhibits a mutualism as the "cleaner shrimp" of many reef-dwelling fishes (Palmtag and Holt 2007). This unique biological characteristic of the species is the formation of long-term pair bond, as in *S. hispidus* (Johnson 1977) and *Hymeoncera picta* (Wickler 1973). *Lysmata debelius* is aggressive to unfamiliar conspecifics but tolerate their partners (Rufino and Jones 2001), so we hypothesized that the species can distinguish their partner from a stranger. This means that the monogamous species, *L. debelius*, has evolved a mechanism to distinguish the paired partner from conspecific intruders. However, the cues involved in the individual recognition is unclear as visual, chemical, and tactile cues were not separated (Rufino and Jones 2001). Typically, olfactory communication is particularly important to solitary-living species (Wyatt 2014). Therefore, we further hypothesized that rather than visual and tactile cues, olfactory chemical cues are predominantly involved on individual recognition of *L. debelius*. To completely understand mate recognition in the fire shimp, *L. debelius*, mating behavior was investigated in the present study as well.

To better understand the evolution of individual recognition driven by social environments in the genus *Lysmata*, we used the socially monogamy shrimp, *L. debelius,* as a model species. Previous observations have been made in *L. wurdemanni* and *L. amboinensis* (Zhang and Lin 2006; Zhang et al. 2007; Wong and Michiels 2011), therefore comparing socially related behaviors in sister species with different mating systems will be invaluable. In order to understand the factors mediating the social monogamy in *L. debelius*, we investigated the role of chemical cues in individual recognition of the fire shrimp during different stages, including intermolt and reproductive molt periods (i.e. mate recognition), courtship and subsequent copulation behaviors of this species were described for the first time in the present study.

Material and methods

Animals

The present study was conducted in the Qionghai Research Center of the East China Sea Fisheries Research Institute, Hainan, China. The fire shrimp, *L. debelius*, ranging from 4.0 to 5.6 cm in total length (TL), were purchased from a local ornamental store. Euhermaphrodite-phase (EP) shrimps of similar size were randomly paired in aquaria (60 × 58 × 33 cm) of a recirculating system. The shrimps were fed adult *Artemia* twice per day. The photoperiod, water temperature, and salinity were 14 h light:10 h dark, 25-26 °C, and 32‰, respectively. No shrimps were repeatedly used for either recognition tests or mating behavior observation. Pre-molt EP shrimp (female role) are simplified as female, and inter-molt EP shrimp (male role) are simplified as male.

Familiarity recognition in *L. debelius*

Assays were used to exclude visual cues involved in the individual recognition in the fire shrimp. The assays were conducted in the aquaria (60 × 58 × 33 cm) where the shrimps were paired for at least 2 weeks. Only male shrimps were used for the assays. One of a paired shrimp (referred to as partner) was moved into an empty tank, and the focal shrimp, termed "resident", remained in the home aquarium. Thereafter, a stranger or "intruder" was introduced into the home aquarium. The total length of the strangers and the residents differed within 1 mm. After recording, the stranger was returned to its original aquarium, and the partner was re-introduced into the home aquarium immediately. The conspecific was placed at a point at least 33 cm away from the resident shrimp. Behavioral interaction between the resident shrimp and its conspecific was recorded using a video camera (Sony PJ670, Japan). To exclude visual cues, videos were taken under a red light of 0.4–3.2 lx (measured with an illuminator, TES-1334A, China). A total of 15 resident shrimps were tested, each shrimp was used once. The interaction between the resident shrimp and stranger or partner was recorded for 30 min following introduction because severe aggression between the resident shrimp and stranger usually occurred within the first 30 min in the preliminary tests. To avoid mortality, observations were terminated if the resident shrimp or stranger was attacked more than three times within the 30 min. The time interval from the introduction of the stranger or partner to the first antenna/antennule contact between the resident shrimp and the stranger or partner was recorded. A dependent *t*-test was employed to compare the two intervals. The strangers were not used as resident animals in other trials.

Four distinguished behaviors were observed and defined as according to interaction intensity between two shrimps. First, wander: one shrimp wandered around in the tank without any contact or interaction with the other one. Second, avoidance: when one shrimp moved to a distance of two antennae/antennules from the other one, it avoided to meet the other shrimp who showed no response. The two shrimps may have had antenna/antennule contact with each other. Third, threat: when two shrimps met after antenna/antennule contact, one raised up its chelipeds, and the other one retreated. Last, aggression: one shrimp raised up its chelipeds and approached to the other one rapidly, followed by mutual fighting. Usually, wander was only observed about 30 min after the stranger or the partner was introduced; once contact between the resident and the stranger or the partner occurred, avoidance, threat, or aggression usually followed.

Chemical cues in individual recognition in *L. debelius*

To test whether chemical cues were involved in individual recognition in the fire shrimp, a Y-maze was designed to evaluate the response of male shrimp to his partner and a stranger (Fig. 1). A separation net was placed at the entrances of both chambers A and B to prevent physical contact. The mesh size of separation net is smaller than the shrimp's appendages so they cannot poke their legs or antennae into the other chamber. An air stone was placed in the end of chamber A or B to create gentle aeration, helping any chemical cues to diffuse. Moreover, a mild water flow was produced by dropping fresh seawater (3 liters/h) to chamber A and B, respectively, ensuring that any chemical cues released by the shrimps in chamber A and B would be slowly transported to chamber C.

The trial included four tests: recognition of a male stranger and his male partner by male, recognition of a female stranger and his male partner by male, recognition of a male stranger and his female partner by male, and recognition of a female stranger and his female partner by male. Each test had 15 observations.

For each test, a bonded pair and one stranger from another bonded pair were transferred from their holding tanks to the Y-maze tank containing 8-liter fresh seawater. The stranger and partner were randomly placed in either chamber A or B, the focal test male (termed focal male) was placed in chamber C. Since the fire shrimp molt at night, all tests were conducted at night. The reproductive status of female shrimps was identified based on molt cycle which is stable at a constant temperature. Shrimps 4–5 days after molting were used as focal male (i.e. cue detector) and male partner or stranger (cue releasers).

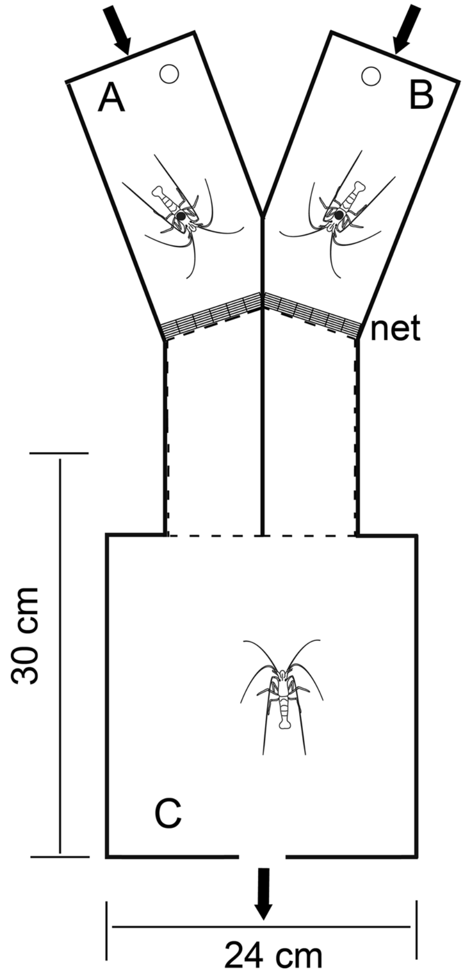

Fig. 1 Y maze designed to evaluate the preference of male *Lysmata debelius* to his partner and the stranger. The pre-molt or inter-molt stranger and partner were placed in chamber A and B randomly. The resident was placed in the distal side of chamber C. Time of the male shrimp stayed in the areas marked with dash lines was analyzed, respectively. Circles represent aeration stones in chamber A and B during the experiments. Arrows represent the water flow direction. Each trail had 15 replicates

The preliminary experiments showed that focal males often wandered around in the maze in the first 30 min after being transferred into the maze, so each focal male was acclimated for 30 min prior to the introduction of the other shrimps. Fifteen replicates were conducted for each test. Behaviors of the focal males were recorded with a video camera (Sony PJ670, Japan) under a red light of 0.4–3.2 lx.

The fire shrimp generally molted between 23:00 and 5:00 and based on the preliminary observations, males displayed behaviors towards female shrimps only during the three hours prior to female molting, hence we recorded at least eleven hours from 19:00 to 6:00. Thus, we analyzed the focal male's behaviors during the first three hours after the introduction of the male stranger and his male partner. For the test with a female shrimp, either stranger or his partner, we observed the behaviors up to post-molt and analyzed the focal male's behaviors three hours prior to each female molting. In the test with a female stranger and his female partner, the focal males preferred the strangers regardless which one molted first (see Results), thus the influence of molting sequence was not a factor. We analyzed the focal males' behaviors three hours prior to each female molting.

Preference or responsiveness of the male was presented with the percentage of time spent in certain areas marked with dashed lines in the front of chamber A or B, respectively (Fig. 1). The focal males that stayed in front of the net (Fig. 1) heading towards chamber A or B for more than 10 s was defined as "stay". During the observation period (3hrs), the time that the male spent in the front of chamber A and B was defined as "stay in chamber A" and "stay in chamber B", respectively. The time spent at neither A or B was excluded.

To eliminate any type of Y-maze effect, a no-choice test was performed prior to the test described above. The focal male was placed in chamber C, then the conditioned water with a male stranger, his male partner, a female stranger, and his female partner was drained into chamber A and B at the same time at an approximate rate of 3 liters/h, respectively. Each type of conditioned water was tested 15 times. To prepare the conditioned water, for male, a male shrimp was placed a container containing 3L seawater for 1 h, and for female, a female shrimp was conditioned in the container up to the female molting. Results indicate that percentage of time the focal male spent at chamber A or chamber B did not differ significantly from each other (Dependent *t*-test, male stranger: chamber A 1960.00 ± 541.00 s, chamber B 1580.00 ± 729.19 s, $t = 0.576$, $df = 14$, $p = 0.623$; male partner: chamber A 2939.25 ± 2373.10 s, chamber B 1585.50 ± 937.76 s, $t = 1.187$, $df = 14$, $p = 0.321$. female stranger: chamber A 1788.00 ± 654.68 s, chamber B 2141.00 ± 874.98 s, $t = 0.505$, $df = 14$, $p = 0.664$; female partner: chamber A 1874.00 ± 1006.56 s, chamber B 1986.00 ± 700.54 s, $t = 0.141$, $df = 14$, $p = 0.90$).

Mating behavior

Fifteen pairs of shrimps were used for the observation. Female shrimps usually molt within 24 hrs after hatching and the molt cycle of female shrimps is about 20 days at 25°C (personal observation). Newly molted EP shrimps are receptive to mate as female for several hours at most. The EP shrimps function as male during inter-molt. Hence, the mating timing is determined based on the molt cycle. Mating behaviors were observed in aquaria (60 × 58 × 33 cm) holding individual pairs. The mating process was recorded with a video camera under a red light of 0.4–3.2 lx. Mating behavior was analyzed based on video clips.

Statistical analysis

All data were expressed as mean ± SD. Normality of the data was evaluated using Kolmogorov–Smirnov test and the homogeneity of variances was assessed using Levene's test with the SPSS statistical software (version 19.0, Chicago, IL, USA). A dependent *t*-test was performed to compare the time the male spent on different targets.

Results

Familiarity recognition in *L. debelius*

The resident, the stranger, and the partner all showed wandering behavior, however, this occurred mostly with the residents. Avoidance and threat behaviors only occurred in the strangers (3/15). Aggression never occurred between the residents and their partners (0/15), but the resident shrimps always fought with the strangers (15/15). The resident shrimps approached the strangers 44–900 s (272.6 ± 64.8 s, $n = 15$) after introduction. For the partners, it took 9–848 s (192.3 ± 55.7 s, $n = 15$) for the first approach. There was no significant difference between the times that it took the residents to make first approach with the strangers versus the partners after their introduction (Dependent *t*-test, $t = 0.893$, $df = 14$, $p = 0.379$).

Chemical cues in individual recognition in *L. debelius*

The focal males spent significantly more time in front of the male partners' chambers (3813.26 ± 1917.30 s) than those of the male strangers (2501.16 ± 1766.06 s) (Dependent *t*-test, $t = 1.767$, $p = 0.049$, $df = 14$) (Fig. 2). In contrast, the focal males spent significantly more time in the front of the chamber holding the female strangers (5044.28 ± 3734.64 s) than those of the male partners (2260.49 ± 1628.21 s) (Dependent *t*-test, $t = 2.233$, $p = 0.042$, $df = 14$) (Fig. 2). When their partners was close to the parturial molt, the focal males spent same amount of time in the front of the chamber holding their female partners (3305.32 ± 2472.63 s) as those of the male strangers (2696.54 ± 1570.93 s), there was no significant difference in statistic (Dependent *t*-test, $t = 0.674$, $p = 0.511$, $df = 14$) (Fig. 2). When both shrimps (partner and stranger) were close to the parturial molt, the focal males always preferred to stay in the front of the stranger's chamber regardless which shrimp molted first. The focal males spent significantly more time in the front of the female strangers' chamber (4698.35 ± 3475.87 s) than those of the female partners (1538.14 ± 1928.66 s) (Dependent *t*-test, $t = 2.929$, $p = 0.01$, $df = 14$) (Fig. 2)

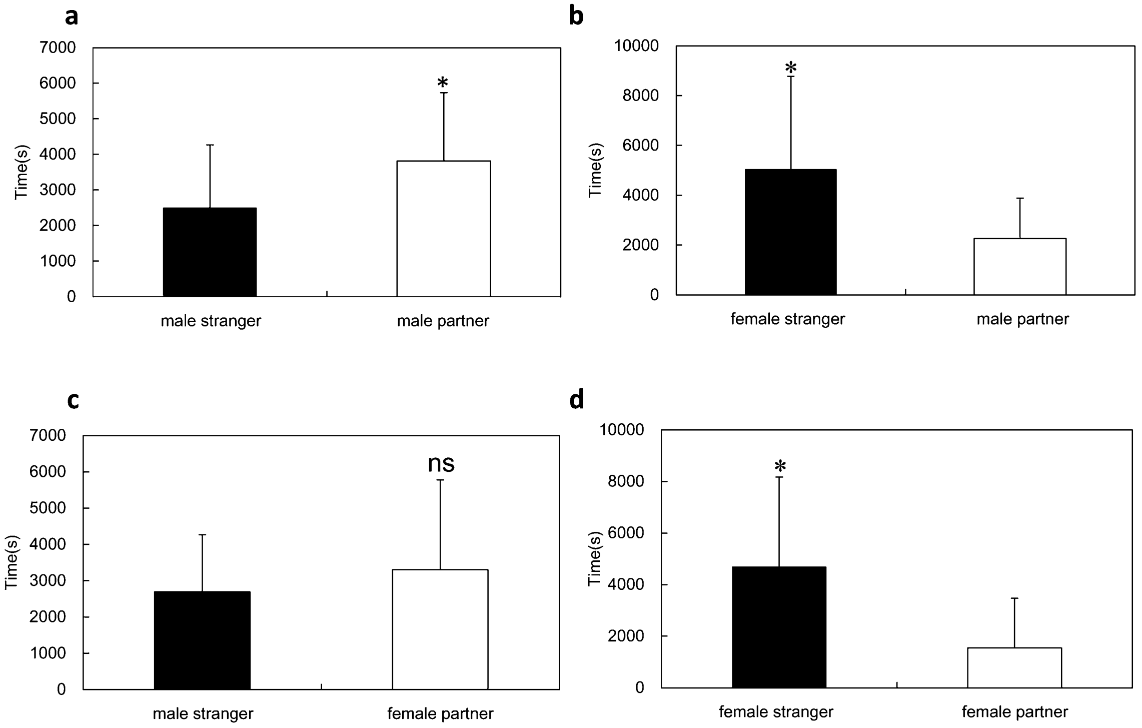

Fig. 2 Time of male shrimp of a pair *Lysmata debelius* spent in the front of the chambers holding a stranger or its partner at different molt stages. Asterisk represents significant difference ($p < 0.05$), ns = not significant ($p > 0.05$). A depedent *t*-test was applied

Mating behavior of *L. debelius*

Prior to the female molting, the male did not display any courtship behaviors such as approach or follow as displayed in the *L. wurdemanni*, an aggregation species (Zhang and Lin 2006). Generally, the male and female stayed together in the aquarium prior to the female molting. However, the male remained 2–8 times the total length of the shrimp from the inactive female, especially 1–3 min prior to the female molting. No interaction between the male and female was observed during the molting period. The female wandered slowly in the tank after molting. When the newly molted female approached the male with antenna/antennule contact, the male would slowly follow the female. The male displayed following behavior 26–168 s post-molt, then tried to copulate with the newly molted female. Once the female stood with its abdomen raised, the male held the female and brought its ventral surfaces into contact. After grasping the female head to head, copulation then occurred, lasting for 1–7 s, during which the spermatophore was transferred from male to female. The female spawned at 3–8 h post-molt. The newly molted female might also jump away to reject the approacheding male in a failed copulation attempt. In four of the fifteen cases, the males failed to copulate with the females, which then typically released unfertilized eggs after several days.

Discussion

As a monogamous species, a paired *L. debelius* always attacked conspecific intruders. They behaved differently when facing a stranger or its partner in different molt statuses, indicating not only that *L. debelius* was able to distinguish familiar partner from unfamiliar stranger but they can also identify molting status as in many other decapod crustaceans (Chak et al. 2015). There was no obvious courtship behavior during the mating process, which is distinctively different from its sister species, *L. wurdemanni,* which have elaborate courtship behaviors such as pure searching. The results suggest that chemical cues play a key role in the individual recognition and mediation of social monogamy in the fire shrimp, *L. debelius*.

Individual recognition and mediation of social monogamy

Our study confirmed that male-role *L. debelius* preferred to stay with their partners when both EP shrimps were at inter-molt phase, which was previously reported by Rufino and Jones (2001). Therefore, our data suggest that the pair-bonded members have the ability to remember familiar mates. Similarly, the pair-living banded coral shrimp *S. hispidus* can discriminate familiar conspecifics from unfamiliar ones (Johnson 1977).

In decapod crustaceans, chemical and visual cues are involved in conspecific recognition (Chak et al. 2015). In *Homarus americanus*, individual recognition and memory are based on the olfactory perception of the urine (Karavanich and Atema 1998). A finding in the hermit crab *P. longicarpus* also shows that individuals were more agonistic when exposed to the odor of their unfamiliar conspecifics than to that of familiar conspecifics (Gherardi and Tiedemann 2004). In the present study, the resident shrimp displayed aggressive behavior towards the stranger but not the partner under a weak red light, suggesting that *L. debelius* does not depend on visual cues to recognize conspecifics. The Y-maze test without physical contact suggests that soluble chemical cues are essential to conspecific recognition in the fire shrimp.

In the Y-maze test, the focal male preferred its partner when both shrimps at chamber A and B were males, but it preferred female stranger regardless of the partner's molt stages when shrimps at chamber A and B were female stranger and its partner. The results suggest there may be two kinds of chemical cues or signals involved, one being a distance sex pheromone secreted only by the female shrimp and another one is for individual recognition ("identification odor"). For the case with the female stranger and male partner, the effect of sex pheromone secreted by the female stranger might be stronger than the cue released by the male partner which is used for individual recognition. When both stranger and partner were females, interestingly, the focal male spent much more time in the front of the chamber holding the female stranger, regardless which one molted earlier. There are two possible causes for the behavior. First, the pre-molt stranger might have released more distance sexual pheromone when it felt its partner was absent. Second, the identification odor that an individual fire shrimp releases is unique to familiarize its partner, as in the hermit crabs *P. longicarpus* (Gherardi and Tiedemann 2004) and *S. hispidus* (Johnson 1977). Obviously, a unique identification odor benefits to maintain a pair bond. Hence, the fact that the focal male spent much more time in the front of the chamber holding the female stranger than that of the female partner might suggest a defense response; since we observed that males intended to fight with newly-molted strangers but not its newly-molted partner. In the other word, mate-guarading should be a prerequisite ability for pair-bonding.

Chemical cues are involved in mate recognition in many decapod crustaceans (Atema 1984; Atema 1995; Kelly et al. 1998; Zhang and Lin 2006; Zhang et al. 2010a, b). In *L. wurdemanni*, behavioral and chemical evidence indicates that both distance and contact pheromones are involved in precopulatory and copulatory behaviors (Zhang and Lin 2006; Zhang et al. 2010a, b). Although it is difficult to conclude that chemical cues are involved in the pre-copulatory period of the *L. debelius* based on the pre-copulatory behavior, the Y-maze tests clearly indicated that waterborne cues are released by the pre-molt female shrimp. The male spent a significant amount more time in front of chamber holding the pre-molt female compared to an inter-molt male. Additionally, we have recently characterized the distance pheromone in the male *L. debelius* (unpublished data). The male did not respond quickly to the newly molted female as in the male *L. wurdemanni,* where copulation immediately occurred once a female molted. However, contact pheromones should contribute to the recognition on the post-molt female the same as in the *L. wurdemanni* according to the post-molt behaviors (Zhang et al. 2011).

Mate recognition in *Lysmata* shrimps with different socal structures

The male *L. debelius* did not display any courtship behavior, such as approaching, following, and chasing the pre-molt female shrimp, which are regular behaviors in the *L. wurdemanni* (Zhang and Lin 2004b; Zhang and Lin 2006), which live in high population densities. Moreover, the male did not actively interact with the newly molted female shrimp. Comparing three species of *Lysmata* shrimps (i.e. the gregarious *L. wurdemanni*, the low density species *L. amboinensis*, and the pair-living *L. debelius*) with different social systems, the response intensity of male to pre- and post-molt female decreases with population intensity, i.e. *L. wurdemanni* > *L. amboinensis* > *L. debelius*. Most likely, this behavioral pattern is shaped by social systems with different intensities of mate competitions (e.g. reviewed by Alcock 2001).

In monogamous species, such as *L. debelius*, the lack of competition from other males might eliminate the need for pre-copulatory behavior (Zhang et al. 2007) as shown by their inactive courtship before mating. A similar mating process was reported in the pair-living *Heptacarpus paludicola* (Bauer 1979). Although a generic association between mating behavior and social environment has been inferred based on data collected from different taxa (e.g. reviewed by Alcock 2001), the present study, combined with the previous work on its sister species, provides a clearer profile of the social-related behavior.

Behavioral differences among species in the genus *Lysmata* might be sexually selected. Two elements, male–male competition and mate choice, are involved in sexual selection (Anderson 1994). Among males, mating success greatly depends on their ability to monopolize resources needed by the females for mating and the ability to recognize matable females (Anderson 1994). In the pure search system, male mating success depends primarily on their ability to find and mate with as many receptive females as possible. Hence, the aggregation species (e.g. *L. wurdemanni*) with the pure search system must have elaborate pre-copulatory behaviors. However, in the monogamous fire shrimp with low mate opportunity, the ability of discriminating their mate partners from strangers and mutual mate-guarding evolved (Kvarnemo 2018).

In *L. wurdemanni*, male pre-copulatory behavior and mating success were closely associated with the number of aesthetascs, chemical sensors for detecting waterborne signals, in the antennules (Zhang et al. 2008). Individuals with a higher number of aesthetascs started approaching/searching females earlier and had higher mating success than ones with lower numbers (Zhu et al. 2012). Furthermore, the number of aesthetascs was greater in group-living species (*L. boggessi* and *L. wurdemanni*) than in the pair-living *L. debelius* (Zhang et al. 2008; Zhu et al. 2012). Hence the inactiveness of *L. debelius* during the mating process may correspond to fewer aesthetascs than in the *L. wurdemanni*, further suggesting that the social environment is a major force to shape the behavior.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethics approval and consent to participate Ethical approval and consent to participate were not required for this work.

Consent for publication Not applicable.

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