Males display “inverse rapping” as a mating behavior to receptive females in the hermit crab

*Pagurus nigrofascia*

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**Abstract:** This paper describes “inverse rapping” as a characteristic mating behavior in *Pagurus nigrofascia*. The behavior involves one hermit crab pulling another crab’s shell towards itself causing the shells to hit against each other. This is the first evidence that males perform inverse rapping as a mating behavior in a *Pagurus* species. Two experiments were conducted to describe the inverse rapping in detail and to discuss its function. In Experiment A, we clarified when (mating season or non-mating season) and to whom (males or females) males displayed this behavior. A focal male that had not been guarding in the field was placed together with another crab and their interaction was observed, especially inverse rapping. Males showed inverse rapping mainly with a female that was close to copulation in the mating season, especially when the male guarded the female. In Experiment B, we examined the female’s response to male inverse rapping and tested the effect of the presence of a neighboring conspecific on the occurrence of the behavior. Most females reduced struggling and/or withdrew into their shells in response to male inverse rapping. The presence of neighboring crabs did not affect inverse rapping. Our findings suggest that inverse rapping is a mating behavior in *P. nigrofascia*, and that inverse rapping may benefit males in the initiation and/or continuation of precopulatory guarding because it can help to restrain struggling females. This behavior has not been observed in other sympatric *Pagurus* species and appears to be a characteristic mating behavior of *P. nigrofascia*.

**Key words:** hermit crab, inverse rapping, mating behavior, *Pagurus nigrofascia*, sexual conflict

**Introduction**

Mating behavior plays an important role in attracting, selecting, and guarding potential mates in sexually reproducing species (Pinheiro & Fransozo 1999; Anthes & Michiels 2007; Thiel & Duffy 2007). Patterns of mating behavior comprise both common patterns shared among related species and species-characteristic patterns. Examples of common patterns include territory defense, mate guarding, and posturing during copulation, and such behaviors would be functional and/or essential for reproduction due to various constraints such as habitat, medium (i.e., in water or air), and body plan. In contrast, species-characteristic patterns can play roles in signaling conspecific identity, genetic quality, or physical conditions of the signalers to potential mates in the context of mate choice, and/or maneuvering potential mates in the context of sexual conflict. For example, mounting a female’s shell is a common feature of the mating behavior of males in littorinid snails (Saltin 2013; Ng & Williams 2015). While males in many ocypodid crabs perform a waving display with their chelipeds, which are raised and lowered to attract females for mating (Crane 1975; Moriito & Wada 2000), species-characteristic features of the display could help females to distinguish conspecific males from those of other species (Crane 1975; Salmon et al. 1978; Detto et al. 2006; Kitaura & Wada 2006). Kitaura & Wada (2006) demonstrated that the waving display of male *Ilyoplax pacifica* clearly differs from that of two morphologically similar species, *I. orientalis* (De Man, 1888) and *I. tansuiensis* Sakai, 1939.

A common feature of the mating behavior of male *Pagurus* hermit crabs is their precopulatory guarding behavior. In this behavior, the male grasps the rim of a gastropod
In a previous study on the mating behavior of *P. nigrofascia* Komai, 1996 (Kido et al. 2019), we found unique behavior in males during the mating season (URL for video given in Table 1). Since this behavior has not been observed in other sympatric *Pagurus* species, namely *P. filholi* (de Man, 1887); *P. mидendorfii Brandt, 1851; *P. lanuginosus* de Haan, 1849; *P. proximus* Komai, 2000; and *P. minutus* Hess, 1865, it is likely a species-specific characteristic of *P. nigrofascia*. This behavior might be the “inverse rapping” described by Hazlett in several hermit crabs (Hazlett 1966, 1972, 1989). In inverse rapping, after a focal hermit crab grasps the shell occupied by another crab, the focal crab extends its body out and pulls the other crab toward itself as the focal crab withdraws into its shell with its abdomen and/or ambulatory legs bent as it holds the shell of the other crab with its ambulatory legs. The shells hit against each other, creating a rapping sound. Hazlett (1989) observed in the hermit crab Clibanarius zebra (Dana, 1852) that the frequency of inverse rapping was higher in successful pairs than unsuccessful pairs and suggested that the male’s inverse rapping might be a precopulatory ritualized behavior of this species. However, there is an alternative hypothesis for the function of inverse rapping—an attacking behavior during shell fights. Hermit crabs perform “shell fighting” over the ownership of empty gastropod shells (Hazlett 1980; Elwood & Neil 1992; Briffa et al. 1998), where the attacker hits its shell many times in a series of boat against the defender’s shell (shell rapping behavior). This behavior has been observed in both the males and females of *P. nigrofascia* (URL for video given in Table 1). Inverse rapping in *P. nigrofascia* may be an action of shell rapping behavior, because Hazlett (1966, 1980) observed inverse rapping in *P. impressus* (Benedict, 1892) and *Anisopagurus pygmaeus* (Bouvier, 1918) (formerly *Pagurus pygmaeus* Bouvier) during shell fighting. Although we did not observe inverse rapping by *P. nigrofascia* females, the sexual behavioral difference might be related to sexual differences in aggression during shell fights (Yoshino & Goshima 2002).

In this study, we examine two hypotheses to explain the inverse rapping behavior of *P. nigrofascia*: (1) mating behavior, and/or (2) shell fighting behavior. We describe the inverse rapping of *P. nigrofascia* in detail, clarify the conditions when males show the behavior and to whom, and compare inverse rapping with shell rapping in this species. To determine the function of inverse rapping, we further examine the response of the other crab to inverse rapping and the effect of a neighboring conspecific on the occurrence of this behavior.

**Materials and Methods**

*Pagurus nigrofascia* is distributed mainly along intertidal rocky shores of Japan, Korea, and China (Komai 1996; Jung et al. 2018; Gong et al. 2019). Hermit crabs used in this study were collected at Kattoshi, on the southwest side of Hakodate Bay, Hokkaido, Japan (41°44′N, 140°36′E). The mating season at this site is from late April to early June (Goshima et al. 1996). During the mating season, males show precopulatory guarding behavior (Suzuki et al. 2012). Females breed once a year after prenuptial molting (Suzuki et al. 2012) and release larvae in the February of the following year (Goshima et al. 1996).

**Experiment A: Conditions under which males show inverse rapping**

To identify the conditions of inverse rapping occurrence, the behavioral interactions between a focal male and an-

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**Table 1.** List of focal male behaviors in the hermit crab *Pagurus nigrofascia*. See also supplementary materials.

| Behavior       | Description                                                                 | Video URL                       |
|----------------|-----------------------------------------------------------------------------|---------------------------------|
| Guarding       | Grasping the rim of the shell of an opponent with its minor (left) cheliped | https://youtu.be/5e27mpwMOgY    |
| Shell fighting | It was consisted with rocking and rapping. Shell rocking usually preceded shell rapping. |                                |
|                | Rocking: Rocking the opponent’s shell around its columnellar axis several times using both chelipeds and ambulatory legs |                                |
|                | Rapping: Holding the opponent’s shell, with facing each other, by steadying with ambulatory legs, and hitting quickly and repeatedly against the opponent’s shell by moving own shell |                                |
| Inverse rapping| Holding the shell occupied by another crab, usually from behind the crab, by steadying with ambulatory legs and hitting its shell once or several times by pulls toward own shell by the movement of abdomen and/or the flexion of ambulatory legs. This behavior did not include Rocking before hitting shell, as in shell fighting. | https://youtu.be/6KqsLsOwrLw    |

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Shell fighting: Guarding Grasping the rim of the shell of an opponent with its minor left cheliped

Inverse rapping: Holding the shell occupied by another crab, usually from behind the crab, by steadying with ambulatory legs and hitting its shell once or several times by pulls toward own shell by the movement of abdomen and/or the flexion of ambulatory legs. This behavior did not include Rocking before hitting shell, as in shell fighting.

*See also supplementary materials.*
other crab were observed during three periods: (1) pre-mating period (March 31 to April 6, 2018); (2) mating period (April 13 to May 24, 2017 and April 14 to May 27, 2018); and (3) post-mating period (November 5 to December 20, 2018). Hermit crabs that were either solitary or in precopulatory guarding pairs were collected at Kattoshi, and each solitary crab or pair was placed in a small vinyl pouch with some seawater while in the field. The crabs were then brought to the laboratory, where each guarding pair or solitary crab was individually placed in a small container (13×9×7 cm) with some natural seawater (approximately 2.5 cm deep) for about an hour. Using a stereomicroscope, solitary crabs were sexed based on the developmental level of the first pleopod, and females were checked to determine if they were carrying eggs on their pleopods. Individuals that were injured and/or missing any chelipeds or pereopods were not used in the experiment.

Females collected during the mating period were categorized into three types: (1) NG-female, females that had not been guarded by males in the field, thus they were solitary and non-ovigerous females; (2) G-female, non-ovigerous females that had been guarded by males; and (3) OV-female, solitary, ovigerous females. This species spawns about an hour. Using a stereomicroscope, solitary crabs were sexed based on the developmental level of the first pleopod, and females were checked to determine if they were carrying eggs on their pleopods. Individuals that were injured and/or missing any chelipeds or pereopods were not used in the experiment.

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Solitary males were used as focal individuals. In each trial, a focal male was placed in a corner of an experimental container (16×12×8 cm) with natural seawater (approximately 3.5 cm deep), and then another crab (male or female) was placed in the opposite corner. During the pre-mating period, each focal male encountered either a solitary male or a solitary female (Table 2). In the mating period, each focal male encountered either a solitary male, an NG-female, a G-female, or an OV-female (Table 2). In the post-mating period, each focal male encountered either a solitary male or a solitary female (Table 2). Each trial was recorded for 30 min with a digital camera (DMC-LF1, LUMIX) or video camera (GZ-R400T, JVC). All individuals were used once in the experiments.

We recorded whether the focal males performed any of the following three behaviors: guarding, shell fighting (rocking and shell rapping), and inverse rapping (Table 1). When inverse rapping was observed, we counted the number of inverse raps in a bout, where the male continued the posture of inverse rapping without interruption with other actions, such as rotating another crab’s shell and palpating the crab with his chelipeds and ambulatory legs.

**Experiment B: Effect of a neighboring conspecific on inverse rapping and female response to male inverse rapping**

In Experiment A, inverse rapping occurred most often when a focal male encountered a G-female during the mating period (see Results below). Inverse rapping might attract the attention of neighboring crabs because the behavior is remarkably loud. Since inverse rapping by males would be related to mating behavior (see Results below), it may be affected by the presence of rival males. In Experiment B, we examined the female’s response to inverse rapping by the focal male, and if the presence of a conspecific neighbor affected the inverse rapping. We collected solitary crabs and precopulatory guarding pairs of *P. nigrofascia* at our study site from April 13 to May 27, 2018. In the laboratory, a focal male and a G-female were placed in an experimental container with either (1) a neighboring male (*N*=85), (2) a neighboring female (*N*=80), or (3) without a neighboring crab (control group; *N*=82). The neighboring crabs comprised solitary crabs collected in the field.

A neighboring crab was first placed into the experimental container for 10 min and then confined within a transparent plastic enclosure (5.5×4×5 cm) in a corner of the container to isolate it from the other two crabs (Fig. 1). In the control group, an empty enclosure was set in a corner of a container for 10 min. A focal male was then placed in an adjacent corner, and a G-female was placed in the corner opposite the container (Fig. 1). Each trial was recorded for 30 min with a digital camera (DMC-LF1, LUMIX) or video camera (GZ-R400T, JVC). The behavior of each focal male was observed in the video recording and classified as in Experiment A. We also recorded any changes in the behavior of G-females before and after the occurrence of male inverse rapping (Table 3).

In the control group, two additional observations were recorded. First, when a focal male performed both precopulatory guarding and inverse rapping, we recorded whether the inverse rapping occurred before or during guarding. Second, if the focal male guarded the G-female, regardless of inverse rapping, after the 30-minute observation period (i.e., the first observation) ended, we left the pair for 30 min, and then observed them for another 30-minute period (i.e., the second observation) to compare the number of raps between the two observation periods. This was done to determine if males showed inverse rapping for more than 30 min after the start of guarding.

After all experiments, the receptivity level of the G-females was assessed based on the time remaining until

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**Table 2.** Summary of crabs encountered focal males in Experiment A during the pre-mating, mating, and post-mating periods. Females in the mating period were categorized into three types: (1) NG-female, females that had not been guarded by males in the field, thus they were solitary and non-ovigerous females; (2) G-female, non-ovigerous females that had been guarded by males; and (3) OV-female, solitary, ovigerous females. This species spawns once a year from late April to early June (Goshima et al. 1996); thus, the amount of time remaining until the next copulation differs for each type of female.

| Experimental period | Male | Female |
|---------------------|------|--------|
|                     | Solitary | Solitary | NG | G | OV |
| Pre-mating          | 45    | 52     | 50 | 51 | 49 | 97 |
| Mating              | 45    | 50     | 51 | 49 | 195 |
| Post-mating         | 55    | 47     | 51 | 49 | 102 |
prenuptial molting occurred. To determine this time period, each G-female was introduced in a small plastic container (13×9×7 cm, 2.5 cm deep of natural seawater) with the male that had guarded the female in the field (if the female was not guarded in the experiment) or the focal male (if the female was guarded in the experiment). The pairs were checked twice a day until the female molted and the male stopped guarding the female. We then measured the shield length (calcified anterior portion of the cephalothorax; hereafter, SL) of each crab to the nearest 0.1 mm under a stereomicroscope. When crabs molted before the measurement, we measured the SL of the exoskeleton. All individuals were used once in the experiments.

To examine the effects of the experimental conditions (0: with a neighboring male; 1: with a neighboring female; 2: control), body size (SLs of focal males and G-females), and female receptivity (the number of days until molting) on the number of raps, we used a hurdle model because our data had many zeros (i.e., focal males showing no inverse rapping). The hurdle model was a two-component hierarchical model: a logistic regression for binary data (i.e., whether the male performed inverse rapping or not) and a regression with a negative binomial distribution for count data (i.e., the number of raps by males performing inverse rapping). All statistical tests were performed in R version 3.6.0 (R Core Team 2019) with the “pscl” package for the hurdle model (Jackman 2017).

**Results**

**Experiment A: Conditions under which males show inverse rapping**

The occurrence patterns of inverse rapping and shell fighting differed greatly (Fig. 2). Inverse rapping was largely limited to G-females during the mating season (Fig. 2a), and shell fighting occurred regardless of another crab and/or the season (Fig. 2b). Inverse rapping and shell fighting were mutually exclusive in all observations except for one; in experimental observation 394, focal males showed inverse rapping in 33 cases (Fig. 2a) and shell fighting (as an attacker) in 31 cases (Fig. 2b). When a focal male encountered a female, all inverse rapping episodes were performed by the focal male to the female (Fig. 2a), whereas both sexes behaved as attackers when shell fighting occurred (Fig. 2b).

When a focal male encountered a female (NG-, G-, OV-female, or solitary), the frequency of inverse rapping was significantly higher in the mating period than in the pre- or post-mating periods (Fisher’s exact test, mating vs.
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Pre-mating, \( P = 0.004 \); mating vs. post-mating, \( P < 0.001 \) (Fig. 2a). The frequency of shell fighting was significantly higher in the mating period than in the pre-mating period (Fisher's exact test, \( P = 0.002 \)), but no difference was found between the mating and post-mating periods (\( P = 0.775 \)) (Fig. 2b).

The frequency of inverse rapping among NG-, G-, and OV-females were significantly different (Fisher's exact test, \( P < 0.001 \)), as G-females showed higher frequencies than that of the other females (Fisher's exact test adjusted by Holm’s method, G-female vs. NG-female, \( P < 0.001 \); G-female vs. OV-female, \( P < 0.001 \); NG-female vs. OV-female, \( P = 1.000 \)) (Fig. 2a). The frequency of shell fighting performed by the focal males (i.e., as attackers) in the mating period differed significantly among the three female types (Fisher's exact test, \( P = 0.017 \)) (Fig. 2b), as focal males performed higher frequencies of shell fighting in the presence of OV-females than NG-females (Fisher's exact test adjusted by Holm's method, \( P = 0.023 \)). The frequency of shell fighting initiated by focal males against G-females did not differ from that against NG-females (\( P = 0.362 \)) and OV-females (\( P = 0.289 \)) (Fig. 2b).

When focal males encountered a G-female, inverse rapping occurred more frequently in males guarding a G-female than in those not guarding a G-female (Fisher’s exact test, \( P < 0.001 \)) (Fig. 3a). Males guarding a G-female seemed to rap more than those not performing guarding behavior, although there was no significant difference between the two types of males (Mann–Whitney \( U \) test, \( W = 39.5, P = 0.188 \), perhaps due to the small sample size (Fig. 3b). The number of raps in a bout of inverse rapping ranged from one to four, and the mode was one (mean±SD=1.37±0.71) (Fig. 4).
Table 4. Results of a hurdle model analysis on the number of inverse rapping by focal males encountering with G-females. Zero model was applied to examine the effect of the experimental conditions, shield length (SL, index of body size) of focal males and G-females, and the number of days until female prenuptial molting (Day) on existence of inverse rapping. Count model was applied to examine the effect of the same explanatory variables on the number of inverse rapping. Experimental conditions were three types: (1) with a neighboring male, (2) with a neighboring female, and (3) control (no neighboring crab).

|                      | Coefficient | SE   | Z     | P     |
|----------------------|-------------|------|-------|-------|
| (a) Zero model       |             |      |       |       |
| Intercept            | −1.717      | 0.993| −1.729| 0.084 |
| Neighboring conditions|            |      |       |       |
| (2) Female vs. (1) Male | −0.225     | 0.332| −0.676| 0.499 |
| (3) Control vs. (1) Male | −0.406     | 0.326| −1.246| 0.213 |
| Focal male SL        | 0.551       | 0.151| 3.643 | <0.001|
| G-female SL          | −0.123      | 0.168| −0.729| 0.466 |
| Day                  | 0.029       | 0.068| 0.43  | 0.667 |
| (b) Count model      |             |      |       |       |
| Intercept            | 0.583       | 1.45 | 0.402 | 0.688 |
| Neighboring conditions|            |      |       |       |
| (2) Female vs. (1) Male | −0.623     | 0.361| −1.725| 0.085 |
| (3) Control vs. (1) Male | 0.175      | 0.374| 0.468 | 0.64  |
| Focal male SL        | −0.413      | 0.206| −2.005| 0.045 |
| G-female SL          | 0.363       | 0.199| 1.823 | 0.068 |
| Day                  | 0.457       | 0.161| 2.836 | <0.005|

Experiment B: Effect of a neighboring conspecific on inverse rapping and female response to male inverse rapping

The presence of neighboring conspecifics did not affect the occurrence or the number of raps during the 30-min observation period regardless of their sex (Table 4). The body size (SL) of focal males had a significant effect on both the occurrence of inverse rapping and the number of raps (Table 4). While larger males were more likely to show inverse rapping (Fig. 5), smaller males repeated more raps when performing inverse rapping (Table 4). In contrast, G-female SL had no effect on the occurrence or number of raps (Table 4). The number of days to female prenuptial molting had a significant effect on the number of raps (Table 4), and males repeated more raps on G-females with more days to prenuptial molting (Fig. 6).

Figure 7 summarizes the behavioral processes in the control group (N=82) and the occurrence of guarding by males, and/or the occurrence of inverse rapping by males. There was no significant trend in rapping by males before (N=14) or after (N=7) guarding (binomial test, P=0.189), and rapping occurred both before and after guarding in 16 cases. There was a significant difference in the frequency of inverse rapping between guarding (37/55) and non-guarding (4/27) cases (Fisher’s exact test, P<0.001).

In the control group, we observed 156 bouts of inverse rapping in 41 cases during the first observation period. Before each bout of inverse rapping, the behavior of G-females was categorized into four types (Table 3): tight withdrawal (31/156), no aggressive response (8/156), struggle (80/156), and undetermined (i.e., either the aperture of the female shell faced downward or the male covered the female with his body) (37/156) (Fig. 8). After inverse rapping, G-females showed four types of responses (Table 3, Fig. 8): (1) no change, the G-female withdrew tightly into her shell before inverse rapping and remained in the shell (N=31); (2) withdrawal, body or appendage(s) were partially out of the shell before inverse rapping and withdrew...
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Fig. 6. Histogram of the number of raps for 30 min with each number of days until female prenuptial molting (Day): (a) Day = 0 (N = 66), (b) Day = 0.5 and 1 (N = 85), (c) Day = 1.5 and 2 (N = 37), and (d) Day > 2 (N = 54). The "Day" was checked twice a day, and the longest day was 12.5. The cases in which the number of raps occurred more than 20 times are condensed into the rightmost column.

We conducted a second observation period for 46 of the 55 cases where guarding was observed during the first observation period; this excluded the nine cases in which guarding ended before the start of the second observation period. Inverse rapping was observed in 11 of the 46 cases, indicating that males performed rapping more than 1 hour after encountering a G-female. However, the number of raps performed by each male was significantly lower in the second observation period than that in the first observation period.
Discussion

*Pagurus nigrofascia* males showed inverse rapping mainly towards G-females in the mating season, especially when the male guarded a G-female. In this species, the occurrence patterns of inverse rapping and shell fighting clearly differed. Our results suggest that inverse rapping is a precopulatory behavior in *P. nigrofascia*. Inverse rapping has been reported in several hermit crabs (Hazlett 1966, 1972, 1980, 1989) and is considered a precopulatory behavior in *Clibanarius zebra* (Hazlett 1989). Although Hazlett (1980) also reported inverse rapping by males in *P. impressus*, the behavior was observed during shell fighting. Thus, the present study provides the first evidence that males perform inverse rapping as a precopulatory behavior in *Pagurus* hermit crabs.

Kido et al. (2019) demonstrated that females typically resist guarding attempts by males in *P. nigrofascia*. In the present study, most females stopped struggling and/or withdrew into the shell in response to male inverse rapping. Thus, inverse rapping by males would benefit the initiation and/or continuation of precopulatory guarding. Female resistance and male coercive behavior have been observed in various animals and is known as sexual conflict (Arnqvist & Rowe 2005; Hall et al. 2008). Furthermore, since many guarding pairs of *P. nigrofascia* are found on the fronds of brown algae where there are few solitary individuals (authors, personal observation), males would climb up the brown algae during guarding, as has been reported in *P. filholi* (Kawaminami & Goshima 2015). Inverse rapping would benefit males if they could restrain females from struggling during guarding and climbing.

Smaller males showed a larger number of raps in the present study. In *P. nigrofascia*, the difference in body size of a mating pair is relatively small (Yoshii et al. 2009; Kojima et al. 2016). Females resist male attempts at guarding regardless of body size (Kido et al. 2019). Therefore, smaller males may need more raps than larger males to reduce female resistance because smaller males would have less impact when performing inverse rapping. Briffa and Elwood (2000) demonstrated that *P. bernhardus* (Linnaeus, 1758) in experimentally rubberized shells were less likely to win shell fights. Alternatively, females might change their intensity of resistance with male size. Further experimental studies are needed to examine these hypotheses.

In the present study, males performed fewer numbers of raps when females were close to molting. This result is inconsistent with previous studies on crustaceans, as male aggressiveness to potential mates increased as the female approached molting (e.g., Minouchi & Goshima 1998; Jormalainen et al. 2000; Miura & Goshima 2016). Females that are close to molting would be of a higher value to males because of the lower guarding costs and higher likelihood of copulation. This would be true for *P. nigrofascia* because males choose females that are close to molting (Suzuki et al. 2012). In hermit crabs, the timing of copulation might be determined by the females (Yamanoi et al. 2006; Okamura & Goshima 2010) since males cannot attach their spermatophores to a female's gonopore unless the female comes out of her shell to accept the spermatophores (Hazlett 1968, 1972). Therefore, males of *P. nigrofascia* might need to avoid excessive rapping as the timing of copulation approaches because inverse rapping causes females to withdraw into their shells.

Inverse rapping might attract the attention of neighboring males since the behavior is loud. However, the presence of neighboring crabs had no effect on the occurrence of inverse rapping. Shell rapping during shell fighting produces a rap sound (Hazlett 1966; Briffa et al. 2003), and the sounds from the striking and knocking of shells have been shown to attract the terrestrial hermit crab *Coenobita compressus* Edwards, 1836 (Laidre 2013). The sound produced by inverse rapping is brief, while shell rapping usually lasts more than several seconds (Elwood & Neil 1992; Ismail 2012), males might not need to be concerned about the sound produced by inverse rapping.

Species-characteristic precopulatory signals are used by many species to identify the species, sex, and quality of potential mates (Pfennig 1998; Rollmann et al. 2003). There are six sympatric species of *Pagurus* hermit crabs in our study site, i.e., *P. nigrofascia*, *P. filholi*, *P. middendorfii*, *P. lanuginosus*, *P. proximus*, and *P. minutus* (Goshima et al. 1998; Wada et al. 2000; Wada & Mima 2003; Oba & Goshima 2004), and the breeding season of all species except *P. middendorfii* overlap. Since inverse rapping has only been observed in *P. nigrofascia*, it may help females to identify potential conspecific mates and/or assess the quality of the potential mates. However, inverse rapping could not be such a signal. The first reason is the low frequency of occurrence of inverse rapping. Sexual signals required for conspecific recognition would be mutually beneficial and be sent in every case during mating behavior. However, we observed that only about half of the males performed inverse rapping, and there was no relationship between inverse rapping and successful copulation. Another reason is that although signals for both conspecific recognition and mate choice are usually emitted before couples are formed, inverse rapping was observed even after guarding in *P. nigrofascia*.

In contrast, inverse rapping may be explained by the sensory exploitation hypothesis. This hypothesis explains male traits as adaptations to exploit female responses that evolved in non-sexual contexts (Andersson 1994). This hypothesis has been supported in several animal taxa (Andersson 1994), including fiddler crabs (Christy & Salmon 1991; Christy 1995). We propose that inverse rapping of *P. nigrofascia* may mimic shell-rapping behavior. Defenders in shell fights initially withdraw into their shells when
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Attackers start shell rapping (Elwood & Neil 1992). Thus, while withdrawing into the shell would be an adaptive response of defenders to rapping in the context of shell fighting, males might use inverse rapping to elicit the withdrawal response in females in order to inhibit the female’s resistance and guard the female. However, further experimental studies are needed to test the sensory exploitation hypothesis in hermit crabs. Recent behavioral studies in hermit crabs have given less attention to specific differences in their behaviors, while there are many studies on the differences in their morphology (Sandberg & McLaughlin 1993; Komai 1996) and life histories (Wada et al. 2005, 2007). We hope that detailed observations on the behavior of each species will lead to new discoveries on the behavioral diversity in hermit crabs and to the establishment of general rules that connect the diversity of morphology, life history, and behavior.

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