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Antenna Length in the Hermit Crab *Pagurus middendorffii* : Sexual Dimorphism and Effect on Two Types of Male–male Competition

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Abstract

Male–male competition is considered a mechanism for sexual selection and the evolution of sexual dimorphism in many animals. There are two types of male–male competition : scramble competition and contest competition. Many studies have focused on contest competition to explain sexual dimorphism of body size and/or weaponry, but it can also result from scramble competition. In this study, we described sexual dimorphism in antenna length of the hermit crab *Pagurus middendorffii* and tested the effects of antenna length in scramble and contest competition. Although antennae were longer in males than in females, longer antennae provided males no advantage in either competition. These results suggest sexual dimorphism of antenna length in this species is maintained by other ecological factors such as advantage in foraging at the rocky shore.

Key words : Sexual dimorphism, Male–male competition, Scramble competition, Contest competition, Antennae, Hermit crab

Introduction

Sexual dimorphism is common in animals. Many studies of vertebrates and invertebrates have described sexual dimorphisms in body size and various traits, such as weapons, ornaments, locomotory and sensory organs (reviewed in Andersson, 1994). Sexual selection, female fecundity and intraspecific niche divergence have often been presented as factors to explain the evolution of sexual dimorphisms (Hedrick and Temeles, 1989 ; Shine, 1989 ; Allen et al., 2011 ; Manicom et al., 2014). Sexual selection through mate choice and/or male–male competition is often regarded as the most important evolutionary factor affecting dimorphism (Andersson, 1994).

There are two types of male–male competition : scramble competition and contest competition. In scramble competition, males compete for early access to females, and sexual selection has been shown to favor males with large body size (Carroll and Salamon, 1995 ; Hanks et al., 1996), small body size (Andersson, 1994), good locomotory organs (Able, 1999) and/or good sensory organs (Hanks et al., 1996). For example, male longhorned beetles, *Phoracantha semipunctata*, have longer antennae than females relative to body size, and males with larger bodies and longer antennae are more successful in scramble competition because they are better at finding females (Hanks et al., 1996). In contest competition, males with large body size and/or weaponry are favored (Andersson, 1994 ; Sneddon et al., 1997 ; Judge and Bonanno, 2008 ; Okada et al., 2011 ; Yoshino et al., 2011). For example, males of the bean bug *Riptortus pedestris* have larger hindlegs than females, and males with larger bodies and hindlegs are more likely to win in contest competition (Okada et al., 2011). Researchers have tended to examine evolutionarily significant sexual dimorphism in body size and weaponry in contest competition (Andersson, 1994 ; Emlen, 2008 ; Snell-Rood and Moczek, 2013), but scramble competition can also be an important factor affecting sexual dimorphism of other traits such as sensory organs.

This study examined sexual dimorphism in antennae length of the hermit crab *Pagurus middendorffii*, a species in which antennae are longer in males than in females (see Fig. 1). In crustaceans, antennae are used to sense physical and chemical stimuli such as tactile information, vibration, and soluble and insoluble chemicals (Dahl et al., 1970 ; Tautz et al., 1981 ; Voigt and Atema, 1992 ; Caskey and Bauer, 2005 ; Koch et al., 2006) and can function in social behavior such as pairing and competition (Vickery et al., 2012). We hypothesize that long antennae in males may function in both scramble and contest competition since they would help earlier detect potential mates (scramble competition) or rivals, and to flee from rivals (contest competition). Few studies, however, have examined the effects of male antennae in either scramble (Bertin and Cézilly, 2003 ; Bertin and Cézilly, 2005) or contest competition for females (Lefebvre et al., 2000).

In this paper, we report on sexual dimorphism in antenna

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length of *P. middendorffii* and test if males become less successful in scramble and/or contest competition after their antennae are cut. Males of this species show precopulatory guarding behavior, grasping the rim of female shells with their minor cheliped during the mating period (Wada et al., 1999 ; Yasuda et al., 2012). Thus, males engage in scramble competition to find females and contest competition when a pair male defends a female from a challenger male. However, to our knowledge, no studies have focused on the effects of antennae length on either type of male–male competition in this species.

Sexual dimorphism in antenna length

Materials and Methods

Solitary individuals and guarding pairs of *P. middendorffii* were collected at Kattoshi, on the west side of Hakodate Bay in southern Hokkaido, Japan (41°44'N, 140°36'E) in 2016 on November 2, 4, 15 and 17, and in 2017 on November 3, 4, 5, 6, 7, 16 and 19 during the mating period at the site (Wada et al., 1995) and brought to the laboratory. We measured the antenna lengths and body size after cracking the shells that the crabs occupied. Flagella of both left and right antennae were cut and photographed with a digital camera (RICHO, WG–30), and flagellum lengths were measured to the nearest 0.1mm with ImageJ, version 1.48. The shield length (the calcified anterior portion of carapace, hereafter SL) of each crab was also measured to the nearest 0.1 mm under a stereoscopic microscope as an index of body size. All crabs were sexed based on the developmental level of the first pleopod. In 2016, we gave each crab a new shell and released them at the sampling site after the measurements. In 2017, we measured only solitary males and pair females used in the following experiments, and the samples were frozen before the measurements.

We examined sexual dimorphism in antennae length as the mean length of the left and right antennae (hereafter AL) using a generalized linear model (GLM) with a normal error distribution, in which the response variable was AL, and the explanatory variables were SL, sex (i.e., male = 0, female = 1), and interaction between SL and sex, considering males of *P. middendorffii* are larger in SL than females (Wada et al. 1995). We used R software, version 3.2.2 and the glm2 package for the statistical analysis.

Results

AL increased with SL in both sexes (males, $N = 258$; females ; $N = 519$, Fig. 1), and there was a significant interaction between SL and sex (GLM, $t = -4.61$, $P < 0.01$, Fig. 1), indicating sexual dimorphism in which the AL was longer in males than females.

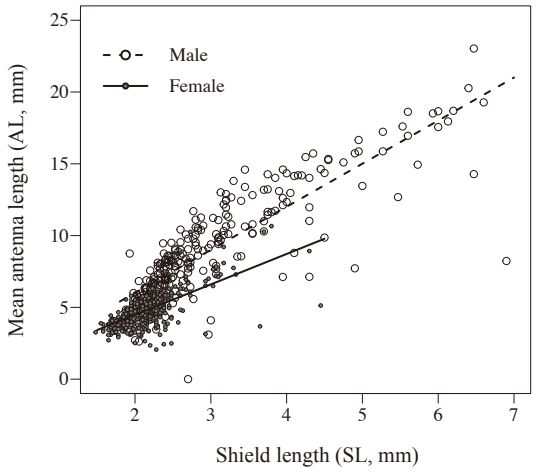

Fig. 1. The relationship between antenna length (AL) and shield length (SL) in both sexes, analyzed by GLM. AL increased with SL in both sexes (males, $N = 258$, AL = 3.00SL + 0.01 ; females, $N = 519$, AL = 2.12SL + 0.24). In the range of female SLs, male predicted AL was always larger than that of females.

Effects of male antenna length on scramble competition

Materials and Methods

Each guarding pair was placed in a small vinyl pouch with seawater and brought back to the laboratory from the sampling site on November 3, 5 and 7, 2017. The pairs were separated, and males were randomly assigned to three groups : control 1, control 2 and experimental. We manipulated the left and right antennae length, after cracking the shells occupied by males of all groups. The antennae remained intact in the control 1 group, had the tips cut off in the control 2 group and had the distal half cut off in the experimental group (Fig. 2). After the antennae were cut, we placed each male in a container (13.5 × 9.5 × 6.5 cm) with natural seawater for at least 24 hours together with 10 vacant shells of the sand snail, *Umbonium costatum*, or *Cantharidus jessoensis*. *C. jessoensis* was used when the males were too small to occupy a sand snail shell. We checked if each male occupied a new shell and used them in the following trials. In addition, each female was also kept in a cup (300 ml) with natural seawater for the trials.

In the trials, we put a male in a corner of an experimental container (45.5 × 31 × 11 cm) with natural seawater and then placed a female that had originally been guarded by another male in the diagonal corner. The female was held with tweezers to prevent it from walking around the container until the end of the trial. Each trial was videotaped for up to 600 seconds with a digital camera (Panasonic, LUMIX DMC–LF1) after the male started walking. If the male touched the female, we ended the trial and recorded the time. After the trials, we reconstructed the original guarding pairs and kept them in containers (13.5 × 9.5 × 6.5 cm). We then assessed

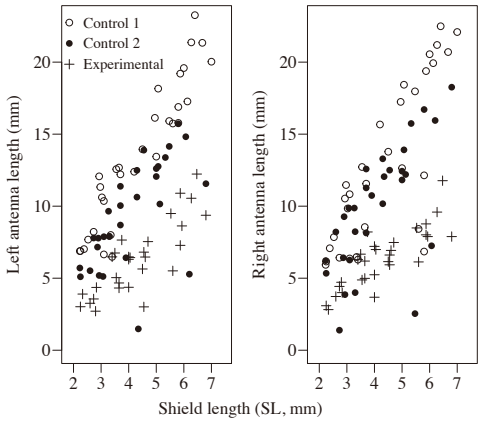

Fig. 2. The relationship between shield length and the length of the remaining antenna (left or right) after the manipulation in the scramble competition (control 1, $N = 31$; control 2, $N = 30$; xperimental, $N = 29$).

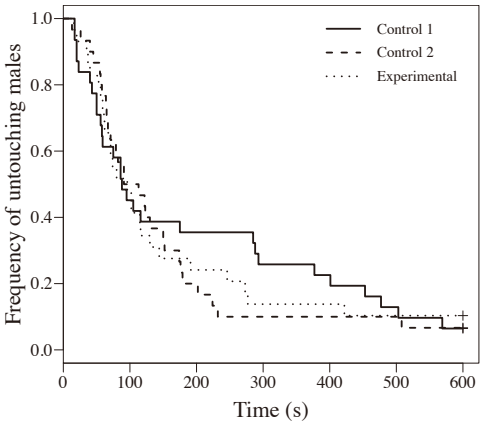

Fig. 3. The curves of the three groups, depicted with Kaplan–Meier method. The curves show how many males touched a female relative to each group size (control 1, $N = 31$; control 2, $N = 30$; experimental, $N = 29$) along the time axis.

guarding durations (hereafter GD) in half-day increments by checking the containers twice a day until all *P. middendorffii* females were released by the guarding males. All crabs were frozen after recording the GD. We also measured the SL of the thawed crabs.

The data were analyzed using the Cox proportional-hazards model (Cox, 1972) in R software. The response variable was time (seconds) to reach the female, and the explanatory variables were the group, male SL, female SL and GD. I excluded the data if females did not spawn eggs or males lacked appendages.

Results

There was no significant difference in time until touching a female between groups when the control 1 group was base line (control 1, $N = 31$; control 2, $N = 30$; experimental, $N = 29$; the Cox proportional-hazards model : control 2, $z = 1.16$; $P = 0.25$; experimental, $z = 1.31$, $P = 0.19$; Fig. 3, Table 1). Male SL had a significant effect on the time ($z = 4.84$, $P < 0.001$, Table 1). The results indicated that neither antenna length nor antenna manipulation affected the time, but large males were more likely to touch a female before smaller males did.

Effects of male antenna length on contest competition

Materials and Methods

Each guarding pair and solitary individual was placed in a small vinyl pouch with seawater and brought back to the lab from the sampling site on November 4, 6, 16 and 19, 2017. The pairs were separated, and the pair males were randomly assigned to two groups : control and experimental. In the control group, about 2 to 3 mm of the left and right antennae of males were cut, and in the experimental group, most of the antennae were cut off after the occupied shells were cracked (Fig. 4). After the manipulation, we placed each pair male in a container (13.5 × 9.5 × 6.5 cm) with natural seawater for at least 24 hours together with 10 vacant shells of the sand snail, *U costatum*, or *C jessoensis*, as we did in the scramble competition. We checked if each male occupied a new shell and used them in the following trials. We also kept each female in a cup (300 ml) and solitary male in a container (13.5 × 9.5 × 6.5 cm) with natural seawater for the trials.

Before each trial, we reconstructed an original pair by placing a male and female in a round container (diameter 25 cm, depth 3 cm) with natural seawater. After the guarding male

Table 1. Effect of male antenna length on time to reach a female, analyzed with the Cox proportional-hazards model. Neither the control 2 nor experimental groups differed significantly from the control 1 group in time to reach a female, but males with large SL were likely to reach a female earlier.

Explanatory variable	Coefficient	*SE*	*z*	*P*
Control 2 vs control 1	0.33	0.28	1.16	0.25
Experimental vs control 1	0.38	0.29	1.31	0.19
Male shield length	0.43	0.09	4.84	< 0.001
Female shield length	−0.29	0.19	−1.49	0.14
Guarding duration	−0.15	0.16	−0.93	0.36

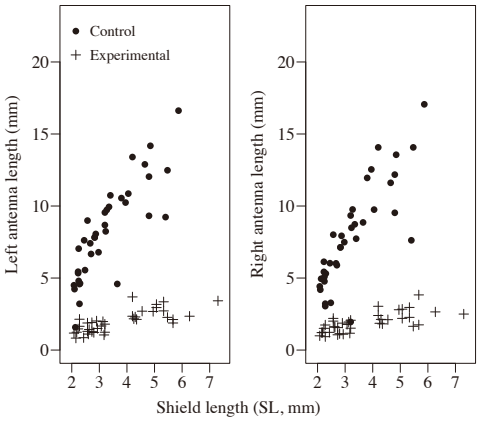

Fig. 4. The relationship between remained left and right antenna lengths and SL after the manipulation in materials and methods 3 (control, $N = 39$; experimental, $N = 35$).

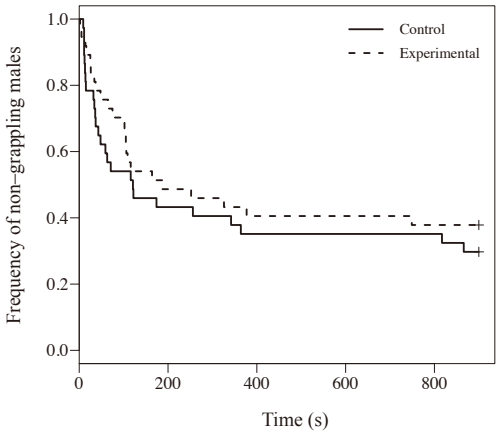

Fig. 5. The curves of the two groups, depicted with Kaplan–Meier method. The curves show how many pair males were involved in grappling relative to each group size (control, $N = 39$; experimental, $N = 35$) along the time axis.

started walking, a solitary male was added into the container as a challenger. The trials were videotaped for 900 seconds with a digital camera (RICOH, WG-40 and Panasonic, LUMIX DMC-LF1) after both males started walking. When the males started grappling, we recorded the time. Because grappling is a risky behavior for a pair male because of the risk of losing the female to the challenger male (Yasuda et al., 2012), they were expected to try to avoid grappling with their antennae. After the trial, I recorded the GD by keeping the original guarding pair in a container (13.5 × 9.5 × 6.5 cm) and measured the SL of each crab after freezing them.

The data were analyzed using the Cox proportional-hazards model in R software. The response variable was time (seconds) for the males to start grappling, and the explanatory variables were the group, pair male SL, challenger SL, female SL and GD. Males lacking appendages were not used in the trials, and the data from females that did not spawn eggs were excluded from the analysis.

Results

Time until grappling started did not significantly differ between groups (control, $N = 39$; experimental, $N = 35$; the Cox proportional-hazards model, $z = -0.62$, $P = 0.54$; Fig. 5, Table 2), although the SL of pair males and challengers had a significant effect on the time (pair male SL, $z = -2.24$, $P = 0.03$; challenger SL, $z = 2.06$, $P = 0.04$; Table 2). The results indicated antenna length did not affect how long the guarding males avoided grappling. However, large pair males were more likely to avoid grappling for longer time, and larger challengers were more likely to start grappling earlier.

Discussion

Although antennae were longer relative to body size in males than females in *P. middendorffii*, no significant advantage of longer antennae in either scramble or contest competition was found. Sexual dimorphism of antennae length in this species is presumably due to other ecological factors other than male-male competition. Males of this species grow faster than females (Wada, 2000), suggesting males need to explore the field more frequently to forage and find new shells. Longer antennae might be advantageous for males when exploring the rocky shore and avoiding obstacles and predators. In the crayfish, *Cherax destructor*, antennae function in exploration (Zeil et al., 1985 ; Bazil and Sandeman, 2000 ; McMahon et al., 2005). Bazil and Sandeman (2000) experimentally showed that the crayfish whose anten-

Table 2. Effect of male antennae length on time until grappling started, analyzed with the Cox proportional-hazards model. The control and experimental groups did not significantly differ in time until grappling started. Larger pair males were more likely to let grappling start later, and larger challengers were more likely to start it earlier.

Explanatory variable	Coefficient	*SE*	*z*	*P*
Experimental vs control	−0.18	0.29	−0.62	0.54
Pair male shield length	−0.40	0.18	−2.24	0.03
Challenger shield length	0.22	0.11	2.06	0.04
Female shield length	−0.44	0.55	−0.81	0.42
Guarding duration	−0.15	0.14	−1.12	0.26

nae were immobilized did not increase exploration behavior in response to a newly added wall in the arena, while the intact individuals did, demonstrating they detected configurational changes in the experiment with their antennae.

Furthermore, the effects of antenna length may be masked by the inappropriate container size, especially in scramble competition. Bertin and Cézilly (2005) used three sizes of tanks (small, medium and large) to assess latency to the first mount in males of the isopod *Asellus aquaticus*. Males with long antennae mounted females earlier than males with short antennae only in the medium–sized tanks. In addition, given that antennae might be useful when individuals cannot depend on their visual sense, the lack of obstacles in the experimental containers in this study might have masked the effects of antenna length. Without obstacles, males might see a female or approaching challenger directly. Thus, the male crabs might have reached the female or been caught by the challenger in similar time regardless of their antenna length.

In the scramble competition, larger males touched females earlier than smaller males did in the experimental condition. *P. middendorffii* shows sexual dimorphism in body size, and larger pair and challenger males have an advantage in contest competition (Wada et al., 1995 ; Wada et al., 1999 ; Yasuda et al., 2012 ; this study). Thus, larger males are more successful in both scramble and contest competitions. In addition, Wada et al. (1999) suggested that pair males could have an advantage in contest competition due to holding a female prior to the approach of a challenger (owner advantage). Therefore, larger males are likely to guard a female first and defend her successfully due to body size and owner advantage. Wada et al. (1995) predicted that only large males can mate, while almost all females could, which would generate sexual selection contributing to maintaining the body size dimorphism.

Sexual dimorphism in animals might result from sexual selection through male–male competition and mate choice, but other factors such as natural selection could also contribute (Hendrick and Temeles, 1989 ; Shine, 1989 ; Allen et al., 2011 ; Manicom et al., 2014). For example, Caravello and Cameron (1987) reported that in males of the Gulf Coast fiddler crab, *Uca panacea*, minor chelipeds are larger in males than females. They suggested males compensate for the loss of foraging ability caused by having an enlarged major cheliped, which is not suitable for foraging. Furthermore, several factors can contribute to maintain sexual dimorphism simultaneously (Hendrick and Temeles, 1989 ; Allen et al., 2011 ; Manicom et al., 2014). Therefore, sexual dimorphism and its factors should be studied by various approaches including observing or testing the effect of natural selection.

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