

Chelipeds are the real weapon: cheliped size is a more effective determinant than body size in male–male competition for mates in a hermit crab

Kenji Yoshino · Tsunenori Koga · Sayaka Oki

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Abstract To understand the evolution of weapons, we must understand both their functions and relative importance compared to body size in determining fighting success. Many decapod crustaceans develop disproportionately large chelipeds for their body size and use them as a weapon in agonistic interaction. There are, however, examples where weapons are merely signals of resource holding potential (RHP) and the RHP is actually determined by body size. We investigated the function and relative efficacy of body size and major cheliped size in male–male contests for females in the hermit crab *Diogenes nitidimanus*. Contests over females took two forms: (1) males preemptively guarded females and opponents did not fight with the guarding male. Cheliped size contributed significantly to the settlement of these contests and probably functioned as a visual signal for the opponents. (2) Guarding males engaged in physical combat with an opponent. In these cases, both body and cheliped sizes affected contest outcomes. The effect size for cheliped size was as strong, or stronger, than that for body size. These results suggest that large chelipeds have evolved as a true weapon and are effective in escalated fights for resources. Therefore they are also efficient visual signals for settling contests with only display. Our results are a rare example that clearly demonstrate that weapons are a more important determinant of fights than body size when both body and weapon size affect resource acquisition.

Keywords Contest · *Diogenes nitidimanus* · Mate-guarding · Weapon

Introduction

Males of many animal taxa have evolved disproportionately large traits than expected for their body size, such as horns, antlers, spurs, tusks, and mandibles (Andersson 1994; Emlen 2008). As these traits are often used in aggressive fights for access to females, they are considered to be weapons that have evolved as a consequence of intra-sexual selection. However, these enlarged structures might be true weapons that are used in physical combat and/or they might be signals of an animal's resource holding potential (RHP) that need not directly increase fighting ability (Berglund et al. 1996; Briffa and Sneddon 2007). To understand the evolution of enlarged weapon-like traits, we must understand both their functions and efficacy in real fights.

Weapon size is usually strongly associated with body size (Jennions and Backwell 1996; Sneddon et al. 1997; Styrsky and Van Rhein 1999; Pomfret and Knell 2006; Judge and Bonanno 2008). As body size is generally the major determinant of RHP of individuals, this association makes it difficult to determine whether weapons really affect the outcomes of agonistic interactions, and how they have evolved. To overcome the problem, several empirical studies have investigated the efficacy of weapons by conducting contests between body-size-matched opponents that differ in the expression of weapon-like traits (Neil 1985; Jennions and Backwell 1996; Barki et al. 1997; Sneddon et al. 1997; Styrsky and Van Rhein 1999; Judge and Bonanno 2008). Body size-matched contests can clarify whether or not these putative weapons are effective in settling contests. If the results show no contribution of

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K. Yoshino (✉)
Institute of Lowland and Marine Research, Saga University,
Saga 840-8502, Japan
e-mail: c1894@cc.saga-u.ac.jp

T. Koga · S. Oki
Faculty of Education, Wakayama University,
Wakayama 640-8510, Japan

weapon size to contest outcomes, the development of weapons would simply represent a correlated response to selection for body size (e.g., Styrsky and Van Rhein 1999) due to a genetic correlation between body size and weapon size. In contrast, even if weapons do affect fight outcome, there remains some doubt that they have evolved because of the advantage they confer in escalated fights, if weapons are less important than body size. In these cases, weapons might have mainly evolved in response to selection in other contexts, such as a signaler–receiver context (Searcy and Nowicki 2005) or through female choice (Berglund et al. 1996; Briffa and Sneddon 2007) rather than direct competition for females.

Crustaceans are an ideal organism to investigate the evolution of weapons because they can easily be manipulated in experiments. Males of many decapod crustaceans develop disproportionately large chelipeds used in aggressive competition for females, and these are usually considered to be weapons. However, are chelipeds really weapons? It is true that large claws in several crustaceans function as weapons (e.g., Jennions and Backwell 1996; Sneddon et al. 1997), but in other species they do not contribute to the outcome of contests that involve aggressive physical contact once the effect of body size is removed (Hughes 1996; Arnott and Elwood 2010). In such cases, enlarged chelipeds merely function as signals of RHP attributed to body size. In fact, chelipeds are often used to transfer information about RHP to an opponent during fights (Hughes 1996; Backwell et al. 2000; Elwood et al. 2006; Lailvaux et al. 2009). Since escalated fights are costly to both contestants (reviewed in Briffa and Sneddon 2007), large chelipeds could have been selected because they are reliable signals of RHP.

D. nitidimanus is a hermit crab species widely distributed on sandflats in Japan. During the reproductive season, males show precopulatory mate guarding behavior in which they grasp the rim of female shells with their minor cheliped (Koga et al. 2010). Guarding males then fight with solitary rivals using their major cheliped while grasping the female's shell with their minor cheliped. Males' major chelipeds are larger than those of females, and show positive allometric growth (Koga et al. 2010). Male chelipeds might be a secondary sexual character that is sexually selected through competition for females (i.e., real weapons). Alternatively, as most of a hermit crab's body is hidden in the shell and direct assessment of body size might be difficult for opponents, chelipeds could function as a visual signal of RHP rather than as a weapon. In this study, we aimed to determine whether male enlarged chelipeds have evolved as signals of RHP or as "true" weapons in *D. nitidimanus*. To do this, we evaluated the function and the relative importance of cheliped size and body size in mating contests by investigating their efficacy

in the contests that are settled by (1) only display or (2) by escalated fights with physical contact. If enlarged chelipeds are merely visual signal of RHP, the efficacy would only be apparent in case (1). If chelipeds are a true weapon, the efficacy would also be detected in case (2), and the effect on fighting success would be larger than that for body size.

Materials and methods

Field sampling and experimental setting

D. nitidimanus is a left-handed hermit crab species (i.e., left chelipeds are larger) that is widely distributed from intertidal sandflat to shallow subtidal zones in Japan. Sampling was performed during low tide in the sandflat of Nunohiki, an area of the Waka-River estuary, Wakayama city, Japan (N34°10'23", E135°10'49"). The reproductive season of *D. nitidimanus* in the Waka-River estuary is from May to October (Koga et al. 2010), during which mate-guarding males are often observed. Mate-guarding is an indicator of male reproductive activity (e.g., Yoshino et al. 2002; Koga et al. 2010). Guarding males often extend their left major cheliped to the opponent, physically preventing rivals from approaching and sometimes flicking them away. This type of use of chelipeds is often observed in other hermit crabs (Elwood et al. 2006). There is a large variation in the size of major chelipeds relative to body size (Koga et al. 2010). Most guarding males are much larger than their female mates, and small males that are similar in size to females are seldom observed guarding (Koga et al. 2010) even though they have matured spermatophores and are physiologically mature (T. Koga unpublished data). We collected guarding pairs by hand in August 4–20, 2005 and July 12, August 12, 23–24, and September 8 in 2006. Collected pairs were taken to the laboratory where they separated and crabs housed individually in small round containers (5 cm in diameter, 3 cm in height) until experiments were conducted. All the males occupied *Umbonium moniliferum* shells and females mainly occupied *Batillaria* spp. shells.

Contest experiments were conducted in the base of a polystyrene arena (15 cm in diameter, 5 cm in height). The base was filled with brackish water from the site so that the shell of experimental crabs was fully covered. Two randomly chosen males were put on opposite sides of the arena so that they did not immediately interact with each other. A female was then placed in the centre of the arena, equidistant from the two males. We observed the trio for 30 min and recorded whether or not the males fought for the female, and which male first guarded and last guarded the female. The number of times males switched in guarding was also recorded. In 2006, we recorded three

30-min trials simultaneously using three digital video cameras (Sony DCR-TRV30, DCR-TRV9, and Panasonic NV-GS100K). The arenas were surrounded by panels so our movements did not disturb the crabs. After the observation period, shell width (SW), body size as shield length (SL; length of anterior calcified part of the cephalothorax), and weapon size as major cheliped length (CHL; maximum length of the propodus) of males were measured with calipers to the nearest 0.1 mm. SL and CHL were measured after removing the shells of the crabs by cracking them with a bench vise. Most females were large enough to induce male guarding behavior and male–male interactions. All crabs were used only once for the experiment. The observed frequencies of guarding behavior in 2005 and 2006 experiments were 96.5% (28/29 contests) and 88.5% (54/61 contests), respectively, and these did not significantly differ (Fisher's exact test, $p=0.43$). Although shell size fit of contestants might affect contest outcomes (Yoshino et al. 2004), we did not manipulate shell condition of males in the present experiment. However, SW adjusted by SL did not differ between contest winners and losers in either 2005 (repeated measures ANCOVA; $F_{1,26}=0.029$, $p=0.87$) or 2006 ($F_{1,52}=1.08$, $p=0.30$). The pooled data also showed no significant difference in shell size between winners and losers ($F_{1,80}=2.2$, $p=0.14$). The mean shell width was 16.0 ± 1.4 mm (SD), and the 95% confidence interval for the mean difference between winners and losers was -0.4 – 0.1 mm. Hence, shell size condition of males did not affect our results, and we do not consider it hereafter.

Data analysis

We calculated coefficients of variation [CV, standard deviation as a percentage of the mean; $100\times(\text{SD}/\text{mean})$] in SL and CHL of the collected guarding males as a rough evaluation of mature male phenotypic variation in the population. To construct the 95% confidence interval of CVs, 5,000 bootstrapping was performed. In the analysis, males from 2005 ($29\times 2=58$ males) and 2006 ($61\times 2=122$ males) were pooled, but males without major chelipeds (i.e., 20 males) were excluded. We analyzed a total of 160 males.

Before evaluating the relative importance of cheliped size and body size in determining contest outcomes, we first confirmed the effect of each variable on contest outcomes using contests where either or both males exhibited guarding behavior. The effect of body size was tested using paired t tests to compare winners and losers. As cheliped size was likely to be correlated with body size, the effect of cheliped size was analyzed in each year by repeated measures ANCOVA. We set cheliped size as a dependent variable, crab status (i.e., winner or loser) as an

explanatory variable, SL as a covariate, and contest identity as the repeated component. If cheliped size affected the contest outcomes, it should differ between winners and losers. There were 16 cases where one or both crabs had no major cheliped (two in 2005, 14 in 2006), so the analyses were based on 66 contests (26 in 2005 and 40 in 2006). The data were pooled as no year difference in the effect of body or cheliped size on contest outcome was detected.

Since both SL and CHL significantly contributed to contest outcomes, we evaluated the relative importance of cheliped and body size in a logistic regression for the 66 contests. We randomly chose one of the two males in each contest as the focal individual. Binary outcome (i.e., win or lose) was then regressed against body size and cheliped size ratios (focal/rival) and these parameters were estimated (Pomfret and Knell 2006). The relative size of partial regression coefficients does not necessarily indicate the influence of the dependent variable, so we calculated the effect sizes for body size ratio and cheliped size ratio, respectively, using formula (11) in Nakagawa and Cuthill (2007) using z value instead of t value. The coefficient of determination was calculated based on Nagelkerke (1991). We also calculated variance inflation factors (VIF) to evaluate collinearity between SL and CHL ratios. VIF is an element of determining standard errors of parameters, and defined as $1/(1-r^2)$, where r is Pearson correlation coefficient between SL and CHL ratios. If predictors are independent, VIF is one and a VIF >10 indicates strong collinearity (Quinn and Keough 2002). To construct confidence intervals for the effect sizes, we repeated these calculations 5,000 times, each time randomly assigning a focal male for each contest. As a result, we evaluated 95% confidence intervals of the predictors by bootstrapping. We also performed the same analysis separately for the 42 escalated contests and the 23 non-escalated contests (but excluding one peculiar case; see Table 1) to evaluate the function of chelipeds in contests. All statistical analyses were performed with R ver. 2.8.1 (R Development Core Team 2008).

Results

Phenotypic variations in male SL and CHL

Figure 1 shows the correlation between SL and CHL in *D. nitidimanus*. The regression line was significant, but the variation in CHL explained by SL was modest (both SL and CHL log-transformed; $F_{1,158}=94.3$, $p<0.001$, $r^2=0.37$). The CVs of SL and CHL were 13.7% and 21.5%, respectively ($n=160$). The bootstrap confidence intervals were 12.2–15.0% for SL and 19.4–23.4% for CHL. No

Table 1 The settlement processes of 66 contests

Settlement patterns	Number of contests
Pre-emptive guarding (no fights)	23
Fight	42
Winning of the first-guarding males with no taking over	25
Winning of the first-guarding males after alternate taking over	6
Losing of the first-guarding males with one taking over	10
Losing of the first-guarding males after alternate taking over	1
Others	1

In most contests, some physical contacts occurred between guarding and the solitary rival male (i.e., fight). Several cases were settled as either crab preemptively guarded the female and no physical contacts occurred afterward (i.e., pre-emptive guarding). In one case, the first-guarding male abandoned females by the approach of the rival male, and the rival guarded the female (others)

overlap between the two intervals indicated that the phenotypic variation of CHL was significantly larger than that of SL.

Settlement patterns of contests

Table 1 shows the settlement pattern of 66 contests. About 35% of cases (23 contests) were settled without any physical contacts when one of the males preemptively guarded the female, while the other 64% of cases (42 contests) showed some physical contacts such as cheliped flicking and/or grappling. The SL ratios of contestants (winner/loser) in the 23 non-escalated contests and 42 escalated contests were 1.09 ± 0.2 (\pm SD) and 1.09 ± 0.1 , respectively. Similarly the CHL ratios were 1.17 ± 0.2 and

1.18 ± 0.2 , respectively. Neither ratios differed between the two types of contests (ANOVA, both $F_{1,63} < 0.026$, $p > 0.87$). In one case, a guarding male abandoned the female at the approach of the rival male who then guarded the female. The video data from 2006 showed that the mean number of interactions per contest was 2.1 ± 1.9 (\pm SD), and in three cases more than five interactions were observed. Of the 42 fights, about 26% (11 contests) were settled when the male that first initiated guarding lost the contest through one (ten cases) or several switches (one case) in the identity of the male guarding. The remaining 72% (31 contests) were settled when the first-guarding males won the contest. No switching of guarding males occurred in 81% of cases (25 contests), but several switching was found in the other six contests (four switches in one contest and two in the other five contests).

Factors determining contest outcomes

The mean SL and CHL with their standard deviations of the crabs used in the analyses were 3.4 ± 0.4 mm and 6.1 ± 1.3 mm, respectively. The SL of winners was significantly larger than that of losers ($t_{65}=4.74$, $p < 0.0001$; Fig. 2), and CHL was also significantly larger in winners even after adjusting for SL (both SL and CHL log-transformed; $F_{1,64}=28.7$, $p < 0.0001$; Fig. 2). The mean difference in SL and CHL corresponded to 6.9% and 12.3% of their mean size, respectively.

The results of logistic regressions for the three analyses are presented in Table 2. Collinearity between CHL and SL ratios was not of serious concern for evaluating the independent effects of CHL and SL ratios since VIFs for all models were between 1.2 and 2.1, which corresponded to a 0.4–0.7 correlation between SL and CHL ratios. In the regression based on all 66 contests, confidence intervals for

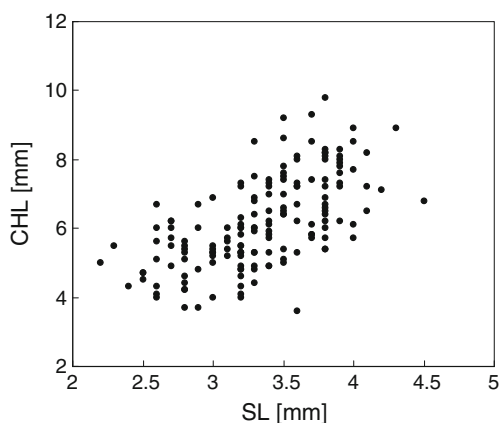


Fig. 1 The relationship between body size (SL) and cheliped size (CHL) of the hermit crab *D. nitidimanus* used in the experiments ($n=160$)

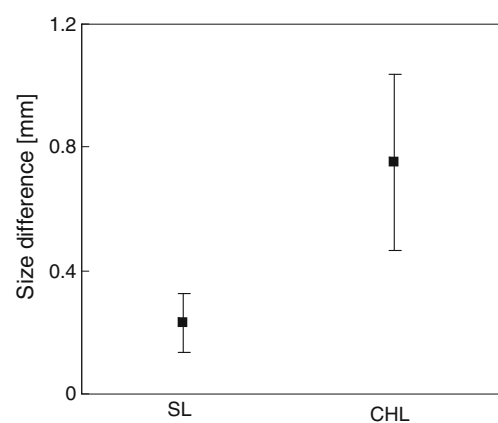


Fig. 2 Size differences in body size (SL) and cheliped size (CHL) between the winners and the losers (winner – loser). (Adjusted) mean differences and their 95% confidence intervals were presented

Table 2 Logistic regression parameters and their effect size (ES_r) for total contests, no fight contests, and contests with fights

Parameters	Mean (CI)	Z (CI)	<i>p</i> value	ES _r (CI)
Total contests (<i>n</i> =66)				
Intercept	-18.4 (-21.0, -17.2)	–	–	–
SL ratio	7.5 (6.4, 9.1)	2.09 (1.79, 2.33)	0.036 (0.019, 0.073)	0.25 (0.22, 0.28)
CHL ratio	10.8 (10.0, 12.6)	3.4 (3.24, 3.52)	0.0008 (0.0004, 0.0012)	0.39 (0.37, 0.40)
Nagelkerke <i>r</i> ²	0.61 (0.58, 0.65)	–	–	–
VIF	1.39 (1.31, 1.48)	–	–	–
No fight (<i>n</i> =23)				
Intercept	-8.6 (-13.5, -6.6)	–	–	–
SL ratio	1.8 (-1.0, 4.9)	0.35 (-0.21, 0.83)	0.71 (0.41, 0.83)	0.08 (-0.04, 0.18)
CHL ratio	6.7 (5.2, 10.9)	1.85 (1.5, 2.09)	0.064 (0.037, 0.13)	0.37 (0.31, 0.41)
Nagelkerke <i>r</i> ²	0.28 (0.15, 0.52)	–	–	–
VIF	1.76 (1.50, 2.09)	–	–	–
Fights (<i>n</i> =42)				
Intercept	-32.1 (-46.6, -19.6)	–	–	–
SL ratio	14.0 (11.3, 22.2)	2.12 (1.8, 2.3)	0.035 (0.021, 0.071)	0.32 (0.28, 0.34)
CHL ratio	18.0 (15.1, 26.4)	2.42 (2.2, 2.6)	0.016 (0.009, 0.027)	0.36 (0.33, 0.38)
Nagelkerke <i>r</i> ²	0.76 (0.72, 0.84)	–	–	–
VIF	1.31 (1.22, 1.42)	–	–	–

The coefficient of determination of each model was presented by Nagelkerke *r*². Means and their 95% confidence intervals (CI) of each parameter and effect size were constructed from 5,000 bootstrap simulations (i.e., 5,000 random assignments of the focal contestant). Wald statistics (*Z*) and *p* values are also presented with confidence intervals for reference

SL shield length, *CHL* cheliped length, *VIF* variance inflation factor for detecting collinearity between *SL* and *CHL* ratios

both *SL* and *CHL* ratios did not include zero, indicating that both parameters are significant predictors of contest outcomes. The Nagelkerke *r*² indicated that *SL* and *CHL* ratios explained about 60% of the variation in contest outcome. Moreover, the effect size for *CHL* ratio was significantly larger than that of *SL* ratio as indicated by the lack of overlap in the two confidence intervals (0.22–0.28 in *SL*, 0.37–0.40 in *CHL*). However, separate regression for the two contest types yielded different results. In 23 contests without physical contacts, only the *CHL* ratio showed a significant effect based on the confidence interval not including zero, while the mean Wald statistics denoted a non-significant *p* value. This non-significance might be due to the small sample size, because the estimated effect size for the *CHL* ratio in this subset of 23 contests is as large as that for all 66 contests. The effect size for *SL* ratio also did not differ from zero, but the interval was about twice to three times wider than that for the other cases. Hence, we cannot accurately estimate the effect of *SL* ratio, but it is clear that the effect was smaller than that for *CHL*. In contrast, both *SL* and *CHL* ratios showed significant, non-zero effect sizes in the 42 escalated fights. Although the difference between them was not significant because of the overlap in their confidence intervals, the effect size for *CHL* was larger than that for *SL*.

Discussion

The effect of cheliped size on fight outcome was larger than that for body size when looking at all 66 contests (based on the 95% confidence intervals—*SL*=0.22–0.28; *CHL*=0.37–0.40). In the 23 non-contact contests, only cheliped size had a non-zero effect (0.31–0.41) on fight outcome, and the confidence interval of body size included zero (–0.04–0.18). While the confidence intervals for the effect of body and cheliped size on fight outcome overlapped in the 42 escalated fights (*SL*=0.28–0.34; *CHL*=0.33–0.38), the effect of *CHL* was still generally larger. Considering these results together suggests that cheliped size is more important than body size in determining contest outcomes. Many studies have shown that body size is a major determinant of the outcome of contests for access to females in hermit crabs (Asakura 1987; Hazlett and Baron 1989; Harvey 1990; Wada et al. 1999; Yoshino et al. 2004). However, no study has shown that chelipeds are more important than body size in determining contest outcome. Our study is the first to report this in hermit crabs.

Large chelipeds might deter opponents by acting as a signal (Andersson 1994; Emlen 2008). The visual deterrence effect of chelipeds is clear in fiddler crabs. Regenerated claws are ineffective in escalated fights compared to

equivalent sized original claws, but are an effective bluff to rival males with original claws (Backwell et al. 2000; Lailvaux et al. 2009). In the snapping shrimp *Alpheus heterochaelis* (Hughes 2000) and the hermit crab *Pagurus bernhardus* (Arnott and Elwood 2010), individuals with larger chelipeds than expected for their body size can convey deceptive information about their real RHP during contests by displaying the cheliped more often. In *D. nitidimanus*, whether agonistic fights occur depends fundamentally on the decision of non-guarding rivals. In the logistic regression for the no fight contests (i.e., when the first male to guard male won without fighting), only CHL ratio influenced the outcome, indicating that non-guarding rivals were reluctant to fight with guarding males that had larger chelipeds, and that cheliped size might therefore function as a visual signal to opponents.

Chelipeds should also function as effective weapons when used in physical contests. The effect size for cheliped ratio was equivalent or larger than that for body size in escalated fights, indicating that chelipeds are not simply a signal of RHP that can be attributed to body size. Larger chelipeds could give a stronger closing force and provide an advantage in contests as found in other crustaceans (e.g., Sneddon et al. 2000; Seebacher and Wilson 2006; Lailvaux et al. 2009). Large chelipeds might also have high performance abilities when used to flick away an opponent during fights. Although the actual physical performance of chelipeds in *D. nitidimanus* remains to be clarified, the fact that cheliped size, corrected for body size, predicted fight outcome indicates that male major chelipeds are a trait under intra-sexual selection and that chelipeds are real weapons.

In several animals, weapons function as ornaments to attract mates (reviewed in Berglund et al. 1996; Briffa and Sneddon 2007; Emlen 2008), but this is unlikely in *D. nitidimanus*. Direct choice of a particular male by females is not known in hermit crabs, although *Pagurus filholi* females could choose males indirectly through male–male competition during guarding (Yamanoi et al. 2006; Okamura and Goshima 2010). Similarly, female behavior should not affect the outcome of the contests we staged. Although female resistance to male mating attempts affects the outcomes of male–male contests in many animal taxa (reviewed in Arnqvist and Rowe 2005), female hermit crabs cannot resist males' guarding attempt unless they are larger than males, but guarding males are larger than females (Asakura 1987; Yoshino et al. 2002; Koga et al. 2010).

The efficacy of *D. nitidimanus* chelipeds in escalated fights represents an intriguing contrast to studies on the snapping shrimp *A. heterochaelis* and the hermit crab *P. bernhardus*. In these species, chelipeds simply function as a visual signal of RHP and do not significantly contribute to the outcomes of escalated fights (Hughes 1996, 2000;

Elwood et al. 2006; Arnott and Elwood 2010). Individuals with larger chelipeds than expected for body size can therefore often deceive opponents about their real RHP (Hughes 2000; Arnott and Elwood 2010). The difference might be explained by the type of resources being disputed. For example, the sand-bubbler crab *Scopimera globosa* becomes more aggressive when competing for mates than for refuges (Koga and Ikeda 2010). We studied *D. nitidimanus* contests over females, which might lead to different results than those in *A. heterochaelis* and *P. bernhardus* fighting for resources in a non-reproductive situation.

The value of contested resources affects the dynamics of contest escalation in many animals (reviewed in Arnott and Elwood 2008). In our experiments, the females in the non-fighting trials might have been less attractive than those in escalated fights. In fact, in several of the escalated contests males were challenged by their rivals. We did not consider the effect of female size or time remaining until she spawned. As no size-assortative mating is found in *D. nitidimanus* (Asakura 1987; Koga et al. 2010), however, large fecund females would not necessarily motivate males to fight more persistently than when competing for small females. In *P. filholi*, males do not decide to guard a female based on her size or the time remaining until spawning (Goshima et al. 1998).

Traits under sexual selection often exhibit high variation (e.g., Hayashi 1985; Alatalo et al. 1988; Koga and Hayashi 1993; Pomiankowski and Møller 1995). According to Pomiankowski and Møller (1995), the average CV of phenotypic variation in sexually selected traits is 22.3% compared with 7.35% in non-sexually selected traits. The CV of CHL is about 21.5% in *D. nitidimanus*, which is consistent with a sexually selected trait.

Persistent directional selection as in the present case (i.e., larger weapon is favored) should reduce trait variation. How then is the large variation in cheliped size maintained in *D. nitidimanus*? One explanation is condition-dependence (Rowe and Houle 1996) due to the costs of weaponry. Without the costs of having large chelipeds, all individuals would grow chelipeds maximally to ensure high mating success. The cost of weaponry is a key element determining their relative growth (van Lieshout and Elgar 2009 and references therein). Doake et al. (2010) report that possession of larger chelipeds than expected for body size imposes significant energetic costs in *P. bernhardus*. Shell condition might also affect cheliped size since cheliped allometry is affected by their shell type (Turra and Leite 2003; Biagi and Mantelatto 2006).

In conclusion, the chelipeds of *D. nitidimanus* appear to function as both a visual signal used to settle contests with displays and a real weapon when fights escalate. In general, the effect of cheliped size on fight outcome was larger than

that of body size. While we focused on male–male competition for females in this study, chelipeds might also be used in contests for other resources. In hermit crabs, shells are an important resource for which there are intensive fights (e.g., Yoshino and Goshima 2002; Briffa and Elwood 2004; Gherardi 2006). However, the large CV and the positive allometry of male chelipeds in *D. nitidimanus* suggest that they have evolved mainly in the context of mating competition.

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References

- Alatalo RV, Höglund J, Lundberg A (1988) Patterns of variation in tail ornament size in birds. *Biol J Linn Soc* 34:363–374. doi:10.1111/j.1095-8312.1988.tb01969.x
- Andersson M (1994) Sexual selection. Princeton University Press, Princeton
- Arnott G, Elwood RW (2008) Information gathering and decision making about resource value in animal contests. *Anim Behav* 76:529–542. doi:10.1016/j.anbehav.2008.04.019
- Arnott G, Elwood RW (2010) Signal residuals and hermit crab displays: flaunt it if you have it! *Anim Behav* 79:137–143. doi:10.1016/j.anbehav.2009.10.011
- Arnqvist G, Rowe L (2005) Sexual conflict. Princeton University Press, Princeton
- Asakura A (1987) Population ecology of the sand-dwelling hermit crab *Diogenes nitidimanus* Terao: 3. Mating system. *Bull Mar Sci* 41:282–288
- Backwell PRY, Christy JH, Telford SR, Jennions MD, Passmore NI (2000) Dishonest signalling in a fiddler crab. *Proc R Soc Lond B* 267:719–724
- Barki A, Harpaz S, Karpus I (1997) Contradictory asymmetries in body and weapon size, and assessment in fighting male prawns, *Macrobrachium rosenbergii*. *Aggress Behav* 23:81–91. doi:10.1002/(SICI)1098-2337(1997)23:2<81::AID-AB1>3.0.CO;2-W
- Berglund A, Bisazza A, Pilastro A (1996) Armaments and ornaments: an evolutionary explanation of traits of dual utility. *Biol J Linn Soc* 58:385–399. doi:10.1111/j.1095-8312.1996.tb01442.x
- Biagi R, Mantelatto FLM (2006) Relative growth and sexual maturity of the hermit crab *Paguristes erythropros* (Anomura, Diogenidae) from South Atlantic. *Hydrobiologia* 559:247–254. doi:10.1007/s10750-005-9115-x
- Briffa M, Elwood RW (2004) Use of energy reserves in fighting hermit crabs. *Proc R Soc Lond B* 271:373–379
- Briffa M, Sneddon LU (2007) Physiological constraints on contest behaviour. *Funct Ecol* 21:627–637. doi:10.1111/j.1365-2435.2006.01188.x
- R Development Core Team (2008) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0. Available at <http://www.R-project.org>
- Doake S, Scantlebury M, Elwood RW (2010) The costs of bearing arms and armour in the hermit crab *Pagurus bernhardus*. *Anim Behav* 80:637–642. doi:10.1016/j.anbehav.2010.06.023
- Elwood RW, Pothanikat RME, Briffa M (2006) Honest and dishonest displays, motivational state and subsequent decisions in hermit crab shell fights. *Anim Behav* 72:853–859. doi:10.1016/j.anbehav.2006.01.025
- Emlen DJ (2008) The evolution of animal weapons. *Ann Rev Ecol Evol Syst* 39:387–413. doi:10.1146/annurev.ecolsys.39.110707.173502
- Gherardi F (2006) Fighting behavior in hermit crabs: the combined effect of resource-holding potential and resource value in *Pagurus longicarpus*. *Behav Ecol Sociobiol* 59:500–510. doi:10.1007/s00265-005-0074-z
- Goshima S, Kawashima T, Wada S (1998) Mate choice by males of the hermit crab *Pagurus filholi*: do males assess ripeness and/or fecundity of females? *Ecol Res* 13:151–161
- Harvey AW (1990) Sexual differences in contemporary selection acting on size in the hermit crab *Clibanarius digueti*. *Am Nat* 136:32–43
- Hayashi K (1985) Alternative mating strategies in the water strider *Gerris elongatus* (Heteroptera, Gerridae). *Behav Ecol Sociobiol* 16:301–306. doi:10.1007/BF00295542
- Hazlett BA, Baron LC (1989) Influence of shells on mating behavior in the hermit crab *Calcinus tibicen*. *Behav Ecol Sociobiol* 24:369–376. doi:10.1007/BF00293264
- Hughes M (1996) Size assessment via a visual signal in snapping shrimp. *Behav Ecol Sociobiol* 38:51–57. doi:10.1007/s002650050216
- Hughes M (2000) Deception with honest signals: signal residuals and signal function in snapping shrimp. *Behav Ecol* 11:614–623
- Jennions MD, Backwell PRY (1996) Residency and size affect fight duration and outcome in the fiddler crab *Uca annulipes*. *Biol J Linn Soc* 57:293–306. doi:10.1111/j.1095-8312.1996.tb01851.x
- Judge KA, Bonanno VL (2008) Male weaponry in a fighting cricket. *PLoS ONE* 3:e3980. doi:10.371/journal.pone.003980
- Koga T, Hayashi K (1993) Territorial behavior of both sexes in the water strider *Metrocoris histrio* (Hemiptera: Gerridae) during the mating season. *J Insect Behav* 6:65–77. doi:10.1007/BF01049148
- Koga T, Ikeda S (2010) Perceived predation risk and mate defense jointly alter the outcome of territorial fights. *Behav Ecol Sociobiol* 64:827–833. doi:10.1007/s00265-009-0899-y
- Koga T, Yoshino K, Fukuda Y (2010) Temporal changes in the reproductive population structures and males' chelae size of the hermit crab *Diogenes nitidimanus*. *Ecol Res* 25:1007–1017. doi:10.1007/s11284-010-0727-x
- Lailvaux SP, Reaney LT, Backwell PRY (2009) Dishonest signaling of fighting ability and multiple performance traits in the fiddler crab *Uca mjoebergi*. *Funct Ecol* 23:359–366. doi:10.1111/j.1365-2435.2008.01501.x
- Nagelkerke N (1991) A note on a general definition of the coefficient of determination. *Biometrika* 78:691–692. doi:10.1093/biomet/78.3.691
- Nakagawa S, Cuthill IC (2007) Effect size, confidence interval and statistical significance: a practical guide for biologist. *Biol Rev* 82:591–605. doi:10.1111/j.1469-185X.2007.00027.x
- Neil SJ (1985) Size assessment and cues: studies of hermit crab contests. *Behaviour* 92:22–38
- Okamura S, Goshima S (2010) Indirect female choice mediated by sex pheromones in the hermit crab *Pagurus filholi*. *J Ethol* 28:323–329. doi:10.1007/s10164-009-0188-2
- Pomfret JC, Knell RJ (2006) Sexual selection and horn allometry in the dung beetle *Euoniticellus intermedius*. *Anim Behav* 71:567–576. doi:10.1016/j.anbehav.2005.05.023
- Pomiankowski A, Møller AP (1995) A resolution of the lek paradox. *Proc R Soc Lond B* 260:21–29
- Quinn GP, Keough MJ (2002) Experimental design and data analysis for biologists. Cambridge University Press, Cambridge, p 537

- Rowe L, Houle D (1996) The lek paradox and the capture of genetic variance by condition dependent traits. *Proc R Soc Lond B* 263:1415–1421
- Searcy WA, Nowicki S (2005) The evolution of animal communication. Princeton University Press, Princeton
- Seebacher F, Wilson RS (2006) Fighting fit: thermal plasticity of metabolic function and fighting success in the crayfish *Cherax destructor*. *Funct Ecol* 20:1045–1053. doi:10.1111/j.1365-2435.2006.01194.x
- Sneddon LU, Huntingford FA, Taylor AC (1997) Weapon size versus body size as a predictor of winning in fights between shore crabs, *Carcinus maenus* (L.). *Behav Ecol Sociobiol* 41:237–242. doi:10.1007/s002650050384
- Sneddon LU, Huntingford FA, Taylor AC, Orr JF (2000) Weapon strength and competitive success in the fights of shore crabs (*Carcinus maenus*). *J Zool* 250:397–403. doi:10.1017/S0952836900003125
- Styrsky JD, Van Rhein S (1999) Forceps size does not determine fighting success in European earwigs. *J Insect Behav* 12:475–482. doi:10.1023/A:1020962606724
- Turra A, Leite FPP (2003) The molding hypothesis: linking shell use with hermit crab growth, morphology, and shell-species selection. *Mar Ecol Prog Ser* 265:155–163
- van Lieshout E, Elgar MA (2009) Armament under direct sexual selection does not exhibit positive allometry in an earwig. *Behav Ecol* 20:258–264. doi:10.1093/beheco/arp013
- Wada S, Tanaka K, Goshima S (1999) Precopulatory mate guarding in the hermit crab *Pagurus middendorffii* (Brandt) (Decapoda: Paguridae): effects of population parameters on male guarding duration. *J Exp Mar Biol Ecol* 239:289–298. doi:10.1016/S0022-0981(99)00045-3
- Yamanoi T, Yoshino K, Kon K, Goshima S (2006) Delayed copulation as a means of female choice by the hermit crab *Pagurus filholi*. *J Ethol* 24:213–218. doi:10.1007/s10164-005-0182-2
- Yoshino K, Goshima S (2002) Sexual dominance in hermit crab shell fights: asymmetries in owner–intruder status, crab size, and resource value between sexes. *J Ethol* 20:63–69. doi:10.1007/s10164-002-0055-x
- Yoshino K, Goshima S, Nakao S (2002) Temporal reproductive patterns within a breeding season of the hermit crab *Pagurus filholi*: effects of crab size and shell species. *Mar Biol* 141:1069–1075. doi:10.1007/s00227-002-0876-8
- Yoshino K, Ozawa M, Goshima S (2004) Effects of shell size fit on the efficacy of mate guarding behaviour in male hermit crabs. *J Mar Biol Assoc UK* 84:1203–1208. doi:10.1017/S0025315404010653h