

# Resource value differentially affects fighting success between reproductive and non-reproductive seasons

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**Abstract** Inter-male competition for resources is usually studied during species' reproductive seasons because fighting is common and conspicuous, but how this competition compares with that during the non-reproductive season is rarely investigated. Here, we compared competition for burrows between the reproductive and non-reproductive seasons in a mud crab. We conducted two natural and three experimental observations: Under natural conditions, we observed fights between residents and intruders in (1) reproductive and (2) non-reproductive seasons, and found similar results in both seasons; two factors, body size difference and residency, contributed equally to fight outcomes; (3) During the reproductive season we created an intruder by capturing a resident male and placing him in the burrow of another resident to induce a fight; (4) We repeated this but first placed a female in the burrow before introducing the intruder; findings for both experiments were similar to those for natural fights; (5) During the non-reproductive season, we repeated the third experiment and found a different result: fight outcome was determined by the difference in body size, not residency. This is the first study to show that differing subjective value of a resource between the reproductive and non-reproductive seasons affects fight outcomes.

**Keywords** Intertidal mud crabs · *Ilyoplax pusilla* · Contest outcomes · Resource value · Residency effect · Body size · Reproductive and non-reproductive seasons

## Introduction

Animals often engage in aggressive interactions to obtain resources required for survival and successful reproduction, such as food, water, shelter and access to mates. The intensity of these interactions may depend on the animals' need for contested resources, which ultimately increases the subjective value of those resources (Arnott and Elwood 2008). Resource necessity may vary with the internal state of the contestants. For example, during the reproductive season, mating partners are the most highly prized resources (Briffa and Sneddon 2007), whereas food is the most important resource during the non-reproductive season (Dearborn 1998).

In agonistic interactions that occur over a limited resource, there are often asymmetries in individuals' fighting abilities (resource holding potential, RHP; Parker 1974) that usually influence fighting success (Arnott and Elwood 2009). Individuals' fighting abilities (RHP) are typically related to body size (Brown et al. 2007) as well as many other factors such as weapon size (Sneddon et al. 1997; Yoshino et al. 2011), age (Koga and Hayashi 1993; Kemp et al. 2006), aggressiveness mediated by hormone levels (Rohwer and Rohwer 1978), energy reserves or stamina (Briffa and Sneddon 2007) and sex (Bryant and Newton 1996). Furthermore, prior ownership of a resource may influence the fighting success by affecting the RHP directly. This has been termed "resource-correlated RHP" (Kemp and Wiklund 2001; Humphries et al. 2006). Another factor, resource value (RV, Maynard Smith 1982), also contributes to an animal's motivation to obtain or retain a resource. When the RV is high, this will be reflected in a high motivation to fight, which may allow individuals to overcome inferior RHP (Davies 1978; Lindstron and Pampoulie 2005; Gherardi 2006; Brown

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et al. 2007; Koga and Ikeda 2010). Although the value of the resource is likely to affect fight outcomes, we know of no studies that compare RV and fight outcomes during the reproductive and non-reproductive seasons, during which the value of the resource often differs.

Here, we examined contests over burrows during the reproductive and non-reproductive seasons in an ocypodid crab. This is an ideal group for this study since males have large claws (chelae) that they use in fights over burrow ownership. They are also easily manipulated and measured (Koga and Ikeda 2010). The burrow is a highly contested resource since it provides shelter from predators and extreme climatic conditions at low tides (Hyatt and Salmon 1978), but in addition, it is the site for mating and incubation. In many ocypodid species, females mate in the males' burrows (Christy 1982; Koga et al. 1993). As a way of getting mates, male–male combat over burrow ownership is especially prevalent during the reproductive season since possession of the burrow is essential for reproductive success (Hyatt and Salmon 1978). We predicted that this additional value of a burrow during the reproductive season will make it an even more valuable resource than in the non-reproductive season.

Here, we observed fights over burrows in a mud crab under both natural and experimental conditions. We conducted observations under natural conditions in which the behaviour of the crabs was only minimally disturbed, during both the reproductive and non-reproductive seasons. We also conducted two sets of experimental manipulations: (1) increasing the resource value for the intruder during both the reproductive and non-reproductive seasons. We did this by digging out, capturing, handling, and releasing the intruders into other residents' burrows. This created an intruder with an increased perception of threat, and we therefore predicted that they would place a higher value on the burrow as a shelter. (2) We increased the value of the resource for the resident. We achieved this by placing a female in the resident's burrow prior to staging a fight with an intruder. We predicted that the presence of the female would increase the RV and therefore affect the resident's motivation to win. This experiment was conducted only in the reproductive season since females are not valuable resources in the non-reproductive season.

For each of these fights, we report on the factors that determine winning (body size asymmetry, residency) and how the outcomes differ between the reproductive and non-reproductive seasons. We predict that smaller males are more likely to lose contests due to their low RHP, but if they place a high value on the burrow (as an intruder or as a resident), then they should win disproportionately more fights than suggested by their inferior RHP.

## Materials and methods

*Ilyoplax pusilla* (family Dotillidae) is a common intertidal mud crab in Japan (Ono 1965). During the reproductive season, males attract females into their burrows for mating by producing an intensive waving display with their large chelae (Wada 1981). Wandering females that are ready to mate will respond to the male's courtship display and enter his burrow. The male then plugs the entrance using mud (Wada 1981), and the pair copulates underground (Koga et al. 1993). In the burrow, the female extrudes eggs 1–3 days after pair formation (Henmi and Murai 1999) and carries them for about 2 weeks (Henmi and Kaneto 1989). After ovulation, the male immediately leaves and occupies another burrow in which he mates with another female (Henmi and Murai 1999).

The study site was the Waka River Estuary, Wakayama, Japan. We observed natural fights in 2011 and experimental fights in 2009 during the reproductive (June–August) and non-reproductive (May, September and October) seasons. All observations were carried out at diurnal low tides. Observations began 2 h before and ended 2 h after low tide.

### Natural fights

We observed fights under natural conditions, without disturbing the normal behaviours of the crabs. To create an intruder, we plugged the burrow of a resident male with a thick paper plug while he was away from his burrow for foraging. The paper plug was sufficient to prevent the resident from retreating back into the burrow, and we then observed these burrow-less males as they sought a resident with which to fight. We did not consider that this process had a significant effect on the perceived predation threat for the crab since predation levels were low under the natural conditions. We waited a maximum of 15 min to observe fights for each intruder. As we did not mark the intruders, body size, carapace colour, or some other distinctive feature that differed between the resident and the intruder was observed very carefully to distinguish them. After the end of a fight, we captured both the winner and loser and measured their carapace width (CW) using a hand caliper to the 0.1 mm level. We observed 47 fights in the reproductive season and 55 fights in the non-reproductive season.

### Experimental manipulation of the resource value

We increased the value of the burrow for the intruder by manipulating his perception of predation threat. We randomly selected a mature, waving male, dug him out of his burrow and marked his carapace with a paint marker for

easy identification. The handling process increases the perception of threat for the male, which would increase the value of the burrow as a potential refuge (Koga and Ikeda 2010). Within a few minutes of capture, we placed the male (hereafter called the intruder) at the entrance of a resident’s burrow and documented the ensuing fight. We noted the winner as the male that remained in the burrow after the fight, and the loser as the male that left the area. We conducted this experiment in both the reproductive and non-reproductive seasons. We observed 50 fights in the reproductive season and 51 fights in the non-reproductive season. For each fight, we captured both crabs and measured their carapace widths after the fight had ended. Individuals were used only once.

We also ran an experiment in which we increased the value of the burrow for both combatants. We again created motivated intruders as described above, but in addition, we placed a female inside the burrow of the targeted resident male. The provision of a female increases the resident’s motivation to defend his burrow (Koga and Ikeda 2010). Adult wandering females (CW >4 mm; Yoshimura and Wada 1992) were captured from the same study area on the same day of the experiment. When placed at the entrance of a male’s burrow, the female immediately entered the burrow to escape from the perceived predation threat. We observed her for a few minutes to check that she did not leave the burrow. If she stayed, the male emerged and plugged the burrow entrance with mud. While the resident was still active, we placed the intruder at the burrow entrance and documented the ensuing fight. In this experiment, both the intruder and resident placed a high value on the resource (the intruder due to increased perception of predation, and the resident due to the presence of a female). We observed 51 fights during the reproductive season. We captured both crabs at the end of fights to measure their CW.

In some cases, we found that resident males avoided direct fighting by blocking the burrow entrance with their chela from inside the burrow entrance. We noted whether a male performed this tactic.

Statistics

We used logistic regression analyses to determine the effect of body size difference, male status (resident or intruder) and the increases of RV on the outcomes of fights. Difference in body size (CW of the resident minus that of the intruder, mm) was the independent variable. Fight outcome for the resident male (win = 1, loss = 0) was the dependent variable, and the effect of predation threat and female mate acquisition were the explanatory variables. The intercept is expressed as the residency advantage in the tables. To clarify the effects of seasons on the outcomes,

**Table 1** Estimated values of the parameters and the standard errors in the logistic regression analysis (for both individual and pooled datasets) of contests for burrows under natural conditions in the reproductive and non-reproductive seasons

Category	Estimated values of the parameters	Standard error	Chi-square	P value
<b>Reproductive season</b>				
Intercept (residency advantage)	1.159	0.478	5.88	0.0153
Difference in body size (CW of the resident minus that of the intruder, mm)	2.315	0.685	11.43	0.0007
<b>Non-reproductive season</b>				
Intercept (residency advantage)	1.345	0.441	9.31	0.0023
Difference in body size (mm)	1.513	0.431	12.28	0.0005
<b>Data pooled for both seasons</b>				
Intercept (residency advantage)	1.246	0.319	15.24	<0.0001
Difference in body size (mm)	1.800	0.365	24.34	<0.0001
Seasons (reproductive/non-reproductive)	0.289	0.260	1.24	0.2660

CW carapace width

analyses were conducted for the reproductive and non-reproductive seasons under both natural and experimental conditions, with a single analysis for each observation, as well as pooling the data for each condition (all natural/all experimental) separately (Tables 1, 2). Data from the natural observations were compared with the experimental results. We also pooled the data to examine the effect of body size, residency, predation risk, female acquisition and seasons on the fight outcomes (lower part of Tables 1, 2). To analyse the effect of body size on burrow blocking in the second experiment, a one-tailed *t* test was used. We tested data for normality before using parametric tests.

Results

Natural fights

A total of 47 and 55 males were observed in the reproductive and non-reproductive seasons, respectively. There was no significant difference in CW (mm) between the residents [7.06 ± 0.81 mm, mean ± standard deviation (SD), *n* = 47] and the intruders (7.36 ± 0.91 mm, *n* = 47, *t* = 1.67, *df* = 92, *P* = 0.0981) during the reproductive

**Table 2** Estimated values of the parameters and the standard errors in the logistic regression analysis (for both individual and pooled datasets) of contests for burrows between the residents and intruders under experimental conditions

Category	Estimated values of the parameters	Standard error	Chi-square	<i>P</i> value
<b>Intruder with increased RV</b>				
Reproductive season				
Intercept (residency advantage)	1.481	0.448	10.92	0.0010
Body size difference (CW of the resident minus that of the intruder, mm)	0.846	0.352	5.78	0.0162
<b>Intruder and resident with increased RV</b>				
Reproductive season				
Intercept (residency advantage)	2.133	0.594	12.91	0.0003
Difference in body size (mm)	1.698	0.552	9.45	0.0021
<b>Intruder with increased RV</b>				
Non-reproductive season				
Intercept (residency advantage)	0.097	0.353	0.08	0.7839
Difference in body size (mm)	2.969	0.995	8.90	0.0029
<b>Data pooled for both seasons</b>				
Intercept (residency advantage)	1.052	0.272	14.92	0.0001
Difference in body size (mm)	1.454	0.294	24.51	<0.0001
Female mate acquisition	-0.037	0.276	0.02	0.8930
Seasons (reproductive/non-reproductive)	-0.936	0.284	10.82	0.0010

RV resource value, CW carapace width

season, but this difference was significant in the non-reproductive season (residents:  $6.63 \pm 0.87$  mm; intruders:  $7.02 \pm 0.81$  mm,  $n = 55$ , respectively;  $t = 2.476$ ,  $df = 108$ ,  $P = 0.0149$ ).

During the reproductive season, both male size and residency affected the outcomes of fights. Residents were more likely to win even when they were smaller. Larger crabs were more likely to win. Similar results were also found during the non-reproductive season (Table 1).

#### Experimental manipulation of the resource value

There were no significant differences in CW between the residents and intruders throughout the experimental treatments, i.e., during the reproductive season (residents:

$7.94 \pm 1.03$  mm; intruders:  $8.33 \pm 1.22$  mm,  $n = 50$ , respectively,  $t = 1.70$ ,  $df = 98$ ,  $P = 0.0922$ , when only the intruder was motivated; residents:  $7.63 \pm 0.87$  mm; intruders:  $7.64 \pm 1.10$  mm,  $n = 51$ , respectively,  $t = 0.082$ ,  $df = 100$ ,  $P = 0.9349$ , when both males were motivated) and in the non-reproductive season (residents:  $7.66 \pm 0.72$  mm; intruders:  $7.52 \pm 0.61$  mm,  $n = 51$ , respectively,  $t = -1.0$ ,  $df = 100$ ,  $P = 0.3186$ , when only the intruder was motivated).

#### During the reproductive season

When the intruder perceived an increased threat of predation, fight outcome was again determined by both body size and residency, similar to the finding for natural observations (Table 2). When the resident's resource value was increased (by giving him a female), the results were again similar to those above, with both body size and residency affecting fighting success (Table 2).

The presence of the female, however, affected the fighting style of the resident male. Residents with females were more likely to block the burrow entrance with their claw. Twelve of the 51 males blocked their burrow entrance when a female was in their burrow (24 %), while only two of the 50 males did so when there was no female present (4 %). This difference was significant ( $P < 0.01$ , Fisher's exact test). Males were more likely to block their burrow entrances when the size difference between rivals (CW of resident minus intruder) was greatest, with smaller residents being more likely to block (mean  $\pm$  SD:  $-0.438 \pm 0.70$ ,  $n = 12$  versus  $0.114 \pm 1.26$ ,  $n = 39$ ;  $t = 1.927$ ,  $P = 0.031$ , one-tailed  $t$  test with uneven variance).

#### During the non-reproductive season

When the intruder perceived an increased threat of predation, there was no residency advantage. The winners were almost always the larger crabs regardless of burrow ownership (Table 2). When the body sizes of the rivals were closely matched, there was an equal chance of winning by the resident and the intruder.

When we pooled the data of natural observations ( $n = 102$ ), only the effects of body size differences and residency were significant, but not the seasons (Table 1). In experiments ( $n = 152$ ), however, there was a significant effect of season in addition to body size and residency, but there was no effect of mate acquisition (Table 2).

## Discussion

We have shown that, in mud crabs, the residency advantage is not consistent, but rather changed between the

reproductive and non-reproductive seasons. When intruders placed a high value on burrow ownership (because they perceived a greater threat of predation), there was no evidence of a residency advantage. In the reproductive season, however, there was a strong residency advantage. This is consistent with differences in the subjective resource value (Arnott and Elwood 2008) of burrows for residents between reproductive and non-reproductive seasons.

The rival with the higher RHP is more likely to win contests (Austad 1983; Haley 1994; Koga and Ikeda 2010). The difference in body size between rivals is often considered an important RHP asymmetry and can even be sufficient to prevent or prematurely end fights (see Archer 1988). Prior residency also has a strong effect on fight outcomes, since it directly affects the RHP (termed the resource-correlated RHP; Kemp and Wiklund 2001; Humphries et al. 2006). An intruder may have an initial size advantage over a smaller resident, but the residency advantage can override this (fiddler crabs: Hyatt and Salmon 1978; Jennions and Backwell 1996; Fayed et al. 2008; white seabream: Caballero and Castro 1999; speckled wood butterfly: Kemp and Wiklund 2004). Since residents have good information about the resources, they may overcome any RHP asymmetry by making accurate decisions in the contests regarding the true quality of the resources (Arnott and Elwood 2008). In the present study, burrows are always important resources for male *I. pusilla*, but during the reproductive season they have the additional value as a mating site.

We found no difference in fight outcomes between the reproductive and non-reproductive seasons in the naturally observed fights, with body size and residency having the same effect on fight outcome in the two seasons. When the motivation was high for the intruder, however, fight outcome was determined by both body size and residency during the reproductive season, but only by body size in the non-reproductive season. The residency effect was not present in the non-reproductive season. This may be because residents valued the burrow more highly in the reproductive season and fought harder to retain it since the loss of a burrow in the reproductive season would have severe consequences for their mating success and hence their fitness.

In several species, increased predation risk elevates the value of a refuge and therefore increases the males' motivation to fight for it (Yoshino and Goshima 2002; Gherardi 2006; Koga and Ikeda 2010). When victory greatly elevates a male's chance of survival, they should fight harder to win (Koga and Ikeda 2010). In the present study, however, predation threat to the intruders was not able to overcome the residency advantage during the reproductive season, even though it did so in the non-reproductive season. It appears that the motivation of residents to retain their

burrows during the reproductive season is extremely strong, and overrides the motivation of threatened intruders. The perceived resource value, which is governed by the internal state of the animal, is likely an important factor determining the intensity of aggression (Arnott and Elwood 2008). The disappearance of the residency advantage in the non-reproductive season may indicate that the value of the burrows decreased for the resident males, as the level of aggression is determined by the RV. Decreased RV appears to have changed the outcome of the fights between the two seasons. This is not surprising, since animals usually pay higher costs when the benefits are greater (Tricarico and Gherardi 2010).

The presence of a potential mate in a territory temporarily increases the value of the territory and leads to higher escalation of a contest than when no female is present (see Tachon et al. 1999; also in male damselfish: Santangelo et al. 2002; Hoem et al. 2007; Koga and Ikeda 2010). In the present study, however, acquisition of the female mate did not affect the fight outcomes. When only the resident male is aware of the female's presence, there is an asymmetry in information between the two contestants. The presence of a female would therefore only affect the fighting behaviour of the resident. Here we show that residents, especially smaller residents, blocked the entrance of their burrow from inside using their chelae, making it difficult for the intruders to invade and replace the owners. This behaviour is very similar to a defence tactic called 'flat-claw' described in *Uca* (Crane 1975); the male crab descends into his burrow and places his major claw such that it lies flat on the surface of the burrow entrance. This tactic was highly advantageous for burrow defence during underground mating in *Uca paradussumieri*, especially when the guarding males were smaller than the intruders (Koga et al. 1999). A similar defence tactic was also reported in *U. mjoebergi*, where the owners sometimes retreat from fights, either blocking the entrance with their claw or wedging into it while claw-grappling with their opponent (Fayed et al. 2008). Although these tactics are very effective in holding burrow ownership regardless of body size, the resident males in the present study did not always show this behaviour. One possible reason is that the blocking may cause more prolonged energetic fighting by the residents, like the flat-claw defence in *U. paradussumieri*, which sometimes induces further attacks by neighbouring males, raising the risk of takeover of both the burrow and mate (Koga et al. 1999).

The value of the contested resource is one of the most important factors influencing contest behaviour (Enquist and Leimar 1987). Many empirical studies have shown that animals adjust their fighting behaviour in line with resource value (reviewed by Arnott and Elwood 2008). In the present study, the residency advantage was so strong in

*I. pusilla* that no difference in outcome of the fights was detected between seasons under natural conditions. However, the artificial predation threats imposed on the intruders in experimental conditions overcame the residency advantage during the non-reproductive season when the value of the burrow was relatively low for the resident, in contrast to the reproductive season when it was high. To our knowledge this is the first study to show that residents lower their perceived resource valuation of burrows in the non-reproductive season.

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