ORIGINAL PAPER

The effect of size and cheliped autotomy on sexual competition between males of the mud crab *Cyrtograpsus angulatus* Dana

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Abstract Size advantage in male–male competition over mates, combined with male preference over large females, is a common feature that can drive to size assortative mating and, eventually, sexual selection. In crabs, appendage autotomy can affect assortative mating and opportunity for sexual selection by affecting size advantage in mating contests. In this work, we evaluate the effect of size and appendage autotomy in generating assortative mating in the mud crab *Cyrtograpsus angulatus*. Field observations of guarding pairs in two different populations show a positive correlation between carapace width of males and females in both the populations. In one of the populations, incidence of appendage autotomy was low and the variability in the size of reproductive males was lower than the variability in the size of randomly collected males (i.e. only larger males were successful in getting a female), whereas there was no differences in the other population (i.e. most male sizes were successful) where the incidence of appendage autot-omy was very high, indicating that the importance of size is higher when the incidence of autotomy is low. In this context, experiments (in both populations) show that, in contests for a female, larger males outcompete smaller ones only when they had intact appendages. When males had missing chelipeds, winning or loosing against smaller males was random. This may lead to a decrease in the importance of male size in populations with high incidence of cheliped autotomy, affecting assortative mating and opportunity for selection and, thus, affecting selective pressures.

Communicated by M. Byrne.

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Introduction

In brachyuran crabs, as in other crustaceans, the duration of female receptivity is often limited to a short period of time (Brockerhoff and McLay 2005) because female reproductive cycles are synchronized with physical factors or because copulation is only possible immediately after molt (Jormalainen 1998). This temporal limitation of sexual receptivity generates highly male biased operational sex ratios, thus producing intense competition among males for access to receptive females (see Parker 1970; Emlen and Oring 1977). The intense competition generates, in turn, the display of male strategies that include male–male agonistic interactions, as fights, and precopulatory and postcopulatory mate guarding (Brockerhoff and McLay 2005). Size of males usually plays a fundamental role concerning both fighting against other males and guarding females; larger males often defeat smaller ones at aggressive interactions, easily dominate females and avoid takeover by other males during guarding (Brockerhoff and McLay 2005). As female fecundity usually increases with size (e.g. Sainte-Marie et al. 1999; Silva et al. 2003), some male selection for large

females is usually found (Reading and Backwell 2007). This size advantage in male–male competition, combined with male choice for larger females (see Reading and Backwell 2007), can generate size assortative mating (i.e. non-random mating with respect to size, see Arnqvist et al. 1996; Jivoff 1997; Sainte-Marie et al. 1999) so that the sizes of the males and the females in mating pairs are positively correlated.

Size assortative mating can be generated by different mechanisms such as physical constraints (e.g. large males are physically unable to copulate with smaller females, Brown 1993; small males cannot carry large females, Adams et al. 1989; Hatcher and Dunn 1997), spatial covariation of sizes (males and females of similar sizes occur in patches; see Crespi 1989), female resistance (females resist male copulation attempts and large females are only dominated by large males; Jormalainen 1998) or male–male competition combined with male choice for large females (Iribarne et al. 1996). Although the same size assortative pattern can be the result of different causes, each cause has different evolutionary implications (see Crespi 1989; Arnqvist et al. 1996). For example, strong male competition and choosiness for mates are expected to increase the variance in mating success (i.e. large males will have more fitness than smaller ones; see Head and Brooks 2006), increasing the opportunity for sexual selection (sensu Arnold and Wade 1984a, b).

Autotomy (i.e. limb or cheliped loss) is an important adaptive mechanism to avoid predation and to limit attack damage that is common on decapod crustaceans (see Smith and Hines 1991; Wasson et al. 2002). Although it may provide a direct immediate survival benefit, cheliped autotomy can also generate long-term costs (Review, Juanes and Smith 1995) that include a decrease in mating success (Smith 1992; Juanes and Smith 1995). Multiple appendage loss, for example, can reduce fecundity in females (Silva et al. 2003) and competitive success in male–male contests (e.g. Smith 1992). This process can have an effect at the population level (Juanes and Smith 1995) because assortative mating may be affected by male fighting success and reduce the importance of size in mate contests (Smith 1992). In such situations, the advantage of large males in mating success is expected to decrease if they are missing appendages, thus affecting the opportunity for sexual selection (see Mills and Reynolds 2003). Thus, while autotomy may decrease mortality, it may decrease the reproductive success generating an added cost to the loss of a limb.

This study investigated the importance of size and appendage autotomy in generating size assortative mating in natural populations of the mud crab *Cyrtograpsus angulatus* and experimentally evaluated the hypothesis that cheliped autotomy can decrease size advantage in male–male contests. The grapsid crab *C. angulatus* lives in intertidal

areas of the South Western Atlantic coast between the southern part of Brazil (Rio de Janeiro, 27°S; Boschi 2000; Iribarne et al. 2003) and the central Argentinean Patagonia (Puerto Deseado, 48°S). This distribution encompasses two biogeographic provinces, the Argentinean Province (southern Brazil to northern Argentinean Patagonia) and the Magallanic Province (Argentinean Patagonian coast and the south of Chile; see Spivak 1997a, b; Boschi 2000). Their main habitat is open-coast rocky shores, but this species also penetrates into brackish waters (Spivak 1988; Iribarne et al. 2003). They are mainly mobile and active in the intertidal zone when the area is underwater, but most often they shelter under rocks or move to the shallow subtidal during low tide (Spivak et al. 1994).

Methods

Study site

Two *C. angulatus* populations were studied. One from Mar Chiquita coastal lagoon (thereafter MCh; Argentina: 37°32′–37°45′S and 57°19′–57°26′W), a brackish water area of about 46 km^2 with muddy sediments and low tidal amplitude (<1 m, Fasano et al. 1982). The other from San Antonio Bay (thereafter SA; Argentina: 40°45′S, 65°55′W), an 80 km^2 embayment affected by up to 9 m semidiurnal tides characterized by sandy pebble flats at lower tidal elevations, and salt marshes dominated by the smooth cordgrass *Spartina alterniflora* at higher tidal elevations (see Daleo et al. 2006). The MCh population is characterized by a high incidence of appendage autotomy (nearly 70% of the population have at least one limb missing, 40% have at least two limbs missing; Spivak and Politis 1989) and individuals are larger (adult sizes from 20 to 53 mm), while SA has a very low incidence of autotomy (less than 50% have at least one limb missing, only 15% have at least two limbs missing) and individuals are smaller (adult sizes from 20 to 40 mm; authors, personal observation). Those populations were chosen given logistic reasons and because they are two of the larger populations of the region (Iribarne et al. 2003).

Assortative mating size and incidence of autotomy

To evaluate the level of assortative mating, mate guarding pairs were manually collected, at both the sites, in the shallow subtidal (i.e. ~0.1 to 0.5 m depth from mean low tidal level) during low tide (from October 2002 to March 2003). Carapace width (distance between the anterolateral teeth measured with a caliper to the nearest 0.05 mm) and number of autotomized appendages were measured for both males and females. Correlation analyses (Zar 1999) were

used to test the null hypotheses of no relationship between male and female sizes for both sites.

To estimate whether the size frequency distribution (thereafter SFD), size variability and incidence of autotomy between guarding individuals and the adult population differed, adult crabs were randomly collected at each site. For each crab, carapace width and number of autotomized appendages were measured (males: MCh, $n = 177$; SA, $n = 136$; females: MCh, $n = 253$; SA, $n = 233$). The null hypotheses of no difference in SFD of randomly collected adults and guarding individuals (for each sex separately) were analyzed with Kolmogorov–Smirnov test (Zar 1999). Size coefficients of variation (size standard deviation × size mean^{-1}) were used to evaluate if there were differences in the size variability of reproductive and randomly collected individuals. The null hypotheses of no differences in the size coefficient of variation between randomly collected and guarding individuals were evaluated with Z test (Zar 1999). The null hypotheses of no differences in autotomy incidence between randomly collected and guarding individuals were analyzed with replicated G test (see Zar 1999) with site as replicates. This analysis is essentially a three-dimensional Chi square test where the existence of differences between the two-sampled sites can be detected (see Zar 1999).

Experimental evaluation of the effect of size and cheliped autotomy on male–male competition

To evaluate the effect of size and number of autotomized appendages on male mating success, we performed experiments in the field (December 2002 to January 2003) using plastic containers (0.5 × 1 m area, 0.2 m depth) following Smith (1992). The plastic containers were deployed in the shore during day low tide, in a depth of 0.05 m, filled with ambient sediment (0.01 m) and water (0.05 m depth). Two randomly collected intermolt adult males, and a female obtained from a guarding pair were placed in each container (38 trials in MCh and 36 in SA). Males were deployed 5 min before the females (given the dimension of the recipient, agonistic interactions were rarely seen at this initial time). Containers were observed for 20 min. If the presence of guarding was noted, carapace width of the crabs was measured. Three different categories were analyzed separately against the 1:1 win–lose probability: (1) small male without missing chelae (SM) versus large male without missing chelae (LM); (2) SM versus large male with autotomized chelae (LMA); and (3) small male with autotomized chelae (SMA) versus LM. We used autotomized chelae (indistinctly left or right) because chelae are crucial in male–male fighting and affect mating success in other crabs (see Smith 1992). Individuals used had no other appendage autotomy. The null hypotheses of no effect of

size and autotomy status on mating success were analyzed with replicated G test (see Zar 1999; with sites as replicates).

Male preference over female size

To evaluate the effect of female size on male choice, experiments similar to the male–male contests described before were conducted but two females were randomly collected from guarding pairs in the field and then deployed with a single male also randomly collected in the field. After 20 min, the sizes of chosen and not chosen females were measured. The null hypothesis of no effect of female size on pairing was analyzed with G test (Zar 1999) against 1:1 win–lose probability. This experiment was only performed at MCh.

Results

Assortative mating, size and autotomy incidence

In both the populations, guarding pairs collected in the field show positive correlation between male and female carapace width (MCh: $r^2 = 0.3$, $df = 262$, $P < 0.001$; SA: $r^2 = 0.23$, $df = 71$, $P < 0.001$; see Fig. 1). SFDs were skewed to larger sizes in guarding males when compared to SFD of randomly collected adult males for both sites (MCh: $D_{MAX} = 0.132$, $N_{guarding} = 264$, $N_{population} = 177$, $P < 0.05$; SA: $D_{MAX} = 0.347$, $N_{guarding} = 73$, $N_{population} = 132$, $P < 0.01$; but differences in size were clearly higher at SA; see Fig. 1). For females, in contrast, there were no differences in SFD of randomly collected and guarding individuals for either population (MCh: $D_{MAX} = 0.09$, $N_{guarding} = 264$, $N_{population} = 180$, $P > 0.05$; SA: $D_{MAX} = 0.137$, $N_{guarding} = 73$, $N_{population} = 175$, $P > 0.1$). There was no difference in the size coefficient of variation between randomly collected and guarding males at MCh ($V_{random} = 0.18$, $V_{guarding} = 0.17$, $Z = 1.3$, $P > 0.05$) but, at SA, was lower for guarding males compared to randomly collected males ($V_{random} = 0.16$, $V_{guarding} = 0.09$, $Z = 4.74$, $P < 0.01$; see Fig. 1). For females, in contrast, there were no differences between randomly collected and guarding individuals at SA ($V_{random} = 0.15$, $V_{guarding} = 0.15$, $Z = 0.28$, $P > 0.1$) but the coefficient was higher for guarding compared with randomly collected females at MCh ($V_{random} = 0.12$, $V_{guarding} = 0.15$, $Z = 3.38$, $P < 0.05$).

As expected, the incidence of autotomy of randomly collected males was higher for MCh compared to SA (G heterogeneity $= 48.02$, $df = 4$, $P < 0.001$). Thus, the analysis was performed separately for each site. The incidence of autotomy was higher in the randomly collected males than in the guarding males at MCh (i.e. guarding
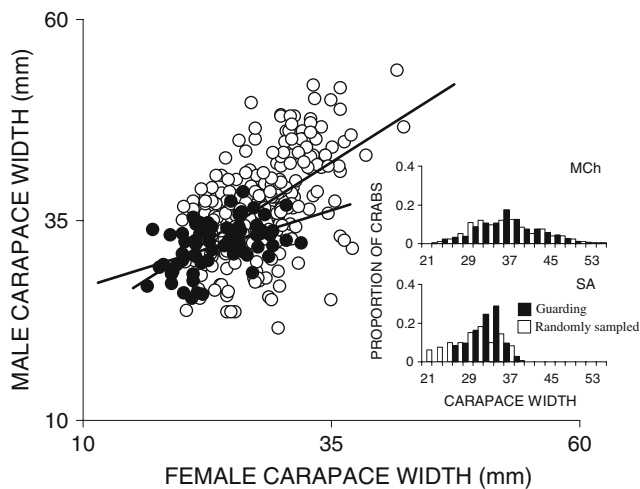
Fig. 1 Female versus male carapace width of *Cyrtograpsus angulatus* guarding pairs from MCh (*empty symbols*) and SA (*black symbols*). *Inset*: size frequency distribution of guarding and randomly sampled males from MCh and SA

males had fewer autotomized appendages than expected by chance; $G = 41.18$, $df = 4$, $P < 0.001$; Fig. 2) while there was no difference in incidence of autotomy between the random sampled and the guarding males at SA ($G = 2.69$, $df = 4$, $P > 0.5$; Fig. 2). For females, there were no differences in the incidence of autotomy between sites (G heterogeneity = 0.4, $df = 7$, $P > 0.9$) and the pooled data show that, in contrast to males, the incidence of autotomy was higher in guarded than in the randomly sampled females ($G = 16.55$, $df = 7$, $P < 0.05$; Fig. 2).

Experimental evaluation of the effect of size and cheliped autotomy on male–male competition

There was no site effect on the outcome of male–male contests for any of the different categories (SM vs. LM: G

heterogeneity = 1.41, $df = 1$, $P > 0.05$; SM vs. LMA: G heterogeneity = 2.04, $df = 1$, $P > 0.05$; SMA vs. LM: G heterogeneity = 0.7, $df = 1$, $P > 0.05$), meaning that the data from the two populations can be pooled. Large males often defeat smaller ones when both had all appendages intact (i.e. SM vs. LM; 30 of 39 contests LM win, $G = 11.93$, $df = 1$, $P < 0.05$; Fig. 3) at even higher rates when smaller males had autotomized limbs (i.e. SMA vs. LM; 12 of 13 LM win, $G = 10.97$, $df = 1$, $P < 0.05$; Fig. 3). However, when large males had cheliped autotomy, the frequency of contest win or loss was not different from the expected 1:1 ratio (i.e. SM vs. LMA; 11 of 21 LMA win, $G = 0.05$, $df = 1$, $P > 0.05$; Fig. 3).

Male preference over female size

When males were given the choice of two females, they chose the larger female more than twice as often as the smaller female (23 larger selected, 9 smaller selected, $G = 6.34$, $df = 1$, $P < 0.05$; Fig. 4).

Discussion

Size assortative mating was detected in both the populations of *C. angulatus*; there was a positive correlation between carapace width of males and females guarding pairs. In SA, the population with lower incidence of autotomy, the size of reproductive males was higher than males randomly collected (only larger males of this population were successful in getting females), whereas the differences at MCh were lower (almost all male sizes were seen pairing). This suggests that the importance of size is higher in SA compared to MCh, probably because autotomy decreased the importance of size, and the incidence of autotomy was higher in MCh. SFD ranges, nevertheless,

Fig. 2 Incidence of appendage autotomy of guarding and randomly sampled *C. angulatus* from two populations (MCh and SA)
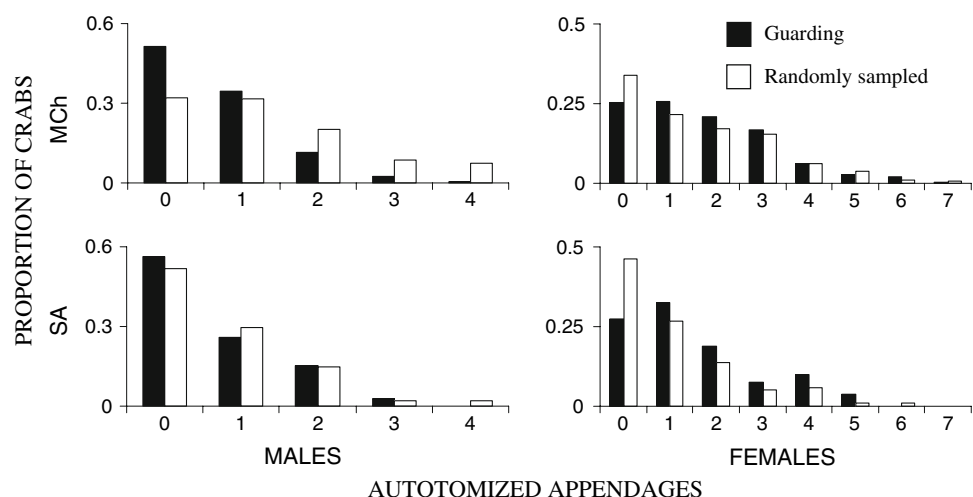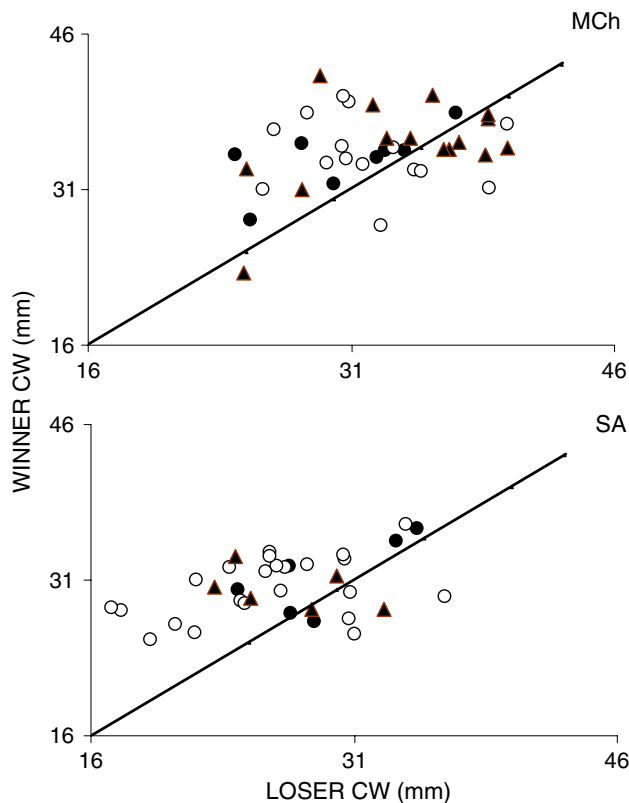
Fig. 3 Loser versus winner carapace width (CW) of *C. angulatus* males from male–male competition experiments. *Empty circles*: small male without autotomy versus large male without autotomy; *black triangles*: small male without autotomy versus large males with autotomized chelae; *black circles*: small male with autotomized chelae versus large male without autotomy. *Lines* inside the graph represent the 1:1 relationship
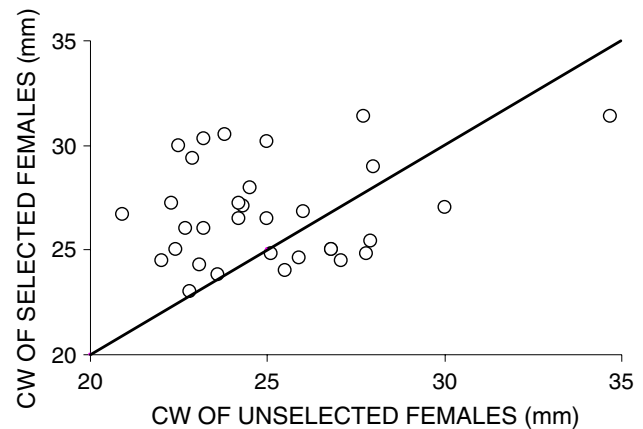

Fig. 4 Selected versus unselected carapace width (CW) of females from male preference experiments. *Line* inside the graph represents the 1:1 relationship

are not the same between sites, being individuals from SA usually smaller, probably because the higher abiotic stress of Patagonian coasts (Bertness et al. 2006). The low frequency of large males, thus, may increase its success independent of autotomy incidence. In this context, standardized experiments made at both sites show that, in contests for females, the larger males outcompete smaller ones when they both had all appendages intact. When males had missing chelae, nevertheless, winning or loosing against smaller males was a random event. One limitation of the experimental design used here is the lack of contests in which both individuals were missing chelae. The inclusion of this group would benefit the analysis of the importance of size and autotomy in male–male contests, as results show that the size is important in contests between individuals with all appendages intact but there is no information about the importance of size in contests when both individuals were missing chelae.

Large body size can be advantageous in contest competition in a variety of organisms, and is very common in crustaceans (e.g. Wada et al. 1997; Brockerhoff and

McLay 2005). This size advantage in male–male competition over mates, combined with male preference over large females (see Reading and Backwell 2007), can generate size assortative mating and seems to be at least one of the causes of the size assortative mating observed in our study. Other causes that were not analyzed in the present study, nevertheless, cannot be excluded. Female resistance and male capacity to carry females during guarding, for example, are factors likely to occur in this system and contribute with the observed size assortative mating. Autotomy is a strategy to avoid predation and limit damage during agonistic interactions (Wasson et al. 2002). Since animals must invest energy to regenerate the missing limb, and there is a period of time without the limb, associated costs may affect feeding, growth, reproduction, competitive ability, predator avoidance, and/or survival (see Juanes and Smith 1995). Autotomy negatively affects male–male competitive success in some crab species (e.g. *Callinectes sapidus*; Smith 1992) and our results show that autotomy can erase the size advantage in male–male competition over females in *C. angulatus*. In some crab species, as the shore crabs *Carcinus maenas*, relative weapon size is a better predictor of competitive success than relative body size in male fights (Sneddon et al. 1997, 2000). In this context, our case can be seen as a particular one where instead of a difference in weapon size, there is a difference in weapon number. The loss of chelae by autotomy, however, did not prevent males from mating. Our field observations show that males missing chelae can perform guarding and experimental results also show that these males can even win in contests against intact males with the full compliment of appendages (especially if the former are larger).

Theory predicts that males should not be selective in mate choice, unless each mating event has a relatively

high cost (Dewsbury 1982). In our study, males prefer larger females over smaller ones, which may be due to the high cost of mate guarding (see Dewsbury 1982) and because fecundity increases with size (Luppi et al. 1997). However, in *C. angulatus*, female fecundity is also dependent on the extent of limb autotomy (i.e. females missing appendages have significantly lower fertility than intact females of the same size; Luppi et al. 1997) thus males may also be expected to prefer females that have all appendages intact. The incidence of autotomy, nevertheless, was higher in guarded than in randomly collected females, indicating that males may not select mates with low levels of autotomy. As male guarding include struggles with females for physical control and fights with other males during takeovers attempts, the higher autotomy level of paired females can be explained if unsolicited mating attempts and male–male dispute during guarding increase autotomy risk of females or if females with missing appendages are easier to dominate and handle (i.e. the resistance of a female missing appendages over male guarding is lower that the resistance of a female with appendages intact).

Results of male–male competition experiments show that autotomy negatively affects the mate competition ability of larger males. The increase of the mating success of small males with all appendages to the detriment of mating success of large males missing chelae will drive to a decrease in the variability of mating success (i.e. in populations with a low incidence of autotomy, larger males may have higher reproductive success than smaller ones, but in populations with a high incidence of autotomy, smaller males may increase their reproductive success). There is no site replication in terms of autotomy incidence (i.e. there is one population with high autotomy incidence and another with low autotomy incidence), but the population with high autotomy incidence showed the lower difference in SFD between guarding and randomly collected males. Although we do not know the causes of the differences in autotomy between our study populations, the experiments show that autotomy decreases variability in mating success. Different explanations, such as high predation pressure, have been proposed, however, for the increase of autotomy rates in some crab populations; see Spivak and Politis 1989).

In conclusion, experimental results, in combination with the observations of natural populations, show that, in the crab *C. angulatus*, size is very important in male–male competition for females, but limb autotomy also has an important effect on the outcome of male–male competition since the effect of size difference may be removed in situations where larger males has lost a claw but smaller males remain intact. Autotomy, thus, can affect the potential for sexual selection on size.

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