

Male size-dependent dominance for burrow holding in the semiterrestrial crab *Neohelice granulata*: multiple tactics used by intermediate-sized males

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Abstract Dominance and the establishment of social hierarchies are frequently related to size: the larger individuals gain greater reproductive success, while the smaller ones display alternative mating strategies. We studied the existence of dominance and the alternative mating strategies among *Neohelice granulata* small (SM) and large (LM) males competing for burrows. LM construct burrows with copulation chambers while SM do not. Field studies showed the existence of a SM's size-range of 30–32 mm carapace width when they change behavior and occupy burrows with copulation chambers (hereafter referred to as the “switch size-range”). We found a restricted size-range in mating pair formation. Laboratory experiments showed that LM dominate SM because SM did not construct burrows in the presence of LM, and LM displaced SM from their burrows. When given the chance, recently mated SM occupied burrows without copulation chambers while not recently mated SM occupied chambered burrows. This is evidence that these males may be displaying a cheating mating strategy to copulate with females looking for these burrows: they occupy but do not own these burrows. SM can also intercept and mate females on the surface. Given the size restriction in pair formation, intermediate-sized males in the switch size-range (30–32 mm carapace width) may copulate with a broader female size-range, larger and smaller than themselves. In this way, SM in the switch

size-range may be acquiring a higher reproductive success by adopting multiple tactics. Male dominance hierarchies have been well documented in crustaceans, except for crabs. Here, we demonstrate male dominance related to the construction and defense of burrows and male size in the crab *N. granulata*. We found that small males of a certain size range adopt an alternative “cheating” mating strategy that can enhance fitness. Therefore, although they are not large and dominant, small males can nevertheless achieve high reproductive success as a result of this alternative reproductive tactic.

Keywords Dominance · Mating strategies · Burrows · Size · Crustaceans

Introduction

Agonistic interactions occur when individuals fight over resources such as direct access to mates or over resources that may assure access to mates (e.g., Parker 1974; Dominey 1984; Christy 2007). In some species, high costs of agonistic interaction are avoided by the establishment of dominance hierarchies (Fletcher and Hardege 2009). Based on game theory and energy cost models (Parker 1974; Maynard Smith 1979; Enquist and Leimar 1987; Riechert 1988), the likelihood of engaging and expending energy in an agonistic interaction will depend on the value of the resource and the probability of success (Riechert 1988; Stuart-Fox 2006). Dominance hierarchies may predict contest outcomes and may be determined by experience (Dugatkin 1997; Hsu and Wolf 1999; Yasuda et al. 2014, 2015); by differences in morphological structures, pheromones, and size (e.g., Rabeni 1985; Pavey and Fielder 1996; Moore and Moore 1999; Kasumovic et al. 2010; Hardy and Briffa 2013); and by other condition-

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dependent characteristics due to age or physiological state (see Dugatkin and Reeve 1998). In crustaceans, the maintenance of dominance hierarchies is determined largely by size (Jachowski 1974; Huntingford et al. 1995; Sato and Nagayama 2011); individuals rarely engage in costly fights and contests are generally resolved quickly by one individual, usually the smaller retreating (Warner 1977).

Dominance hierarchies may have important consequences for the pattern of mating. Causes of assortative mating in arthropods may be due to multiple mechanisms including mate choice, mate availability, and mating constraints (Crespi 1989). If dominance hierarchies are established before female choice, then inter-sexual selection may operate over the subgroup of dominant males (Reichard et al. 2005). Under this situation in which strong sexual selection promotes high variance in reproductive success, alternative mating tactics are likely to evolve (Shuster and Wade 2003). Furthermore, females may also mate with subordinate males to increase genetic diversity (Fletcher and Hardedge 2009) or avoid male aggressiveness (Moore and Moore 1999). Diverse animal taxa show distinct patterns of male mating behavior that are associated with differences in phenotype or behavior (e.g., Gadgil 1972; Campanella and Wolf 1974; Thornhill 1981; Maynard Smith 1982; Parker 1982; Hews et al. 1997; Moore et al. 1998; Johnson et al. 2000). Alternative mating tactics may be the outcome of genetically different strategies coexisting in evolutionary equilibrium (frequency-dependent models; Gross and Charnov 1980; Ryan et al. 1992; Gross 1996) or the effect of a plastic response in which each tactic is triggered under different conditions or status (status-dependent or environmental threshold strategy; Hazel et al. 1990; Gross 1996). As stated previously, in many crustacean species, size is a good phenotypical trait indicating dominance. Therefore, dominant males are often larger than other males and may have higher mating rates than small males (e.g., Koga and Murai 1997; Gosselin et al. 2003; Carver et al. 2005; Sato and Goshima 2007; Lemaitre et al. 2009; Hardy and Briffa 2013). Large dominant males may have access to females or may monopolize or defend resources to mate with females. Small subordinate males may obtain at least some reproductive success by adopting an alternate strategy, by sneaking copulations (Alcock et al. 1977; Howard 1978; Hayashi 1985; Diesel 1986), or by attempting to gain access to females when costs of undergoing agonistic interactions are low.

Given that size in crustaceans is highly correlated to age, a male is expected to switch from a subordinate tactic to the dominant one when he is able to successfully fight with other males (Alcock et al. 1977; Thornhill 1981; Taborsky 1994). In dominance hierarchies, establishing dominance can carry high costs in time, energy, and risk of injury; thus, it is expected that dominance provides increased access to resources (Wilson 1975). Animals that use resources such as shelters or burrows may be able to use them to gain a tactical edge over an

opponent (Fayed et al. 2008). Burrows are resources that primarily provide shelter from predation in open-water species and from harsh physical conditions in the more terrestrial species (Richardson 2007). Several studies conducted in semiterrestrial cyclopods and grapsoids show that the burrows are also used for mating purposes, being the place where copulation occurs (Seiple and Salmon 1982; Backwell and Passmore 1996; Brockerhoff and McLay 2005a; deRivera 2005; Christy 2007). Grapsoid crabs exhibit a considerable diversity of reproductive strategies in which males actively approach and secure females thereby promoting intra-sexual competition through agonistic encounters (Seiple and Salmon 1982; Brockerhoff and McLay 2005b; Sal Moyano et al. 2012a). Dominant individuals can obtain and maintain greater control over critical ecological resources, for example burrows, which can result in more copulations and higher reproductive success (Ellis 1995).

The mating system of *Neohelice granulata* (Dana 1851) is based on the defense of “burrows” constructed by the large males (LM, carapace width > 34 mm). These burrows can be used as a sheltered/protected copulatory chamber or “boudoir” for mating purposes (Sal Moyano et al. 2012a). Copulatory chambers have a concealed chamber in the upper or median part of the burrow (see Sal Moyano et al. 2012a). By contrast, small males (SM, carapace width < 32 mm) construct burrows as straight tubes, without chambers, and their copulations can occur (1) on the surface, by interception of receptive females, or (2) in burrows of LM since SM were found occupying empty burrows constructed by LM (Sal Moyano et al. 2012a). However, no previous studies have been conducted to analyze the correlation between male size (large and small) and their occurrence in burrows with or without copulation chambers. Moreover, the male size-range at which the switch between constructing copulation chamber and occupying an empty chambered burrow occurs (“switch size-range”) has not been studied previously. Thus, we define “switch size-range” throughout the manuscript as the size range where SM can be frequently found inside burrows with copulation chambers constructed by LM. Although the memory ability of dominant and subordinate male *N. granulata* of similar sizes after agonistic encounters was studied (Kaczer et al. 2007), no studies were performed to analyze the existence of dominance between different sized males in the use of burrows. *N. granulata* receptive females are the searching sex, choosing LM burrows to copulate with the resident (Sal Moyano et al. 2014). Nevertheless, there are no data about the existence of a size limit between sexes to copulate which probably could affect the selection of males or females in mating pair formations.

In this context, we hypothesize that *N. granulata* LM are dominant over SM and, consequently, SM display alternative mating strategies. The aim of the present manuscript was to study the existence of dominance and alternative mating

strategies among *N. granulata* males of different sizes in the use of burrows. As specific aims, we studied whether (1) there is a switch size-range in SM regarding the burrow type (with or without copulation chamber) they occupy in field, (2) there is a correlation between the size of male and female partners, (3) SM construct burrows in the presence of LM, (4) LM displace SM from their burrows, (5) LM with only one chela or a regenerated smaller one displace SM from their burrows, and (6) SM occupy empty LM burrows for mating purposes.

Materials and methods

Study area

The study was carried at Mar Chiquita, which is a coastal lagoon (MCL) located in Buenos Aires Province, Argentina (37°45'S, 57°19'W). It is a body of brackish water (46 km²) of low tidal amplitude (ca. 1 m) permanently connected to the sea (Reta et al. 2001). The upper intertidal zone is a mixed *Spartina densiflora* and *Sarcocornia perennis* marsh, and the mid- and lower intertidal zones is mud flat (Isacch et al. 2006). Crabs occupy the upper and mid-intertidal zones, generating extensive beds of burrows (Spivak et al. 1994; Luppi et al. 2013).

Field sampling

In order to study the occurrence of different male sizes (large or small) in the different burrow types (with and without a copulation chamber), and to characterize if there is a switch size-range in SM regarding the burrow type they occupy in field, sampling was carried out during the 2014/2015 reproductive season (extended from September 2014 to March 2015). The data were obtained during three different sampling days in January and March. Burrows were sampled randomly and data on the size of male and the presence or absence of a copulation chamber inside the burrow were obtained. The presence of a copulation chamber was recognized after probing the interior of the burrow with a stick to detect the presence of a widening of the chamber in its median or upper part (see Sal Moyano et al. 2012a). Crabs inside the burrows were taken out and their carapace width (CW) measured with a caliper accurate to 0.1 mm. A total of 276 burrows occupied by males were sampled.

Bayesian methods are preferred over classic statistics for this type of analysis because the results can easily be interpreted in terms of relative probability (Hilborn and Mangel 1997; Wade 2000; Quinn et al. 2006). For this reason, we used a Bayesian approach with models based on binomial distribution to compare the theoretical proportion of crabs with the ability to build a burrow chamber (sizes larger than 34 mm of CW; Sal Moyano et al. 2012a) with the occurrence

of chambered burrow and the male size (organized in groups of 2 mm) found inside them in field.

In order to study the size differences between sexes of mating pairs encountered randomly in field, couples found copulating (sternum-to-sternum position of the male and the female) or inside a burrow with the female receptive and the male displaying post-copulatory guarding behavior (see Sal Moyano et al. 2012a) were sampled and their CW measured.

Collection, maintenance of crabs, and laboratory experiments

Laboratory experiments were run from September 2014 to March 2015 (reproductive season 2014/2015). *N. granulata* crabs were collected by hand from the field in MCL 5 days prior to the beginning of the experiments and transported to laboratory. In the laboratory, individuals were maintained in seawater aerated aquaria (30 × 35 × 25 cm, containing 3 cm depth of seawater) and sexes were kept separated. No more than four crabs of similar size (all SM or LM males or females) were placed in each acclimation aquarium (approximately 36 crabs m⁻²) avoiding effects of density and size on behavior because in field, density of burrows is high, reaching up to 60 burrows m⁻² (Iribarne et al. 1997). No sediment was added to the acclimation aquaria in order to avoid the construction of burrows and, thus, establishing a possible dominance hierarchy. Individuals were fed daily with pet-food pellets, and water was changed after feeding. Crabs were maintained under natural daylight conditions and temperatures that ranged between 22 and 28 °C (mean 24 °C). Individuals were measured using the CW as the reference variable. Only mature crabs of both sexes were used during experiments (>19 mm CW; López Greco and Rodríguez 1998). Two categories of males were employed for the experiments: small males (SM) with a CW <32 mm and large males (LM) with a CW >34 mm.

Experiments were conducted in experimental aerated plastic aquaria (40 × 60 × 25 cm) containing 20 cm of sediment obtained from MCL in one side and a rock (approximately 10 × 20 × 6 cm), as an alternative refuge, on the other side. Burrows could reach more than 70 cm depth (Iribarne et al. 1997), but the copulation chamber is generally constructed in the entrance of the burrows, in the first 10 cm (Sal Moyano et al. 2012a); thus, 20 cm depth of sediment was considered sufficient to allow the construction of a chambered burrow. Different laboratory experiments were conducted in order to test the specific objectives proposed.

Large males construct burrows with copulation chambers while SM construct straight burrows, and it is assumed that SM do not invest energy in constructing burrows with chambers because LM could contest and win these burrows (Sal Moyano et al. 2012a). To analyze the dominance existence of LM over SM, we designed experiment 1 in order to test if SM construct burrows in the presence of LM. The first day the

experiment began, we randomly took two males from two different acclimation aquaria; they were measured and classified as SM and LM. Both males were placed in the experimental aquarium for 48 h, when the experiment was terminated. The outcome of the experiment was to record where the LM and SM were found: under the refuge or inside a burrow if they constructed one. The control consisted of adding only a SM to the aquarium.

Experiment 2 was designed to test if LM dominate and displace SM from burrows with copulation chambers. Burrows with copulation chambers were constructed artificially: a straight tube was first constructed using a trowel, and then the chamber was constructed using a spoon. The chamber was located in the upper part of the burrow, after 4 cm from the entrance, in order to allow inspection of crabs inside it. We randomly took a SM from an acclimation aquarium, placed it in the experimental aquarium, and left it for 72 h in order to allow the SM to get inside the burrow and use it as the owner of the burrow. During the 72 h, the experiment was checked daily to detect if the SM was found inside the artificially constructed burrow or another burrow had been constructed by the SM. Only in three cases did the SM construct and occupy a new burrow; thus, these were not considered in the statistical analysis. The experiment started after the addition of a randomly selected LM from an acclimation aquarium to the experimental one (before adding the LM, we checked to see that the SM was inside the artificially constructed burrow) and lasted 6 h. Every 10 min, the position of the crabs (LM and SM inside or outside the burrow) was recorded and their behavior described by an observer. According to previous studies, the observer was located 1 m from the experimental aquarium, enough distance to see the crabs but to avoid affecting their behavior (e.g., Sal Moyano et al. 2012a). The outcome of the experiment was whether the LM or the SM was found inside the burrow at the end of the experiment.

Experiment 3 was designed to test if LM missing one chela or with one smaller regenerated chela can dominate and displace SM from burrows with copulation chambers. Large males missing one chela or were heterochelous were captured from the field, isolated, and acclimated under the same laboratory conditions described above for the rest of the crabs in the acclimation aquaria, and used in the experiments. The experimental design was identical to experiment 2.

Experiment 4 was designed to test if SM occupy burrows with copulation chambers for mating purposes. Two treatments were conducted using (A) not recently mated SM and (B) recently mated SM. Recently mated SM were obtained by randomly selecting a SM from the acclimation aquaria, placing it in an aquarium with a receptive female and observing successful copulation. Receptivity of females was recognized by the detection of mobile vulvae opercula which could be pushed inwards like a trapdoor when examined under a binocular microscope: the pleon was lifted and the two opercula

were gently probed daily using fine forceps (see Sal Moyano et al. 2012b). Copulation was considered to have occurred when both the male and female pleon were observed open and the male gonopods were inserted into the female vulvae. Immediately after the copulation ended and the pair separated, the male was used for the experiments. Experimental aquaria contained a SM burrow (straight tube) and a LM burrow (tube with a copulation chamber). Both types of burrows were constructed artificially and manually: the former were straight tubes constructed with a trowel, while the latter were constructed by the same way described in experiment 2. Both types of burrows had the same diameter of the entrance of 4 cm. The experiment started after addition to the experimental aquarium of only one randomly selected SM from the acclimation aquaria, either not recently mated for treatment A or a recently mated SM for treatment B, and terminated 48 h later. The outcome of the experiment was a record in which of the two burrows the SM was found.

Twenty replicates for each experiment were performed. In experiments 2–4, new burrows were constructed for each replicate. For experiment 4, burrows were constructed in the right and left corners of the aquarium with sediment, at a distance of 5 cm from aquarium walls, and construction of both burrow types varied between right and left of the aquaria for each replicate. For statistical analyses, chi-square with Yates's correction or binomial tests of proportions were performed to analyze differences in each experiment. For experiments 2 and 3, differences in the time spent by LM to displace SM from the burrow were analyzed using a *t* test.

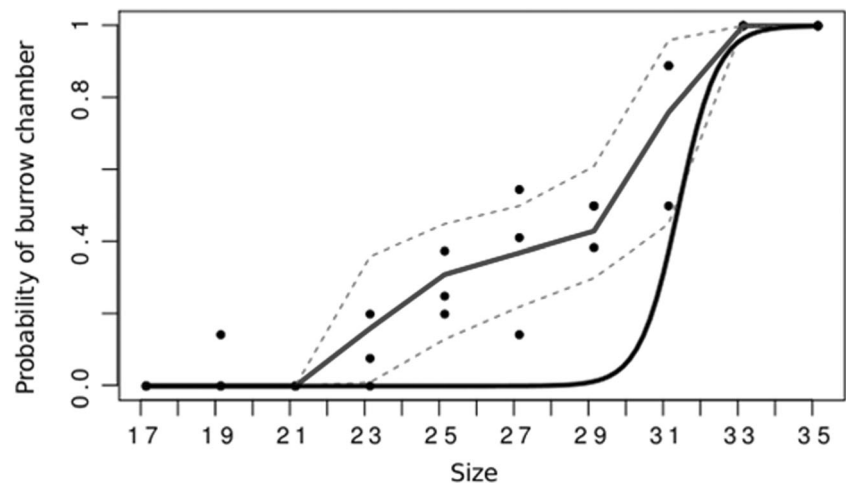
To minimize observer bias, blinded methods were used when all behavioral data were recorded and/or analyzed.

Results

Field sampling of burrows and mating pairs

The theoretical probability of the crabs' ability to build a burrow with a copulation chamber related to their size is shown in Fig. 1. When adding to the model the crabs of different sizes found inside burrows with copulation chambers, Bayesian analysis showed that posterior probability of a crab being found in a burrow with a copulation chamber had a positive relation to size (Fig. 1). The confidence intervals were different among the 22–30 and 30–32 mm sizes (Fig. 1). Thus, it showed that the posterior probability of crabs ranging from 30 to 32 mm CW to be found inside a burrow with a copulation chamber is higher than crabs of 22–30 mm CW (see Table 1). In this way, males ranging between 30 and 32 mm CW were considered to be the size-range in which behavior could switch because of more frequently occupied empty burrows with copulation chambers constructed by LM.

Fig. 1 Logistic regression of presence/absence of a burrow chamber related to size (CW, mm). The *sigmoidal lowest black line* shows the theoretical probability of the crab ability to build a burrow with a copulation chamber. The *intermediate black line* shows the Bayesian posterior probability of all individuals to be found inside a burrow with a copulation chamber. The *dotted gray lines* show the intervals of credibility of Bayesian posterior probability



Maximum size divergence between sexes in 24 mating pairs found in field was 5.6 mm of CW; thus, there was a restricted size range in mating pair formation. In two cases, males were 0.4 and 1.2 mm smaller than females, while in the rest of the mating pairs, males were always larger than females (varying from a minimum difference of 0.9 mm to a maximum one of 5.6 mm). Males larger than 30 mm CW were always found copulating with females larger than 27 mm and were found inside burrows with copulation chambers. Males smaller than 28 mm CW were always encountered copulating with females smaller than 28 mm CW, and they were found in the surface.

Laboratory experiments

Experiment 1: SM were found under the refuge and did not construct burrows in the presence of LM, while LM constructed burrows with copulation chambers and were found inside them ($\chi^2 = 5$, $p < 0.05$, Fig. 2a). However, in the absence of

LM, SM constructed burrows without copulation chambers and were found inside them ($\chi^2 = 7.2$, $p < 0.05$, Fig. 2a).

Experiment 2: LM displaced SM from burrows with copulation chambers ($\chi^2 = 12.8$, $p < 0.001$, Fig. 2b). Displacement of SM occurred at the beginning of the experiment, mostly in the first 40 min. Displacement occurred in two different ways: either the LM tried to get into the burrow and contacted the SM through their legs or chela, and immediately after contact, the SM abandoned the burrow without interacting with the LM (40 % of the cases); or the SM tried to defend the burrow through agonistic interactions using its smaller chela, but the LM always won the contest, forcing the SM out of the burrow using its bigger chela (60 % of the cases).

Experiment 3: LM with one chela or with one smaller regenerated chela displaced SM from burrows with copulation chambers ($\chi^2 = 8$, $p < 0.01$, Fig. 2c). Only in two cases (not considered in the statistical analyses) both males were found inside the burrow with a copulation chamber. Displacement of SM occurred 80 min after the beginning of the experiment. Displacement occurred principally by agonistic interactions between both male types: the LM used the only chelae available or the non-regenerated smaller one during the interaction.

Differences in the time required to displace SM by LM were found between experiments 2 and 3: LM with two big normal chelae displaced SM faster than LM with only one chela or with a smaller regenerated one ($t = 2.25$, $p < 0.05$).

Experiment 4: in treatment A, not recently mated SM were found inside burrows with copulation chambers ($\chi^2 = 12.8$, $p < 0.001$, Fig. 2d), while in treatment B, recently mated SM were found in burrows without copulation chambers ($Z = 2.53$, $p < 0.05$, Fig. 2d).

Table 1 Bayesian posterior probability estimation of burrow chamber related to size class (CW, mm)

Size	PP	IC	Abi
16–18	0	–	Without
18–20	0	–	Without
20–22	0	–	Without
22–24	0.16	0.1–0.36	Without
24–26	0.31	0.13–0.45	Without
26–28	0.37	0.22–0.5	Without
28–30	0.43	0.3–0.61	Without
30–32	0.76	0.45–0.96	Without
32–34	1	–	With
34–36	1	–	With

PP posterior probability, IC intervals of credibility, Abi crabs found with the ability to build a copulation chamber inside the burrow (Sal Moyano et al. 2012a)

Discussion

Here, we found that SM *N. granulata* hide under a refuge in the presence of LM. This result corroborates a hypothesis

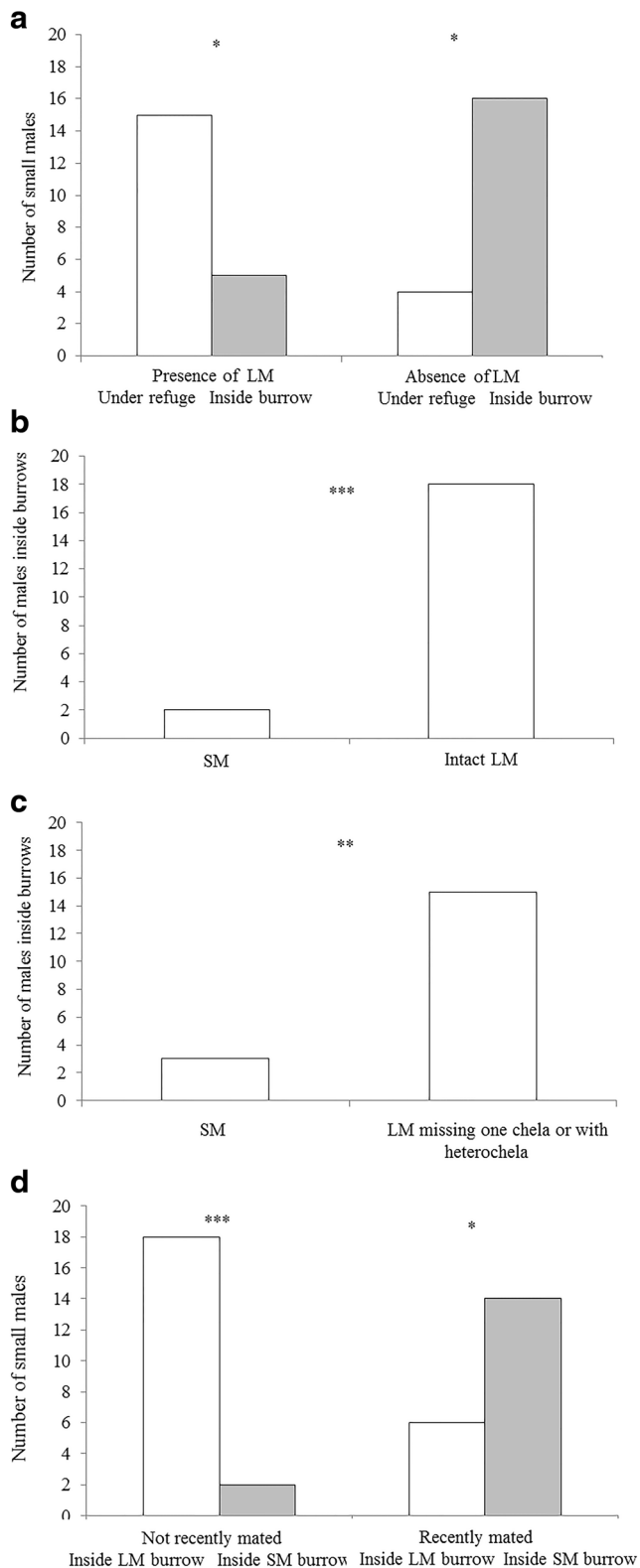


Fig. 2 Laboratory experiments of *Neohelice granulata* males. **a** Experiment 1: small males (SM) found under the refuge or inside the burrow in the presence or absence of large males (LM). **b** Experiment 2: number of SM or intact (with both chelae) LM found inside burrows with copulation chambers. **c** Experiment 3: number of SM or LM missing one chela or with a regenerating one found inside burrows with copulation chambers. **d** Experiment 4: number of SM not recently mated or recently mated found inside LM or SM burrows. Significant differences: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

interactions in male–male contest (Sal Moyano et al. 2012a). By this way, it was demonstrated here that SM recognize the dominance of LM and do not construct burrows in the presence of LM, while they did in the absence of LM (experiment 1). In this sense, a previous study conducted on this species showed that subordinate males present higher memory ability than dominants after agonistic encounters (Kaczer et al. 2007). Crustaceans reduce the costs of agonistic encounters by establishing social size hierarchies, as occurs in the crayfish, *Pacifasticus tenuisculus*, where aggressive interactions were significantly shorter in a stable hierarchy (Ahvenharju and Ruohonen 2007). The recognition of dominance rank was demonstrated in some crustaceans such as lobsters (Karavanich and Atema 1998), crayfish (Gherardi and Daniels 2003; Fujimoto et al. 2011; Sato and Nagayama 2011), and shrimps (Correa et al. 2003).

Dominant males are generally the largest ones (Pavey and Fielder 1996), gaining control over higher-value resources (Berrill and Arsenault 1982; Fletcher and Hardedge 2009). In the case of *N. granulata*, dominance is directly related to the phenotypical trait “size” because LM are the only ones who construct burrows with copulation chambers, a valuable resource for attracting females for mating. Here, we showed that LM displaced SM from burrows, even when having only one chela or a regenerated smaller one (although it took longer), by two different ways: through agonistic interactions or, by contrast, the SM abandoned the burrow avoiding interaction with the LM after contact between both males types (experiments 2 and 3). Even though constructing a burrow with a copulation chamber assures “secure” copulation with a female and allows the development of a post-copulatory guarding behavior diminishing sperm competition (Sal Moyano et al. 2012a), SM do not have any chance of winning a contest with LM because physical capabilities related to size determine the outcome of the contest. However, SM showed alternative behavior of fighting or retreating. It could be suggested that these two alternatives might be related to the fact that SM, while fighting, may be obtaining information about the opponent and gaining experience and, while retreating, may be recognizing their dominance showing submission. Small males’ being submissive in response to aggressive behavior was previously found in hermit crabs and crayfish (Reese 1964; Huber et al. 1997). Prior experience, age, as well as size and genetic differences may affect the flexible behavior of males (Brockmann 2002).

established in a previous study conducted on this species in which it was supposed that SM did not invest energy in constructing burrows with copulation chambers because LM could easily fight and win the burrow through agonistic

The size of males found in burrows with copulation chambers in the field agrees with a previous study conducted on this species in which field experiments demonstrated that males larger than 34 mm CW construct burrows with copulation chambers (Sal Moyano et al. 2012a). In the case of smaller males, it was observed that there is a size range between 23 and 32 mm CW in which males could be found in burrows with or without copulation chambers. However, SM construct burrows as straight tubes, without copulation chambers (Sal Moyano et al. 2012a). We propose that in *N. granulata* males, there is a threshold or size-range at 30–32 mm CW in which their behavior changes because they were frequently found in burrows with copulation chambers although they do not construct them. Based on the threshold or switch model for the evolution of a phenotype-correlated decision mechanism for mating strategies (Parker 1982; Brockmann 2002), in *N. granulata*, males should maximize their fitness by constructing burrows with copulation chambers when being larger than 34 mm of CW and by occupying an empty burrow with a copulation chamber constructed by a LM or by intercepting a receptive female while looking for a burrow when being smaller than 32 mm of CW.

As dominant males are often larger than other males and are superior to subordinates in contests over females in various animal taxa (e.g., Forslund 2000; Hagelin 2002; Hardy and Briffa 2013), they mate more often than subordinates (Sato and Goshima 2007). Travis and Woodward (1989) demonstrated that LM always copulate with females, SM never copulate, and males of intermediate size switch from one behavior to the other depending on context. In *N. granulata*, we found that there is a restricted size range in mating pair formation; thus, the largest males in the population ($32 < CW < 36$ mm) may copulate with the largest females ($27 < CW < 33$ mm) inside their burrows with copulation chambers because females look for these burrows, thereby obtaining higher fecundity and the greater reproductive success.

The smallest sexually mature males ($19 < CW < 32$ mm) in the population may copulate with the smaller sexually mature females ($19 < CW < 30$ mm) by developing an alternative mating strategy such as intercepting females on the surface or by occupying empty chambered burrows constructed by LM. However, from all SM, the ones in the switch size-range of 30–32 mm CW are the most capable of winning a LM empty burrow. This supports our result indicating that SM occupying LM empty burrows were predominantly the larger ones. This alternative mating strategy could be defined as “cheat mating” because SM avoid energy costs related to the construction of a chambered burrow and cheat females which are looking for LM burrows. Besides, recently mated SM did not occupy empty LM burrows (experiment 4) supporting our hypotheses because it demonstrates that not recently mated SM may look for empty LM burrows to occupy with mating purposes in mind. A previous study demonstrated that LM

transfer larger ejaculates than SM (Sal Moyano et al. 2015), which also support the hypothesis about the “cheating behavior” of SM. Effective copulation between females and SM inside empty burrows with copulation chambers constructed by LM was demonstrated previously in a field study (Sal Moyano et al. 2012a). The cheating mating strategy was previously described in spider crabs and named as “sneaking” when SM mimic females avoiding aggressive behavior from LM and may be able to increase their mating opportunities (Diesel 1986; Laufer and Ahl 1995).

In the case of mature SM ranging from 19 to 30 mm of CW, based on the result showing that males smaller than 28 mm were observed copulating on the surface, they would be more likely copulating by interception of receptive females on surface. The result indicating that SM from 23 to 29 mm can be found inside empty burrows with copulation chambers may show that these males are looking and trying to occupy these burrows, although if a “larger” SM (principally those 30–32 mm CW) find them, they would be displaced in a male–male contest. This may explain again why we more frequently found the larger SM inside LM burrows in field. Distinct mating strategies are sequential depending on male size because there is limited size copulation compatibility: SM mate with small females by intercepting them in the surface, while LM mate with large females by constructing chambered burrows. It was demonstrated in male horseshoe crabs that they change their reproductive tactics as they grow older (condition-dependent tactics; Brockmann and Penn 1992). However, in the case of SM in the switch range, because of their intermediate size, they may be employing the two mating strategies of intercepting females on the surface while looking for empty LM burrows (less frequently) or cheating by occupying empty LM burrows (more frequently).

The SM in the critical size-range may benefit because they can copulate with (1) a broader female size range, with females smaller and larger than themselves while small males cannot copulate with the largest females and the largest males cannot copulate with the smallest females because of the pairing size restriction, and (2) the largest females that look for LM burrows to copulate. The existence of empty LM burrows may be related to the fact that these males die more frequently because of age. Also, studies of activity patterns in *N. granulata* showed that LM is the most active group (Luppi et al. 2013); thus, because of moving, it could be more likely to lose their burrows. Besides, burrow fidelity studies demonstrated that LM are the group less faithful to their burrows (Nuñez in preparation). In conclusion, although not being the dominant largest males in the population, SM reaching the switch size-range may increase their reproductive success by displaying alternative mating strategies. The mating behavior is sufficiently plastic to allow any male bearing spermatozoa, independently of size, to take advantage of the reproductive opportunities (Elnor and Beninger 1995).

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Compliance with ethical standards

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Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval All applicable international, national, and/or institutional guidelines for the care and use of animals were followed.

Informed consent Informed consent was obtained from all individual participants included in the study.

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