

*Mating system of the burrowing crab  
Neohelice granulata (Brachyura:  
Varunidae) in two contrasting  
environments: effect of burrow architecture*

**M. P. Sal Moyano, M. A. Gavio &  
T. A. Luppi**

**Marine Biology**

International Journal on Life in Oceans  
and Coastal Waters

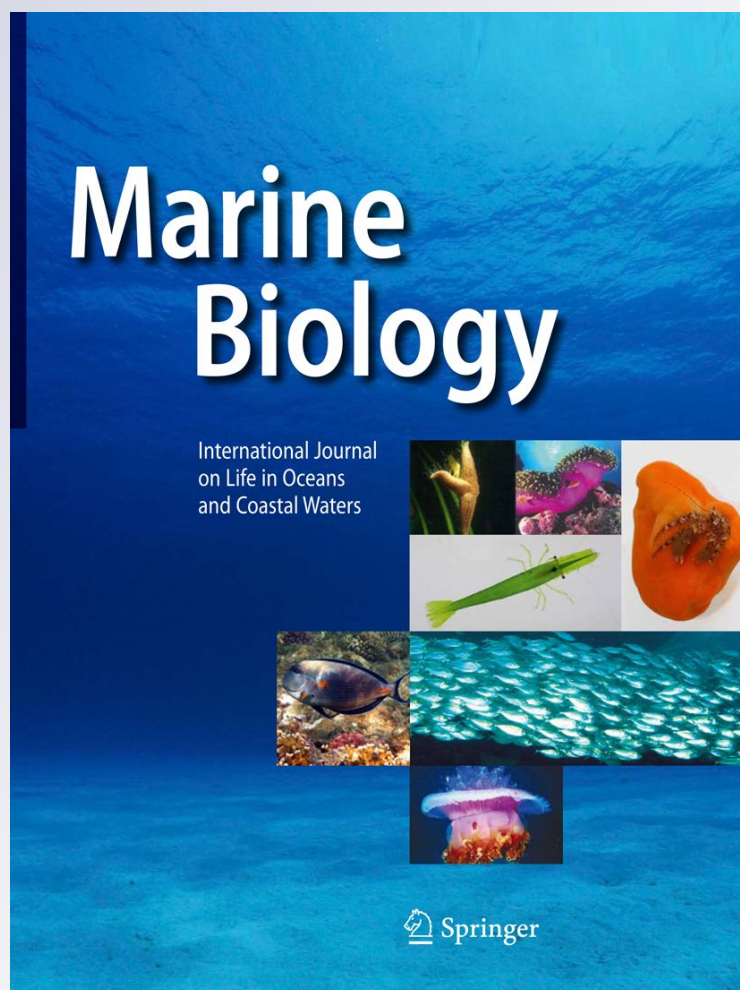
ISSN 0025-3162

Volume 159

Number 7

Mar Biol (2012) 159:1403-1416

DOI 10.1007/s00227-012-1917-6



**Your article is protected by copyright and all rights are held exclusively by Springer-Verlag. This e-offprint is for personal use only and shall not be self-archived in electronic repositories. If you wish to self-archive your work, please use the accepted author's version for posting to your own website or your institution's repository. You may further deposit the accepted author's version on a funder's repository at a funder's request, provided it is not made publicly available until 12 months after publication.**

# Mating system of the burrowing crab *Neohelice granulata* (Brachyura: Varunidae) in two contrasting environments: effect of burrow architecture

M. P. Sal Moyano · M. A. Gavio · T. A. Luppi

Received: 2 November 2011 / Accepted: 6 March 2012 / Published online: 23 March 2012  
© Springer-Verlag 2012

**Abstract** Few studies conducted in crustaceans have demonstrated how habitat features could shape the mating systems. Here, the burrow of *Neohelice granulata* was considered as a resource used for mating, and its architecture was characterized in two contrasting study sites: Mar Chiquita Lagoon (MCL), an estuary composed of muddy sediments, and San Antonio Oeste (SAO), a marine bay composed of gravel sediment. Burrow features differed between study sites and occupant gender. Large males constructed burrows with a chamber in MCL and with a widened entrance in SAO, while small males constructed the same narrow burrows as females at both study sites. Field experiments demonstrated that burrows with chambers or widened entries are places used for copulation, although successful post-copulatory guarding was displayed only in those with chambers. The intensity of the agonistic encounters and the success of males in winning resources (burrows/females) also depend on the habitat characteristics. *N. granulata* shows a resource defense mating system where males employ different mating strategies according to the burrow architecture to ensure mating success.

## Introduction

The mating system of a population depends on the behavioral strategies used by individuals in obtaining mates, in the context of a limited set of ecological conditions such as the abundance and distribution of resources (Emlen and Oring 1977). For a given species, the nature of the sexual association between males and females is set by intrasexual competition and mate choice. These associations vary considerably creating a wide diversity of mating systems (Thornhill and Alcock 1983). Christy (1987) classified the mating systems of brachyuran crabs into three main types based on the kind of competition between males to gain access to females and female mate choice. Two of them that were categorized as “female-centered competition” and “resource-centered competition” are similar to those already established by Emlen and Oring (1977). Additionally, Christy (1987) proposed a third type that he termed “encounter rate competition.” Mating associations corresponding to those three types were reported for a number of grapsoid crabs (see Brockerhoff and McLay 2005a and references therein).

Regarding the resource-centered competition type, burrows are resources that primarily provide shelter, initially from predation in open-water species, and increasingly from harsh physical conditions in the more terrestrial species (Richardson 2007). Additionally, in many crab species, the distribution of shelters or the type of habitat used for the construction of burrows plays an important role in mating as an adaptation to the particular habitat in which the individual lives (Seiple and Salmon 1982; Salmon 1983; Wirtz and Diesel 1983; Abele et al. 1986; Christy 1987; Lindberg and Stanton 1989). Detailed studies describing burrow architecture demonstrate that it varies according to the different habitat sediment composition (Morrisey et al.

---

Communicated by M. Huettel.

---

M. P. Sal Moyano (✉) · M. A. Gavio · T. A. Luppi  
Instituto de Investigaciones Marinas y Costeras (IIMyC),  
Consejo Nacional de Investigaciones Científicas y Técnicas  
(CONICET), Estación Costera J.J. Nágera,  
Mar del Plata, Argentina  
e-mail: salmoyan@mdp.edu.ar

M. P. Sal Moyano · M. A. Gavio · T. A. Luppi  
Departamento de Biología, Facultad de Ciencias Exactas y  
Naturales, Universidad Nacional de Mar del Plata,  
Funes, 3350, 7600 Mar del Plata, Argentina

1999; Katrak et al. 2008; Li et al. 2008; Needham et al. 2010). In addition, several studies of ocypodids show that the burrow form is different between sexes, having an enlarged terminal chamber where matings occur in male burrows (Christy 2007). Moreover, comparison of male burrow features indicates that burrow structure can affect female choice (Backwell and Passmore 1996; deRivera 2005). A few studies of grapsoids have recorded that mating occurs not only on the surface, but also inside the burrows (Seiple and Salmon 1982; Brockerhoff and McLay 2005a), although neither the detailed burrow shape was characterized nor it differed between sexes and the particular reproductive strategy of the species.

Mating associations are the result of complex processes in which both the reproductive strategies and the mating behaviors displayed by mating partners play an important role (Brockerhoff and McLay 2005b). Grapsoid crabs exhibit a considerable diversity of reproductive strategies, in which males actively approach and secure females thereby promoting intrasexual competition through agonistic encounters. Agonistic interactions occur when individuals fight over resources such as mates, food or shelters. Dominant individuals can obtain and maintain greater control over critical ecological resources, which can result in more matings and higher reproductive success (Ellis 1995). Hence, burrows could be important resources for mating purposes, defended by males and promoting intrasexual male competition.

In addition to typical male–male competition, males can also compete by means of sperm competition when multiple mating occurs and sperm from numerous individuals vie for unfertilized eggs inside females seminal receptacles (Parker 1970). Based on the connection of the ovary to the seminal receptacle, Diesel (1991) characterized the female brachyuran seminal receptacle into dorsal and ventral morphological types. Accordingly, the first or the last male to inseminate the female is believed to have an advantage in fertilizing the oocytes. The risk of sperm competition within the female seminal receptacle can be reduced by post-copulatory guarding by males (Jivoff 1997). Post-copulatory guarding has been observed in only a few grapsoid species such as *Hemigrapsus crenulatus* and *H. sexdentatus*, although this may be partly due to the lack of studies (Brockerhoff and McLay 2005a). The development of a male post-copulatory guarding behavior has been considered as an optimal adaptive behavior, and it may be favored when males secure females in burrows.

The burrowing and semiterrestrial crab *Neohelice granulata* is considered a keystone species from South American salt marshes, mud flats and estuaries, ranging from the northern Patagonia, Argentina (42°25'S; 64°36'W), through Uruguay, to Rio de Janeiro, Brazil (22°57'S; 42°50'W) (Spivak 2010). It is distributed in high densities in habitats

of varying salinity, temperature and tidal patterns, inhabiting both the *Spartina* salt marsh and the intertidal mud flats, generating extensive beds of burrows (Spivak et al. 1994; Spivak 1997). Burrows reach high densities, up to 60 burrows m<sup>-2</sup> (Iribarne et al. 1997), and vary in size and form depending on the habitat where they are constructed: mud flat or *Spartina* salt marsh (Olivier et al. 1972; Iribarne et al. 1997; Escapa et al. 2007; Fanjul et al. 2008). Several studies were conducted in *N. granulata* populations 800 km apart along the Argentinean coast, occupying contrasting habitats: one located in the Mar Chiquita Lagoon (MCL), an oligo-polyhaline estuary, and the other in San Antonio Bay, an eu-hyperhaline system. The first habitat is composed of muddy fine sediments with high penetrability, typical of a low-energy habitat, while the latter has gravel coarse sediment with low penetrability, typical of a high-energy habitat. Those studies identified population differences in many reproductive traits associated with the type of habitat. The reproductive season started later and was shorter in San Antonio; in females from Mar Chiquita, secondary vitellogenesis continues even when the reproductive season ends and the ovaries remain fully developed throughout the non-reproductive season and are ready to spawn in the following spring, while females from San Antonio do not attain a fully developed ovary during winter, causing a delay in the beginning of the reproductive period (Ituarte et al. 2006). Additionally, fecundity is higher in females from Mar Chiquita, while egg and larvae volume is higher in San Antonio (Bas et al. 2007, 2008). These traits were mainly associated with the different food supply since the organic matter of muddy substrata is higher in Mar Chiquita (Bas et al. 2005). However, the way in which the habitat features such as the burrow architecture could influence the mating system and the mating strategies developed by both sexes has never been assessed until now.

According to the mating system theory proposed by Emlen and Oring (1977) and the reproductive associations between males and females of Brachyura proposed by Christy (1987), we hypothesized that *N. granulata* would show a resource defense mating system (burrows being valuable shelters that are controlled by males), although the environment may constrain or favor particular mating tactics via its effect on burrow architecture. We predicted that: (1) males and females may construct burrows of different shape, (2) burrow features would vary between study sites according to the different grain size and penetrability of the sediment, (3) males would develop a post-copulatory behavior involving female guarding inside the burrow to avoid sperm competition and (4) agonistic interactions would occur between males to defend burrows and gain females. In this context, the objective of the present study was to characterize the burrow architecture of *N. granulata*



constructed by different sexes in two habitats (mud flat and salt marsh), two study sites (Mar Chiquita and San Antonio Oeste) and by relating the burrow form to the reproductive strategies, guarding behavior and mating system.

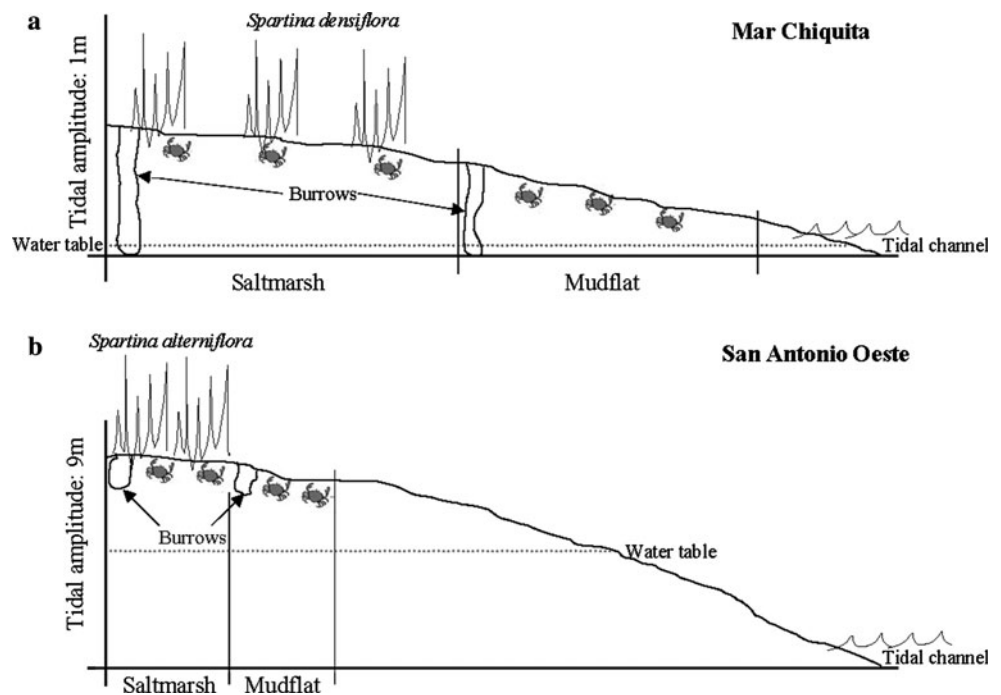
**Materials and methods**

**Study sites**

The study was carried out in two coastal areas: one at Mar Chiquita, which is a coastal lagoon located in Buenos Aires Province, Argentina (37°45'S, 57°19'W), and the other one at San Antonio Oeste (SAO), which is a bay located in the northwest of San Matías Gulf, Río Negro Province, Argentina (40°46'S, 64°50'W). Mar Chiquita is a body of brackish water (46 km<sup>2</sup>) 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 (Isacch et al. 2006), and the mid- and lower intertidal zones is mud flat. Crabs occupy the upper and mid-intertidal zones. Burrows reach more

than 70 cm depth and are connected with the water table in both habitats (Iribarne et al. 1997; Fanjul et al. 2008) (Fig. 1a). Sediments are fine with low (salt marsh) or nil (mud flat) content of gravel and with high penetrability (salt marsh lower than mud flat) and organic matter content (Table 1). By contrast, the other area, SAO, is a marsh lacking freshwater input, except for the scarce rains (200 mm/year), with a semidiurnal macrotidal (ca. 9 m) regime. The upper intertidal is a *S. perennis* marsh, and the middle intertidal divides into a *Spartina alterniflora* marsh (Isacch et al. 2006) and a mud flat. Crab burrows occupy both the upper and mid-intertidal zones (Bas et al. 2005). The shape of crab burrows in this area has not been described yet; however, burrows are short and are not connected with water table (Fig. 1b). The sediment organic matter content (salt marsh higher than mud flat) and penetrability (salt marsh lower than mud flat) are low, and content of gravel is high (salt marsh lower than mud flat) (Table 1). In both areas, burrows ameliorate the harsh physical conditions when salt marsh and mud flat are uncovered by water by diminishing the range of variation of temperature and/or salinity (Silva et al. 2009; Luppi unpubl data).

**Fig. 1** Schematic representation of each study site. **a** Mar Chiquita and **b** San Antonio Oeste



**Table 1** Sediment features of salt marsh and mud flat from Mar Chiquita and San Antonio Oeste

	Mar Chiquita (1)		San Antonio Oeste (2)	
	Salt marsh	Mud flat	Salt marsh	Mud flat
Penetrability (kp/cm <sup>2</sup> )	9.5 ± 1.49	1.7 ± 0.48	32.3 ± 4.3	26.3 ± 1.1
Organic matter content (%)	3.8 ± 0.56	4.1 ± 0.21	1.84 ± 0.03	0.9 ± 0.07
Gravel content (%) (grain > 2 mm)	3 ± 0.4	0	4.5 ± 0.23	13.3 ± 0.88

Data from (1) Spivak et al. (1994) and (2) Bas et al. (2005)

## Sampling

Sampling was carried out during the reproductive seasons of 2008/2009 and 2009/2010 in MCL and 2009/2010 in SAO. Individuals were measured with a caliper using the carapace width (CW) as the reference variable. Only functional mature crabs were considered (>19 mm CW, López Greco and Rodríguez 1998), and according to preliminary studies, different categories of individuals were distinguished for both MCL and SAO, respectively: (1) ovigerous females (OF), 23.4–31.7 mm CW in MCL and 22.3–27.5 mm CW in SAO; (2) non-ovigerous females (NOF), 22.1–30.9 mm CW and 21–25.6 mm CW; (3) small males (SM), 25.9–32.6 mm CW and 21.4–27.5 mm CW and (4) large males (LM), 34.3–36.2 mm CW and 28.1–34 mm CW, respectively.

## Characterization of burrows

Characterization of burrow architecture was assessed by two approaches both in the *Spartina* salt marsh and on the mud flat at both study sites (MCL and SAO), which consisted of: (1) sample burrows located in randomly placed transects named “random burrows” and (2) a designed experiment in order to associate the burrow form with the category of crab that constructed it, named “exclusion burrows.” The experiment consisted of placing a crab of each category (OF, NOF, SM and LM) inside a single round exclusion cage (30 cm diameter, buried 15 cm deep) constructed of plastic mesh (10 mm opening), on transects located in the burrowing area in small patches without burrows, allowing the crab to construct a burrow. According to the mean burrow depth values of the randomly selected burrows in (1), the exclusion burrows were measured daily with a tape measure without disturbing the crab (all crabs remained inside burrows while being measured) until they reached similar depths with respect to the random ones. Exclusion burrows were maintained between 1 and 2 days in SAO and between 6 and 11 days in MCL. The cages were then removed, and the burrows constructed were examined. For characterization of both random and exclusion burrows, the crab inside them was taken out by hand when it was near the surface or with a piece of wire when it was deep inside the burrow (without modifying the burrow form), sexed and measured. In order to obtain the burrow form, casts were made using expansible polyurethane foam, and after a hardening time of 30 min, casts were hand-excavated from the sediment and transported to the laboratory. Maximum and minimum diameters as well as length were recorded from the casts using a caliper. The number of branches and entrances of each burrow cast were also registered. To recognize the presence of a widening as a chamber in burrows and differentiate them from narrow burrows,

the difference between the maximum and minimum width of the cast was considered as a dependent variable and identified as “burrow width differentia.” Thus, large differences in the burrow width differentia would indicate the presence of a widening in the burrow, while small differences would indicate the presence of a narrow burrow, independently of the crab size (large or small). Generalized linear models (GLMs) were performed in order to test simultaneously the effects and interactions between the differing independent factors: “habitat” (salt marsh and mud flat), “category of crab” (OF, NOF, SM and LM), “experimental design” (random or exclusion burrows) and “study site” (MCL and SAO), and with respect to the dependent variable, “burrow width differentia.” For the dependent variable “length of the casts,” GLMs were conducted in order to test the effect and interactions of the same independent factors described above. Nine to 15 replicates were obtained for each crab category, for the random and exclusion burrows, in both the salt marsh and mud flats, in MCL and SAO.

A subsample of 26 and 23 exclusion burrow casts from MCL and SAO, respectively, was used to calculate the relation between the number of days that a crab used in the construction of a burrow and the burrow length as a measurement of the crab effort invested in its construction and compared between study sites using a *t* test.

## Male burrow form and mating behavior

To experimentally evaluate the relationship between male burrow form and mating, including post-copulatory guarding behavior, a crab caging exclusion experiment was performed at both study sites, MCL and SAO, during the reproductive seasons of 2009/2010 and 2010/2011. Experiments included SM, LM, narrow burrows and burrows with a widening as a chamber and arranged in four treatments: (1) one SM placed in a narrow burrow, (2) one LM placed in a burrow with a chamber, (3) one SM placed in a burrow with a chamber and (4) one LM placed in a narrow burrow. Exclusion cages (1 m<sup>2</sup>, 15 cm depth) constructed with plastic mesh (10 mm opening) were located on the mud flat. All crabs encountered inside the burrows enclosed in cages were removed, and according to the treatment, the type of burrows needed was left intact, while the rest were eliminated by filling them with sediment from surrounding areas. Burrows were probed with a stick in order to detect either the presence of a widening as a chamber inside them or whether they had a narrow burrow shape. For burrows with chambers, only those holding them in the upper part of the burrow length were used in the experiments, since copulation (if it occurred in the chamber) could be visually recognized from the surface (see section “Results”). According to the treatment, SM or LM, denoted as the “resident male,”

was added to the exclusion cage and occupation of the burrow was registered. Then, a receptive female, recognized by the presence of mobile opercula (Sal Moyano unpubl data), was added. The observer was located 30 cm from the exclusion cage, enough distance to see the crabs but to avoid affecting their behavior. The place where copulation occurred (inside/outside burrows) was recorded, and the cases in which copulation was not observed were not registered. Successful mating was considered to have occurred when both the female and male pleons were opened and the male gonopods inserted into the female vulvae. The number of males that copulated inside versus outside burrows was recorded and compared among treatments and between each study site, MCL and SAO, through a log-linear analysis (Norman and Streiner 1996; Zar 1999), considering the null hypothesis of independence between the number of individuals copulating inside burrows and (1) the study site, (2) the treatments. A posterior chi-square test of independence was conducted to analyze whether the number of males that copulated inside versus outside burrows depended on the type of treatment.

Once copulation ended, the existence of a post-copulatory guarding behavior was recorded in each experiment during 1 h. Successful post-copulatory mate guarding was considered to have occurred when the male retained the female with its chela, between its pereopods or blocked the burrow entrance preventing female escape (when copulation occurred inside burrows) until the end of the experiment. The place where the post-copulatory guarding was displayed (inside/outside burrows) was recorded. The number of males that showed post-copulatory guarding behavior inside or outside burrows was compared among treatments and between study sites through a log-linear analysis, considering the null hypothesis of independence between the number of individuals displaying a post-copulatory guarding behavior and (1) the study site, (2) the treatments. A posterior *G* test was conducted to analyze whether differences in the development of a post-copulatory guarding behavior inside/outside burrows were dependent on the type of treatment.

After the first male had successfully copulated with (and guarded) the female, a second male of similar size as the resident male was added; this second male was denoted “intruder” and identified by marking with dots of colored nail polish. The outcome of each trial was determined as follows: the male, resident or intruder located inside the burrow, holding the female (inside or outside the burrow) or both of them after 1 h, was considered the “winner” of the encounter, while the crab anywhere outside the burrow or not holding the female was considered the “loser” of the encounter. Independent of the treatments, after addition of the intruder male, the number of males (resident versus intruder) that won the resources “burrow” or “female” was

recorded and compared between MCL and SAO using a chi-square test of independence. If differences were encountered between study sites, the observed and the expected frequencies of resident versus intruder males winning each resource were compared using a chi-square test of adherence. Since few resident males from SAO won both resources, which did not allow us to compare statistically the type of male (resident or intruder) that won both resources at each study site, regardless of the type of male, the number of males, resident and intruder that won both resources (burrow and females) was pooled and compared between both study sites using a chi-square test.

Number and duration of agonistic interactions between the resident and the intruder males were recorded and compared between MCL and SAO using a *t* test after natural log transformation of the data. The number of agonistic interactions refers to each time the pair of males contacted with their chelae and separated, while duration of agonistic interactions refers to the duration of the encounters in each trial. Most of the agonistic interactions occurred outside or near the surface of the burrow and could be easily quantified. However, in a few cases and only during a few seconds, both males entered deeply inside the burrow and interactions could not be recorded. Ten replicates per treatment were obtained. All trials were conducted during low tide, on sunny or cloudy days and temperature ranged from 23 to 28 °C.

## Results

### Variation in the burrow form between individuals and study sites

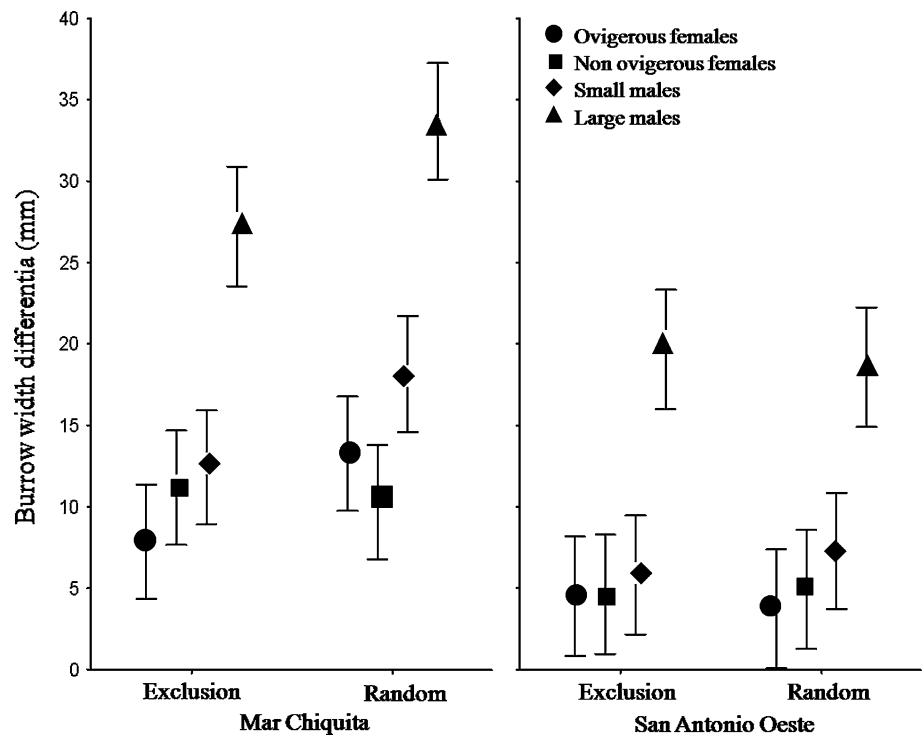
Regarding the dependent variable “burrow width difference,” GLM showed a significant effect of the factors “category of crab,” “experimental design” and “study site,” while “habitat” had no effect (Table 2). The significant effect of the factor “category of crab” indicated that burrow form varied between the differing category of individuals, in the random or exclusion burrows, at both study sites (Table 2, Fig. 2). Thus, two types of burrow form were found at both study sites. In MCL, burrows had a widening as a “chamber” in the upper or middle part of the cast length, and they were associated with LM, or burrows had a narrow tube form corresponding to OF, NOF and SM (Fig. 3a). In SAO, burrows presented a widened or a narrow entrance, and they corresponded to LM or OF, NOF and SM, respectively (Fig. 3b). A size difference between the maximum and minimum cast width of 18 mm or larger was considered as a chamber for both study sites. Maximum and minimum difference of the cast width was 55 mm and 1.3 mm for MCL and 29.7 and 0.1 mm for SAO, respectively. The significant interaction

**Table 2** Generalized lineal model showing the effect of the independent factors “habitat,” “category of crab,” “experimental design” and “study site” and their interactions with respect to the dependent variable “burrow width differentia” defined as the difference between the maximum and minimum burrow cast width

Effect	SS	Degree of freedom	MS	F	P
Intercept	53,415.87	1	53,415.87	771.62	***
(1) Habitat	11.15	1	11.15	0.16	ns
(2) Category of crab	16,502.09	3	5,500.70	79.46	***
(3) Experimental design	357.15	1	357.15	5.15	**
(4) Study site	5,457.42	1	5,457.42	78.83	***
1 × 2	42.12	3	14.04	0.20	ns
1 × 3	0.11	1	0.11	0.00	ns
2 × 3	174.38	3	58.13	0.83	ns
1 × 4	346.24	1	346.24	5.00	**
2 × 4	373.62	3	124.54	1.79	ns
3 × 4	364.97	1	364.97	5.27	**
1 × 2 × 3	52.21	3	17.40	0.25	ns
1 × 2 × 4	294.04	3	98.01	1.41	ns
1 × 3 × 4	6.34	1	6.34	0.09	ns
2 × 3 × 4	228.40	3	76.13	1.09	ns
1 × 2 × 3 × 4	24.18	3	8.06	0.11	ns
Error	20,905.94	302	69.22		

Significant P values:  
\*\* P < 0.01, \*\*\* P < 0.001

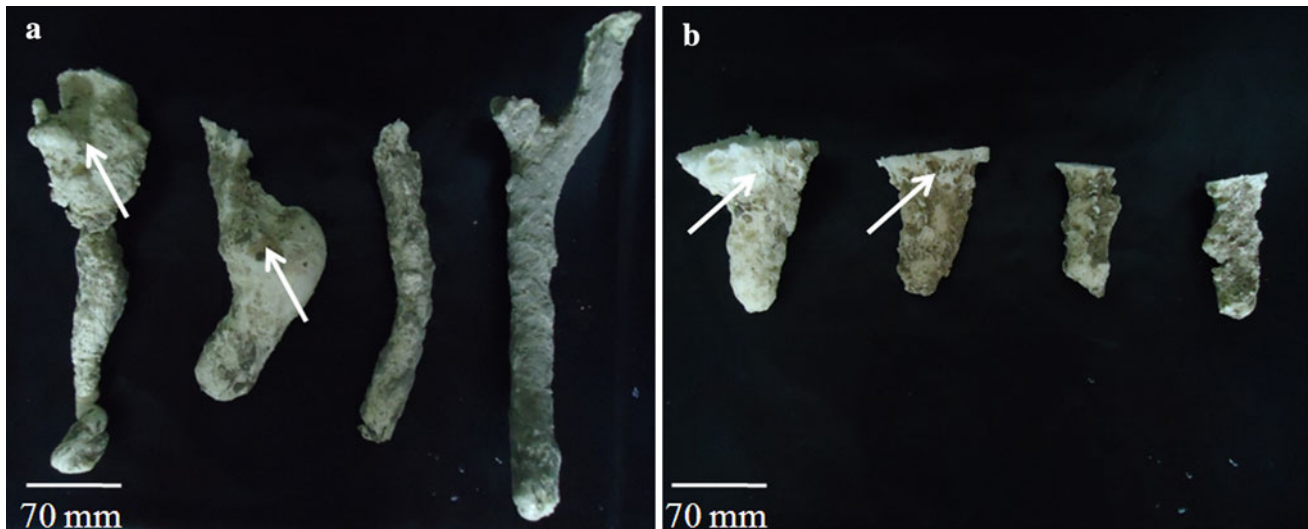
**Fig. 2** Generalized lineal model showing the interactions between the independent factors: “category of crab” including ovigerous females, non-ovigerous females, small males and large males, “experimental design” including random or exclusion burrows, and “study site” corresponding to Mar Chiquita and San Antonio Oeste; and with respect to the dependent variable, “burrow width differentia,” defined as the difference between the maximum and minimum burrow cast width



between the factors “experimental design” and “study site” (Table 2) was caused by LM having burrows with chambers in MCL and widened entries in SAO, while NOF and OF had narrow burrows at both study sites. By contrast, SM were encountered in burrows with chambers in the random sampling although they constructed narrow burrows at the exclusion sites in MCL, while they constructed narrow

burrows in SAO (Fig. 2). Although no significant effect was observed for “habitat,” the significant interaction between “habitat” and “study site,” shown in Table 2, was because in MCL there was a small variation in burrow width differentia between habitats, being larger in the salt marsh than in the mud flat, while in SAO no differences were found between them.





**Fig. 3** Burrow casts of *Neohelice granulata*. **a** Burrows casts constructed in Mar Chiquita Lagoon. Two types of burrow form were encountered: with a widening as a chamber in the upper or median part of the casts length (see *arrows*) and without a widening, as narrow

tubes. **b** Burrows casts constructed in San Antonio Oeste. Two types of burrow form were found: with a widened entrance (see *arrows*) and with a narrow entrance

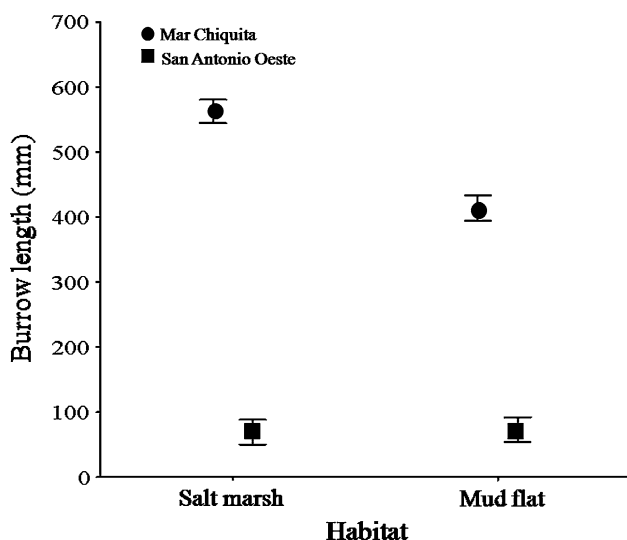
**Table 3** Generalized lineal model showing the effect of the independent factors “habitat,” “category of crab,” “experimental design” and “study site” and their interactions with respect to dependent variable “length” of the burrow casts

Effect	SS	Degree of freedom	MS	F	P
Intercept	25,821,670	1	25,821,670	3,355.629	***
(1) Habitat	432,570	1	432,570	56.214	***
(2) Category of crab	18,451	3	6,150	0.799	ns
(3) Experimental design	2,609	1	2,609	0.339	ns
(4) Study site	14,343,100	1	14,343,100	1,863.943	***
1 × 2	6,394	3	2,131	0.277	ns
1 × 3	2,679	1	2,679	0.348	ns
2 × 3	4,066	3	1,355	0.176	ns
1 × 4	479,357	1	479,357	62.294	***
2 × 4	11,203	3	3,734	0.485	ns
3 × 4	1,652	1	1,652	0.215	ns
1 × 2 × 3	7,229	3	2,410	0.313	ns
1 × 2 × 4	8,203	3	2,734	0.355	ns
1 × 3 × 4	3,581	1	3,581	0.465	ns
2 × 3 × 4	4,881	3	1,627	0.211	ns
1 × 2 × 3 × 4	12,037	3	4,012	0.521	ns
Error	2,308,509	300	7,695		

Significant *P* values:  
 \*\*\* *P* < 0.001

Regarding the burrow length, GLM showed a significant effect and interaction of the factors “habitat” and “study site,” while no effect was encountered for the “category of crab” and “experimental design” (Table 3). Differences between habitats were found in MCL: burrows were larger in the salt marsh than in the mud flat, while in SAO no differences were found (Fig. 4). Differences between study sites showed that burrow casts from MCL were much longer than the ones from SAO. Maximum and minimum burrow length was 779

and 240 mm for MCL and 105 and 46 mm for SAO, respectively. The non-significant effect of the factors “category of crab” and “experimental design” showed that the burrow length did not vary between the different categories of individuals and the random or exclusion burrows, at both study sites. Regarding the number of branches or entrances, some casts from MCL presented one or two branches and in some cases two entrances, while casts from SAO always lacked branches and never had more than one entrance.



**Fig. 4** Generalized linear model showing the interactions between the independent factors: “habitat” including the salt marsh and the mud flat, and “study site” corresponding to Mar Chiquita and San Antonio Oeste; and with respect to the dependent variable, “burrow length”

Differences were found in the crab effort (calculated as the relation between the number of days that a crab spent in the construction of a burrow and the burrow length) between study sites: individuals from SAO spent more time in building a burrow than the ones from MCL ( $t = 3.93$ ,  $P < 0.001$ ; mean  $\pm$  SD, MCL =  $0.014 \pm 0.007$ , SAO =  $0.022 \pm 0.01$ ).

#### Variation in burrow form: effects on copulation, post-copulatory guarding and agonistic encounters

The number of males that copulated inside versus outside burrows was independent of the study site ( $\chi^2 = 0.55$ ,  $P = 0.45$ ), but dependent on the treatment ( $\chi^2 = 46.88$ ,  $P < 0.001$ ). Regardless of the size of males (LM or SM) when the burrow had a chamber or a widened entrance (treatments 2 and 3), copulation occurred inside it, while in narrow burrows (treatments 1 and 4) copulation occurred outside them, on the surface (MCL:  $\chi^2 = 27.5$ ,  $P < 0.0001$ ; SAO:  $\chi^2 = 19.48$ ,  $P < 0.001$ ) (Fig. 5a–d; Table 4).

The number of males that showed post-copulatory guarding was dependent on the study site ( $\chi^2 = 16.36$ ,  $P < 0.001$ ) and on treatments ( $\chi^2 = 41.04$ ,  $P < 0.001$ ). Males from MCL displayed post-copulatory guarding behavior, while males from SAO showed no post-copulatory guarding ( $\chi^2 = 13.22$ ,  $P < 0.001$ ). For males from MCL, post-copulatory guarding was dependent on the type of treatment ( $G = 33.06$ ,  $P < 0.001$ ). In treatments 2 and 3 where burrows had a chamber and copulation occurred inside them, we also observed post-copulatory guarding: males occupied the entrance of the chamber and blocked females from running away (Fig. 5e, f; Table 4). In treat-

**Fig. 5** *Neohelice granulata* male burrows and mating behavior. **a** A small male (arrow) in the entrance of a narrow burrow, without a chamber, in Mar Chiquita Lagoon (MCL). **b** A large male (LM) in a burrow with a chamber in its upper part in MCL. **c** A exclusion cage used for the behavioral experiments, the observer was located 30 cm from of the exclusion cage. **d** A LM copulating with a female in a burrow chamber in MCL. **e** A LM with a female displaying a post-copulatory guarding behavior in a burrow chamber in MCL. **f** A LM displaying a post-copulatory guarding behavior inside a burrow chamber, holding a female with his chela and preventing her escape in MCL. **g** A LM copulating with a female in the widened entrance of a burrow in San Antonio Oeste. **h** A mating pair copulating outside burrows

ments 1 and 4 where copulation occurred outside burrows (Fig. 5g), males caged females within their legs or held them with their chela, but rarely did they retain the female during the entire experimental time (Table 4).

After addition of the intruder male, there were differences in the number of males (resident versus intruder) that won the resource “burrow” between both study sites ( $\chi^2 = 6.19$ ,  $P < 0.05$ , Fig. 6a). In MCL, there were no differences between the type of male that won the burrow ( $\chi^2 = 0.9$ ,  $P = 0.34$ ), while in SAO, the resident males were more successful in defending and winning the burrows with respect to intruders ( $\chi^2 = 8.1$ ,  $P < 0.05$ ). Moreover, there were differences in the number of males that won the females between both study sites ( $\chi^2 = 8.378$ ,  $P < 0.05$ , Fig. 6b). In MCL, there were no differences between the type of male that won the female ( $\chi^2 = 0.1$ ,  $P = 0.75$ ), while in SAO, the intruder males were more successful in winning the female with respect to the resident males ( $\chi^2 = 19.6$ ,  $P < 0.0001$ ). The number of males winning both resources, burrows and females, was significantly higher in MCL than in SAO ( $\chi^2 = 7.714$ ,  $P < 0.05$ , Fig. 6c). Thus, males from MCL more frequently obtained females and burrows, while males from SAO obtained females or burrows, but rarely both of them. The number and duration of agonistic interaction between the resident and the intruder male were significantly higher in SAO than in MCL ( $t = 4.72$ ,  $P < 0.001$ , Fig. 7a;  $t = 4.37$ ,  $P < 0.001$ , Fig. 7b; respectively).

## Discussion

The mating strategies of species depend on the ecological and behavioral potential to monopolize mates (Emlen and Oring 1977). The different habitats and behaviors needed to survive in them appear to play an important role in shaping the different mating systems (Brockerhoff and McLay 2005a). Here, we studied two populations of *Neohelice granulata* inhabiting contrasting study sites, and we found differences related to: (1) the form of burrows between study sites and among the different categories of individuals



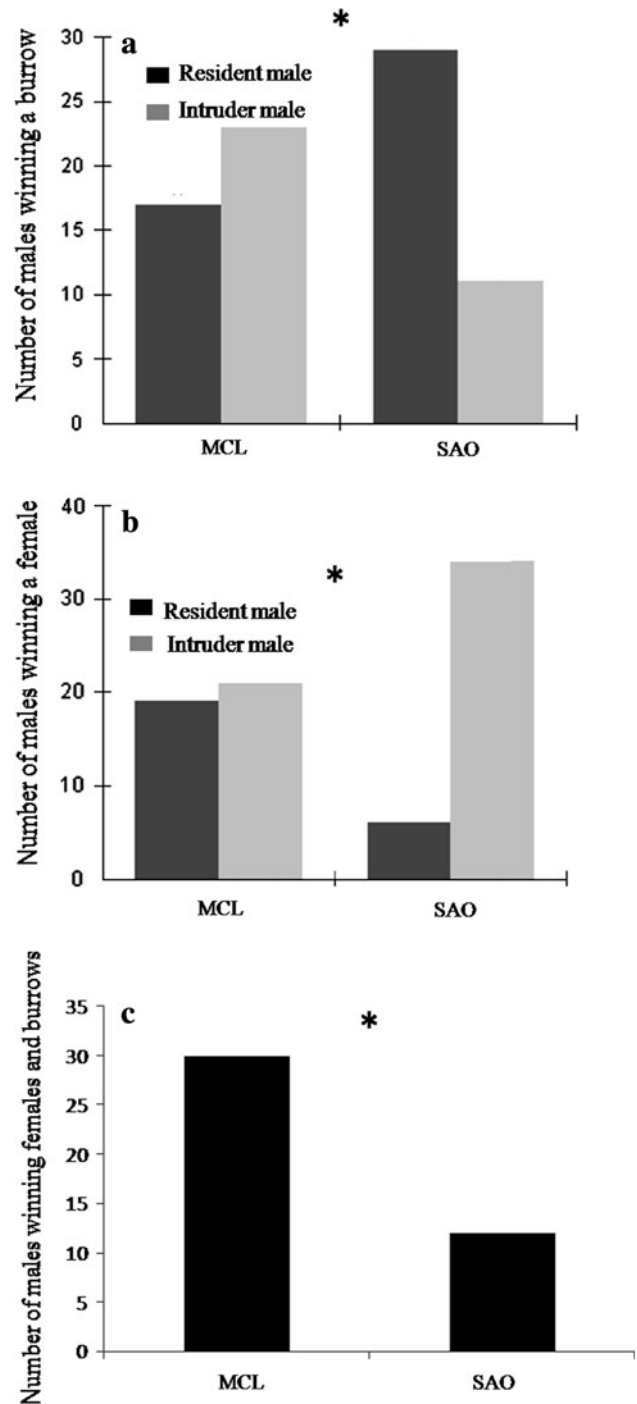


**Table 4** Observed frequencies of the number of individuals that copulated inside and outside burrows in Mar Chiquita Lagoon (MCL) and San Antonio Oeste (SAO), and observed frequencies of the number of individuals that display successful post-copulatory guarding inside and outside burrows or not displaying it, in MCL and SAO, in treatments 1 (T1), 2 (T2), 3 (T3) and 4 (T4)

Observed frequencies of individuals	T1	T2	T3	T4
<i>MCL</i>				
Copulating inside burrows	0	9	7	0
Copulating outside burrows	10	1	3	10
<i>SAO</i>				
Copulating inside burrows	0	7	6	0
Copulating outside burrows	10	3	4	10
<i>MCL</i>				
Post-copulatory guarding inside burrows	0	9	8	0
Post-copulatory guarding outside burrows	3	0	1	8
Without post-copulatory guarding	7	1	1	2
<i>SAO</i>				
Post-copulatory guarding inside burrows	0	4	3	0
Post-copulatory guarding outside burrows	1	0	0	2
Without post-copulatory guarding	9	6	7	8

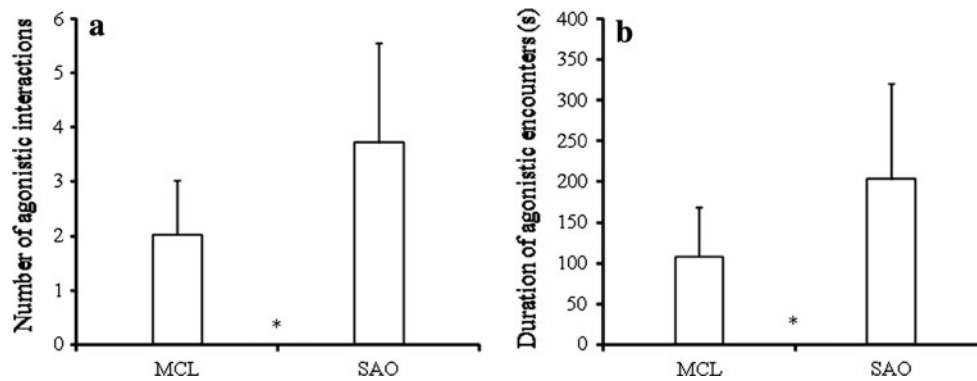
that constructed them, (2) the development of a successful post-copulatory guarding behavior and (3) the agonistic behavior of males, indicating that variation of mating strategies may be associated with different study sites. Thus, the environment appears to constrain or favor particular mating tactics via its effect on burrow architecture, similar as found for host effects on symbiotic crustaceans (Baeza and Thiel 2007).

The differences in burrow form between both study sites could be related to the different texture of the sediment: while fine sediments of MCL allow the construction of deep burrows, coarse sediments of SAO prevent them from being so deep. Moreover, in MCL, chambers can be constructed along the length of the burrow, while in SAO chambers may be constructed at the entrance, as widened entries, due to their short length of the burrows. This pattern of variation in the burrow form associated with habitat characteristics as the sediment composition was also reported for other grapsoids such as *Austrohelice crassa* (Morrisey et al. 1999; Needham et al. 2010) and *Helograpsus haswellianus* (Katrak et al. 2008). Similarly, studies conducted on thalassinidean shrimps found deeper burrows in muddy shore habitats compared to sandy ones, indicating that sediment type affects the burrow features (Griffis and Chavez 1988; Li et al. 2008). The difference in the length of *N. granulata* burrows between habitats (mud flat and salt marsh) was also reported by Iribarne et al. (1997). Additionally, habitat differences in the inclination and entrances



**Fig. 6** *Neohelice granulata* males. **a** Comparison between the number of resident versus intruder males winning burrows in Mar Chiquita Lagoon (MCL) and San Antonio Oeste (SAO). \* Significant differences were found ( $\chi^2 = 6.19, P < 0.05$ ). **b** Comparison between the number of resident versus intruder males winning females in MCL and SAO. \* Significant differences were found ( $\chi^2 = 8.378, P < 0.05$ ). **c** Comparison between the number of males that won both burrows and females, in MCL and SAO. \* Significant differences were found ( $\chi^2 = 7.714, P < 0.05$ )





**Fig. 7** Agonistic interactions between *Neohelice granulata* males. Mean values and standard deviation of the: **a** number of agonistic interactions between resident and intruder males of the Mar Chiquita Lagoon (MCL) and San Antonio Oeste (SAO): number of times that each pair of males contacted with their chelae and separated. \* Signifi-

cant differences were found ( $t = 4.72$ ,  $P < 0.001$ ) **b** Duration (s) of the agonistic encounters between resident and intruder males from MCL and SAO in each trial. \* Significant differences were found ( $t = 4.37$ ,  $P < 0.001$ )

of the burrow were associated with different trophic modes (Iribarne et al. 1997). It was also demonstrated that the length and maximum width of the burrows varied between the salt marsh and tidal creeks, promoting marsh erosion (Escapa et al. 2007). Those studies found differences in the burrow shape related to the habitat sediment characteristics, although none of them examined whether the burrow form may affect behavioral strategies and mating as we shown here for *N. granulata*.

The differences in burrow form of the different categories of *N. granulata* individuals also affected the mating behavior of crabs: large males constructed burrows with a chamber or a widened entrance where copulation with females occurred, while small males constructed the same narrow burrow form as females and copulation occurred at the sediment surface. Few studies conducted on grapsoid crabs have reported that copulation occurs inside burrows: underground mating was observed for *A. crassa* (Brockerhoff and McLay 2005a) and probably also occurs in *Sesarma reticulatum* (see Seiple and Salmon 1982), although copulation sites (inside or outside the burrows) were apparently not related to burrow form. The case for ocypodids is different. For example, in *Uca annulipes*, burrow architecture differed between sexes, with male burrows being larger than female burrows, albeit this difference was attributed to the male's spatial requirements as a consequence of its large cheliped and body size (Lim and Diong 2003), and not associated with mating. In *Ocypode ceratophthalma*, differences in the burrow architecture between juvenile and adult crabs, but not between sexes, were reported and associated with the respiratory behavior (see Chan et al. 2006). In the case of *Uca pugilator*, males create deeper burrows with chambers during the breeding season presumably for mating purposes (Christy 1982).

For *N. granulata*, we registered differences between sexes and sizes of males: large or small adult males con-

struct different types of burrows. Since burrows are important resources for mating, large and small males follow different mating strategies. It is expected that small males do not invest energy in constructing burrows with chambers because larger males could contest and win these burrows. It appears that large males construct and defend burrows with chambers used for mating, while small males mate with receptive females outside burrows, encountering them by chance (intercept mating, sensu Christy 1987). Habitat type is expected to influence a male's strategy to maximize his reproductive success (Brockerhoff and McLay 2005a). In relatively permanent habitats, males may defend long-lasting burrows as sites for mating (Seiple and Salmon 1982; Zimmerman and Felder 1991). Burrow quality could be considered as an important criterion in female mate choice, due to burrow structure potentially influencing reproductive success (Christy 1982; Backwell and Passmore 1996). Although in the fiddler crab *Uca annulipes* no relationship between male size and burrow quality was encountered, it was suggested that females use at least two independent criteria when choosing potential mates, based on male size or burrow features (Backwell and Passmore 1996). In this study, *N. granulata* male size (large versus small) was related to burrow architecture. Possibly, females are selecting mates based on a combination of resource quality (burrows) and male size. Burrow chambers may be an "honest" indicator of male quality to females, indicating that males are capable of constructing burrows with chambers in which to mate.

At MCL, differences between random and exclusion burrows were found: some random burrows of small males had a chamber, but exclusion burrows of small males never had a chamber. Possibly at this site, some small males occupied burrows originally constructed by large males. The high density of crabs that characterize that area (see Iribarne et al. 1997; Spivak 2010) could be important in causing



high mobility and interactions that occur between males to gain burrows. Males of different sizes are observed during low and high tide getting in and out of burrows, defending or contesting ownership. The high mobility of crabs at MCL may be favored by the limited costs of constructing burrows at this site, explaining the variation observed in the burrow form and the male resident. In contrast, in SAO, only large males were encountered in burrows with a widened entrance in both random and exclusion burrows. In this case, large males occupants may be defending burrows constructed by themselves, and since this involves a higher energy cost, they defend their own burrows once they have built them.

Moreover, the behavioral experiments showed that resident males from SAO won burrows, while the intruders won females. This might indicate that burrow owners (resident males) defend them, being able to copulate with a receptive female that approaches the burrow. In the presence of an intruder male, the resident males most likely choose to defend their burrows rather than females. At SAO, the primary function of burrows maybe related to protection from desiccation, which can be associated with greater exposure of crabs during low tide, rather than for mating purposes. On the other hand, in MCL, resident or intruder males could win either burrows or females, thus indicating more flexible interactions related to a lower energy cost associated with the construction of a burrow in this habitat.

The higher number and duration of agonistic encounters in males from SAO compared to males from MCL also indicate that the aggressiveness of males might be related to site-specific differences. Contest characteristics may differ between populations according to (1) the conditions determining the reward for winning the contest (e.g. more favorable operational sex ratio or duration of the breeding period) and (2) the fitness costs of aggressive behavior and the chances of winning the conflict (e.g. secondary sexual structures) (Jormalainen et al. 2000). Investment in contest behavior should coevolve with other characters that affect contest outcome (Jormalainen et al. 2000). Consequently, contest behavior of males in the two *N. granulata* populations may depend on different habitat characters: the longer exposure during low tide and the greater effort invested in the construction of a burrow could explain the higher aggressiveness of males from SAO.

Pre- and post-copulatory guarding are optional and highly flexible behaviors, the duration of which is influenced by socio-sexual context (Sainte-Marie et al. 2008). In *N. granulata*, post-copulatory guarding behavior was related to the burrow form and, consequently, to the study site. In MCL, the existence of a closed chamber may allow males to successfully defend and retain a receptive female in their burrows, while in SAO the open chamber at the

entrance could be related to the lower efficiency or lack of post-copulatory guarding behavior. The large proportion of males (resident or intruder) from MCL winning both burrows and females also indicate that the presence of a closed chamber improves male defense of females, thus developing a successful post-copulatory guarding behavior. Prolonged post-copulatory guarding as an expected strategy to increase a male's fertilization probability was previously reported for the varunids *Hemigrapsus crenulatus* and *H. sexdentatus* (Brockerhoff and McLay 2005a). Post-copulatory mate guarding may help to ensure paternity for the guarding male by preventing rival males from inseminating the female, thus reducing the risk of sperm competition (Parker 1970; Smith 1984). López Greco et al. (1999) found that the seminal receptacle of *N. granulata* females belongs to the ventral type defined by Diesel (1991). Consequently, in *N. granulata*, differences in the development of a post-copulatory guarding behavior between populations have important implications in the mating system: in MCL, males may be more successful in assuring paternity of offspring compared to males from SAO.

Different populations of the same species should feature different mating systems whenever individuals in each population or species are experiencing dissimilar ecological conditions; thus, shifts from one to another mating system should depend not only on environmental conditions but also on how flexible a species is in terms of behavior, physiology or sexual attributes (Baeza and Thiel 2007). We conclude that in *N. granulata*, since burrows constructed by males are resources used for mating and have an effect on the efficiency of post-copulatory guarding, they could influence the paternity of the brood. The intensity of agonistic encounters and the propensity of males to fight for resources such as burrows, females or both not only depend on the social environment (number and size of competitors), but also on habitat characteristics. Thus, males must employ different mating strategies according to the habitat type to ensure mating success.

**Acknowledgments** We wish to thank to Micaela Vallina, Ximena Sirimarco, Paula Orlando, Paola Silva and Matías Maggi for their help on field work. We gratefully acknowledge Antonio Baeza for revising an early version of the manuscript, and Martin Thiel and Colin McLay for their helpful advice and for kindly correcting our English text, which highly improved this manuscript. This work is part of the PhD thesis of M.P.S.M. Financial support was given to M.P.S.M. by Neotropical Grassland Conservancy and Idea Wild; to M.A.G. by the Universidad Nacional Mar del Plata, Project EXA 459/09; and to T.A.L. by Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Project PIP 176. M.P.S.M. had a fellowship from CONICET.

**Ethical standards** The experiments comply with the current laws of the country in which they were performed.

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

## References

- Abele LG, Campanella PJ, Salmon M (1986) Natural history and social organization of the semiterrestrial grapsid crab *Pachygrapsus transversus* (Gibbes). *J Exp Mar Biol Ecol* 104:153–170
- Backwell PRY, Passmore NI (1996) Time constraints and multiple choice criteria in the sampling behavior and mate choice of the fiddler crab, *Uca annulipes*. *Behav Ecol Sociobiol* 38:407–416
- Baeza JA, Thiel M (2007) The mating system of symbiotic crustaceans: a conceptual model based on optimality and ecological constraints. In: Thiel M, Duffy JE (eds) *Evolutionary ecology of social and sexual systems: crustaceans as model organisms*. Oxford University Press, Oxford, pp 249–267
- Bas C, Luppi T, Spivak E (2005) Population structure of the South American estuarine crab, *Chasmagnathus granulatus* (Brachyura: Varunidae) near the southern limit of its geographical distribution: comparison between northern populations. *Hydrobiologia* 537:217–228
- Bas CC, Spivak ED, Anger K (2007) Seasonal and interpopulational variability in fecundity, egg size, and elemental composition (CHN) of eggs and larvae in a grapsoid crab, *Chasmagnathus granulatus*. *Helgol Mar Res* 61:225–237
- Bas CC, Spivak ED, Anger K (2008) Variation in early developmental stages in two populations of an intertidal crab, *Neohelice (Chasmagnathus) granulata*. *Helgol Mar Res* 62:393–401
- Brockerhoff AM, McLay CL (2005a) Comparative analysis of the mating strategies in grapsid crabs with special references to the intertidal crabs *Cylograpsus lavauxi* and *Helice crassa* (Decapoda: Grapsidae) from New Zealand. *J Crust Biol* 25:507–520
- Brockerhoff AM, McLay CL (2005b) Mating behaviour, female receptivity and male–male competition in the intertidal crab *Hemigrapsus sexdentatus* (Brachyura: Grapsidae). *Mar Ecol Prog Ser* 290:179–191
- Chan BKK, Chan KKY, Leung PCM (2006) Burrow architecture of the ghost crab *Ocypode ceratophthalma* on a sandy shore in Hong Kong. *Hydrobiologia* 560:43–49
- Christy JH (1982) Burrow structure and use in the sand fiddler crab, *Uca pugilator* (Bosc). *Anim Behav* 31:687–694
- Christy JH (1987) Competitive mating, mate choice and mating associations of brachyuran crabs. *B Mar Sci* 41:177–191
- Christy JH (2007) Predation and the reproductive behavior of fiddler crabs (Genus *Uca*). In: Thiel M, Duffy JE (eds) *Evolutionary ecology of social and sexual systems: crustaceans as model organisms*. Oxford University Press, Oxford, pp 211–231
- deRivera CE (2005) Long searches for male-defended breeding burrows allow female fiddler crabs, *Uca crenulata*, to release larvae on time. *Anim Behav* 70:289–297
- Diesel R (1991) Sperm competition and the evolution of mating behavior in Brachyura, with special reference to spider crabs (Decapoda, Majidae). In: Bauer RT, Martin JW (eds) *Crustacean sexual biology*. Columbia University Press, New York, pp 145–163
- Ellis L (1995) Dominance and reproductive success among nonhuman animals: a cross-species comparison. *Ethol Sociobiol* 16:257–333
- Emlen ST, Oring LW (1977) Ecology, sexual selection, and the evolution of mating systems. *Science* 197:215–223
- Escapa M, Minkoff DR, Perillo GME, Iribarne O (2007) Direct and indirect effects of burrowing crab *Chasmagnathus granulatus* activities on erosion of southwest Atlantic Sarcocornia-dominated marshes. *Limnol Oceanogr* 52:2340–2349
- Fanjul E, Grela MA, Canepuccia A, Iribarne O (2008) The Southwest Atlantic intertidal burrowing crab *Neohelice granulata* modifies nutrient loads of phreatic waters entering coastal area. *Estuar Coast Shelf S* 79:300–306
- Griffis RB, Chavez FL (1988) Effects of sediment type on burrows of *Callinassa californiensis* Dana and *C. gigas* Dana. *J Exp Mar Biol Ecol* 117:239–253
- Iribarne O, Bortolus A, Botto F (1997) Between-habitat differences in the burrow characteristics and trophic modes in the Southwestern Atlantic burrowing crab *Chasmagnathus granulata* (Brachyura: Grapsoidae: Varunidae). *Mar Ecol Prog Ser* 155:137–145
- Isacch JP, Costa CSB, Rodríguez-Gallego L, Conde D, Escapa M, Gagliardini DA, Iribarne OO (2006) Association between distribution pattern of plant communities and environmental factors in SW Atlantic saltmarshes. *J Biogeogr* 33:888–902
- Iuarte RB, Bas C, Luppi TA, Spivak ED (2006) Interpopulational differences in the female reproductive cycle of the Southwestern Atlantic Estuarine crab *Chasmagnathus granulatus* Dana, 1851 (Brachyura: Grapsoidae: Varunidae). *Sci Mar* 70:709–718
- Jivoff P (1997) The relative role of predation and sperm competition on the duration of the post-copulatory association between the sexes in the blue crab, *Callinectes sapidus*. *Behav Ecol Sociobiol* 40:175–185
- Jormalainen V, Merilaita S, Hardling R (2000) Dynamics of intersexual conflict over precopulatory mate guarding in two populations of the isopod *Idotea baltica*. *Anim Behav* 60:85–93
- Katrak G, Dittmann S, Seuront L (2008) Spatial variation in burrow morphology of the mud shore crab *Helograpsus haswellianus* (Brachyura, Grapsidae) in South Australian saltmarshes. *Mar Freshwater Res* 59:902–911
- Li HY, Lin FJ, Chan BKK, Chan TY (2008) Burrow morphology and dynamics of mudshrimp in Asian soft shores. *J Zool* 274:301–311
- Lim SSL, Diong CH (2003) Burrow-morphological characters of the fiddler crab, *Uca annulipes* (H. Milne Edwards, 1837) and ecological correlates in a lagoonal beach on Pulau Hantu, Singapore. *Crustaceana* 76:1055–1069
- Lindberg WJ, Stanton G (1989) Resource quality, dispersion and mating prospects for crab occupying bryozoan colonies. *J Exp Mar Biol Ecol* 128:257–282
- López Greco LS, Rodríguez EM (1998) Size at the onset of sexual maturity in *Chasmagnathus granulatus* Dana, 1851 (Grapsidae, Sesarminae): a critical overall view about the usual criteria for its determination. In: *Proceedings of the 4th international crust congress*, pp 675–689
- López Greco LS, López GC, Rodríguez EM (1999) Morphology of spermathecae in the estuarine crab *Chasmagnathus granulata* Dana 1851 (Grapsidae, Sesarminae). *J Zool Lond* 249:490–493
- Morrisey DJ, DeWitt TH, Roper DS, Williamson RB (1999) Variation in the depth and morphology of burrows of the mud crab *Helice crassa* among different types of intertidal sediment in New Zealand. *Mar Ecol Prog Ser* 182:231–242
- Needham HR, Pilditch CA, Lohrer AM, Thrush SF (2010) Habitat dependence in the functional traits of *Austrohelice crassa*, a key bioturbating species. *Mar Ecol Prog Ser* 414:179–193
- Norman GR, Streiner DL (1996) *Bioestadística*. Harcourt, Madrid
- Olivier SR, Escofet A, Penchaszadeh P, Orensanz JM (1972) Estudios ecológicos en la región estuarial de Mar Chiquita (Buenos Aires, Argentina). I: Las comunidades bentónicas. *An Soc Cient Arg* 93:237–261
- Parker GA (1970) Sperm competition and its evolutionary consequences in the insects. *Biol Rev* 45:525–567
- Reta R, Martos P, Perillo GME, Piccolo MC, Ferrante A (2001) Características hidrográficas del estuario de la Laguna de Mar Chiquita. In: Iribarne O (ed) *Reserva de Biosfera Mar Chiquita*. Editorial Martín, Mar del Plata, Argentina, pp 31–52
- Richardson AMM (2007) Behavioral ecology of semiterrestrial crayfish. In: Thiel M (ed) *Evolutionary ecology of social and sexual systems: crustaceans as model organisms*. Oxford University Press, Oxford, pp 319–338
- Sainte-Marie B, Gosselin T, Sè vigny JM, Urbani N (2008) The snow crab mating system: opportunity for natural and unnatural selection in a changing environment. *B Mar Sci* 83:131–161

- Salmon M (1983) Courtship, mating systems and sexual selection in decapods. In: Rebach S, Dunham DW (eds) *Studies in adaptation: the behavior of higher crustacea*. Wiley, New York, pp 143–169
- Seiple W, Salmon M (1982) Comparative social behavior of two grapsid crabs, *Sesarma reticulatum* (Say) and *S. cinerum* (Bosc). *J Exp Mar Biol Ecol* 62:1–24
- Silva PV, Luppi TA, Spivak ED, Anger K (2009) Reproductive traits of an estuarine crab, *Neohelice* (= *Chasmagnathus*) *granulata* (Brachyura: Grapsoidea: Varunidae), in two contrasting habitats. *Sci Mar* 73:117–127
- Smith RL (1984) Human sperm competition. In: Smith RL (ed) *Sperm competition and the evolution of animal mating systems*. Academic Press, New York, pp 601–660
- Spivak ED (1997) Cangrejos estuariales del Atlántico sudoccidental (25°41'S) (Crustacea: Decapoda: Brachyura). *Inv Mar Valparaiso* 25:105–120
- Spivak ED (2010) The crab *Neohelice* (= *Chasmagnathus*) *granulata*: an emergent animal model from emergent countries. *Helgol Mar Res* 64:149–154
- Spivak E, Anger K, Luppi T, Bas C, Ismael D (1994) Distribution and habitat preferences of two grapsid crab species in Mar Chiquita Lagoon (Province of Buenos Aires, Argentina). *Helgol Meeresunters* 48:59–78
- Thornhill R, Alcock J (1983) *The evolution of insect mating systems*. Harvard University, Cambridge, Massachusetts
- Wirtz P, Diesel R (1983) The social structure of *Inachus phalangium*, a spider crab associated with the sea anemone *Anemonia sulcata*. *Z Tierpsychol* 62:209–234
- Zar JH (1999) *Biostatistical analysis*. Prentice Hall Press, New Jersey
- Zimmerman TL, Felder DL (1991) Reproductive ecology of an intertidal brachyuran crab, *Sesarma* sp. (nr. *reticulatum*), from the Gulf of Mexico. *Biol Bull* 181:387–401