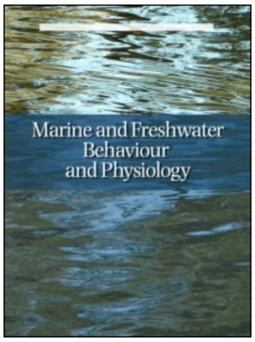

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Burrow ornamentation in the fiddler crab (*Uca leptodactyla*): female mate choice and male–male competition

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ABSTRACT

Non-biological ornamentation is found in the nests and burrows of different kinds of animals. We evaluated here whether sand hoods constructed by male fiddler crabs (*Uca leptodactyla*) are one of the signals used by males to attract females during courtship. We observed females when they were walking among the males, and we quantified the proportion of females that visited male burrows with and without ornamentation and the choice to stay in a male's burrow. Females visited more burrows with hoods than burrows without hoods, and they chose significantly more builder males. Male investment in ornamentation nevertheless decreased when the proportion of females increased in the area. Male investment was not correlated with the proportion of non-builder males nearby, but was positively correlated with overall density. The density sex ratio, however, was more male-biased in high-density than in low-density areas suggesting that even if building attracts females, the function could be related to male competition for mates.

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KEYWORDS
Fiddler crab; *Uca*; hood; intraspecific competition; attractiveness; semi-dome ornamentation

Introduction

Extended phenotypes are traits found outside an individual's body that are maintained by sexual selection or as a result of the selection of other traits (Bailey 2012). These non-biological ornaments can be found in the nests and burrows of different kinds of animals (Ostlund-Nilsson & Holmlund 2003; Slatyer et al. 2008; Doerr 2010). For example, male three-spined sticklebacks, *Gasterosteus aculeatus*, build nests using sediment and pieces of plants (Barber et al. 2001; Morrell et al. 2012), male fiddler crabs, *Uca musica*, build sand hoods upon their burrows (Christy et al. 2002, 2003b), and male great bowerbirds, *Ptilonorhynchus nuchalis*, build and adorn their bowers with colored objects (Doerr 2010, 2012). For mate choice, which is usually made by females, these ornaments have been considered relevant. Although these ornamentations are not always used in sexual communication (Christy et al. 2003a; Slatyer et al. 2008), they are also used, for example, as a

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shelter when there is predation risk, even for non-builder species (Christy et al. 2003a; Kim et al. 2007), to decrease access to resources for competitors (Wada & Murata 2000; Slatyer et al. 2008), or to protect territory (Zucker 1974).

Some species of fiddler crabs, which are semi-terrestrial crabs, build sand ornamentations on the burrow entrance. The ornamentations are named according to the shape, such as hoods or semi-domes (Kim et al. 2007; Muramatsu 2009), pillar (Backwell et al. 1995; Zhu et al. 2012), and chimney (Slatyer et al. 2008; Gusmão-Junior et al. 2012). These ornaments are destroyed by each flooding high tide and are then reconstructed as soon as the crabs start their activities outside the burrow at low tide (Christy 2007).

In the reproductive season, both sexes of fiddler crab can search for mates, and the searching sex may change in the same species and/or among species according to burrow density, mating location (surface or burrow), substrate size, carapace width, wave intensity, and eyestalk length (deRivera & Vehrencamp 2001; Ribeiro et al. 2010). For the subgenus *Leptuca*, an American clade of genus *Uca*, which contains the species that is the focus of this study, the females often search for a mate (deRivera & Vehrencamp 2001). A female begins to search for a mate during the reproductive season. Males approach a wandering female, and after assessment of the males' morphological traits (enlarged claw) and courting behavior (enlarged claw waving display), choose which burrow to visit (Christy 1988; Backwell & Passmore 1996; Murai & Backwell 2006). In this kind of mate searching, the burrow ornamentation can be a way to assess male quality in builder species because the construction and the maintenance of the ornaments generate costs for those that build (Muramatsu 2009).

The burrow ornamentation, the enlarged claw, and the waving display would be male multisensory signals, which, even if sent to different receptors, might be maintained by female mate choice due to sexual selection. We postulated that males of *Uca leptodactyla* with ornamented burrows are more likely to be chosen by females and that ornament construction would increase when the proportion of surrounding females increased. We also postulated that the hoods have "dual function" because some signals can be used either in male–male or male–female interactions (Delaney et al. 2007). The aims of this study were therefore (1) to determine whether the sand hoods constructed by *Uca leptodactyla* males are one of the signals used by males to attract females during courtship (multisensory signals), and (2) determine whether the hoods might be a signal in male competition.

Materials and methods

Study area and crabs

The study was conducted on a sandy bank without vegetation (238 m^2) of the Rio Una estuary (24°18′ S, 47°00′ W) in 2011. The location is in the Juréia-Itatins Ecological Station, a conservation unit in Peruíbe, São Paulo, Brazil (Link to supplementary Figure S1). Our study animal was the fiddler crab *U. leptodactyla*, one of the 10 species of the genus *Uca*, which occurs in Brazil. They live in estuarine zones and are distributed from Mexico to Florianópolis, Santa Catarina, Brazil. They are found in areas without vegetation coverage and with a sandy substratum with little or no mixing with mud (Melo 1996). *U. leptodactyla* is the only fiddler crab species in the study area.

Experimental design

All of the observations occurred on the sediment surface in the daylight at low tide, which is when the animals become active outside their burrows (Crane 1975). The reproductive males change their carapace color from gray to white (Link to supplementary Figure S2) and start to build burrow ornaments. In this area, we observed three different shapes of hood: (1) a wall shape, where the crab just adds a small quantity of sediment in the burrow opening; (2) a semi-dome (or hood) shape, which is the only description for the species in the literature (Crane 1975); (3) an intermediate shape, which is similar to a triangular form (Link to supplementary Figure S3). Only the semi-domes were studied for our behavioral analysis.

The density of crabs in the study area was 62.22 ± 14.20 crabs/m^2. To assess female choice, we visually identified and followed 15 females that were feeding continuously when outside their burrows. We followed them until they chose a mate. To examine the mate selection process, we quantified the number of male burrows with and without ornaments that were visited by each female until a mate selection was made. The mate choice was defined here as "female permanently inside male burrow during the next low tide." After a female entered a male burrow its owner could remain in the burrow or go back to the sediment surface. At this stage, the ratio of males without and with hooded burrows was approximately 3:1 and the ornamented burrows represented 24% of the total number of male burrows.

We also evaluated whether male investment in ornamentation increased when the proportion of females or other non-building males increased in adjacent areas. We addressed this question by counting the number of ornament builder males, non-builder males, and females in each of 27 quadrats (75 × 75 cm) during the reproductive season. The data obtained were used to calculate the proportion of each class. To investigate whether density influences the data, we also used the quadrats to compare the proportion of females, builder males, and non-builder males in the quadrats as a function of density. As not all males in the population show building behavior (Zucker 1974; Christy 1988; Salmon & Zucker 1988; Backwell et al. 1995), we classified non-builder males as those that did not built an ornament until the end of the low tide.

Data analyses

The proportion of visits and female mate choices for males with and without ornamented burrows were compared to the hypothesized probabilities of the success of ornamented and non-ornamented burrows of $p = 0.24$ and $p = 0.76$ for this population using an Exact binomial test. A Spearman's rank correlation test was used to assess the correlation between the proportion of females and built ornaments, between the proportion of non-builder males and built ornaments in the same area, and between the proportion of each class and the area density. The significance level was set at $p < 0.05$.

Ethics statement

Our study complies with the Ethical Principles in Animal Research adopted by the National Council for the Control of Animal Experimentation – Brazil (CONCEA). Permission to use the mangrove area, as well as to manipulate the crabs in the conservation unit, was given

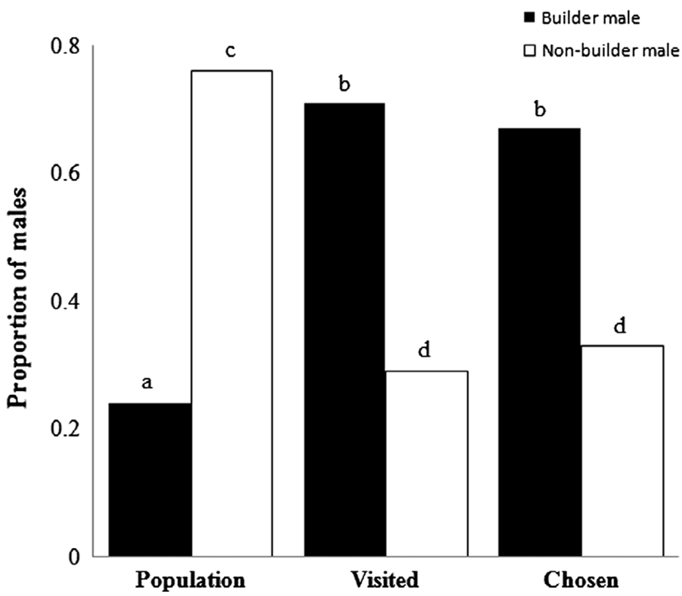

Figure 1. Female choice for hooded or non-hooded male burrows.
Notes: Proportion of males of *Uca leptodactyla* with or without ornamented burrows in the population ($p < 0.05$), folowed by proportion of males visited ($p < 0.05$) and chosen ($p < 0.05$) by females. Same letters above bars indicate no significant differences.

by the scientific technical committee (COTEC) of the Secretariat for the Environmental (SMA), process 260108 – 003.357/2011.

Results

The female mate choice started when several males approached a wandering female. The female eventually chose to follow one of the males to its burrow entrance. She would then visit the burrow or not, irrespective of whether the burrow was ornamented. Females visited and remained in more ornamented than unornamented burrows (Exact Binomial Test: $p < 0.000$). On the other hand, females also visited non-builders less than predicted (Exact Binomial Test: $p = 0.001$) and chose (Exact Binomial Test: $p = 0.001$) less non-builder males than predicted for the population Figure 1.

There was a negative correlation between the proportion of females and the proportion of ornamented burrows constructed in the same area (Spearman rank correlation: $r_s = -0.621$, $N = 27$, $p = 0.0005$; Figure 2(A)) but there was no correlation between the proportion of non-builder males and the proportion of ornaments constructed by builders (Spearman rank correlation: $r_s = -0.047$, $N = 27$, $p = 0.813$; Figure 2(B)). The population density had a negative correlation with the female proportion (Spearman rank correlation: $r_s = -0.452$, $N = 27$, $p = 0.018$; Figure 3(A)) and a positive correlation with builder males (Spearman rank correlation: $r_s = 0.487$, $N = 27$, $p = 0.010$; Figure 3(B)) but there was no correlation with non-builder males (Spearman rank correlation: $r_s = 0.111$, $N = 27$, $p = 0.581$; Figure 3(C)).

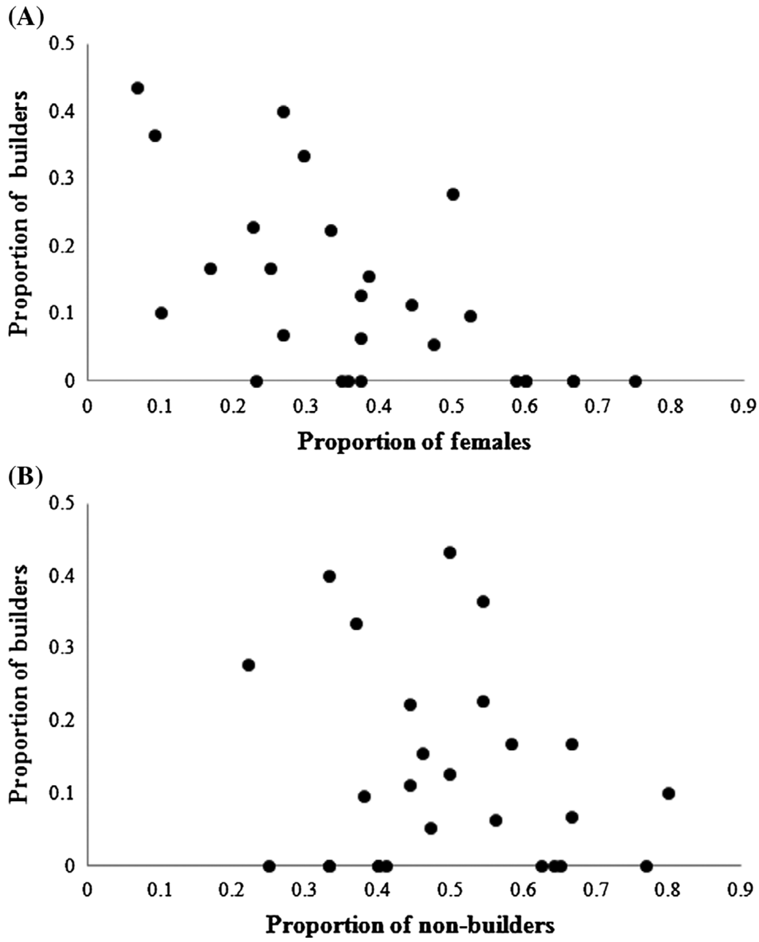

Figure 2. Ornamentation function in the reproductive period.
Notes: Correlation among the proportion of *Uca leptodactyla* builder males and: (A) neighboring females ($p < 0.05$); (B) neighboring non-builder males ($p > 0.05$).

Discussion

In this study, we showed that burrows with hoods built by *U. leptodactyla* males during the breeding season influence female mate choice, because females visited, and then chose, more males with ornamented burrows than males with burrows without ornamentation. Although builders were not more likely to build ornaments in their burrows when the proportion of non-builder males increased in the same area, they invested less in ornamentation when the proportion of females increased in their surroundings. The data on the correlation between class proportion and population density show that the ornamentation investment is positively linked to increasing density, but this only increases if there is an increase in males. While ornaments are clearly used by females to assess male quality (Backwell et al. 1995; Matsumasa et al. 2013), our findings also suggest that competition among males can influence crab behavior. While a focus of the present study, the nature of competition among males is an evident question for future investigation.

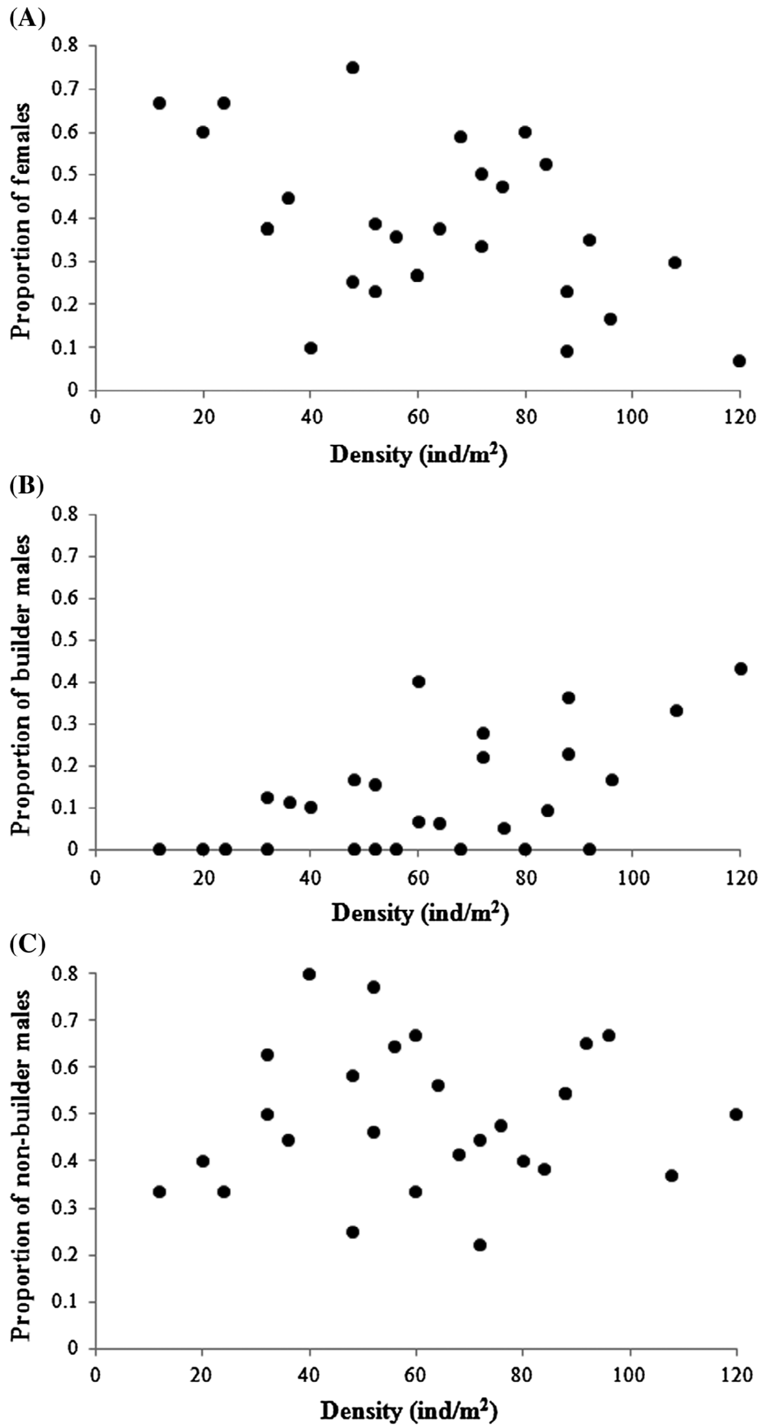

Figure 3. Effect of population density on crabs' proportion.

Notes: Correlation among the proportion of each class of *Uca leptodactyla* and the population density: (A) Females ($p < 0.05$); (B) Builder males ($p < 0.05$); and (C) Non-builder males ($p > 0.05$).

An individual can send different signals for different receivers, for example, mates or competitors. These different signals in traits and behavior can be maintained at the same time, because they reach different members of the social environment linked to sexual attraction and/or resource maintenance. Each trait could thus indicate individual quality, as well as the cost of maintenance (Andersson 1994). For bowerbirds, *Ptilonorhynchus violaceus*, decorated bowers represent an honest signal of male quality for females (reproduction) as much as a signal for males (resource competition), because the presence of objects in the bower shows the male's success in finding objects for decoration and in defending the bower against ornamentation theft by other males (Doerr 2010). Here, we observed that females preferred to visit males with ornamented burrows rather than males with non-ornamented burrows, indicating that the burrow ornamentation is important for the reproductive process as well as for burrow maintenance and protection.

For many species, ornamentation indicates the health of males, which means that females have direct benefits when accessing the males chosen on the basis of these traits (Préault et al. 2005). In the fiddler crab, *Uca annulipes*, the male body size and the quality of the male burrow are used together by females to assess and choose a mate (Backwell & Passmore 1996). The female first chooses one of the males in the assembly by his size, and then goes inside this male's burrow to assess the quality of the burrow (Backwell & Passmore 1996). For the three-spined stickleback, *G. aculeatus*, the size of the nests constructed by males is closely related to the males' health and kidney size (Barber et al. 2001). As the maintenance and construction of these ornaments is a costly activity, this behavior is performed only by healthy males (Muramatsu 2009). In our study, males with ornamented burrows were more visited by females than those with non-ornamented burrows even though they represented less than 25% of the total male population. This suggests that ornaments render males more attractive to females. These results confirm what has been described for other species of this genus (Christy et al. 2002, 2003b; Murai & Backwell 2006).

Females are attracted to males that construct ornaments, but the building behavior may also be maintained for other reasons besides sexual selection (Christy et al. 2003b). As the proportion of hooded burrows was negatively correlated with the female:male ratio in our study, we assumed that building investment did not depend on the presence of females. However, there was no relationship between the proportion of hooded burrows and the proportion of neighboring males with non-ornamented burrows. Besides that, the proportion of non-builder males was not correlated with population density, but the density was positively correlated with the ornamentation investment, and was negatively correlated with the proportion of females in the area. This suggests that the hood construction may be influenced only by the increased number of males, since the density growth is a result of male input. Individuals of 40 species of *Uca* build sedimentary structures on their own burrow (unpublished data, Pardo et al.), but in addition to our example, in only two species was the ornament assumed to be a result of male–male competition (Zucker 1974; Christy 1988). In *U. terpsichores*, the burrow of shelter building males reduces the defended area because only the entrance of the shelter is defended. This decreases the aggression among neighbors (Zucker 1974). Females of *U. beebei* also use pillars as landmarks, but the construction of the pillars may have evolved due to competition among males to attract females (Christy 1988). The females are thus able to choose their mate based on the presence or absence of ornaments in a male's burrow, whereas a male can build a hood in the presence of other potential competitor males so signaling the quality.

In summary, we showed that hoods built by *U. leptodactyla* males attracted females in the breeding season. This is similar to previous observations in other species of *Uca* sp. (Backwell et al. 1995; Christy et al. 2001, 2003b; Muramatsu 2009). Although the females can mate more often with builder males, the males invest less in ornamentation when the proportion of neighboring females increases but invest equally when the number of neighboring non-builder males increases or decreases. The density also affects the proportion of ornamentation building behavior, but the increased density is only caused by an increase in males in that population. This suggests that even if the behavior is maintained by sexual selection, competition can also influence the outcome. Future studies could be done to test the effect of competition on the behavior.

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Disclosure statement

No potential conflict of interest was reported by the authors.

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