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Neohelice granulata burrow fidelity behaviour related to landscape heterogeneity

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Abstract

Neohelice granulata provides an interesting animal model for studying behavioural process because it is widely distributed, ensuring variability related to different environmental conditions. The aim of this study was to analyse variation in site fidelity with relation to landscape heterogeneity. Field observations were carried out in three geographically distant marshes in Argentina (Mar Chiquita, San Antonio Oeste, and Riacho San José), which differ in their environmental characteristics and where crabs display different reproductive strategies. We analysed potential variation in burrow fidelity with relation to body size, sex and presence of vegetation (mudflat and saltmarsh) at all study sites. In addition, we analysed the influence of tidal flooding on fidelity in the Mar Chiquita saltmarsh. To achieve these goals, we used a mark–recapture method in which we tagged approximately 100 crabs during mid-summer for each zone at each site (a total of 668 crabs) for geographical comparison and approximately 370 crabs to evaluate the influence of tidal flooding. We found more faithful individuals in Mar Chiquita than in San Antonio Oeste and Riacho San José. For the San Antonio Oeste and Riacho San José populations and for Mar Chiquita previous to flooding samples we also found differences in site fidelity related to crab body size. At San Antonio Oeste and Riacho San José the relationship between size and proportion of faithful crabs was negative (smaller crabs were more faithful than larger crabs). In Mar Chiquita, a higher proportion of fidelity previous to flooding and a size-dependent response to flooding were detected, suggesting that fidelity may be modulated by tides having different effects on crabs with different body sizes. Equal proportions of males and females displaying site fidelity were observed at all study zones and sites. Our study suggests that *N. granulata* burrow fidelity behaviour changes with latitude and landscape (mudflat or saltmarsh) and can be sensitive to variables such as body size and frequency of flooding.

Keywords: Flooding, Fidelity behaviour, Intertidal, Crabs

Background

Site fidelity (i.e. homing to a constant rest site) refers to an organism being associated to a particular place for a given period of time [1]. Site fidelity in non-sessile species may be achieved by the use and/or defence of resources at a given site without travelling very far from it [2]. In species that do travel long distances away from their site, site fidelity may also occur if their cognitive abilities enable them to use environmental cues to return home. The expression of site fidelity behaviour may greatly depend on the potential of resource holding, which is a measure of an animal's ability to win a fight against an opponent [3, 4]. Resource holding may be determined by the costs and benefits of holding sites or resources such as access to shelter, food, mates, and breeding and/or mating sites in order to monopolise their properties [5]. As a result, intraspecific variation in resource holding behaviour is likely to occur if the costs and benefits of holding sites vary across different time and spatial scales.

Intertidal mudflats and marshes provide suitable systems for exploring the site fidelity of species given the spatial and temporal heterogeneity in their environmental conditions (including resource availability). Various studies were conducted on site fidelity behaviour of several crab species in this type of environment [6–8]. Some species, such as certain ocypodid crabs and tropical mangrove crabs display strong site fidelity [9–12], while

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others, such as some grapsid and majid species, typically show moderate or no site fidelity [13–16]. The proportion of individuals that exhibit site fidelity can vary among populations. For example, the fidelity behaviour of mangrove tree crabs (*Aratus pisonii*) can vary across its distribution range, being higher in mangrove populations than in saltmarsh populations [17]. On the other hand, site fidelity in the land crab *Cardisoma guanhumi* varies during its reproductive season [18]. Plasticity in crab site fidelity, such as that displayed by *A. pisonii* and other crab species [19], is understood as a strategy to maximise food acquisition [9, 20] or minimise predation risk [21, 22]. Although understanding of site fidelity in non-sessile species has increased in recent years, it is still challenging to identify the biotic and/or abiotic factors influencing the expression of differential behavioural strategies within a species. Studies based on crab species that dwell in different habitats across a large distribution range might help to provide more details on how ecological factors influence alternative behaviours.

Neohelice granulata is one of the more abundant semi-terrestrial brachyuran crabs (Brachyura: Varunidae) in South America. This species distributes from southern Brazil to southern Argentina, where it inhabits the intertidal zone of low mudflats and saltmarshes [23]. *N. granulata* males and females are typically found in or near their burrows they dig in the substratum. Burrows appear to be key resources to these crabs, providing shelter against adverse environmental conditions [24, 25] and predatory attacks from several species of birds and fish [26–30]. Burrows also provide an area for sexual encounters and a safe place where females breed their embryos [31, 32]. *N. granulata* build burrows differentially depending on the environmental characteristics: while in some populations males build burrows with a mating chamber to protect the pair during mating [32, 33], in others, they build burrows with a widened entrance but without a mating chamber [31]. Burrows with a mating chamber facilitate pre and post-copulatory behaviours, that in turn allow greater sperm transfer. Winners of agonistic encounters for the possession of burrows with mating chambers are typically those largest male individuals. Therefore, burrows with mating chamber are always occupied by males larger than 30 mm of carapace width [32], which are consequently more likely to be selected by females during mate searching [31, 34–36]. Recent studies reported that *N. granulata* individuals often make short-term explorations to find food and then use their own footpath to return to the burrow [36]. Luppi et al. [25] showed that the dynamics in the transit of individuals between intertidal zones such as mudflats and saltmarshes and across different tidal regimes can be high and variable depending on the geographic site. In many populations of this species tide covers most burrows daily, and when this happen crabs leave their burrows and roam between the mudflat and the saltmarsh. Soon after tide withdraws, crabs are observed intensely searching for burrows. In those populations in which males build mating chambers, males (especially large individuals) look first for burrows with mating chambers, but if do not find any they either build a chamber in an existing burrow or dig a new burrow in case they are unable to find an unoccupied one. In the light of the above, populations of *N. granulata* provide an ideal study system for investigating whether geographical and local heterogeneity related to resource holding may determine potential interpopulation differences in burrow fidelity. Here, we analyse the level of burrow fidelity exhibited by *N. granulata* crabs in relation to landscape heterogeneity. To achieve this goal, we selected three different geographical sites, which differ in their environmental characteristics and where crabs display different reproductive strategies. We analysed potential burrow fidelity variation in relation to body size, density, sex and presence of vegetation (mudflat and saltmarsh) at all study sites. In addition, we analysed the influence of tidal flooding in saltmarshes on burrow fidelity.

Materials and methods

Study sites

This study was conducted in Mar Chiquita (MCH, 37°45′S, 57°19′W), San Antonio Oeste (SAO, 40°46′S, 64°50′W) and Riacho San José (RSJ, 42°25′S, 64°37′W) (Fig. 1) in February and March 2014 (in which is a

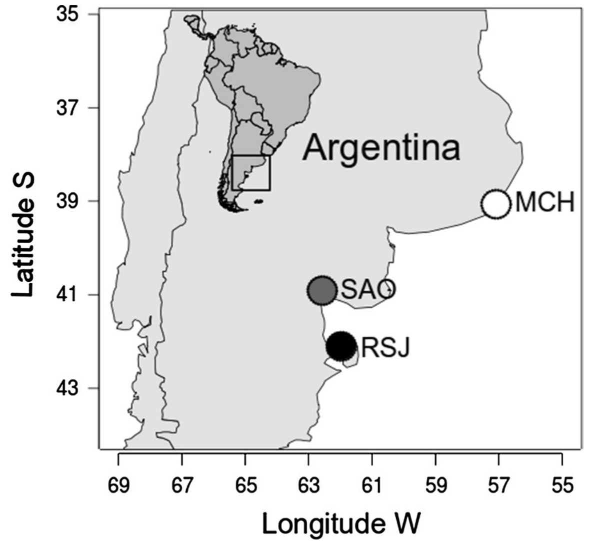

Fig. 1 Map of observation locations on the Argentinean coast. *MCH* Mar Chiquita, *SAO* San Antonio Oeste, *RSJ* Riacho San José. Different colour dots show different sites

period where this populations are in the reproductive period [24]). All sites exhibit different environmental characteristics:

Mar Chiquita is a coastal lagoon with a large intertidal area (46 km^2) and semidiurnal microtidal regime (0.3–1 m amplitude, Servicio de Hidrografía Naval, http://www.hidro.gov.ar/, accessed August 24, 2018) connected with the open sea by a narrow channel of about 5 km long. Mean rainfall is 800 mm year^{-1}. The lower and middle intertidal zones are mudflats, while the upper-intertidal zone is a mixed *Spartina densiflora* and *Sarcocornia perennis* marsh [37]. Sediments are fine with high organic matter content and high penetrability [38]. Crabs occupy the upper- and mid-intertidal zone. Burrows are deep with maximum depth 70 cm, and include a mating chamber to protect the pair during mating [32, 33].

San Antonio Oeste is a bay with a very large intertidal area (143 km^2) that opens to San Matías Gulf. It is located in a very dry area (average rainfall: 240 mm year^{-1}) with no freshwater input. It has a semidiurnal macrotidal regime (9 m amplitude, Servicio de Hidrografía Naval, http://www.hidro.gov.ar/, accessed August 24, 2018) and an extensive sand-cobble intertidal flat. The upper intertidal zone is a *S. perennis* marsh and the mid-intertidal zone is divided into a *S. alterniflora* marsh [37] and a mudflat that continues throughout the lower intertidal zone. The organic matter in the sediment and penetrability are very low [39]. As occurs in MCH, crab burrows occupy both the upper- and mid-intertidal zones, but burrows in SAO reach a maximum depth of 25 cm and do not include a mating chamber at the entrance [32].

Riacho San José is a bay with a smaller intertidal area (2 km^2) that opens into the San José Gulf and is located in a very dry area (average rainfall: 200–225 mm year^{-1}) with no freshwater input. It has a semidiurnal macrotidal regime (4.69 m amplitude, Servicio de Hidrografía Naval, http://www.hidro.gov.ar/, accessed August 24, 2018), with extensive sand-cobble intertidal flats. The upper intertidal zone is a *S. perennis* marsh and the mid-intertidal zone is divided into a *S. alterniflora* marsh [37] and a mudflat that continues throughout the lower intertidal zone. As at the other sites, there are burrows in both the upper- and mid-intertidal, with maximum depth 30 cm [40]. Burrows are built with a mating chamber to protect the pair during mating [32, 33].

In order to study burrow fidelity, we used a mark–recapture method in which we tagged approximately 100 crabs in each zone (mudflat and saltmarsh) at each site (MCH, SAO and RSJ).

"Faithful" individuals were those that were found again in their burrows while "unfaithful" individuals were those that were not found in their burrows at the time of our measurement. At each site and zone we marked a set of approximately 30 individuals during three different and separated days. For each of these days we registered the faithful individuals (i.e. those tagged crabs found inside their burrows, see Table 1) after 24, 48 and 72 h (i.e. every two tidal cycles). The number of individuals marked daily depended on the available working time due to the tidal regimes of different tidal cycles (see Table 1).

Before starting with the observations, crabs were carefully extracted without damaging the burrow structure. For this, the crabs inside the burrow was taken out by

Table 1 Descriptive data of geographical and of the tidal flooding observation of "faithful" crabs returning to burrow

Source	Zone	Day of observation		
		One	Two	Three
MCH	Mudflat	0.21 (n = 33)	0.35 (n = 33)	0.34 (n = 32)
	Saltmarsh	0.48 (n = 39)	0.50 (n = 41)	0.65 (n = 80)
	Total	0.38 (n = 72)	0.49 (n = 74)	0.55 (n = 112)
SAO	Mudflat	0.00 (n = 37)	0.04 (n = 24)	0.02 (n = 41)
	Saltmarsh	0.055 (n = 38)	0.12 (n = 25)	0.075 (n = 37)
	Total	0.03 (n = 75)	0.08 (n = 49)	0.05 (n = 78)
RSJ	Mudflat	0.00 (n = 36)	0.055 (n = 35)	0.11 (n = 35)
	Saltmarsh	0.11 (n = 34)	0.05 (n = 41)	0.08 (n = 33)
	Total	0.03 (n = 70)	0.04 (n = 76)	0.07 (n = 68)
MCH saltmarsh	Previous flooding	0.62 (n = 31)	0.46 (n = 97)	0.35 (n = 88)
	After flooding	0.34 (n = 26)	0.43 (n = 65)	0.26 (n = 62)
	Total	0.48 (n = 57)	0.44 (n = 162)	0.30 (n = 150)

Data are from two zones (mudflat and saltmarsh) in three locations in Argentina, from north to south: Mar Chiquita (MCH); San Antonio Oeste (SAO) and Riacho San José (RSJ) from two environmental conditions in the saltmarsh zone of MCH: tidal situation previous and after flooding. The number in each bristle board denotes the percentage of site fidelity crabs and within the parentheses the total number of individuals tagged on the corresponding day hand when it was near the surface, in some cases we used wire method sensu Sal Moyano et al. [31] to prevent the rapid retraction of the crab inside the burrow by nailing the wire to the sediment into the burrow behind the individual. Immediately after retrieval, carapace width (CW) was measured with a calliper (0.1 mm accuracy) and sex was determined. The time of the extraction did not exceed 3 min, and once it was returned the re-entry to the burrow and its permanence was verified.

We used sexually mature male and female crabs ranging from 22 to 32 mm in CW [41]. Crabs were marked by gluing (cyanoacrylate) a small colour-coded plastic tag on the cardiac region of the carapace, which is considered innocuous [9]. In order to identify the burrow corresponding to each tagged crab, a labelled stake was placed near the burrow.

In order to control the potential density-dependence effect on site fidelity, we evaluated the differences in the density of populations among sites and zones. For this purpose, in a mudflat and salt marsh at each site (MCH, SAO and RSJ), the density of *N. granulata* was estimated at the beginning of the study by counting all individuals with a carapace larger than 20 mm within ten 50 × 50 cm randomly placed square frames.

Influence of tidal flooding on burrow fidelity

The zones we chosen for sampling (i.e. mudflat and vegetated area of the salt marsh located immediately upward of the mudflat) varied in the frequency of "flooding" among sites. While this portion of the saltmarsh floods daily during high tides in SAO and RSJ, the MCH saltmarsh only floods a few times per month during extreme tides [38]. Burrows and crabs associated to *S. densiflora* are only flooded during these particular events. Taking advantage of this environmental context, we decided to perform further samplings in MCH to evaluate whether the proportion of faithful crabs changed with flooding frequency. For this purpose, we marked crabs in the high salt marsh zone: (1) on days with regular tides (previous to flooding), and (2) on days with spring tides (after to flooding) (Table 1). In these two situations, faithful individuals were recorded with the same general methodology as described above.

Data analysis

Bayesian methods are preferred over classic statistics because the results can easily be interpreted in terms of relative probability [42–44]. For this reason, we used a Bayesian approach with models based on binomial distribution to describe the burrow fidelity behaviour of *N. granulata* on each level of observation.

Our observational data were obtained from individuals that were measured on the same days. In order to incorporate the potential additional variation due to factor day (e.g. time of marking, number of individuals, climatic conditions of each day, among others), we used a hierarchical Bayesian model (Additional file 1: S1 [45]).

For the geographical fidelity analysis, hierarchical Bayesian regression models were performed to determine whether the proportion of "faithful" crabs (dependent variable) varies due to the combination of population density, size and sex (independent variables) in the mudflat and saltmarsh at each site. In the case of tidal fidelity analysis (i.e. tide flooding analysis), hierarchical Bayesian regression models were performed to determine whether the proportion of "faithful" crabs (dependent variable) varies due to the combination of density population, size and sex (independent variables) without and with exceptional tidal events. In the case of population density data, prior to performing the hierarchical Bayesian models, we analysed whether this factor varied significantly among zones and sites.

We used Bayesian methods in JAGS [46] to estimate the posterior probability distributions of all parameters modelled through Monte Carlo-Markov chain (MCMC) algorithm implemented in the program. We called JAGS from within program R [47] with the library version 4-6 (http://mcmc-jags.sourceforge.net, accessed August 24, 2018). All prior distributions were uninformative distributions specified to have little influence on the posterior probability distributions. An example of JAGS code for the fidelity rate estimation is provided in the Additional file 1: S1. We ran 100,000 generations of three Markov chains, a priori discarding the first 10,000 (i.e. 10%) as burn-in. Convergence was diagnosed for the all models by visual inspection of the MCMC through the Gelman–Rubin statistic in which numbers less than 1.1 indicate good convergence [48].

In all cases, the importance of each explanatory variable in the minimum adequate models was assessed by comparing a reduced model (with all terms involved and the factor of interest removed) against the full model, using deviance information criterion (DIC) developed by Spiegelhalter et al. [49], which evaluates model fit and complexity such that smaller values are preferable. We computed DIC weight (w_i) for each candidate model [50] through its computed DICc and the Δ values. Weights ranging from 0 to 1 are interpreted as the weights of evidence in favour of model *i* as the best model among the set of all candidate models examined [51]. Finally, the models with the smallest DIC and the highest w_i values were chosen as the models that "best" represented the data. If the top models had close convergence, we implemented a model averaging process to calculate the relative importance (RI) of the explanatory variables. To do so, we used the models that constitute a cumulative DIC weight of 0.95 [51]. We considered it as a strong explanatory variable if the RI was close to 0.9, moderate for an RI of 0.9–0.6, and weak if the RI was less than 0.6 [51]. All statistical analyses were conducted in R 3.3.1 [47].

Results

The overall rate of fidelity recorded was very low particularly at periods greater than 24 h. For 48 and 72 h the rate of fidelity recorded was less than 0.1 whereby the analysis for those time periods were not very informative (due to the high number of zeros), thus we restrict the analysis to the results of 24 h.

During the study we found a little number of gravid females, which with the same criteria to the 48 and 72 h data set it was not incorporated to the analysis. However, it should be noted that gravid females in all the cases were more faithful than non-gravid ones (Additional file 1: Fig S2).

Recovery rates of crabs to their burrows varied according to geographic sites (MCH, SAO and RSJ) and zones (mudflat and saltmarsh). Respect to sites, the highest proportion of "faithful" individuals was recorded at MCH (0.47 ± 0.086, average and SD of three observation days, see Table 1), followed by SAO and RSJ (0.053 ± 0.020 and 0.049 ± 0.025, respectively, average and SD of three observation days, see Table 1). Respect to zones, at MCH, the highest proportion of "faithful" individuals was recorded at saltmarsh (0.56 ± 0.085 average and SD of three observation days, see Table 1) followed by mudflats (0.32 ± 0.053, average and SD of three observation days, see Table 1). But at SAO and RSJ the proportion of "faithful" individuals was similar between both zones (mudflat; 0.020 ± 0.020 and 0.055 ± 0.051 and saltmarsh; 0.028 ± 0.080 and 0.016 ± 0.060 respectively, average and SD of three observation days, see Table 1).

According to the Bayesian models, the relative importance (RI) of population density and crab sex variables on the proportion of faithful crabs was weak for all the study zones at each site (RI < 0.6, Table 2), indicating that these variables may not affect site fidelity. Similarly, body size also showed a weak RI in MCH (mudflat and saltmarsh RI < 0.6). However, in SAO and RSJ the RI was from moderate to high values (see Table 2) and in all cases with a low probability (less than 0.15) to find faithful crabs with an exponential decay related to carapace width, indicating that smaller crabs were more likely to be faithful than larger ones for these sites (see Table 2; Fig. 2).

Influence of tidal flooding on burrow fidelity

Recovery rates varied according to the flooding situation; the highest proportion of faithful individuals was recorded on days "previous to flooding" (0.46 ± 0.137, average and SD of three observation days, see Table 1) than "after to flooding" (0.34 ± 0.085, average and SD of three observation days, see Table 1).

According to the Bayesian models, the RI of population density and crab sex variables on proportion of faithful crabs was weak, for both situations either "after

Table 2 The four best Bayesian models for the three sources of information (Sites)

Source	Model	Mudflat						Saltmarsh					
		Den	Sex	Size	DIC	Δ	w_i	Den	Sex	Size	DIC	Δ	w_i
MCH	1	−	−	+	109.7	0.0	0.28	−	+	−	161.92	0.0	0.31
	2	−	+	−	110.05	0.38	0.23	+	−	−	162.09	0.17	0.28
	3	+	−	+	110.53	0.85	0.18	−	−	−	163.71	1.79	0.13
	4	+	−	−	110.85	1.17	0.16	+	+	+	164.29	2.37	0.09
RI		0.39	0.34	0.54				0.46	0.51	0.21			
SAO	1	+	+	+	20.06	0.0	0.20	−	+	+	22.22	0.0	0.21
	2	+	−	−	20.18	0.12	0.18	+	+	+	22.50	0.29	0.18
	3	+	−	+	20.38	0.32	0.17	+	−	+	22.68	0.47	0.16
	4	−	+	+	20.48	0.42	0.16	−	−	+	22.84	0.62	0.15
RI		0.57	0.42	*0.71*				0.57	0.54	*0.7*			
RSJ	1	−	+	+	17.65	0.0	0.23	−	+	+	34.53	0.0	0.19
	2	−	−	+	17.71	0.05	0.23	+	−	−	34.63	0.10	0.18
	3	+	−	+	17.78	0.13	0.22	−	−	+	34.64	0.11	0.18
	4	+	+	+	18.51	0.91	0.15	+	+	+	34.90	0.37	0.15
RI		0.52	0.45	*0.83*				0.57	0.48	*0.66*			

+/− indicates whether or not the factor was included in the model. Relative importance of the explanatory variables (*RI*). Strong or moderate explanatory variable influence on the average model is highlighted in italic

DIC—deviance information criterion; Δi—deviance information criterion differences; w_i—normalised weights of DIC

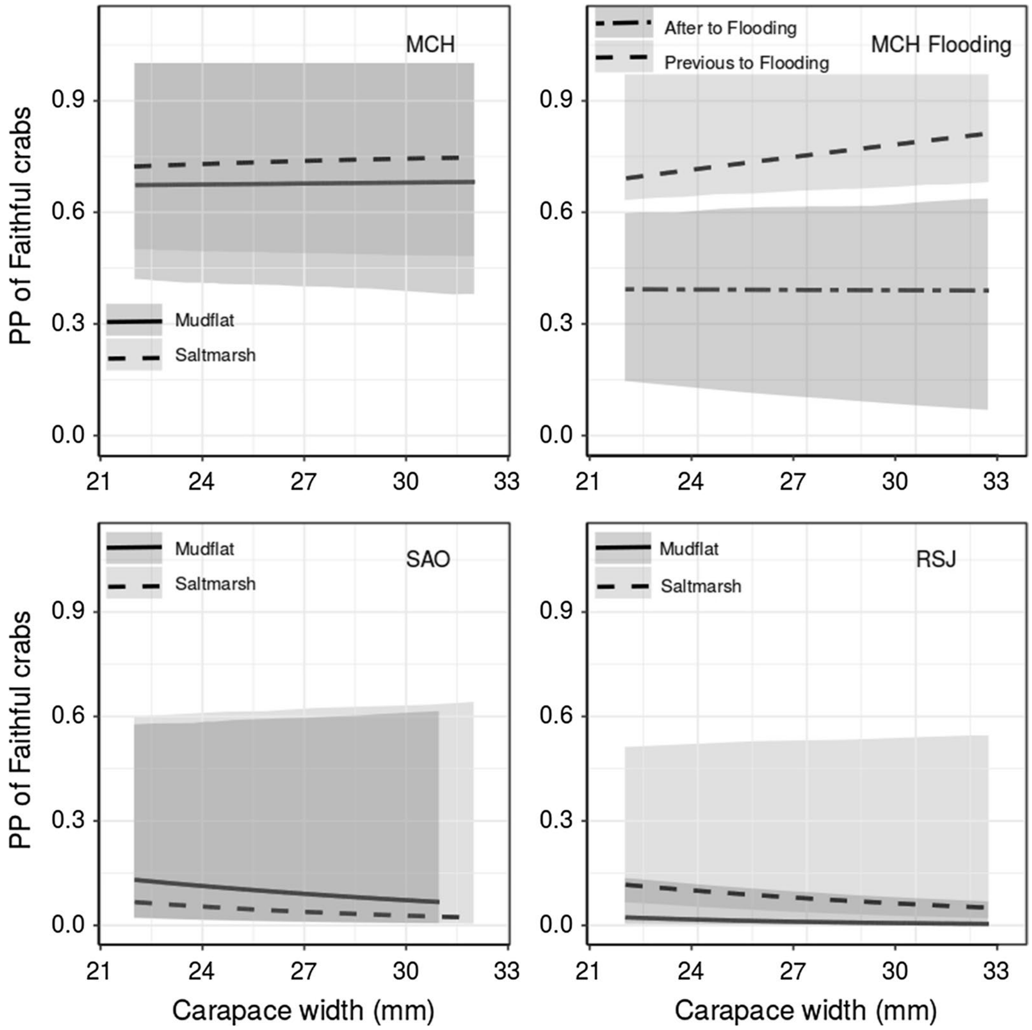

Fig. 2 Bayesian regression model graph of "faithful" crabs and body sizes at the different geographical sites for each zone (mudflat and saltmarsh) and at different flooding situations. The y-axis shows the posterior probability (PP) estimated of "faithful" crabs and the x-axis shows carapace width. Estimated "faithful" PP (black line) with 95% credible interval (shaded area) represent two zones (mudflat and saltmarsh) in three locations in Argentina, from north to south: Mar Chiquita (MCH); San Antonio Oeste (SAO) and Riacho San José (RSJ) from two environmental conditions in the saltmarsh zone of MCH: tidal situation previous and after flooding

to flooding" or "previous to flooding" (RI < 0.6, Table 3). Meanwhile, RI for body size was weak (< 0.6) "after to flooding" and moderate (0.77) "previous to flooding" (Table 3). This would indicate that at "previous to flooding" events, there is high probability (more than 0.5) to find faithful crabs and this probability increase with the carapace width, indicating that larger crabs were more likely to be faithful than smaller ones (see Table 3; Fig. 2).

Discussion

The low recovery rates for tagged crabs observed at all sites indicate that the semiterrestrial crab *N. granulata* displays low fidelity during its daily activity pattern (after 48 h less than 1% for all study populations, Table 1). In a previous work on this species [25] it has been reported that individuals can show a high mobility rate between different patches (saltmarsh and mudflat) in short periods of time (e.g. along of tidal cycle) and this is probably related to the use of different types of habitats to eating, resting and reproducing, as it was also observed in ecologically equivalent species (such as *A. cinereum*) [52]. This high rate of mobility that crabs in *N. granulata* exhibit could explain the low fidelity we found here. *N. granulata* uses two dominant feeding strategies (detritivorous and herbivore) that are context-dependent; when habitats are covered by tides crabs predominantly

Table 3 The four best Bayesian models for the two sources of information (flooding)

Source	Model	Previous to flooding						After to flooding					
		Den	Sex	Size	DIC	Δ	w_i	Den	Sex	Size	DIC	Δ	w_i
Saltmarsh	1	−	+	−	145.06	0.0	0.43	−	−	+	97.77	0.0	0.28
	2	−	−	−	145.72	0.66	0.32	+	+	+	98.07	0.30	0.24
	3	+	+	−	148.70	3.64	0.07	+	−	+	99.06	1.29	0.15
	4	−	−	+	149.56	4.50	0.05	−	+	+	99.81	2.04	0.10
RI		0.17	0.58	0.17				0.56	0.44	*0.77*			

+/−indicates whether or not the factor was included in the model. Relative importance of the explanatory variables (*RI*). Strong or moderate explanatory variable influence on the average model is highlighted in italic

DIC—deviance information criterion; Δi—deviance information criterion differences; w_i—normalised weights of DIC

feeds on leaves of *Spartina* sp. [53] while when the tide withdraws they feed mud [54] which could lead to higher rates of migratory movements during high tide [25].

Stachowicz and Hay [16] proposed that crabs with generalist feeding habits exhibit reduced mobility and strong fidelity behaviour to a particular area. Despite the fact that *N. granulata* has an omnivorous–detritivorous feeding habit [54, 55] our data indicate that site fidelity in *N. granulata* is weak. Low burrow fidelity has also been observed in other marsh Graspid species such as *S. reticulatum*, *A. cinereum* and *Hemigrapsus sanguineus* [14, 51]. Similarly to *N. granulata*, these species show "unfaithful" daily behaviour, being capable of travelling long distances within their habitat [14, 56], as well as having omnivorous–detritivorous feeding habit [56, 57] indicating that the Stachowicz and Hay's model cannot be applied.

The strength of site fidelity for burrow holding may be a function of the costs and benefits incurred by different strategies such as (1) constructing a new burrow, (2) acquiring and restoring an unoccupied burrow, or (3) continuously maintaining and defending the individual's own burrow. In addition, even when the time and energy required to dig a new burrow may be negligible, the availability of free appropriate space to dig a new burrow or the likelihood of finding an unoccupied one may be some of the variables that influence which strategy is chosen. For example, fiddler crabs are known to have strong site fidelity [58] to their burrows, which they use as a refuge during both high and low tides, as protection from physiological stress [59] and a place for mating [60]. With some exceptions [20], fiddler crabs feed on the sediment located within a radius that rarely extends beyond 1 m from the opening of their burrows [61]. During feeding bouts, fiddler crabs are constantly retracting in response to any predation risk or any attempted theft by an intruder [8, 58]. In fiddler crabs, the likelihood of finding an unoccupied burrow may be low because unoccupied burrows that are not plugged are irretrievably crumbled and destroyed by the incoming tide. In addition, coalitions between neighbours [62] may prevent burrowless crabs from digging new burrows in their neighbourhood, forcing them to marginal areas. Therefore, losing or discarding a burrow may be more costly for fiddler crabs than for *N. granulata* because they lose the physical resource as well as the site where it was located. In contrast, *N. granulata* does not plug burrows during high tide and the likelihood of finding an unoccupied burrow may be much higher than in fiddler crabs. Therefore, the weak site fidelity in *N. granulata* may be caused by the resulting balance between the costs and benefits of guarding or defending a resource that may not be as scarce as it is for fiddler crabs. In environments in which the individuals of *N. granulata* are exposed to many hours of desiccation, it is common that there are almost no individuals outside the burrows and do not conglomerate in other places either, thus, in a broad sense, it can be assumed that the number of burrows are equivalent to the number of crabs. When certain zones are covered by tides a high and variable proportion of individuals leaves the burrows and has the capacity to move long distances, losing spatial contact with the original burrow. However, the total number of burrows is still equivalent to the number of crabs, so they are redistributed among the existing burrows, and the searching time and type of burrow obtained will depend on the individual relative size. For example, a male crab with a carapace width (CW) higher than 30 mm has competitive advantages of occupying a burrow with mating chamber after having abandoned its original burrow, and only at exceptional cases, we can found crabs with a smaller CW on burrows with mating chamber [32].

Our results showed that *N. granulata* displays different degrees of site fidelity at a geographical scale and with a variable effect of body size. In general terms, the proportion of "faithful" crabs was higher in MCH than SAO and RSJ. Within SAO and RSJ populations, smaller crabs were more "faithful" than larger ones. In this regard, many intertidal species have developed a variety of adaptations to regulate their body temperature and evaporation [63]. In the context of resource holding behaviour, the "environmentally stressful response" hypothesis predicts that individuals make behavioural decisions in order to reduce desiccation risk [64–66]. Burrows are thus essential to these crabs for avoiding adverse environmental conditions [24, 38]. A higher rate of site fidelity is thus expected in populations living under harsher climate conditions. Although the climate is less harsh in MCH than in SAO and RSJ (in terms of evaporative rate) [66, 67], its mesotidal regime results in crabs spending days without being flooded, mainly in the saltmarsh area. Under this scenario, sites with higher flooding tidal frequencies (macrotidal regimes such as SAO and RSJ) may reduce the window of exposure time to desiccation and could therefore promote lower site fidelity, thus showing that the frequency of flooding may be more important than the local evaporative rate. Indeed, the data gathered in MCH with and without a flooding strongly support the idea of the importance of tidal flooding on crab fidelity to burrows, since there are fewer "faithful" crabs during exceptional tidal events (*i. e* less desiccation risk during these events).

Neohelice granulata builds its burrow differently depending on the environmental characteristics (attributed mainly to different granulometry, texture and hardness of the sediment): while at some sites such as MCH and RSJ males make burrows with a mating chamber to protect the pair during mating [32, 33], at others, such as SAO, males build burrows with a widened entrance and without a mating chamber [32]. Mating chamber of MCH are maintained during all seasons independently to reproductive period, whereby in addition to the reproductive role [32], it could have another possible role, such as protection from predators, which also differed among sites (MCH have higher density of predatory avian species than SAO) [68]. In the context of resource holding behaviour, a higher rate of site fidelity is expected in populations with mating chamber because crabs assume costs of building chambers and also obtain benefits of breeding success [32]. However, the proportion of "faithful" crabs was independent of the population's capacity to build chambers (MCH and RSJ), which may suggest that the importance to occupy a burrows with mating chambers is not as important as the environmental conditions and/or presence of predatory avian species of each saltmarsh.

Although the proportion of fidelity in SAO and RSJ always was lower than in MCH, both sites had a negative association between the probability of fidelity and crab body size. On the other hand, at MCH, there was a positive association between the probability of fidelity and body crab size for individuals under non-flooding conditions. Here, there is a case of intraspecific variation in resource holding behaviour that is dependent on body size, varying across different spatial scales (evident in SAO and RSJ vs. MCH) and flooding condition (evident in MCH). In the literature the presence of predators is reported as a factor modulating fidelity behaviour [69]. In our study case, although there are differences in the occurrence of avian predators [68] it is not clear how it may explain body-size dependent fidelity behaviour between sites. In contrast to what would be expected, sites characterized by a low density of predatory avian species [68] as SAO were those found to have body-size dependent fidelity. It is likely that other factors as different degrees of cannibalism may help to explain the relationship between site fidelity and body size. Therefore, the mobility of small individuals, at populations with high cannibalism (such as SAO [54, 70] and RSJ [Pers. Obs.]), may be less intense than those of adult due to the vulnerability to cannibalization by larger individuals [71]. Cannibalism in *N. granulata* is apparently density independent (since we find the lowest density of individuals where high degrees of cannibalism are reported, see Additional file 1: Fig. S3) and is rather related to proportion of organic matter content in the sediment [54, 70]. Within this context, smaller crabs could be using burrows more frequently as refuge. However, further experiments are necessary to determine whether cannibalism drives the site fidelity behaviour of smaller crabs in this population.

In the case of MCH with a positive association between the probability of fidelity and crab body size in the low tidal area, and with the exposition to a large number of predatory avian species (such as gulls *Larus atlanticus*, oystercatchers *Haematopus palliatus*, and chimangos *Milvago chimango*) [68], the flooding events could be the opportunity for large individuals (which are more often consumed by birds) to move about while avoiding avian predation. Similar results were reported for hermit crabs, whose dispersion and circadian rhythm are synchronised with tides, providing an advantage for dispersal and/or avoiding predators [72–75]. Thus, further experiments are needed to determine whether site fidelity behaviour (during low tide) decreases the risk of avian predation at this site.

To conclude, our study suggests that *N. granulata* has low burrow fidelity but the degree and dependency on body size changes according to the site. We suggest that abiotic factors such as flooding frequencies (affecting the individual desiccation risk) and biotic factors such as risk of predation-cannibalism at each site may be responsible for the differences found. In line with Cannizzo and Griffen [17], our results give a good example of how the expression of a characteristic behaviour may vary within a species depending on the environment and intrinsic characters. This probably plays an important role in structuring the spatial distribution of *N. granulata* along their natural range of distribution.

Additional file

Additional file 1: S1. Model specification of analyses of the number of "faithful" crabs. **Fig. S2.** Plot of the Posterior Probability of the number of "faithful" female crab related to reproductive status. **Fig. S3.** Evaluation of the differences in the population densities among sites and zones.

Abbreviations

MCH: Mar Chiquita; SAO: San Antonio Oeste; RSJ: Riacho San José; CW: carapace width; DIC: deviance information criterion; h: hour; w_i: weights; RI: relative importance; SD: standard deviation; PP: posterior probability.

Authors' contributions

JDN designed the experiment, collected the samples, conducted the analyses, interpreted the data and wrote the manuscript. PDR, EHO and TAL assisted with the field sampling, experimental desing and the writing of the manuscript. All authors read and approved the final manuscript.

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Competing interests

The authors declare that they have no competing interests.

Availability of data and materials

The data supporting the conclusions of this paper are available in the mainpaper and Additional file 1.

Consent for publication

The authors declare that they agree to publish in this journal.

Ethics approval and consent to participate

All applicable international, national, and/or institutional guidelines for the care and use of animals were followed. This article does not contain any studies with human participants performed by any of the authors.

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