Nauplius
THE JOURNAL OF THE
BRAZILIAN CRUSTACEAN SOCIETY

e-ISSN 2358-2936
www.scielo.br/nau
www.crustacea.org.br

ORIGINAL ARTICLE

Burrow fidelity in the blue crab, *Cardisoma crassum* Smith, 1870 (Brachyura: Gecarcinidae) from the Ponuga River, Veraguas, Panama

Roberto C. Lombardo[1, 2] orcid.org/0000-0002-0279-8621
Maryory Rojas[1] orcid.org/0000-0001-6425-1114

1 Universidad de Panamá, Centro Regional Universitario de Veraguas, Departamento de Biología Marina y Limnología. Santiago de Veraguas, Calle 10, via San Francisco, + (507) 958-5569, Panamá.
RCL E-mail: roberto.lombardo@up.ac.pa
MR E-mail: maryory.rojas@up.ac.pa

2 Centro de Capacitación, Investigación y Monitoreo de Biodiversidad del Parque Nacional Coiba (CCIMBIO-Coiba). Santiago de Veraguas, Calle 10, via San Francisco, Edificio J., Panamá.

ZOOBANK: http://zoobank.org/urn:lsid:zoobank.org:pub: EB273D88-1242-4C47-8F02-BBB8E3BBA921

ABSTRACT

From January to June 2021, mark-recapture and biometric data were collected from a population of blue crab, *Cardisoma crassum* Smith, 1870, from Ponuga, in Veraguas, Panama. Recapture histories of 163 crabs indicate strong burrow fidelity. During the dry season (January-March) burrow fidelity was 73.2 %, while in the rainy season (April–June) it was 50.7 %. Population was estimated at 2,569 crabs in $10.93^{\text{-ha}}$ with a density of 0.024 ind. m^{-2}. Cephalothorax width averaged 63.62 ± 6.37 mm for males (50.95–78.01 mm, $N = 83$) and 61.90 ± 5.47 mm for females (53.21–77.78 mm, $N = 80$). Blue crab reproductive season was traditionally known to take place just during the rainy season. Here, we report ovigerous females in February and March (dry season), suggesting reproduction may occur throughout the year in Panama. This is the first report of burrow fidelity and continuous biometry measurements in natural conditions for *C. crassum*. Burrow fidelity seems to be closely related to abiotic factors and is different between dry and rainy seasons.

KEYWORDS

Biometry, cephalothorax width, population estimate, recapture, sex ratio

Corresponding Author
Roberto C. Lombardo
roberto.lombardo@up.ac.pa

SUBMITTED 07 October 2021
ACCEPTED 18 February 2022
PUBLISHED 28 November 2022

DOI 10.1590/2358-2936e2022033

INTRODUCTION

Crustacean decapod species are ecologically important within mangrove ecosystems; many are also important food and economic resources for coastal human communities (Fischer *et al.*, 1995; Arzola-González *et al.*, 2010). Several decapods clearly exhibit site fidelity (Cannicci *et al.*, 1995; Vannini and Cannicci, 1995), which can change adaptively (Ens *et al.*, 1993) with landscape and variables such as body size, frequency of habitat flooding (Cannizzo and Griffen, 2016; Nuñez *et al.*, 2018), and reproductive events (Green, 2004; Moraes-Costa and Schwamborn, 2018).

Crab site fidelity is important because it can affect the structure of prey through philopatric, site-specific predation (Poirier *et al.*, 2017). Crabs can affect plant species composition by seed predation and/or selectively grazing on plant propagules (Smith, 1987; Smith *et al.*, 1989). This can favor or limit particular plant species recruitment, playing a significant role in structuring mangrove communities (Smith, 1987; Smith *et al.*, 1989; Wolcott and O'Connor, 1992; Lindquist *et al.*, 2009).

The blue crab *Cardisoma crassum* Smith 1870 is a common resident of mangrove ecosystems in the Panamanian Pacific. Its distribution ranges from Espiritu Santo Island, Baja California (Mexico) to San Pedro de Vice in Piura, Peru (Fischer *et al.*, 1995; Alemán and Ordinola, 2017).

Blue crabs are mainly herbivores (Vargas-Téllez and Vázquez-López, 2016; Alemán and Ordinola, 2017). The burrows dug by *C. crassum* are complex, often over 2 meters deep and normally located in drier, high areas of mangroves with a water reservoir at the bottom of the burrow (Bright, 1977). Resident blue crabs can occasionally block their burrows by plugging the entrance with excavated mud, forming low mounds (R. Lombardo, personal observation).

Available information on *C. crassum* is comprised of a limited number of ecological studies (Hidalgo, 2012; Alemán *et al.*, 2018), in addition to population and fishery (Vázquez-López *et al.*, 2014; Vargas-Téllez and Vázquez-López, 2016; Alemán and Ordinola, 2017; Vega *et al.*, 2018), and growth research (Tabares-Berón, 2014; Vázquez-López and Ramírez-Pérez, 2015; Molina-Ortega and Vázquez-López, 2018; Zambrano and Olivares, 2020). In Panama, Vega *et al.* (2018) conducted the only study to date on a blue crab artisanal fishery on the northeastern side of the Montijo Gulf.

These studies report valuable measurements; however, behavioral studies of *C. crassum* are lacking, and this aspect might have particular importance due to the observed relationship between individual crabs and their burrows (R. Lombardo, personal observation).

Burrow structure and use by multiple species of other gecarcinid crabs have been studied (Herreid and Gifford, 1963; Braithwaite and Talbot, 1972; Bright, 1977; Bliss *et al.*, 1978; Green, 2004); however, to our knowledge, there is no published information about site fidelity and ecological interactions affecting this behavior in *C. crassum*.

Data on behavioral ecology together with biometry data are important for resource management because changes in behavior may affect the vulnerability of a species to overharvesting (Moraes-Costa and Schwamborn, 2018). Moreover, information about population fluctuations in biometry (size at sexual maturity, sex ratio and growth rate) allows us to propose adequate measures to promote sustainable stock use (Cardona *et al.*, 2019; Quiñones-Llópiz and Rodriguez-Fourquet, 2019; Schwamborn and Moraes-Costa, 2021). Currently, the blue crab fishery is not regulated, and the stock status is unknown in Panama (Vega *et al.*, 2018).

The construction and maintenance of burrows can be costly activities due to the time and energy invested; hence sustained use, burrow fidelity and defense against usurpers are expected (Christy, 1987; Tina *et al.*, 2017). The high value (survival and reproductive) that burrows represent for crabs (Christy, 1987, 2007; Green, 2004; Zeil and Hemmi, 2006) and the effort required for construction and maintenance (Bright, 1977), can give rise to strong intraspecific and interspecific competition (Linsenmair, 2007).

This scenario implies that changes in burrow fidelity by *C. crassum* could have significant impact on mangrove structure, as well as on the crabs themselves with unknown consequences. For example, mangrove plant species composition could shift due to changes in grazing intensity (Wolcott and O'Connor, 1992; Lindquist *et al.*, 2009), or blue crab predation risk can increase due to changes in burrow fidelity (Koga *et al.*, 2001).

Therefore, our main objective was to establish recapture histories of marked blue crabs to evaluate burrow fidelity. In doing so, data on biometric variables was gathered to further characterize the population under study.

Material and Methods

Study site

The study site is located at the Ponuga River (watershed 122) in Veraguas, Panama (Fig. 1A). The mangroves in the study site grow on alluvial plain sediments and stabilized riverbeds (Instituto Geografico "Tommy Guardia", 1988).

The sampling polygon is part of a highly intervened mangrove area, bordering cattle ranching grounds, which only flood during the highest tides (Fig. 1B). The total polygon area was calculated using ArcGIS 10.7.1. (Esri, 2019).

Tree species such as *Prioria copaifera*, *Rhizophora racemosa*, *Pelliciera rhizophorae*, *Avicennia germinans*, shrub-forming ferns *Acrostichum aureum* and *Hymenocallis littoralis* lilies, dominate the plant assemblage (R. Lombardo, personal observation).

January to March comprise the dry season with 14 days of rain$^{\text{-month}}$ on average and a maximum rainfall of 118.9 mm. In 2021, the rainy season was from April to June with 27.8 days of rain$^{\text{-month}}$ on average and 553.4 mm of rainfall, with a peak of 781.5 mm of rainfall in June (ETESA, 2021).

Sampling procedure

Sampling was carried out at the end of each month from January to June 2021 for five days. Within the sampling site, a trail of burrows was established based on visual confirmation of occupation, entrance size and recent activity signs.

Besides visual confirmation of *C. crassum* presence, burrow occupation signs may also include freshly excavated mud outside the burrow, fresh feces pellets and/or fresh plant remains at the entrance (Fig. 2A, B). When a burrow met these criteria, a wooden artisanal trap of 25.5 cm width and 13.3 cm length (Fig. 2C) was set to capture crabs without injury and/or destroying the burrow.

During sampling, each trap was baited and positioned at the entrance of a burrow for 24 h and inspected every hour (6:15 a.m. to 5:00 p.m.). Bait items consisted of yuca (*Manihot esculenta*), coconut (*Cocos nucifera*) and ripe plantain (*Musa paradisiaca*). The proportion of successful/failed trap setting was recorded. Past 5:00 p.m., traps were left baited and activated through the night. If unsuccessful they were relocated to a different burrow the next morning.

Mark-recapture procedure

Once trapped, data recording began in situ with the date and time of capture; crabs were then inspected for missing appendages, as a proxy for overall individual condition. The sex of crabs was determined by the shape of the abdomen (Fischer *et al.*, 1995), and female reproductive status was recorded as: ovigerous or spawned (Solano and Moreno, 2009).

Major chelae height (QH), cephalothorax length (CL), cephalothorax width (CW), third and fourth propodal length (P3 and P4) as well as third and fourth carpal length (C3 and C4) were measured with a digital vernier caliper (0.1 mm). Afterwards, individuals were given a numeric mark with quick drying white enamel paint and a double layer of sealant varnish (Fig. 2D). After the paint dried, individual total weight (TW) was recorded using a digital balance (0.01 g).

Processed crabs were then released into the burrow of origin, which was also marked with the corresponding ID number and its location coordinates noted (Garmin Etrex 20 GPS). If crabs were recaptured, the above-described routine was repeated using yellow enamel paint instead.

Burrow fidelity

Fidelity was defined as the number of accumulated recaptures in the same burrow by a specific individual. We revisited all marked burrows and assessed burrow fidelity by calculating the proportion of blue crabs (pooled and by sexes) that were recaptured in their corresponding burrow, expressed as the total proportion of individuals recaptured at each previous sampling campaign.

Crabs from marked burrows that were later found blocked (Fig. 2B) were excluded from the total proportion of recaptured individuals due to impossible recapture and ID uncertainty; if the burrow was found reopened, then recapture was attempted.

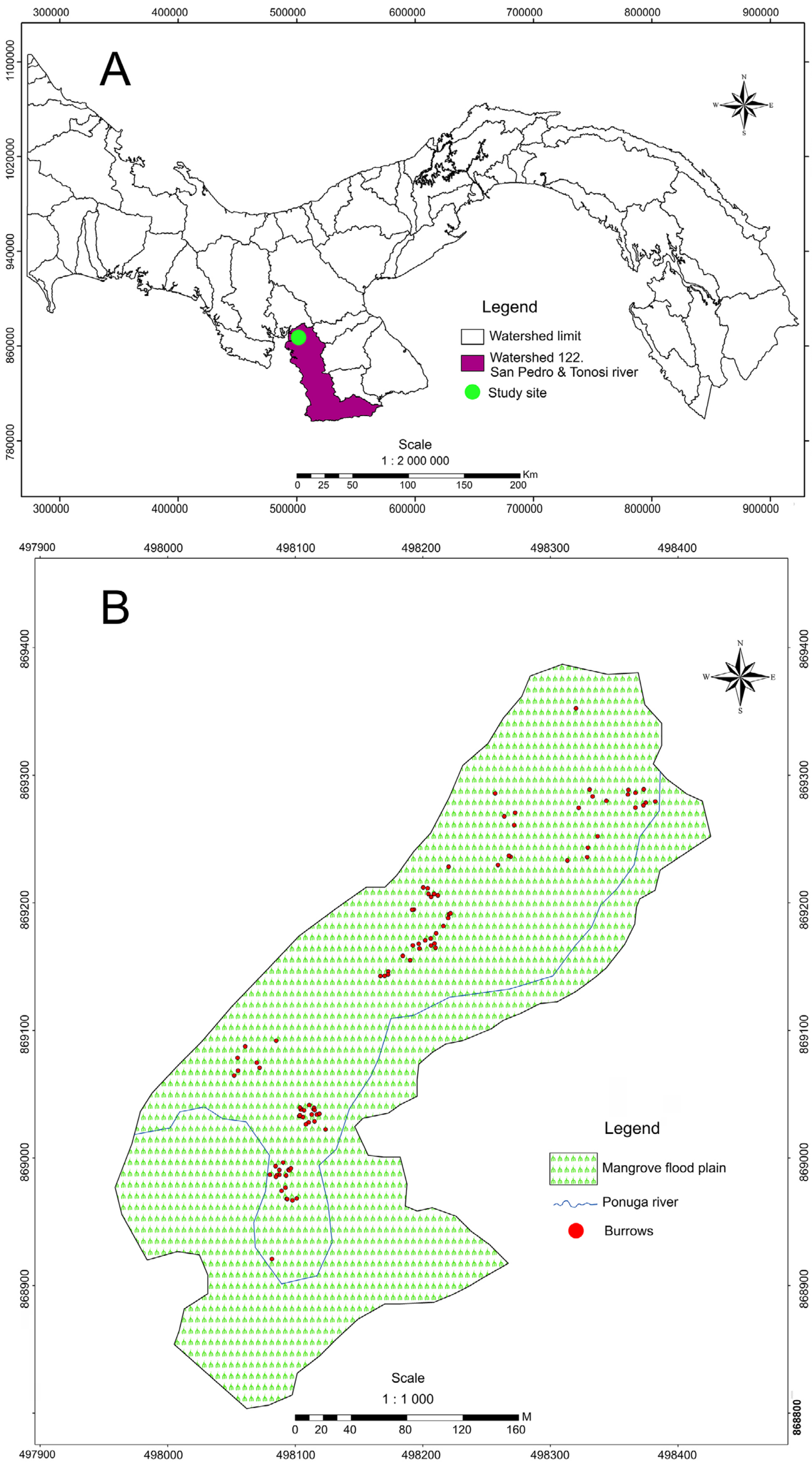

Figure 1. Sampling site located in the estuarine region of Ponuga, Veraguas, Panama. Site location (green circle) within watershed #122 (**A**). *Cardisoma crassum* burrow layout within 10.93^{-ha} sampling polygon (**B**). Cartographic parameters: UTM projection (Universal Mercator transverse -17N, horizontal datum: World Geodetic System 1984 (WGS-84), vertical datum: Medium sea level of WGS-84 geoid.

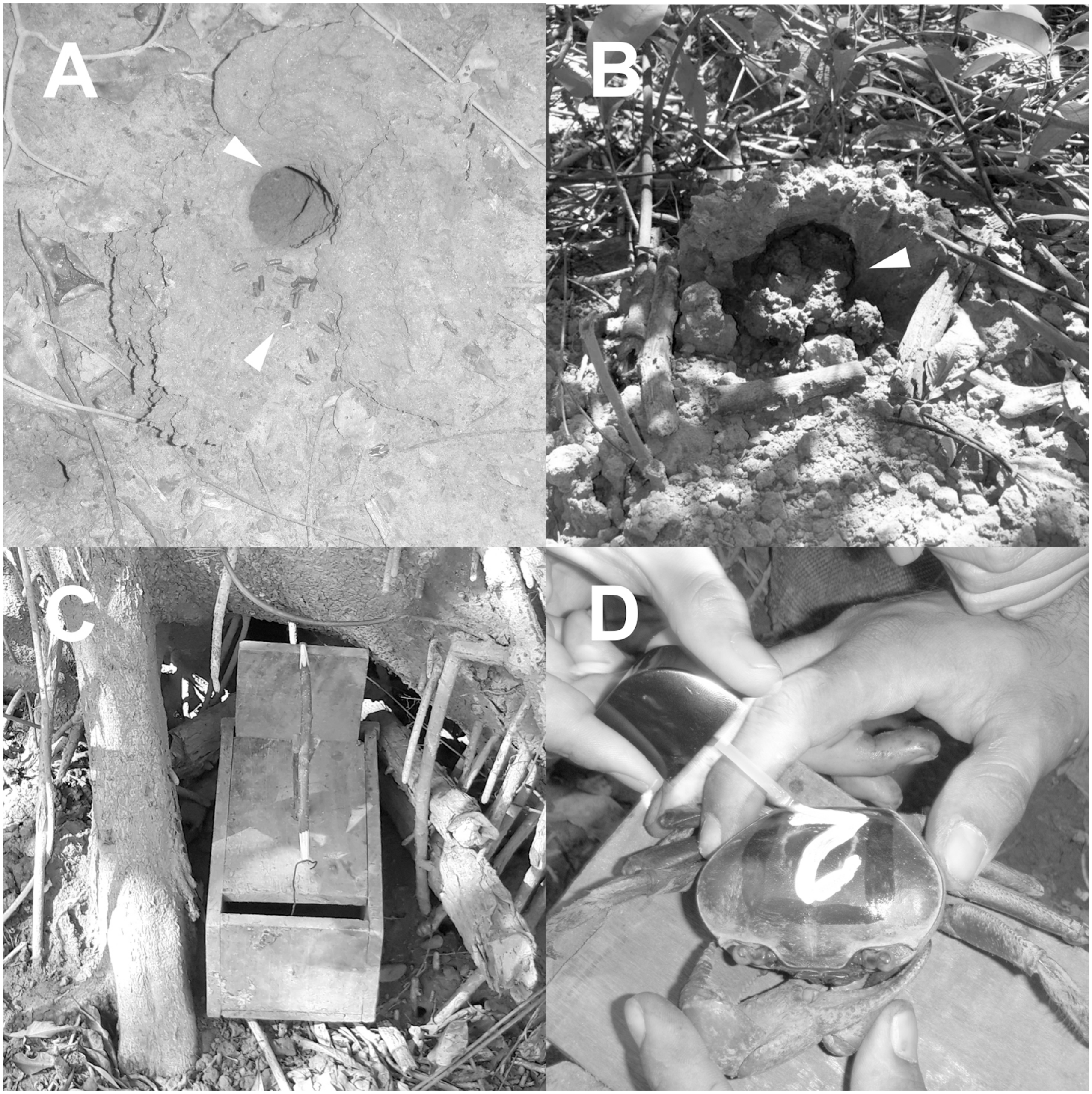

Figure 2. *Cardisoma crassum* burrow features. Active burrow with feces in the entrance (**A**). Blocked burrow with fresh plug during dry season (**B**). Artisanal wooden trap (**C**). Enamel paint and sealant application (**D**).

Instances of mortality indicated by remains of marked crab carapaces were considered as recaptures if found in the immediate vicinity (< 1 m) of the corresponding marked burrow. We also recorded instances of individuals captured in a burrow other than its marked one, as well as unmarked (new) individuals found in a previously marked burrow.

Biometry

Sex ratios per month were tabulated and compared across months with Chi-square tests. Descriptive statistics of all individual first captures were generated and possible differences in biometry between the sexes were explored with the Student's t-test. Comparison of these biometric data variables across sampling campaigns was conducted using one-way ANOVA.

Linear regression (stepwise) was used to identify the best predictors of CW. Since cephalothorax width is the most common proxy for crab fishery assessment, it was considered as the independent variable for the analysis using the pooled data as well as by sex. Regression was used to estimate the relationship between burrow entrance diameter (BD) and biometric variables. Differences in biometric variables were explored comparing their recorded increments across accumulated recapture events. For CW increments a one-way ANOVA and Tukey's pairwise comparison test were used, while TW increment data were analyzed using Welch's ANOVA with the Games-Howell pairwise comparison to adjust for sample size and non-normality. Differences in TW between sexes were explored with a Mood's median test.

Relative condition factor

The relative condition index (Huxley, 1950; Le Cren, 1951) was used to infer the general status (Froese, 2006; Bello-Olusoji *et al.*, 2010; Wang *et al.*, 2011; Molina-Ortega and Vázquez-López, 2018) of the *C. crassum* population in our study site, with the following equation:

$$K_n = \frac{TW}{a \cdot CW^b}$$

where K_n represents the estimated relative condition factor, *a* and *b* are the exponential forms of the intercept and slope, from the logarithmic length-weight equation (Le Cren, 1951). Relative condition factors were calculated separately for the pooled data and by sex. The resulting condition factors were compared with a Mann-Whitney test. We also evaluated these condition factors across sampling campaigns (different months) and compared them with a Mood's median test accordingly.

Estimates of population size and density

Capture histories from our mark-recapture procedure were recorded on a 1–0 format from January to June for each individual. The blue crab population at each month was estimated using the Jolly-Seber method for multiple mark-recapture events from an open population (Pollock *et al.*, 1990; Seber, 2002).

Within R, the FSA package was used to summarize the capture history data file through the function "capHistSum()". Then, the function "mrOpen()" was applied to estimate the population size (N) at each sample period, the apparent survival rate (φ) and number of immigrating individuals to the population (B) between sampling campaigns. The function "confint()" allowed calculation of 95 % confidence intervals for each of the population estimates and related parameters (Ogle *et al.*, 2021; R Core Team, 2021).

The population estimates obtained correspond to the burrow trail area (2 m width × total trail length). To obtain abundance and density estimates for the entire sampling site, equivalence between estimated trail population and the polygon area was used (Seber, 2002).

A separate 100 m^{-2} plot was also established within the study site to record the number of burrows, which were active, blocked, and inactive during the study period. This allowed calculating *C. crassum* burrow density (indirect population estimate) and detect changes in activity pattern.

RESULTS

Sampling procedure

A total of 163 individuals were sampled during the study period of which, 83 were males and 80 females with a statistically even sex ratio at 1.03:1 ($\chi^2 = 0.055$, $P = 0.814$).

Trap success (336/676) and failure (340/676) proportions were not significantly different ($\chi^2 = 0.024$, $P = 0.878$). Bait and trap success were not associated ($\chi^2 = 1.53$, $P = 0.47$) but there was a significant association between trap success and month (June ratio: 1.97, $\chi^2 = 31.40$, $P < 0.001$). The highest trap success was 66.3 % in June, while the lowest was 38.8 % in January. There was no association between individual's sex and bait preference for plantain, coconut or yuca ($\chi^2 = 2.06$, $P = 0.36$).

In January, 21.3 % of crabs had one missing pereiopod with males and females at an even proportion. The corresponding values for February and March were 10.5 % and 13.3 % at an even sex ratio, respectively. April had 11.5 % of crabs missing a limb, all females, while May had 13.0 % at an even sex ratio. In June, no first capture crabs with missing limbs were recorded. The proportion of crabs missing limbs was not associated with the month ($\chi^2 = 3.28$, $P = 0.66$), but there was a decrease in the proportion of missing limb individuals and their accumulated recaptures during the sampling period ($\chi^2 = 13.91$, $P = 0.008$).

Sex, month and their interaction had no effect in TW (two-way ANOVA; month: $F_{(1,5)} = 0.34$, $P = 0.88$; sex: $F_{(1,1)} = 0.49$, $P = 0.49$; interaction: $F_{(1,5)} = 0.26$, $P = 0.93$) or CW of crabs missing pereiopods (two-way ANOVA; month: $F_{(1,5)} = 0.45$, $P = 0.81$; sex: $F_{(1,1)} = 0.05$, $P = 0.83$; interaction: $F_{(1,5)} = 0.28$, $P = 0.92$).

We confirmed 10 mortality events by predation on marked individuals, one in February (female), five in March (males) and four in April (2 males and 2 females). Remains consisted of empty carapaces and/or chelae in the immediate vicinity of corresponding (intact) burrows.

Burrow fidelity

Out of 163 individuals in the study, 83 were recaptured (51 %) at varying frequency. The highest frequency of multiple recaptures was attained by one female (#38), captured in the same burrow during six consecutive months. Seven individuals were recaptured five times, 11 individuals four times, 23 three times, 41 crabs were recaptured twice, and 79 just once for a total of 315 accumulated recapture events.

When correcting for burrow blockage, the proportion of blue crabs (pooled) that were recaptured in their corresponding burrow, expressed as the total proportion of individuals recaptured at each month, changed.

For example, in February there were 47 marked crabs (from January) available for recapture. In the February sampling, 19 of these 47 burrows were found blocked with mud by the resident crabs; thus, we excluded them from the proportion calculation of recaptured vs. total available burrows (corrected), for that month. The burrow fidelity proportion was then calculated based on 28 individuals, for instance, crabs in February had 64.3 % burrow fidelity (18/28 recapture proportion; Fig. 3A).

During the dry season (January-March) burrow fidelity was 73.2 % (H_0: p = 0.6; $P = 0.022$), while in the rainy season (April-June) it was 50.7 % (H_0: p = 0.6; $P = 0.006$). Dry and rainy season fidelity proportions were significantly different (H_0: p = 0; $P < 0.001$), however, the sex of individuals and burrow fidelity were not associated ($\chi^2 = 0.390$, $P = 0.532$).

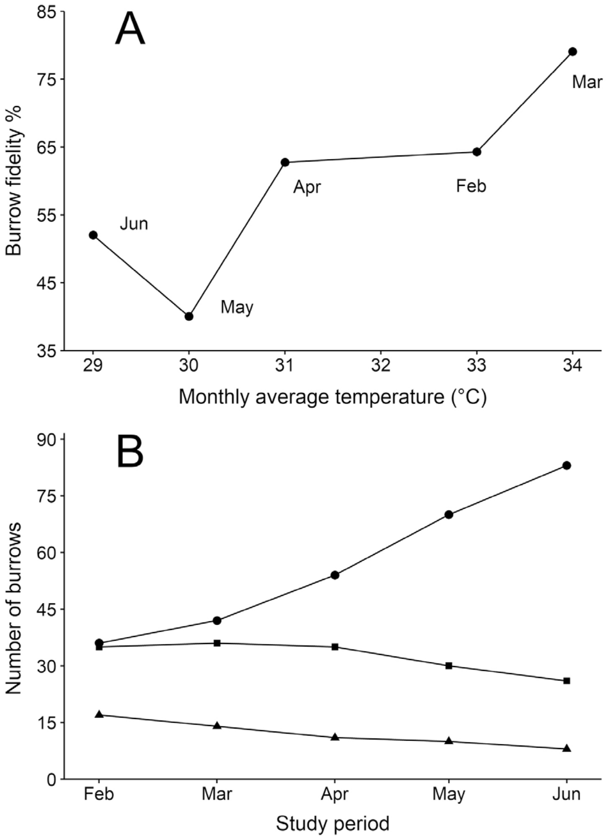

Figure 3. Monthly (January to June 2021) burrow fidelity and temperature correlation in *Cardisoma crassum* from Ponuga, Veraguas, Panama (**A**). Number of active, inactive, and blocked burrows in a 100 m^{-2} plot along the sampling period (**B**). Active burrows (circle); inactive burrows (square); blocked burrows (triangle).

Fidelity was positively correlated with overall temperature records (ETESA, 2021) for the region during the study period (Pearson, $r_{(4)} = 0.887$, $P < 0.05$; Fig. 3A); month, precipitation, and number of active burrow correlations with fidelity were found to be negative, but not significant.

We recorded 23 instances of burrow ownership change, with one in February, two in March, four in April, 13 in May, and three in June. These proportions were significantly different ($\chi^2 = 88.1$, $P < 0.001$), but the sex ratio of new tenants remained even ($\chi^2 = 0.043$, $P = 0.835$).

The proportion of female to male tenant switch in burrow occupancy was 26.1 %, male to female 21.7 %, male to male 21.7 % and female to female 30.4 %, but there was no difference between these proportions ($\chi^2 = 2.08$, $P = 0.56$). There was no difference in CW or TW between previous and the new occupant crabs

(CW; t = -0.23, df = 44, *P* = 0.819 and TW; t = -0.29, df = 44, *P* = 0.78).

Biometry

The pooled mean CW was 62.84 ± 6.01 mm (50.95–78.01 mm, *N* = 163). Significant difference was found in biometric variables across months except in CL (one-way ANOVA, $F_{(1,162)} = 1.83$, $P = 0.11$). Male CW averaged 63.62 ± 6.37 mm (50.95–78.01 mm, *N* = 83) and 61.90 ± 5.47 mm for females (53.21–77.78 mm, *N* = 80). There was a weak, but not significant, trend indicating larger male CW (t = 1.85, *P* = 0.07). Comparison between male and female biometric variables indicated significant differences in QH, P3, P4 and TW (Tab. 1), with males being larger and heavier.

The relationship between biometric variable predictors and CW was confirmed ($r^2 = 0.847$, $F_{(4,162)} = 219.68$, $P < 0.001$) along with the following equation:

$$CW = 25.46 + 0.09365\ TW + 0.2421\ CL + 0.411\ P4 + 0.343\ P3$$

TW, CL and P3 were the best predictors of male ($r^2 = 0.826$, $F_{(3,80)} = 121.98$, $P < 0.001$) and female CW ($r^2 = 0.836$, $F_{(3,69)} = 111.78$, $P < 0.001$) (Fig. 4).

Large burrow entrance diameter (BD) did not translate to large resident crabs ($r^2 = 0.159$, $F_{(4,19)} = 1.01$, $P = 0.416$) as 80 % of burrow diameters (113.01 mm) were above the CW maximum value, and this proportion was significant (H_0: p = 0.5; *P* = 0.006). On average, *C. crassum* CW was 18.06 mm smaller than their BD (Tab. 2).

There was a difference between CW monthly increments (one-way ANOVA, $F_{(1,134)} = 10.06$, $P < 0.001$). The April–May period had the highest CW average increase 1.01 ± 0.349 mm (1.77–0.36 mm, *N* = 16), while the lowest average CW increment was recorded in January–February with 0.57 ± 0.63 mm (2.23–0.10 mm, *N* = 17). This difference was significant as well (Tukey, difference of means = 0.676, t = 6.0, *P* < 0.001) (Fig. 5A, App. 1). In six months, blue crabs increased their average CW by 1.49 ± 0.98 mm (3.83–0.00 mm, *N* = 80). Male and female CW increased by 1.56 ± 1.11 mm (3.83–0.00 mm, *N* = 44) and 1.38 ± 0.79 mm (3.75–0.21 mm, *N* = 36), respectively, although there was no significant difference between them.

We detected significant differences between monthly TW increments (Welch's ANOVA, $F_{(1,4)}$

Table 1. Male and female mean, standard deviation (SD), maximum and minimum values of total weight (g) (TW), cephalothorax width (CW), cephalothorax length (CL), main chela height (QH), third and fourth propodal length (P3 and P4) and third and fourth carpal length (C3 and C4) (mm) of *Cardisoma crassum* from Ponuga, Veraguas, Panama. Asterisk indicates significant t-test male-female comparisons where males were larger and heavier.

Biometric variable	Parameter				*t*-test
	Maximum	Minimum	Mean	SD	
♂ TW*	235.01	61.11	128.96	40.67	t = 2.91, *P* = 0.004
♀ TW	206.11	61.05	112.53	30.95	
♂ CW	78.01	50.95	63.62	6.37	t = 1.85, *P* = 0.067
♀ CW	77.78	53.21	61.90	5.47	
♂ CL	61.12	34.77	48.38	5.52	t = 1.49, *P* = 0.137
♀ CL	58.80	33.69	47.13	5.18	
♂ QH*	43.45	13.90	31.32	5.93	t = 4.56, *P* < 0.001
♀ QH	41.23	14.31	27.06	5.94	
♂ P3*	24.70	14.40	19.71	2.01	t = 2.49, *P* = 0.014
♀ P3	26.78	14.50	19.36	2.32	
♂ C3	22.20	13.03	17.31	1.80	t = 1.58, *P* = 0.115
♀ C3	23.56	11.99	16.80	2.24	
♂ P4*	22.69	14.14	18.97	1.98	t = 2.36, *P* = 0.019
♀ P4	24.56	14.58	18.54	2.00	
♂ C4	21.40	11.80	17.02	1.90	t = 1.58, *P* = 0.115
♀ C4	22.46	11.14	16.53	2.06	

= 20.70, $P < 0.001$). In January–February crabs had the highest TW average increase of 3.20 ± 1.99 g (6.1–0.61 g, $N = 16$), while the lowest average TW increment was found in May–June with 0.93 ± 0.24 g (1.44–0.37 g, $N = 49$). This difference was statistically significant (Games-Howell, difference of means = -2.27, t = 4.55, $P = 0.003$) (Fig. 5B). In six months, blue crabs increased their average TW by 2.93 ± 2.44 g (9.05–0.30 g, $N = 79$) with no statistically significant difference in TW increment between males (3.04 ± 2.63 g, 8.97–0.3 g, $N = 43$) and females (3.04 ± 2.67 g, 12.11–0.42 g, $N = 37$) (Mood's median test, χ^2 = 0.01, $P = 0.918$).

Relative condition factor

The mean relative condition factor K_n calculated using the resulting CW–TW *a* and *b* parameters ($a = -7.056$, $b = 2.854$) (App. 2) was 1.01 ± 0.14 (0.47–1.96, $N = 163$). There was no statistically significant difference of the K_n factor between males (1.01 ± 0.16, $N = 83$) and females (1.01 ± 0.11, $N = 80$) (Mann-Whitney test, W = 6799, $P = 0.983$); but there was a statistically significant difference among monthly condition factor K_n medians (Mood's test, $\chi^2 = 12$, $P = 0.035$).

Estimates of density and population size

The burrow trail totaled 1,375.74 m with an area of 2,751.48 m^{-2} and a density of 0.06 ind. m^{-2}. The crude population estimate was 6,474 crabs considering a total polygon area of $10.93^{\text{-ha}}$. The Jolly-Seber population estimate (Tab. 3) was 2,569 crabs (± 95 % confidence interval: 1,618–3,520) in $10.93^{\text{-ha}}$ with a density of 0.024 individuals m^{-2} (± 95 % confidence interval: 0.015–0.032).

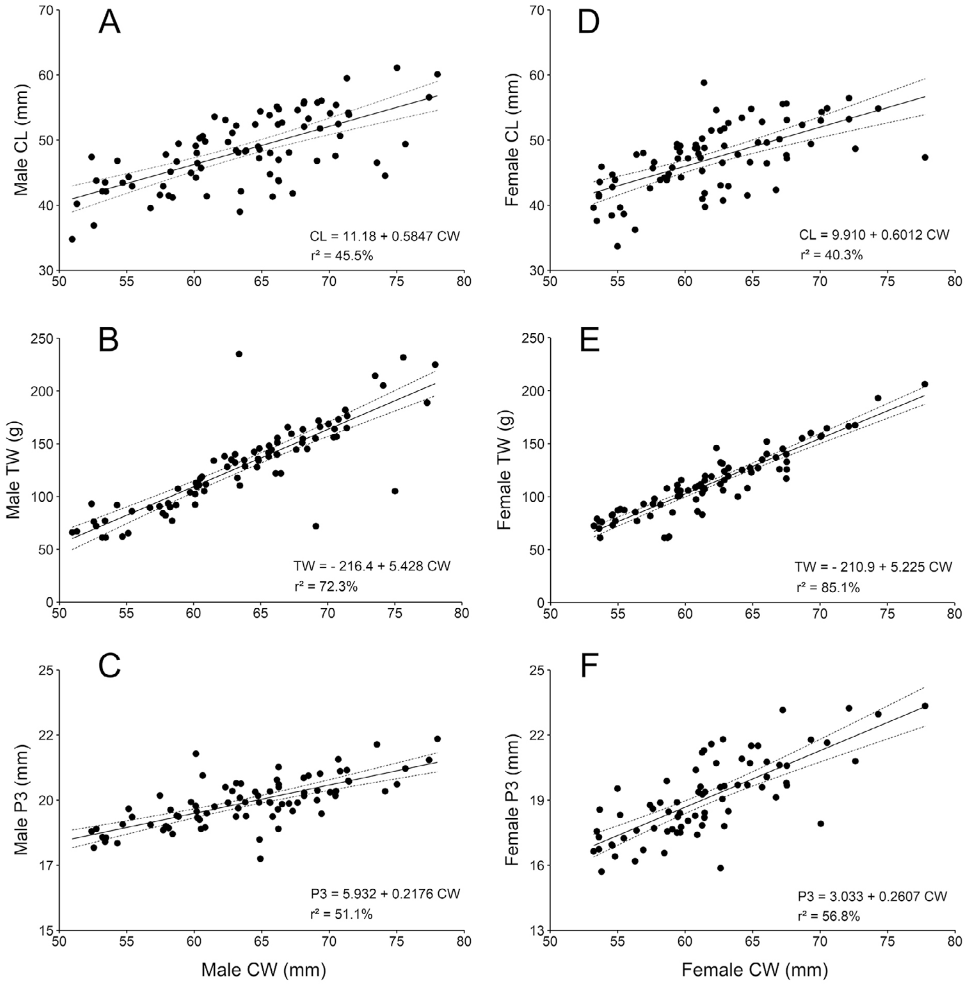

Figure 4. Cephalothorax width predictors in *Cardisoma crassum* from Ponuga, Veraguas, Panama. Left side panels correspond to males (**A–C**). Right side panels to females (**D–F**). CW, cephalothorax width; CL, cephalothorax length; TW, total weight; P3, third propodus.

Table 2. Burrow entrance diameter (BD) comparison with three biometric response variables: cephalothorax width (CW), cephalothorax length (CL) and chela height (QH) of *Cardisoma crassum* from Ponuga, Veraguas, Panama.

Biometric variable (mm)	Max.	Mean	Size diff. with burrow		BD to variable ratio (max.)	Number of burrows > variable (max.)
			Max.	Mean		
BD	113.01	82.41				
CW	70.80	64.35	42.21	18.06		16, $P = 0.006$
CL	54.90	47.60	58.11	34.81		19, $P = 0.001$
QH	39.79	31.94	73.22	50.47		20, $P < 0.001$
BD/CW					1.60	
BD/CL					2.06	
BD/QH					2.84	

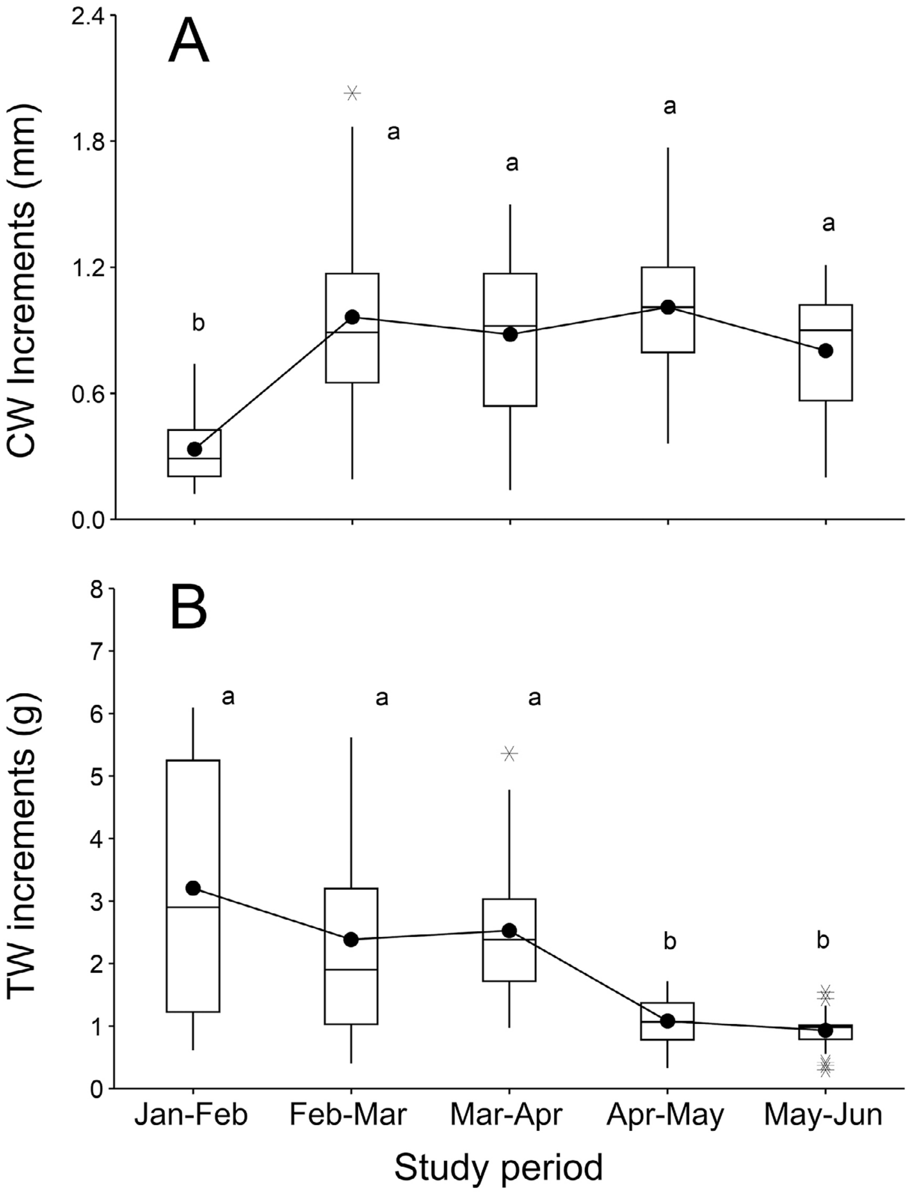

Figure 5. Monthly (January to June 2021) biometric variable increment rate of *Cardisoma crassum* from Ponuga, Veraguas, Panama. Cephalothorax width growth rate (**A**). Total weight gain rate. Bars not sharing superscripts represent statistically different means (**B**).

Table 3. Jolly-Seber population estimate parameters: marked population size (M), population estimate (*N*), proportion estimates of the population surviving between samples (φ), estimated new arrivals to the population (B) as well as lower and upper 95 % confidence limits (LCL and UCL) for *Cardisoma crassum* from Ponuga, Veraguas, Panama.

Sampling	M	Population estimate (N)			Survival (φ)			Immigration		
		N	LCL	UCL	φ	LCL	UCL	B	LCL	UCL
Jan					0.51	0.36	0.67			
Feb	24.2	49.7	39.4	59.9	0.90	0.75	1.05	13.60	3.10	24.00
Mar	38.8	58.3	49.4	67.1	0.72	0.58	0.87	23.50	17.50	29.40
Apr	39.0	65.7	60.6	70.8	0.52	0.38	0.65	51.10	41.40	60.90
May	33.6	85.0	73.9	96.1						

At the 100 m^{-2} plot, there were 36–83 active burrows between February and June; 35–26 and 17–8 burrows were inactive and blocked, respectively. Total burrow density was 1.01 m^{-2}; however, there were only 57 active burrows on average for 0.57 burrows m^{-2} and an estimated population of 62,294 crabs in 10.93^{-ha}.

The number of active, blocked and inactive burrows at the 100 m^{-2} plot was significantly different during the study period (one-way ANOVA, $F_{(2,14)} = 18.54$, $P < 0.001$). The number of active burrows changed significantly according to the month ($\chi^2 = 11.17$, $P = 0.025$), with June having the highest number of recorded burrows (117), of which 83 were active (71 %) (Fig. 3B).

There was no variation in sex ratio within months ($\chi^2 = 1.88$, $P = 0.866$) even though the total number of males (100/162) and females (89/151) recaptured was higher in the rainy season ($\chi^2 = 8.91$, $P = 0.003$ and $\chi^2 = 4.83$, $P = 0.028$). The number of males and females captured, and the season were independent ($\chi^2 = 0.254$, $P = 0.614$).

Three ovigerous females were captured during the study period. Female #44 (CW 63.36 mm) was recaptured with an egg mass in February and last captured in March without eggs. Female #9 (CW 62.81 mm) was recaptured in March with an egg mass, and it was last recaptured in April without eggs. Female #69 (CW 58.63 mm) was captured in March carrying an egg mass, but it was not recaptured afterwards.

Discussion

Fidelity to a specific physical feature, such as burrows, trees and specific mudflat areas has been reported in *Cardisoma guanhumi* Latreille, 1828 (see Forsee and Albrecht, 2012; Moraes-Costa and Schwamborn, 2018), *Cancer magister* Dana, 1852 (see Stone and O'Clair, 2002), *Gecarcoidea natalis* (Pocock, 1889) (see Green, 2004), *Aratus pisonii* (H. Milne Edwards, 1837) (see Cannizzo and Griffen, 2016), and *Neohelice granulata* (Dana, 1851) (see Nuñez *et al.*, 2018).

Here we report for the first time burrow fidelity for *C. crassum*. The stability of the substratum, food availability and the mating system are factors regulating persistence of burrows and their overall value to crabs (Christy, 1982, 1987; Zeil and Hemmi, 2006). In the Montijo Gulf, substratum characteristics in the high fringes of mangroves change drastically between the dry and rainy seasons. During the rainy season the substratum is soft yet very stable, while in the dry season it hardens (A. Vega, personal communication). Substratum hardness may be a limiting factor for burrow building (Christy, 1982).

This pattern, as well as changes in temperature, may explain the variability in the observed burrow fidelity between seasons. As temperature increased and the substratum hardened in the dry season, burrow fidelity increased. When the rainy season arrives, physiological constraints imposed by temperature on crabs may relax (Greenaway, 1988) and the relative cost of abandoning burrows decreases since it may be less costly to occupy a vacant one or build a new one (Christy, 1982; Koga *et al.*, 2001; Schlacher *et al.*, 2016).

Changes in burrow ownership support this hypothesis since most of these changes occurred in the rainy season. The new tenant sex ratio remained even, suggesting burrow value and availability might affect both sexes equally. The change in sequence of previous and new tenant sex was not skewed and there was no significant difference in size or weight, which can be indicative of opportunistic burrow occupation (Govender and Rodríguez-Fourquet, 2008; Schlacher *et al.*, 2016).

Opportunistic burrow occupation is also supported by the fact that small individuals were captured from burrows with large entrance diameters (entrance size and crab size were not correlated), suggesting burrows are reused and occupied by crabs opportunistically (Carmona-Suárez and Guerra-Castro, 2012; Schlacher *et al.*, 2016; Moraes-Costa and Schwamborn, 2018).

Intense extraction pressure can be problematic for the burrow fidelity of blue crabs. The signature of such pressure can be detected in sex ratio shifts (Ewers-Saucedo, 2019). The sex ratio of our population was even, which contrasts with other *C. crassum* populations (see below) and closely related species studies. Monthly sex ratio changes in *C. guanhumi* have been reported (Shinozaki-Mendes *et al.*, 2013), while in *Cardisoma armatum* (Herklots, 1851), migration associated with mating events is known to alter the sex ratio (Etchian *et al.*, 2016).

Large-scale life history patterns play an important role in the prevalence of evolutionary versus ecological determinants of sex ratio bias in crustaceans (Ewers-Saucedo, 2019). Differential growth and mortality, different maximum sizes, and longevity may account for variation in sex ratios (Wenner, 1972; Diele *et al.*, 2005; Ewers-Saucedo, 2019).

Three *C. crassum* studies have reported male-biased sex ratios. In Panama, Vega *et al.* (2018) found a male-biased sex ratio (1.6:1), while Alemán *et al.* (2018) in Peru and Zambrano and Olivares (2020) from Ecuador reported heavily male-biased sex ratios of 3.8:1 and 3.4:1, respectively. On the other hand, *C. crassum* studies by Vázquez-López and Ramírez-Pérez (2015), as well as Molina-Ortega and Vázquez-López (2018), found female-biased sex ratios of 1:1.45 and 1:1.74, respectively.

Populations with female-biased sex ratios were found under intense illegal commercial fishing, thus high male mortality would explain the bias towards females since large males are preferentially extracted. In contrast, crab populations with male-biased sex ratio are associated with highly preserved sites where mortality by predation and/or fishing is low (Diele *et al.*, 2005; Hernández-Maldonado and Campos, 2015; Alemán *et al.*, 2018; Moraes-Costa and Schwamborn, 2018). For example, Alemán *et al.* (2018) reported male-biased sex ratio for *C. crassum* in Tumbes, Peru, where the population had low mortality rates because the fishery was centered on *Ucides occidentalis* (Ortmann, 1897) instead.

If crab populations with male-biased sex ratio are linked to low fishing and predation mortality and female-biased sex ratios are indicative of heavily fished populations, then the even sex ratio in the present study may be indicative of a population undergoing increased fishing mortality, where larger males have been previously extracted. This might be the case since fishers used our site periodically, and natural mortality was low. Moreover, independence between trap performance, bait type and sex of individuals between seasons indicate no sampling effects, as likely cause for the observed sex ratio in our study.

A larger size reached by males has been observed in other closely related species such as *C. armatum* (see Etchian *et al.*, 2016), *C. guanhumi* (see Hernández-Maldonado and Campos, 2015; Govender, 2019), *Gecarcinus ruricola* (Linnaeus, 1758) (see Hartnoll *et al.*, 2007), and *Johngarthia lagostoma* (H. Milne Edwards, 1837) (see Hartnoll *et al.*, 2009). Such size asymmetry is attributed to sexual selection pressure (mate guarding and combat) (Christy, 1987). Although this was not the focus of our study, mortality related to decreased burrow fidelity, e.g., migration (Green, 2004; Hartnoll *et al.*, 2007, 2009) and mate choice (Bliss *et al.*, 1978; Christy, 1982, 2007; Koga *et al.*, 2001), might play a role in maintaining size class differences in *C. crassum*. This is the case at least for females known to take part in seaward movements for release of their larvae (Vázquez-López and Ramírez-Pérez, 2015), where predation risk might increase.

Data obtained from our mark-recapture study provide the first continuous measurements of CW, TW and condition factor in *C. crassum*. Contrasting monthly variation in these measurements suggest that environmental changes related to dry and rainy season (Pinheiro and Fiscarelli, 2009; Vázquez-López and Ramírez-Pérez, 2015) have an important impact on the overall condition of both, male and female crabs.

Blocked burrows can house molting individuals (Green, 2004; Quiñones-Llópiz and Rodriguez-Fourquet, 2019), and February (the dry season) was precisely the month with the highest number of blocked burrows in our 100 m^{-2} plot. Burrow fidelity may minimize heat stress (Greenaway, 1988; Nuñez *et al.*, 2018) and predation risk during the molting process (Christy, 1987; Koga *et al.*, 2001; Green, 2004). The relationship between burrow fidelity and survival warrants further studies since land crabs are notorious for their longevity (10–13 years) (Hartnoll *et al.*, 2007; Cardona *et al.*, 2019; Vogt, 2019).

Population density reports for *C. crassum* vary. For example, Alemán *et al.* (2018) found 0.7 ind. m^{-2} and Vázquez-López *et al.* (2014) estimated 1.66 ind. m^{-2}; both estimates were indirect. Correcting for the total area, our *C. crassum* population density was lower at the crude, Jolly-Seber and active burrow (indirect) estimates. Any comparison should be interpreted with caution since our crude and Jolly-Seber estimates include crabs in the range of 78.01–50.95 mm, while our indirect estimate from the active burrows at the 100 m^{-2} plot is inclusive of all possible individual sizes. Nonetheless, the low density at our site raises concerns about the status of this fishery resource.

Studies from Mexico (Vázquez-López *et al.*, 2014; Vázquez-López and Ramírez-Pérez, 2015; Vargas-Téllez and Vázquez-López, 2016; Molina-Ortega and Vázquez-López, 2018) reported ovigerous females during the rainy season, while Alemán *et al.* (2018), in Peru, mentioned egg-bearing females during the dry season. Our study revealed the presence of ovigerous females in February and March (dry season), while another study from Panama (Vega *et al.*, 2018) reported ovigerous females in the rainy season (August–September), suggesting there can be more than one reproductive event in Panama.

Cardisoma crassum showed strong burrow fidelity with a tendency to decrease during the rainy season; however, fidelity remained at 50 % suggesting that this behavior is adaptive. Additional studies are needed to investigate the relationship between burrow fidelity and intraspecific and interspecific interactions in this species. For instance, it is unknown if limbs were lost during conspecific or prey-predator interactions, and interestingly, the proportion of individuals with a missing limb and their accumulated recaptures decreased. This hints at the potential costs of burrow fidelity, which can also prove to be a rewarding future research topic.

ACKNOWLEDGEMENTS

We thank the Rojas family for their hospitality during fieldwork, Jaime Rivera for GIS assistance and Dumas Galvez for an early manuscript review. We are grateful to Andry Marín, Juan Campos and Alfredo Pinzón for their assistance during fieldwork. Our gratitude goes to the anonymous reviewers for their time and valuable comments to improve an earlier version of the manuscript.

ADDITIONAL INFORMATION AND DECLARATIONS

Author Contributions

Roberto Lombardo: Conceptualization, Methodology, Formal analysis, Investigation, Writing, Supervision, Resources. Maryory Rojas: Investigation, Data curation, Resources.

Consent for publication

All authors agree to the current version of the manuscript and consent publication of the paper.

Competing interests

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data are available from the authors upon request.

Funding and grant disclosures

There is no funding or grant to report.

Study association

The main author and co-author are affiliated to Panama University.

Study permits

All procedures involving live animals were compliant with Panamanian law. No crabs were harmed during research.

References

Alemán, S. and Ordinola, E. 2017. Ampliación de la distribución sur de *Ucides occidentalis* (Decapoda: Ucididae) y *Cardisoma crassum* (Decapoda: Gecarcinidae). *Revista Peruana de Biologia*, 24: 107–110.

Alemán, S.; Vera, M.; Cisneros, P.; Montero, P. and Ordinola, E. 2018. Algunas características biológico-poblacionales del cangrejo sin boca *Cardisoma crassum* (Crustacea: Gecarcinidae) en los manglares de Tumbes, Perú. *Boletín Instituto del Mar del Perú*, 33: 43–52.

Arzola-González, J.F.; Flores-Campaña, L.M. and Vázquez-Cervantes, A. 2010. Crustáceos decápodos intermareales de las islas de la costa de Sinaloa, México. *Universidad y Ciencia*, 26: 179–193.

Bello-Olusoji, O.A.; Anifowose, O.J. and Sodamola, M.Y. 2010. Length-weight relationships, condition factor and fecundity of the West Africa freshwater crab, *Sudanonautes africanus* (Milne-Edwards 1883), in Western Nigeria. *West African Journal of Applied Ecology*, 16: 65–74.

Bliss, D.E.; Van Montfrans, J.; Van Montfrans, M. and Boyer, J.R. 1978. Behavior and growth of the land crab *Gecarcinus lateralis* (Fréminville) in southern Florida. *Bulletin of the American Museum of Natural History*, 160: 113–151.

Braithwaite, C.J. and Talbot, M.R. 1972. Crustacean burrows in the Seychelles, Indian Ocean. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 11: 265–285.

Bright, D.B. 1977. Burrowing Central American mangrove land crabs and their burrow associates. *Marine Research in Indonesia*, 18: 87–99.

Cannicci, S.; Dahdouh-Guebas, F.; Anyona, D. and Vannini, M. 1995. Homing in the mangrove swimming crab *Thalamita crenata*. *Ethology*, 100: 242–252.

Cannizzo, Z.J. and Griffen, B.D. 2016. Changes in spatial behaviour patterns by mangrove tree crabs following climate-induced range shift into novel habitat. *Animal Behaviour*, 121: 79–86.

Cardona, L.; Campos, N. and Hernández, E. 2019. Parámetros de crecimiento de *Cardisoma guanhumi* en el Departamento del Magdalena, Colombia. *Boletín de Investigaciones Marinas y Costeras*, 48: 27–41.

Carmona-Suárez, C.A. and Guerra-Castro, E. 2012. Comparison of three quick methods to estimate crab size in the land crabs *Cardisoma guanhumi* Latreille, 1825 and *Ucides cordatus* (Crustacea: Brachyura: Gecarcinidae and Ucididae). *Revista de Biologia Tropical*, 60: 139–149.

Christy, J.H. 1982. Burrow structure and use in the sand fiddler crab, *Uca pugilator* (Bosc). *Animal Behaviour*, 30: 687–694.

Christy, J.H. 1987. Competitive mating, mate choice and mating associations of brachyuran crabs. *Bulletin of Marine Science*, 41: 177–191.

Christy, J.H. 2007. Predation and the reproductive behavior of fiddler crabs (Genus *Uca*). p. 211–231. In: E.J. Duffy and M. Thiel (eds), Evolutionary ecology of social and sexual systems: Crustaceans as model organisms, New York, Oxford University Press.

Diele, K.; Koch, V. and Saint-Paul, U. 2005. Population structure, catch composition and CPUE of the artisanally harvested mangrove crab *Ucides cordatus* (Ocypodidae) in the Caeté estuary, North Brazil: Indications for overfishing? *Aquatic Living Resources*, 18: 169–178.

Ens, B.J.; Klaassen, M. and Zwarts, L. 1993. Flocking and feeding in the fiddler crab (*Uca tangeri*): Prey availability as risk-taking behaviour. *Netherlands Journal of Sea Research*, 31: 477–494.

Environmental Systems Research Institute (Esri). 2019. ArcGIS Version 10.7.1. Redlands, CA, Esri Inc. Available at: https://www.esri.com/en-us/arcgis/products/arcgis desktop/resources. Accessed on 21 August 2021.

Etchian, O.A.; Dakouri, R.; Ble, C.M.; Lawal-Are, A.O. and Cuesta, J.A. 2016. Some ecological aspects of the gecarcinid land crab, *Cardisoma armatum* Herklots, 1851 (Crustacea, Brachyura, Gecarcinidae) from the estuarine region of the Comoe River, Côte d'Ivoire. *International Journal of Biological and Chemical Sciences*, 10: 457–474.

Empresa de Transmisión Eléctrica (ETESA). 2022. Datos climáticos históricos, Available at: https://www.hidromet.com.pa/es/clima-historicos. Accessed on 7 October 2021.

Ewers-Saucedo, C. 2019. Evaluating reasons for biased sex ratios in Crustacea. *Invertebrate Reproduction and Development*, 63: 222–230.

Fischer, W.; Krupp, F.; Schneider, W.; Sommer, C.; Carpenter, K.E. and Niem, V.H. 1995. Pacífico centro-oriental. Volumen I. Plantas e invertebrados. 1st ed. Guía FAO para la identificación de especies para los fines de la pesca. Rome, FAO, 646p.

Forsee, R.A. and Albrecht, M. 2012. Population estimation and site fidelity of the land crab *Cardisoma guanhumi* (Decapoda: Brachyura: Gecarcinidae) on Vieques Island, Puerto Rico. *Journal of Crustacean Biology*, 32: 435–442.

Froese, R. 2006. Cube law, condition factor and weight-length relationships: History, meta-analysis and recommendations. *Journal of Applied Ichthyology*, 22: 241–253.

Govender, Y. 2019. Long-term monitoring of crab *Cardisoma guanhumi* (Decapoda: Gecarcinidae) captures in Jobos Bay estuary, Puerto Rico. *Revista de Biologia Tropical*, 67: 879–887.

Govender, Y. and Rodríguez-Fourquet, C. 2008. Techniques for rapid assessment of population density and body size of the land crab *Cardisoma guanhumi* (Lattreille, 1825) in Puerto Rico. *Tropical Estuaries*, 1: 203–209.

Green, P.T. 2004. Burrow dynamics of the red land crab *Gecarcoidea natalis* (Brachyura, Gecarcinidae) in rain forest on Christmas Island (Indian Ocean). *Journal of Crustacean Biology*, 24: 340–349.

Greenaway, P. 1988. Ion and water balance. p. 211–248. In: B.R. McMahon and W.W. Burggren (eds), Biology of the land crabs, Cambridge, Cambridge University Press.

Hartnoll, R.G.; Baine, M.S.P.; Britton, A.; Grandas, Y.; James, J.; Velasco, A. and Richmond, M.G. 2007. Reproduction of the black land crab, *Gecarcinus ruricola*, in the San Andres

Archipelago, Western Caribbean. *Journal of Crustacean Biology*, 27: 425–436.

Hartnoll, R.G.; Broderick, A.C.; Godley, B.J. and Saunders, K.E. 2009. Population structure of the land crab *Johngarthia lagostoma* on Ascension Island. *Journal of Crustacean Biology*, 29: 57–61.

Hernández-Maldonado, A. and Campos, N.H.C. 2015. Estado actual de la población adulta del cangrejo semiterrestre *Cardisoma guanhumi* (Latreille) en la isla de San Andrés, Caribe Colombiano. *Boletin de Investigaciones Marinas y Costeras*, 44: 185–198.

Herreid, C.F. and Gifford, C.A. 1963. The burrow habitat of the land crab, *Cardisoma guanhumi* (Latreille). *Ecology*, 44: 773–775.

Hidalgo, W.V. 2012. Bases para el manejo del cangrejo azul (*Cardiosma crassum*) en la zona del bajo Borbón, Provincia de Esmeraldas. *Revista Científica Interdisciplinaria Investigación y Saberes*, 1: 43–53.

Huxley, J.S. 1950. Relative growth and form transformation. *Proceedings of the Royal Society of London. Series B - Biological Sciences*, 137: 465–469.

Instituto Geográfico Nacional Tommy Guardia. 1988. Atlas Nacional de la Republica de Panamá. Panamá, Universidad de Panamá, 3rd ed., 222p.

Koga, T.; Backwell, P.R.Y.; Christy, J.H.; Murai, M. and Kasuya, E. 2001. Male-biased predation of a fiddler crab. *Animal Behaviour*, 62: 201–207.

Le Cren, E.D. 1951. The length-weight relationship and seasonal cycle in gonad weight and condition in the perch (*Perca fluviatilis*). *British Ecological Society*, 20: 201–219.

Lindquist, E.S.; Krauss, K.W.; Green, P.T.; O'Dowd, D.J.; Sherman, P.M. and Smith, T.J. 2009. Land crabs as key drivers in tropical coastal forest recruitment. *Biological Reviews*, 84: 203–223.

Linsenmair, K.E. 2007. Sociobiology of terrestrial Isopods. p. 339–364. In: E.J. Duffy and M. Thiel (eds), Evolutionary ecology of social and sexual systems: Crustaceans as model organisms, New York, Oxford University Press.

Molina-Ortega, M.G. and Vázquez-López, H. 2018. Relative growth of *Cardisoma crassum* Smith, 1870 (Decapoda: Gecarcinidae) in the estuary El Salado, Puerto Vallarta, Jalisco Mexico. *BIOCYT Biología Ciencia y Tecnología*, 11: 808–823.

Moraes-Costa, D. and Schwamborn, R. 2018. Site fidelity and population structure of blue land crabs (*Cardisoma guanhumi* Latreille, 1825) in a restricted-access mangrove area, analyzed using PIT tags. *Helgoland Marine Research*, 72: 1–15.

Nuñez, J.D.; Ribeiro, P.D.; Ocampo, E.H. and Luppi, T.A. 2018. *Neohelice granulata* burrow fidelity behaviour related to landscape heterogeneity. *Helgoland Marine Research*, 72:17.

Ogle, D.; Doll, J.; Wheeler, P. and Dinno, A. 2021. FSA: Fisheries Stock Analysis Version 0.9.1.9000. R Core Development Team. Available at: https://github.com/fishR-Core-Team/FSA. Accessed on 6 August 2021.

Pinheiro, M.A.A. and Fiscarelli, A.G. 2009. Length-weight relationship and condition factor of the mangrove crab *Ucides cordatus* (Linnaeus, 1763) (Crustacea, Brachyura, Ucididae). *Brazilian Archives of Biology and Technology*, 52: 397–406.

Poirier, L.A.; Symington, L.A.; Davidson, J.; St-Hilaire, S. and Quijón, P.A. 2017. Exploring the decline of oyster beds in Atlantic Canada shorelines: Potential effects of crab predation on American oysters (*Crassostrea virginica*). *Helgoland Marine Research*, 71: 13.

Pollock, K.H.; Nichols, J.D.; Brownie, C. and Hines, J.E. 1990. Statistical inference for capture-recapture experiments. *Wildlife Monographs*, 107: 1–97.

Quiñones-Llópiz, J.D. and Rodriguez-Fourquet, C. 2019. Dinámica y estructura de la población del cangrejo terrestre *Cardisoma guanhumi* (Latreille , 1825) en la Reserva Natural del Humedal Punta Tuna en Maunabo , Puerto Rico. *Primer Congreso de Manglares de América*, 98–110.

R Core Development Team. 2021. A language and environment for statistical computing Version 4.0.5. Vienna, Austria, R Foundation for Statistical Computing, 2021. Available at: https://www.R-project.org. Accessed on 25 July 2021.

Schlacher, T.A.; Lucrezi, S.; Peterson, C.H.; Connolly, R.M.; Olds, A.D.; Althaus, F.; Hyndes, G.A.; Maslo, B.; Gilby, B.L.; Leon, J.X.; Weston, M.A.; Lastra, M.; Williams, A. and Schoeman, D.S. 2016. Estimating animal populations and body sizes from burrows: Marine ecologists have their heads buried in the sand. *Journal of Sea Research*, 112: 55–64.

Schwamborn, R. and Moraes-Costa, D.F. 2021. Growth and mortality of the endangered land crab *Cardisoma guanhumi* assessed through tagging with PITs and novel bootstrapped methods. *Pan-American Journal of Aquatic Sciences*, 16: 57–78.

Seber, G. 2002. The estimation of animal abundance and related parameters. New York, USA, The Blackburn Press, 2nd ed, 654p.

Shinozaki-Mendes, R.A.; Silva, J.R.F.; Santander-Neto, J. and Hazin, F.H.V. 2013. Reproductive biology of the land crab *Cardisoma guanhumi* (Decapoda: Gecarcinidae) in north-eastern Brazil. *Journal of the Marine Biological Association of the United Kingdom*, 93: 761–768.

Smith, T.J. 1987. Seed predation in relation to tree dominance and distribution in mangrove forests. *Ecology*, 68: 266–273.

Smith, T.J.; Chang, H.T.; McIvor, C.C. and Robblee, M.B. 1989. Comparisons of seed predation in tropical, tidal forests from three continents. *Ecology*, 70: 146–151.

Solano, F. and Moreno, J. 2009. Cangrejo rojo (*Ucides occidentalis*) un análisis durante el periodo de veda reproductiva, 2009. *Boletín Científico y Técnico*, 20: 37–47.

Stone, R.P. and O'Clair, C. 2002. Behavior of female dungeness crabs, *Cancer magister*, in a glacial southeast Alaska estuary: homing, brooding site fidelity, seasonal movements, and habitat use. *Journal of Crustacean Biology*, 22: 481–492.

Tabares-Berón, P.A. 2014. Efecto de la proteina en la tasa de crecimiento del cangrejo azul (*Cardisoma crassum*). *Revista Científica Sabia*, 1: 87–95.

Tina, F.W.; Jaroensutasinee, M. and Jaroensutasinee, K. 2017. Burrow excavation and mudballing behaviour of the fiddler crab *Uca annulipes* (H. Milne Edwards, 1837) from southern Thailand. *Crustaceana*, 90: 735–743.

Vannini, M. and Cannicci, S. 1995. Homing behaviour and possible cognitive maps in crustacean decapods. *Journal of Experimental Marine Biology and Ecology*, 193: 67–91.

Vargas-Téllez, I. and Vázquez-López, H. 2016. Fecundity of *Cardisoma crassum* Smith, 1870 in an estuary of the Mexican Pacific. *Biología, Ciencia y Tecnología*, 9: 632–641.

Vázquez-López, H. and Ramírez-Pérez, T. 2015. Aspects of growth in the terrestrial crab *Cardisoma crassum* Smith, 1870 (Crustacea: Brachyura: Gecarcinidae) from El Salado estuary, Puerto Vallarta, Jalisco, México. *Mitteilungen Klosterneuburg*, 65: 82–99.

Vázquez-López, H.; Vega-Villasante, F.; Rodríguez-Varela, A. del C. and Cruz-Gómez, A. 2014. Population density of the crab *Cardisoma crassum* Smith, 1870 (Decapoda: Gecarcinidae) in the estuary El Salado, Puerto Vallarta Jalisco, México. *International Journal of Innovative and Applied Research*, 2: 1–9.

Vega, Á.J.; Mena, C. and Robles, Y. 2018. Pesca artesanal de *Cardisoma crassum* (Cangrejo) y *Ucides occidentalis* (Mangote) en el sector nororiental del Golfo de Montijo, Pacifico de Panamá. *Tecnociencia*, 20: 5–22.

Vogt, G. 2019. A compilation of longevity data in decapod crustaceans. *Nauplius*, 27.

Wang, Q.; Yang, J.X.; Zhou, G.Q.; Zhu, Y.A. and Shan, H. 2011. Length-weight and chelae length-width relationships of the crayfish *Procambarus clarkii* under culture conditions. *Journal of Freshwater Ecology*, 26: 287–294.

Wenner, A.M. 1972. Sex ratio as a function of size in marine Crustacea. *The American Naturalist*, 106: 321–350.

Wolcott, D.L. and O'Connor, N.J. 1992. Herbivory in crabs: Adaptations and ecological considerations. *Integrative and Comparative Biology*, 32: 370–381.

Zambrano, R. and Olivares, S. 2020. Alometría y madurez sexual morfométrica de *Cardisoma crassum* (Decapoda: Gecarcinidae) en la costa continental norte de Ecuador. *Geomare Zoologica*, 2: 25–33.

Zeil, J. and Hemmi, J.M. 2006. The visual ecology of fiddler crabs. *Journal of Comparative Physiology A: Neuroethology, Sensory, Neural, and Behavioral Physiology*, 192: 1–25.

APPENDIX

Appendix 1. Table with monthly mean, standard deviation (SD), maximum and minimum values of total weight (g) (TW), cephalothorax width (CW), cephalothorax length (CL), main chela height (QH), propodium length (P3 and P4) and carpal length (C3 and C4) (mm) of *Cardisoma crassum* from Ponuga, Veraguas, Panama. Pairwise comparison (PWC) column indicates significant difference (one-way ANOVA, $P < 0.05$) between months with month order representing large to smaller mean values along with Tukey test and P-value.

Biometric variable	Parameter				PWC	Tukey test
	Maximum	Minimum	Mean	SD		
TW	235.01	61.05	121.12	37.05	Apr–Jan	$t = 2.89, P = 0.050$
CW	78.01	50.95	62.84	6.01	Jun–Jan	$t = 2.89, P = 0.039$
CL	61.12	33.69	47.77	5.36	$P = 0.110$	
QH	43.45	13.90	29.29	6.31	Mar–Jan	$t = 3.93, P = 0.002$
					Apr–Jan	$t = 3.94, P = 0.002$
					May–Jan	$t = 3.66, P = 0.005$
					Jun–Jan	$t = 5.00, P < 0.001$
					Jun–Feb	$t = 3.17, P = 0.023$
P3	26.78	14.40	19.56	2.17	Jun–Jan	$t = 5.33, P < 0.001$
					Jun–Feb	$t = 4.42, P < 0.001$
					Jun–Mar	$t = 3.64, P= 0.005$
					Jun–Apr	$t = 3.86, P= 0.002$
					Jun–May	$t = 5.03, P< 0.001$
C3	23.56	11.99	17.08	2.05	Jun–Jan	$t = 4.21, P = 0.001$
					Jun–Feb	$t = 5.31, P < 0.001$
					Jun–Mar	$t = 4.92, P < 0.001$
					Jun–Apr	$t = 4.81, P < 0.001$
					Jun–May	$t = 4.83, P < 0.001$
P4	24.56	14.14	18.79	2.02	Jun–Jan	$t = 5.96, P < 0.001$
					Jun–Feb	$t = 4.66, P < 0.001$
					Jun–Mar	$t = 4.61, P < 0.001$
					Jun–Apr	$t = 4.56, P < 0.001$
					Jun–May	$t = 5.24, P < 0.001$
C4	22.46	11.14	16.81	2.01	Jun–Jan	$t = 4.96, P < 0.001$
					Jun–Feb	$t = 5.26, P < 0.001$
					Jun–Mar	$t = 4.58, P < 0.001$
					Jun–Apr	$t = 5.23, P < 0.001$
					Jun–May	$t = 5.10, P < 0.001$

Appendix 2. Table with length-weight relationship (LWR) on *Cardisoma crassum* biometric variables: cephalothorax width (CW), cephalothorax length (CL), chela height (QH), propodium length (P3 & P4) and carpal length (C3 & C4) (mm) from Ponuga, Veraguas, Panama.

LWR	**Linear regression equation**	**Intercept**	**Slope**	**r^2**	**t-test for allometry (Ho: b = 3)**	**$TW = a \cdot L^b$**
CW	log(TW) = -7.056 + 2.854·log(CW)	-7.056	2.854	$0.7757, P < 2.2^{-16}$	$t = -1.21, df = 162, P = 0.115$	$0.00086 \cdot L^{2.854}$
♂	log(TW) = -7.056 + 2.854·log(CW)	-6.907	2.824	$0.7497, P < 2.2^{-16}$	$t = -0.97, df = 81, P = 0.168$	$0.00100 \cdot L^{2.824}$
♀	log(TW) = -7.008 + 2.837·log(CW)	-7.008	2.837	$0.805, P < 2.2^{-16}$	$t = -1.03, df = 78, P = 0.153$	$0.00090 \cdot L^{2.837}$
CL	log(TW) = -1.031 + 1.498·log(CL)	-1.031	1.498	$0.304, P= 2.1^{-14}$	$t = -8.43, df = 162, P = 9.02^{-15}$	$0.35651 \cdot L^{1.498}$
♂	log(TW) = -0.971 + 1.492·log(CL)	-0.971	1.492	$0.273, P= 4.0^{-7}$	$t = -5.57, df = 81, P = 1.60^{-7}$	$0.37855 \cdot L^{1.492}$
♀	log(TW) = -0.725 + 1.407·log(CL)	-0.725	1.407	$0.328, P= 2.9^{-8}$	$t = -6.98, df = 78, P = 4.28^{-10}$	$0.48452 \cdot L^{1.407}$
QH	log(TW) = 2.107 + 0.789·log(QH)	2.107	0.789	$0.356, P < 2.2^{-16}$	$t = -26.42, df = 161, P = 9.9^{-61}$	$8.22279 \cdot L^{0.789}$
♂	log(TW) = 1.731 + 0.899·log(QH)	1.731	0.899	$0.333, P= 1.1^{-8}$	$t = -14.87, df = 81, P = 3.6^{-25}$	$5.64573 \cdot L^{0.899}$
♀	log(TW) = 2.449 + 0.684·log(QH)	2.449	0.684	$0.331, P= 2.9^{-8}$	$t = -20.92, df = 77, P = 8.4^{-34}$	$11.5733 \cdot L^{0.684}$
P3	log(TW) = -0.914 + 1.909·log(P3)	-0.914	1.909	$0.4633, P < 2.2^{-16}$	$t =-6.76, df = 162, P = 1.18^{-10}$	$0.40104 \cdot L^{1.909}$
♂	log(TW) = -1.386 + 2.081·log(P3)	-1.386	2.081	$0.4312, P= 1.58^{-11}$	$t = -3.46, df = 81, P = 0.0004$	$0.25005 \cdot L^{2.081}$
♀	log(TW) = -0.320 + 1.693·log(P3)	-0.320	1.693	$0.5097, P= 1.06^{-13}$	$t = -6.95, df = 78, P = 4.93^{-10}$	$0.72615 \cdot L^{1.693}$
P4	log(TW) = -1.118 + 2.004·log(P4)	-1.118	2.004	$0.4855, P < 2.2^{-16}$	$t = -6.14, df = 162, P = 3.06^{-9}$	$0.32690 \cdot L^{2.004}$
♂	log(TW) = -0.830 + 1.919·log(P4)	-0.830	1.919	$0.3879, P= 3.25^{-10}$	$t = -4.03, df = 81, P = 6.18^{-5}$	$0.43609 \cdot L^{1.919}$
♀	log(TW) = -1.295 + 2.052·log(P4)	-1.295	2.052	$0.6147, P < 2.2^{-16}$	$t = -5.15, df = 78, P = 9.37^{-7}$	$0.27403 \cdot L^{2.052}$
C3	log(TW) = 0.726 + 1.422·log(C3)	0.726	1.422	$0.3023, P = 2.44^{-14}$	$t = -9.30, df = 162, P = 4.57^{-17}$	$2.06680 \cdot L^{1.422}$
♂	log(TW) = 0.244 + 1.604·log(C3)	0.244	1.604	$0.261, P= 8.04^{-7}$	$t = -4.65, df = 81, P = 6.22^{-6}$	$1.27634 \cdot L^{1.604}$
♀	log(TW) = 1.256 + 1.219·log(C3)	1.256	1.219	$0.335, P= 1.87^{-8}$	$t = -9.15, df = 78, P = 2.69^{-14}$	$3.51275 \cdot L^{1.219}$
C4	log(TW) = 1.024 + 1.324·log(C4)	1.024	1.324	$0.2719, P = 8.14^{-13}$	$t = -9.85, df = 162, P = 1.60^{-18}$	$2.78292 \cdot L^{1.324}$
♂	log(TW) = 1.155 + 1.292·log(C4)	1.155	1.292	$0.2001, P= 2.24^{-5}$	$t = -5.95, df = 81, P = 3.22^{-8}$	$3.17371 \cdot L^{1.292}$
♀	log(TW) = 1.132 + 1.270·log(C4)	1.132	1.270	$0.3389, P = 1.47^{-8}$	$t = -8.61, df = 78, P = 3.07^{-13}$	$3.10247 \cdot L^{1.270}$