

Distribution patterns of the ghost crab *Ocypode cursor* on sandy beaches of a tropical island in the Cabo Verde archipelago, Eastern Central Atlantic

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The spatial distribution of the ghost crab *Ocypode cursor* was determined for beaches on eastern Boa Vista Island, Cabo Verde Archipelago. The main objectives were to analyse the across-shore distribution by means of burrow counts and to identify preferential zones and spatial segregation. Six beaches were investigated using 20 across-shore beach transects. It was demonstrated that ghost crabs occur throughout the entire intertidal zone, with higher densities in a 9–13 m band above the waterline. There was an exponential relationship between the carapace length of captured crabs and the diameter of their burrows. Mean burrow diameter was correlated with burrow density and increased linearly with distance from the waterline, although small burrows, representing individuals smaller than the median size, occurred across the beach. Burrow diameter and depth were positively correlated, with larger holes indicating larger crabs and deeper burrows. Deeper burrows were more common in the upper intertidal zone. These results are similar to those described for ghost crab populations elsewhere and contribute to an understanding of the ecology of the species in the local context.

Keywords: burrows, crustacean, density, intertidal distribution, population structure

Introduction

Ghost crabs, belonging to the genera *Ocypode* and *Hollocypode*, attain large sizes and are conspicuous inhabitants of sandy beaches worldwide, from tropical to temperate zones (Sakai and Türkay 2013; Lucrezi 2015). They are opportunistic omnivorous crustaceans, whose diet includes eggs and early juveniles of turtles, carrion and the food remains of humans (Trott 1999). They are preyed on by other crabs, fishes, reptiles, birds and mammals (Lucrezi and Schlacher 2014; Marco et al. 2015). Their roles as both predators and prey and also, by eating organic detritus that drifts into the littoral zone, as cleaners, make them important components of sandy beach food webs (Wolcott 1978; Strachan et al. 1999; Valero-Pacheco et al. 2007; Türeli et al. 2009; Lucrezi and Schlacher 2014).

In common with other sandy beach fauna, ghost crabs are subject to anthropogenic disturbances and have been considered exceptional bioindicators of sandy beach quality (Schlacher et al. 2011). Habitat destruction, tourist presence, vehicle traffic, erosion, pollution, climate change and other stressors have been cited as important anthropogenic drivers capable of shifting the structure and population dynamics of sandy beach inhabitants (Brown and McLachlan 2002; Lecari and Defeo 2003; Schoeman et al. 2014). Under certain circumstances, disturbances are reflected early in changes in demographic features, including abundance and distribution of a species (Caswell 2001; Veloso et al. 2011). Hence, assessment of population

parameters, such as distribution, is a valuable tool for understanding the degree of security or threats a species faces, with trends over time providing useful information for the conservation and management of endangered species (Santangelo et al. 2007; Costa et al. 2014).

Ghost crabs occupy a broad band of the coastal zone, from the low intertidal zone up to 400 m inland. There is considerable interspecific variability in across-shore distribution, with some having a more restricted distribution, whereas others are more widely distributed. On beaches where more than one species occur, spatial segregation among species has been observed (Lucrezi and Schlacher 2014). Intraspecific differences in across-shore distributions among populations from different geographic areas have also been reported (Alberto and Fontoura 1999; Lucrezi 2015). In addition, in Costa Rica sex-based differences were observed for *Ocypode gaudichaudii*, with females dominating the lower intertidal zone and males dominating the upper shore (Milne and Milne 1946; Trott 1998).

Burrow size (mostly for *Ocypode quadrata*), as well as the age of ghost crabs, have been reported to be negatively correlated with distance from the dune base (Milne and Milne 1946; Fisher and Tevesz 1979; Duncan 1986; Alberto and Fontoura 1999; Turra et al. 2005; Souza et al. 2008; Branco et al. 2010; Ocaña et al. 2012; Maia-Carneiro 2013; Corrêa et al. 2014). Duncan (1986), and more recently Maia-Carneiro et al. (2013), proposed that protection

against tidal flooding (damage from wave energy) and competitive exclusion for space and food, are responsible for the predominance of larger crabs in the zone near dunes. These authors also speculated that faster, smaller crabs preferentially occupy areas near the waterline, because of their limited capacity to dig burrows in the more compacted sediments of the higher beach zone, or in order to avoid desiccation.

Counting and measuring burrows of ocypodid crabs is a feasible method for non-destructive data collection (Warren 1990). Three other methods have been used to obtain data on ghost crabs: (i) hand capture of crabs found outside the burrows (e.g. Branco et al. 2010); (ii) excavation of burrows for hand capture of hidden crabs (e.g. Ewa-Oboho 1993); and (iii) the use of traps (e.g. Schlacher et al. 2011). All these methods imply handling of crabs to take measurements, which is stressful for them (Elwood et al. 2009). During handling, crabs can shed chelae, an extreme escape response known as autotomy (Zhou and Shirley 1995). Maladaptive or harmful responses can also follow handling, such as decreased ability to avoid threats, reduced resistance to disease, reduced growth, feeding and fecundity rates, or physiological stress responses that could lead to mortality (Stoner 2012). Moreover, excavation for sampling destroys their labour-intensive burrows, probably creating an additional stress and modifying their habitat. Although Silva and Calado (2013) and Pombo and Turra (2013) cautioned against possible imprecisions from counting and measuring burrows, this method is still widely used as a proxy for density, to elucidate aspects of population biology and environmental impacts (Branco et al. 2010; Schlacher et al. 2011; Noriega et al. 2012; Lucrezi 2015).

The tufted ghost crab *Ocypode cursor* (L.) occurs along the tropical and subtropical west coast of Africa (Lucrezi and Schlacher 2014), from southern Mauritania to northern Namibia, as well as in the eastern Mediterranean (Fischer et al. 1981; Manning and Holthuis 1981; Ziese 1985; Glaubrecht 1992). Although not mentioned in the Eastern Central Atlantic identification sheets by Fischer et al. (1981), the species occurs on all islands of the Cabo Verde Archipelago in the tropical Eastern Atlantic. The African ghost crab *O. africana* is sympatric with *O. cursor* along parts of the West African coast, though they have different across-shore distributions, with the former digging its burrows farther from the sea (Rathbun 1921).

In late 1970, preliminary studies on the distribution, population structure and burrow shape of *O. cursor* were carried out on northern Israeli beaches (Shuchman and Warburg 1978; Warburg and Shuchman 1979), followed by behavioural (Strachan et al. 1999) and spatial ecology studies (Türeli et al. 2009) on other Mediterranean coasts. Extensive investigations of *O. cursor* were conducted recently in Cabo Verde (Boa Vista Island), which focused on basic ecology, predation on turtle nests (JAL Da Graça, University of Cabo Verde, unpublished data¹; Vieira 2011),

population structure and morphometrics (N de C Delgado, University of Cabo Verde, unpublished data²).

Ocypode cursor is abundant on Cabo Verde's beaches, especially pristine ones (Barros 2001; Marco et al. 2011), and predated intensively on the nests of loggerhead turtles *Caretta caretta*, which is currently the sole large carnivore found on those beaches (Marco et al. 2015).

The aim of this study was to analyse the across-shore distribution of *O. cursor* in the Cabo Verde Archipelago, (i) to investigate whether there is a preferential zone of occurrence and (ii) to explore size-based spatial segregation, i.e. whether smaller individuals (based on burrow diameter) prefer digging burrows near the waterline and bigger crabs prefer being near the upper intertidal zone. Moreover, we analysed whether the depth of burrows is related to the distance from the waterline and to the size of the crabs.

Material and methods

Study area

The Cabo Verde Archipelago is a small island chain located in the Eastern Central Atlantic, 570 km west of the African mainland. It comprises 10 volcanic islands and eight islets, with a total area of 4 033 km² and c. 965 km of coastline (Duarte and Romeiras 2009). The climate in the region is subtropical, with two weather regimes (seasons) alternating during the year: a moderately mild season (December–June, with an average sea surface temperature [SST] of 22–23 °C) and a warm season (July–November; SST 26–27 °C), incorporating a rainy season from August to October. It is situated at the southern limit of the Canary Current, on the eastern border of the North Atlantic Gyre, and is influenced seasonally by the North Equatorial Counter Current (Pelegrí and Peña-Izquierdo 2015). The archipelago has a semi-diurnal microtidal regime with a maximum range of 1.4 m (Gomes et al. 2015). This study was conducted on Boa Vista Island (16°06' N, 22°48' W), which has an area of 630 km² and is the easternmost and third largest island of the archipelago (Figure 1). Situated on the largest insular shelf in Cabo Verde, Boa Vista is one of the regions of the archipelago with the highest marine biodiversity (Almada 1993; Roques et al. 2014). The main features of the island are the flat and white sandy beaches that cover half of the island's coastline, estimated at c. 160 km (Almeida et al. 2012), and very large dunes with oases of date palms (Roques et al. 2014).

Ghost crab sampling was carried out at Porto Ferreira, along Simon Nho Narda, Figura, Flor, Bufador, Pedra Fernande and Mosquito beaches, which vary in length and width (mean width: 20 m). All beaches are undeveloped and are characterised by the presence of backshore dunes. Based on visual observations, other than Mosquito Beach, all beaches displayed a steep slope and strong wave action on the days of sampling (Table 1).

¹ Da Graça JAL. 2011. Avaliação da Intensidade da Predação e o Comportamento de Caranguejo Fantasma (*Ocypode cursor*) sobre os ninhos da Tartaruga *Caretta caretta* em Boavista, Cabo Verde. Relatório de estágio do Curso de Bacharelato em Biologia Marinha e Pescas. Mindelo: DECM, Universidade de Cabo Verde

² Delgado N de C. 2012. Contribuição para o conhecimento da biologia do caranguejo fantasma (*Ocypode cursor* L.) na ilha de Boavista (Cabo Verde): estrutura populacional e morfométrica. Relatório de estágio do Curso de Licenciatura em Biologia Marinha e Pescas. Mindelo: DECM, Universidade de Cabo Verde

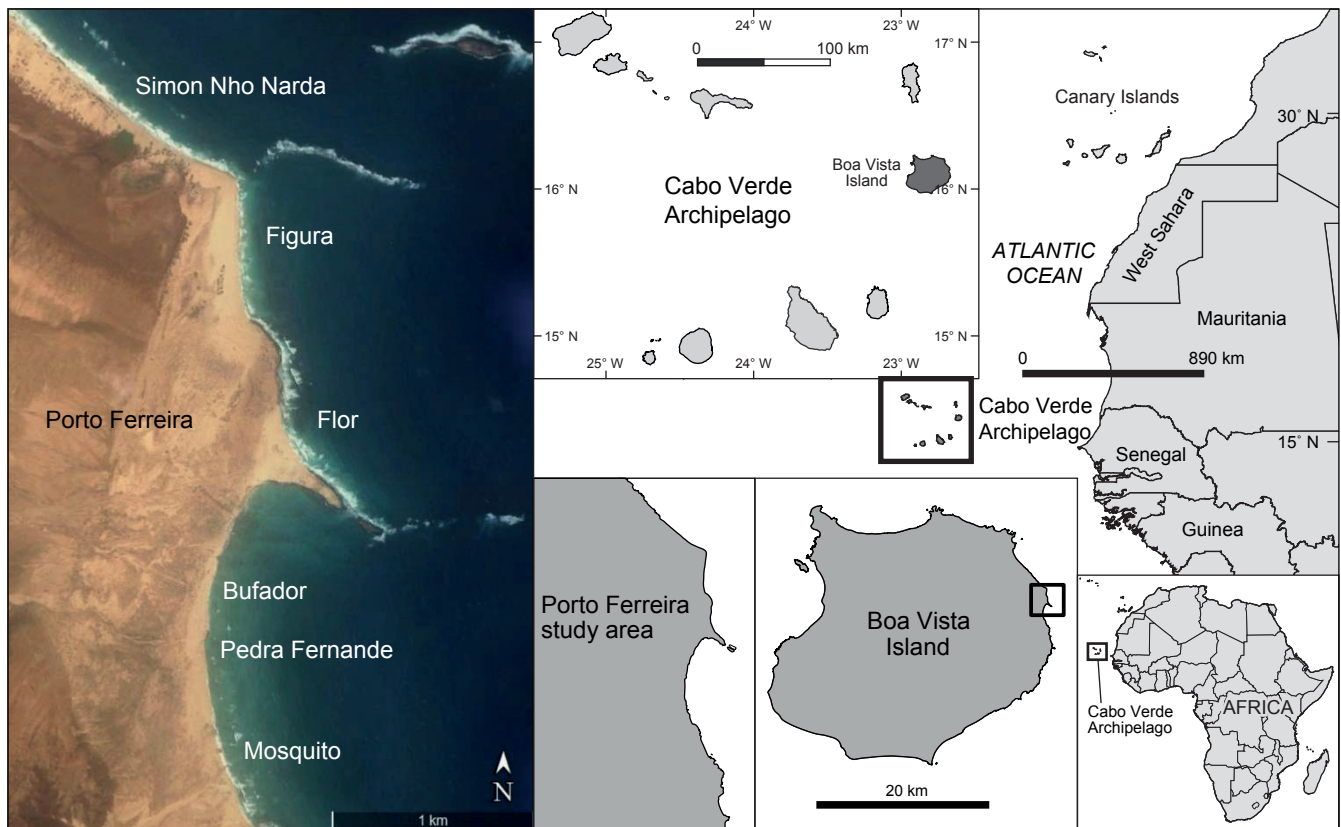


Figure 1: Location of Boa Vista Island, study area of Porto Ferreira and beaches studied in Cabo Verde Archipelago. Aerial orthophoto extracted from © Google Earth, accessed January 2015

Table 1: Number of burrows by transect for each beach at Porto Ferreira, Boa Vista Island (Cabo Verde), during July–October 2011, and some physical features of the beaches studied. Slope and wave action are presented as category variables for comparative purposes

Beach name	Length (m)	Slope	Wave action	Number of burrows					Total
				Transect					
				1	2	3	4	5	
Bufador	667	+++	+++	88	19	13	–	–	120
Figura	684	+++	+++	26	21	27	36	–	110
Flor	286	+++	+++	14	16	27	32	–	89
Mosquito	382	+	+	6	13	–	–	–	19
Pedra Fernande	286	+++	+++	18	19	–	–	–	37
Simon Nho Narda	914	+++	+++	25	8	16	11	13	73
Total									448

Sampling design

Sampling was carried out from July to October 2011. Randomly placed transects of 20 m × 4 m (80 m²) were used to determine the distribution of burrows across the intertidal zone during low spring tides. The number of transects varied according to the length of the beach, other than at Mosquito Beach. Mosquito Beach is divided naturally into two sections by a stream, with a predominance of turtle nests in one section. Sampling was done only in the section of beach where there were no turtle nests, in order to avoid affecting simultaneous research in the other section on the effect of predation by ghost crabs on juvenile turtles.

Subdivisions of 1 m × 4 m (sampling units) were used to count burrows. Mean density and diameter of burrows were calculated by quadrats ($n = 20$ per transect) across the distance from the waterline, with densities expressed as number per m². The diameter of burrows was measured with a vernier calliper, and the length and the angle of burrows was measured with a ruler and protractor, respectively, to calculate the maximum linear depth of the main chamber (sine of the angle × length). Burrow diameter was grouped into intervals of 5 mm to facilitate analysis of distribution across the intertidal zone. Correlation analyses were conducted using mean values per interval. In order to investigate correlations between burrow dimensions

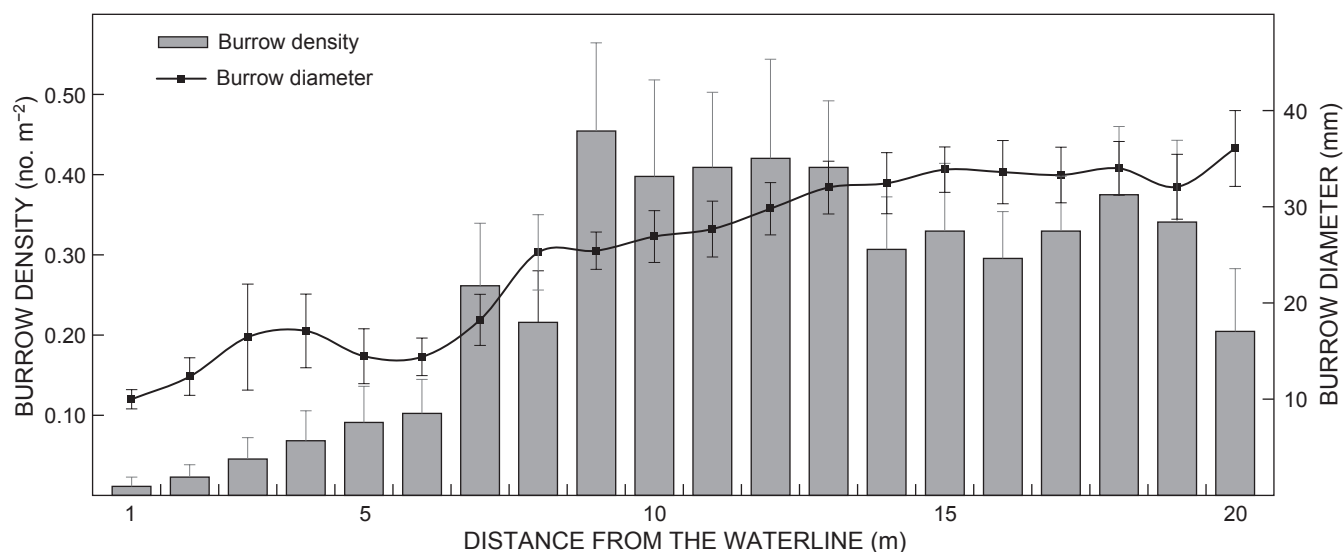


Figure 2: Across-shore distribution of mean density and mean aperture diameter of burrows of ghost crab *Ocypode cursor*. Error bars denote SE

and the size of ghost crabs, 24 animals from all beaches were captured by hand after excavating the burrows. Captured crabs were measured (carapace length [CL], from eyes to abdomen) with a vernier calliper and weighed using a spring balance. The animals were then released. Temperature inside the burrows was measured with a digital thermometer at the time crabs were captured.

Results

The number of transects per beach ranged from 2 to 5, with burrows counted in 20 transects conducted in total (Table 1). A total of 448 burrows were measured, ranging from 6 to 88 per transect.

The density of burrows increased with distance from the waterline towards the base of the dunes. Greatest densities were found in a 9–13 m band above the waterline (Figure 2). The mean diameter of burrows was 29.1 mm (SE 0.8, range 4.2–74.1 mm). Similar to the density distribution, the mean burrow diameter increased almost linearly with distance from the waterline (Figure 2). Burrows >37.6 mm were found c. 20 m away from the waterline, whereas those <13.4 mm were approximately 1 m from the waterline.

The relationship between measured CL and burrow diameter was exponential (Figure 3). Small burrows (<32 mm diameter), representing individuals that are below the median as observed in size class histograms (data not shown), occurred throughout the across-shore gradient, whereas larger individuals occurred only from 7 m to the upper shore (Figure 4).

Carapace length (estimated from burrow diameter) and burrow depth were positively and linearly correlated. Burrow depth ranged from 2.2 cm to 108 cm, with a mean value of 19.98 cm (SE 0.6) (Figure 5). Burrows of greater diameter occurred more frequently in the upper intertidal zone, i.e. >15 m above the waterline (Figure 6a).

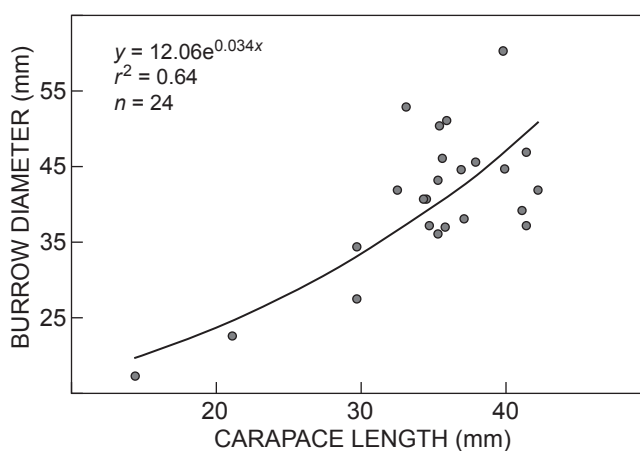


Figure 3: Relationship between measured carapace length and burrow diameter of *Ocypode cursor*

Burrow diameter and depth were positively correlated with crab size, as measured and estimated, respectively, indicating that the larger the ghost crab, the greater the diameter and depth of its burrow. The smallest crab measured (19 mm CL) had a burrow depth of 2.5 cm, whereas the largest (37.7 mm CL) had a burrow depth of 107.7 cm. There was a positive linear correlation between burrow depth and burrow diameter (Figure 6b). Mean burrow temperature ranged from 25 °C to 27 °C, with higher temperatures occurring in the upper intertidal zone (Figure 7).

Discussion

Ocypode cursor at Boa Vista Island preferred the zone between 9 and 13 m above the waterline, with densities

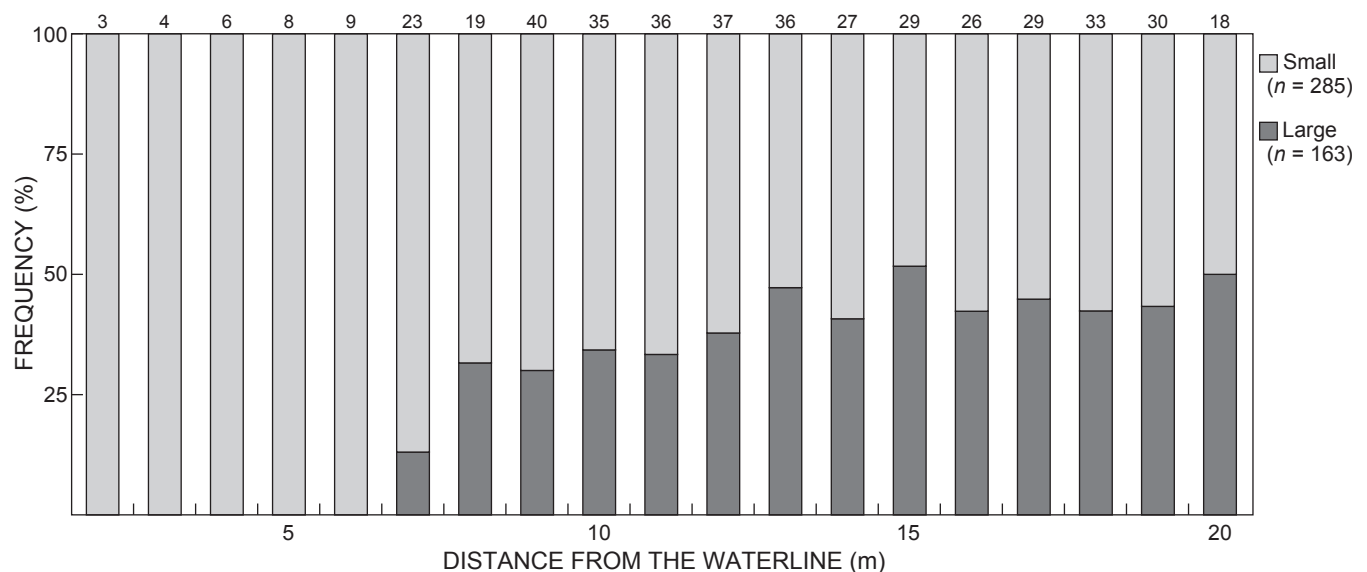


Figure 4: Spatial variation in the across-shore distribution of small (CL ≤ 32 mm) and large individuals (CL > 32 mm) of *Ocypode cursor*. Carapace length was estimated from burrow diameter. Numbers indicate the numbers of burrows counted

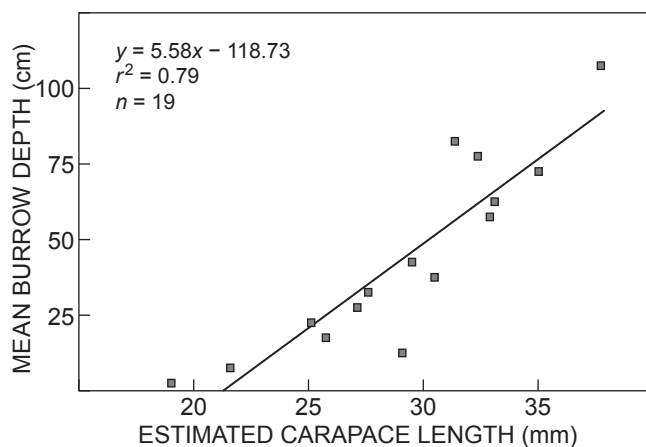


Figure 5: Relationship between burrow depth and estimated mean carapace length of *Ocypode cursor*

decreasing both above and below this band. Both density and burrow diameter decreased from 9 m to the waterline. Alberto and Fontoura (1999) described a similar pattern for *O. quadrata* on the Brazilian coast, reporting that the preferential distribution of that species is in the mid-intertidal zone. On South African beaches, Lucrezi (2015) found that 50% of burrows occurred above the berm zone and 40% in the upper beach, 20 m away from the dune bases. The occurrence of optimal zones for ghost crab burrows can vary through time and for distinct morphodynamic beach types (Lucrezi and Schlacher 2014). For instance, in studying the *O. cursor* population on Israeli shores, Shuchman and Warburg (1978) found that, in autumn, ghost crab burrows were located at least 15 m above the waterline and were evenly distributed throughout the remaining supratidal zone. Because beaches are highly

dynamic environments, it is possible that differences in the across-shore distribution reported for ghost crabs are due to stochastic sampling. Ghost crabs move across the shore in response to tidal oscillation and storm-tide events in order to obtain protection from flooding and to avoid damage from wave energy (Maia-Carneiro et al. 2013). Therefore, if sampling is undertaken soon after such events, crabs might appear to be restricted to the upper shore. However, studies on tidal migration are not conclusive (Lucrezi et al. 2009), and therefore long-term studies covering periods both of normal conditions and extreme events are necessary to test this hypothesis.

Small burrows occurred in all intertidal zones, but larger burrows were not found lower than 6 m from the waterline. Menezes et al. (2007) and Corrêa et al. (2014) found a similar pattern for *O. quadrata* on Brazilian beaches. The same was found for *O. cursor* from northern Cyprus (Strachan et al. 1999) and Israel (Shuchman and Warburg 1978). The reason for this is probably the limited capacity of smaller ghost crabs to dig burrows in the more compacted sediments of the higher beach zone. Turra et al. (2005) proposed that spatial distribution could be related to the ability of larger ghost crabs to withstand a wider humidity gradient, with smaller individuals being less resistant to desiccation. Clum (2005) found that a relationship between burrow size and location in the across-shore spatial gradient occurred only in beaches 43–110 m wide, but a reason for this was not postulated. Schöne (1968) and Branco et al. (2010) suggested that the explanation for the spatial distribution of ghost crabs is more complex, being influenced by competition, resource availability, density and anthropogenic factors.

A significant positive relationship between CL and burrow diameter of *O. quadrata* and *O. cursor* was shown by Turra et al. (2005) and Strachan et al. (1999), respectively. Thus, it is possible to estimate crab size from burrow openings,

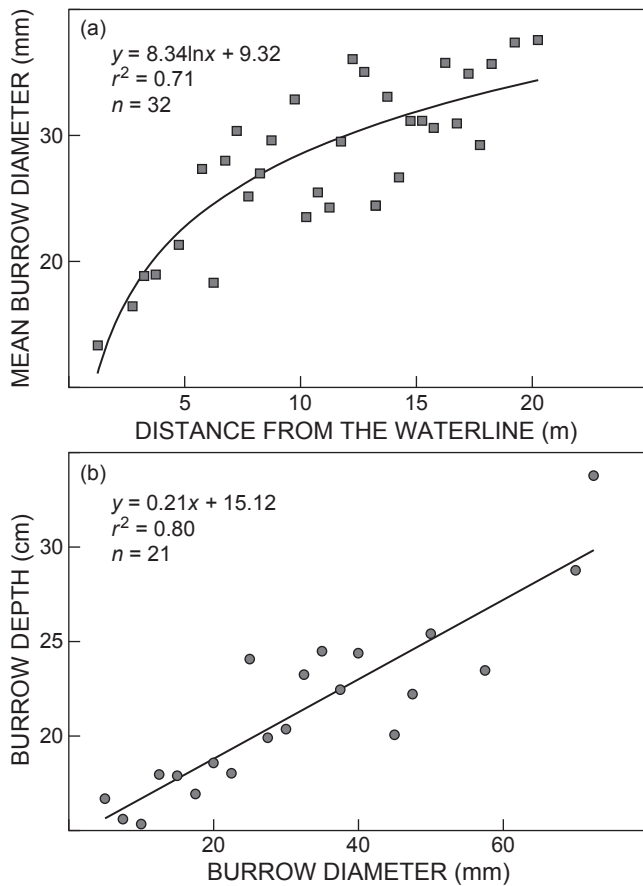


Figure 6: Relationship between (a) distance from the waterline (grouped by intervals of 0.5 m) and mean burrow diameter and (b) mean burrow depth and burrow diameter (grouped into 5 mm intervals) for *Ocypode cursor* burrows ($n = 448$ burrows)

and this relationship was verified here by capturing specimens of *O. cursor* in their burrows on Boa Vista Island.

Strachan et al. (1999) and Türelı et al. (2009) showed that burrow depth is related to the distance from the waterline and to the size of crabs. Consistent with this, we have shown that the mean depth of burrows was positively correlated with the estimated size of *O. cursor*, and the mean diameter of burrow openings was smaller near the waterline. This agrees with a study on South African beaches (Lucrezi 2015), and might be explained by hydrodynamics near the waterline. The daily destruction of burrows by waves near the waterline might force crabs to reconstruct burrows repeatedly, which would limit their depth. In addition, according to Barrass (1963), larger crabs are found more frequently farther away from the waterline, which lessens their exposure to storm waves and extreme tides and enables them to maintain deeper burrows.

Temperature can play an important role in the survival, growth, reproduction, activity and small-scale distribution of local populations of ghost crabs. The air temperature range for different species in different localities is 12–50 °C (Lucrezi and Schlacher 2014). Temperature changes are buffered inside burrows, however. In Cyprus, Strachan et al. (1999) reported variations of <3 °C over a

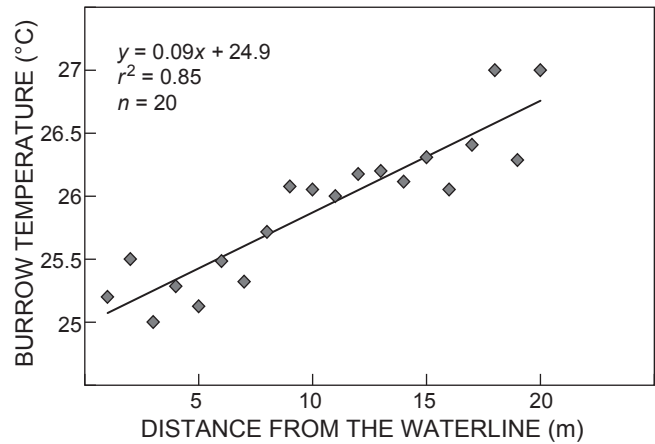


Figure 7: Relationship between temperature of *Ocypode cursor* burrows and distance from the waterline

period of 24 hours, despite a greater range in ambient air temperature. The role of burrow temperature in across-shore distribution remains unclear. Differences in the mean temperature of burrows at Boa Vista Island at sunrise did not exceed 2 °C along the across-shore gradient, with higher temperatures occurring in the upper intertidal zone.

Understanding the ecological factors that drive the distribution of ghost crabs is crucial to protecting these animals from anthropogenic threats, as well as to elucidate their roles as predators and their influence on marine and terrestrial foodwebs. This study of size-based, across-shore distribution of *Ocypode cursor* on Boa Vista Island contributes to an understanding of the ecology of the species in the local context, and provides baseline information for monitoring potential change.

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