BIOECOLOGY OF THE GHOST CRAB *OCYPODE QUADRATA* (FABRICIUS, 1787) (CRUSTACEA: BRACHYURA) COMPARED WITH OTHER INTERTIDAL CRABS IN THE SOUTHWESTERN ATLANTIC

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ABSTRACT Data sets on the natural dynamics of beach ecosystems are scarce and fragmentary. Such data are necessary for implementing more efficient monitoring programs that quantify the dynamics of key ecological attributes on sandy beaches. This article contributes to the bioecology of ghost crabs from subtropical Praia Brava, Itajaí, Santa Catarina. *Ocypode quadrata* occurs in sandy beaches along the tropical–temperate western Atlantic, from Rhode Island (US) to Rio Grande do Sul (Brazil). During 14 consecutive months, a total of 649 specimens were captured: 255 females (39%), 241 males (37%), and 153 juveniles of undetermined sex (24%). Highest densities were recorded in June and November, with a total of 1,900 burrows distributed along the beach (56.95%) and dunes (43.05%). Sixteen natural diet items were identified for this crab, with a larger participation of *Apis* spp. (38.97% of relative volume). In the local food web, the ground-burrowing owl *Speotyto cunicularia* was the main crab predator. This article indicates that the ghost crab represented the second most consumed food item of the owl (29.24%), only surpassed by rodent remains, which occupied 50.32% of its stomach volume. The natural diet and the main predator of the ghost crab had not been observed along the coast of Brazil. Knowledge of natural diet is fundamental for understanding distribution patterns, migrations, and molting cycles. Further information on population structure (abundance peaks in spring and summer; a negative allometric growth pattern), spatial distribution (predominance of females in August and May, and of males in July; size of specimens increases toward higher intertidal levels), sexual proportion throughout the year (reproduction is continuous), form and disposition of burrows (reduced abundance toward the higher tidal levels), and relative importance for the diet of the main predator (both predator and prey are nocturnal) may be used as instruments for evaluating the occupational impact and for conserving natural dune and beach environments along sandy beach ecosystems. In conclusion, ghost crabs provide an alternative source of food for the ground-burrowing owl, a predator that may represent an important population controlling factor, other than the human-induced impacts on sandy beaches. Although burrowing crabs are the most conspicuous and ecologically important invertebrates of intertidal beaches along tropical and temperate regions, factors that regulate abundance are still controversial, whereas the biotic community interactions in sandy beaches remain barely known.

KEY WORDS: anthropogenic effects, population structure, reproduction, trophic structure, ghost crab, *Ocypode quadrata*

INTRODUCTION

Sandy beach ecosystems (Defeo et al. 2009) and mangrove forests (Valiela et al. 2001) represent the most conspicuous coastal systems in tropical environments. Along with terrestrial rain forests and marine coral reefs, they are among the world's most threatened major environments. The biological communities in both of these land–sea transitional environments are dominated by different groups of burrowing crabs. Understanding the functioning of these communities may be important for wetland and coastal management under the conflicting pressures of economic value and ecological services (Valiela & Fox 2008). An important theme in the ecology of soft sediments in the southwestern Atlantic is the study of physical and biological disturbances affecting the distribution and abundance of the infauna. Predation (Paine 1966, Hunt & Scheibling 1997) and bioturbation (Ólaffson et al. 1994) are the best known causes affecting the structure and dynamics of soft-bottom communities.

In southwestern Atlantic mangrove areas, the most studied semiterrestrial burrowing crabs are the varunid *Neohelice granulata* (Dana, 1851), the grapsid *Cyrtograpsus angulatus* Dana, 1851, and the ocypodids *Uca uruguayensis* Nobili, 1901, and *Uca rapax* (Smith, 1870). Biotic and abiotic impacts have been approached in several articles. The population structure of *N. granulata* has been studied by Bas et al. (2005). It was shown that this dominant crab coexists with *C. angulatus*, but the burrows of the latter species are displaced from soft-bottom habitats to refuge in sandy–muddy areas when coexisting with *N. granulata* (Iribarne et al. 2003). *N. granulata* is more flexible in its diet than the predominantly herbivorous *C. angulatus,* and a higher frequency of empty stomachs were found in males of *N. granulata* in crab beds, indicating that feeding habit may, at least in part, explain the adaptations to these different substrata (Martinetto et al. 2007). *N. granulata* has strong effects on the sediment dynamics (Botto et al. 2005, Escapa et al. 2008, Fanjul et al. 2008) and is efficient in trapping debris (Iribarne et al. 2000), affecting the distribution and survival of the fiddler crab *U. uruguayensis* (Botto & Iribarne 2000, Daleo et al. 2003) and other inhabitants of the benthic communities in mudflats (Botto & Iribarne 1999). For example, a habitat-generated bottleneck appears to occur between settlement and recruitment in the reef-building serpulid polychaete *Ficopomatus enigmaticus* (Fauvel, 1923), in response to settlements of the crab *C. angulatus*

(Casariego et al. 2004). On the other hand, the densities of the polychaete *Laeonereis acuta* Treadwell, 1923, and of the tanaid *Kalliapseudes schubartii* Mañé-Garzón, 1949, are reduced around burrows of this crab in southern Brazil (Rosa & Bemvenuti 2004). Although meiofauna nematodes appear unaffected by this crab, ostracod, copepod, and turbellarian densities were significantly lower in mudflat habitats disturbed by the crab (Rosa & Bemvenuti 2005). On the other hand, *N. granulata* increases the feeding rate and consequently enhances the body condition of the polychaete *L. acuta* inside crab beds (Palomo et al. 2004), but affects the clam *Tagelus plebeius* (Lightfoot, 1786) negatively (Lomovasky et al. 2006). The plant cover by the cordgrass *Spartina densiflora* Brong, 1829, is strongly correlated with the spatial distribution of the burrowing crab *N. granulata* (Bortolus et al. 2002), and the crab is also responsible for inducing phenotypic changes in *S. densiflora* (Bortolus et al. 2004, Daleo & Iribarne 2009). These crabs further affect the use and foraging activities of migratory shorebirds (Botto et al. 2000). Interestingly, *N. granulata* can decrease the impact of predation by shorebirds on polychaetes (Palomo et al. 2003a). Shorebirds avoid areas of high crab burrow densities on mudflats (Iribarne et al. 2005). It has also been shown that sediment bioturbation in crab beds of *N. granulata* reduces ant predation of intertidal polychaetes (Palomo et al. 2003b), but facilitates fish predation on benthic polychaetes in crab beds, reducing their abundance (Martinetto et al. 2005).

Regarding population and reproductive cycles, studies of *U. rapax* suggest that females might remain in their burrows during the incubation period (Castiglioni & Negreiros-Fransozo 2005, Castiglioni & Negreiros-Fransozo 2006a, Castiglioni & Negreiros-Fransozo 2006b, Castiglioni et al. 2007).

Sandy beach ecosystems dominate the coastlines of the world (McLachlan & Brown 2006). These natural habitats are being destroyed at an accelerating rate as a result of rapidly expanding human populations (Defeo et al. 2009). Sandy beaches become increasingly overexploited for the consumption of natural resources as humans shift toward the coast (Roberts & Hawkins 1999). As an inevitable consequence of economic expansion, intensive coastal development results in widespread modification of the beach ecosystems. It thus becomes critical to understand how sandy beach ecosystems and their natural products function and respond to such unprecedented environmental change (Defeo et al. 2009). It also becomes important to understand how these sand communities compare with the equally endangered intertidal wetlands (Valiela et al. 2004).

Coastal areas, and particularly sandy beaches, are prime destinations for outdoor recreation activities, yet these zones have diverse, dynamic, and, often, sensitive ecosystems (Beatley et al. 2002). Visitors use and impact coastal beaches by driving off-road vehicles, walking on beaches or dunes, trampling the vegetation, inducing soil erosion, and inflicting other drastic changes on coastal habitats. Such anthropogenic effects represent an important and growing concern for coastal management.

Crabs of the genus *Ocypode* (Fabricius, 1787) are commonly found along tropical and subtropical beaches around the world. They are represented in the western Atlantic by *Ocypode quadrata*, which occurs from Rhode Island (US) to Rio Grande do Sul (Brazil) (Melo 1996). They build burrows in the supralittoral, from the water level up to the hillside dunes (Rathbun 1918).

Ocypode quadrata, popularly known as the "ghost crab" (commonly as *Maria-farinha* or *caranguejo-fantasma* in Brazil),

has nocturnal habits and forages on bivalves such as *Donax hanleyanus* Philippi, 1842, and the mole crab *Emerita brasiliensis* Schmitt, 1935, in Brazil (Veloso et al. 2006); and on organic detritus (Robertson & Williams 1982, Trott 1999). They are thus important for relaying energy among different trophic levels (Phillips 1940, Fales 1976, Wolcott 1978).

However, ghost crabs were considered to have essentially no terrestrial competitors or predators. With few predators or competitors, a flexible feeding behavior, and the ability to endure starvation for long periods, *O. quadrata* would represent an ideal top carnivore in a simple, filter-feeding-based food chain of the dune and forebeach ecotone (Wolcott 1978). As such, it has been used as an indicator of the health of the dune and forebeach environment.

Blankensteyn (2006) observed predation by hawks and seagulls in Santa Catarina, and inferred that the worldwide nocturnal behavior of *Ocypode* spp. could have evolved as a protection mechanism against predation. Gianuca (1997) actually mentioned predation by owls in Rio Grande do Sul, but the implications of the existence of other than human factors in population regulation of *O. quadrata* remained unnoticed.

In Brazil, the spatial distribution and age structure (Gianuca 1997, Veloso et al. 1997, Alberto & Fontoura 1999, Turra et al. 2005, Perez & Vianna 2007, De Araújo et al. 2008), reproductive cycle (Negreiros-Fransozo et al. 2002), and use of the crab as an indicator of anthropogenic impacts (Barros 2001, Turra et al. 2005, Blankensteyn 2006, Neves & Bemvenuti 2006) have been studied. However, the natural diet and the predators of this crab had not yet been considered in more detail along our coast.

Ocypode quadrata has received special attention, mainly in North America, regarding its biology and distribution (Sawaya 1939, Phillips 1940, Wolcott 1978), reproduction (Haley 1969, Haley 1972, Williams 1984), feeding habits (Fales 1976, Wolcott 1978, Trott 1999, Robertson & Williams 1982) behavior (Sawaya 1939, Phillips 1940, Milne & Milne 1946), running capabilities (Perry et al. 2009), and impact of car traffic and bather treading along the beach (Steiner & Leatherman 1981, Wolcott & Wolcott 1984, Moss & McPhee 2006).

Recent discovery of Holocene to Pleistocene fossils of *O. quadrata* in Florida (Portell et al. 2003) have led to new insights regarding the biology of these crabs. These semiterrestrial crabs need to wet their gills in the surf zone after high tides have receded. *O. quadrata* is able to extract interstitial water from damp sand (Wolcott 1976). They also burrow into the high-level dune sand to seek protection from predators. These 2 distinct behavioral patterns are thought to have produced the ichnofacies *Psilonichnus* and *Skolithos* fossil traces, respectively (Martin 2006).

Knowledge of feeding habits of crabs is fundamental for the understanding of their distribution patterns, migrations, and molting cycles (McLaughlin & Hebard 1961). Information on population structure, spatial distribution, form and disposition of burrows, natural diet, and the relative importance of predators may be used as an instrument for evaluating the occupational impact and for conserving natural dune and beach environments along sandy coastal ecosystems.

MATERIALS AND METHODS

Ocypode quadrata was sampled monthly from May 2003 to June 2004 at Praia Brava (26°55′56″S to 26°57′36″S; 48°37′38″W to 48°37′41″W), Itajaí, Santa Catarina. The beach

was divided into 7 equal-size longitudinal sections of 400 m; each of these sections was divided transversally into a beach and a dune area (Fig. 1, upper right insert).

During the day the number and diameter of the burrows in each area was obtained, using transects 1 m wide, positioned perpendicularly to shore. Areas I and VIII are amplified in the lower half of Figure 1; the transect is illustrated in the lower right insert of Figure 1. This transect consists of 2 parallel sides with a fixed distance of 1.00 m. The lengths of the transect varied for each area (measuring 17.70 ± 5.17 m on the beach sand and 30.49 ± 12.07 m on dunes) as follows: 28.7 m (area I), 16.6 m (area II), 18.9 m (area III), 14.9 m (area IV), 15.3 m (area
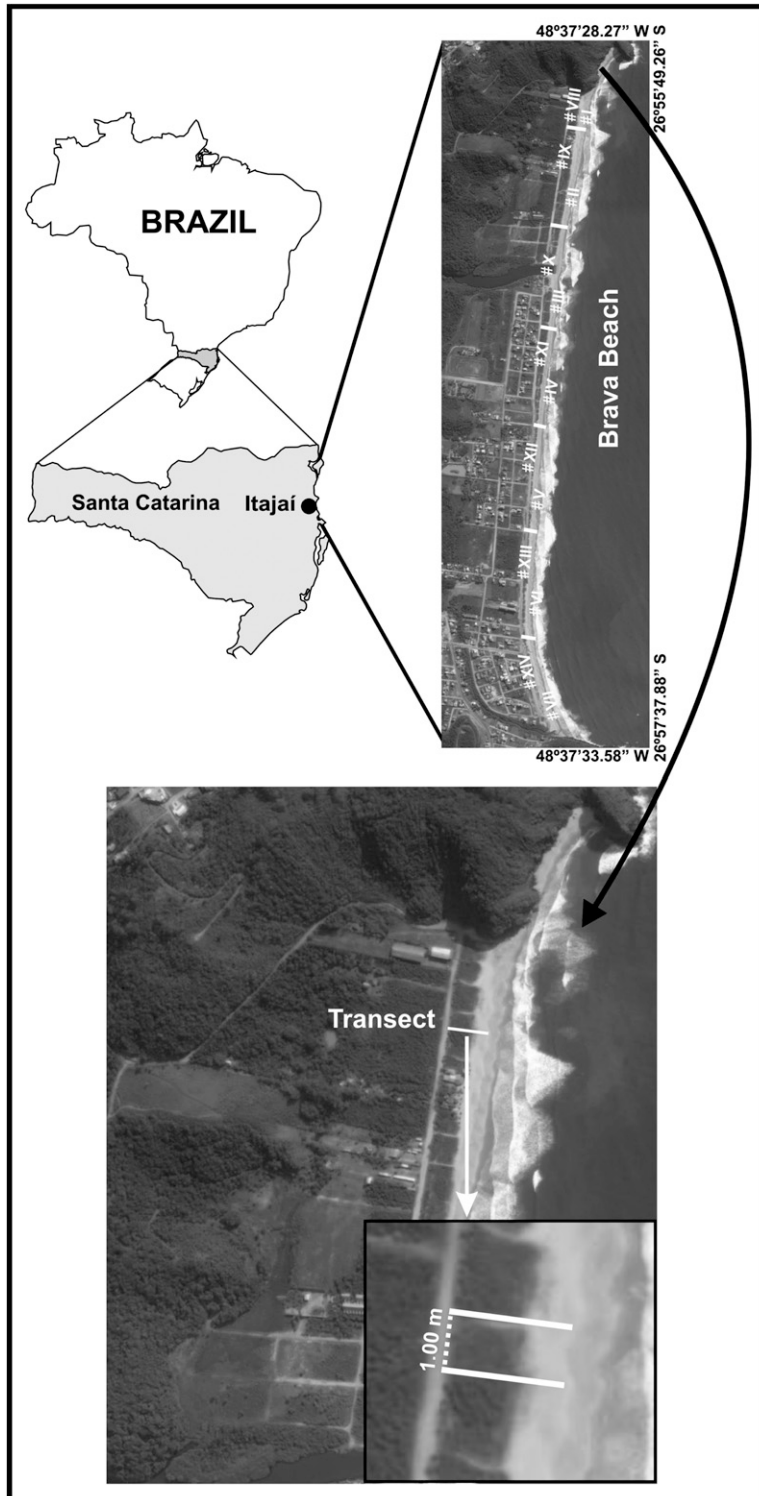

Figure 1. Map indicating study site, sampling areas, and transect used for obtaining samples.

V), 13.1 m (area VI), 16.4 m (area VII), 41.7 m (area VIII), 46.6 m (area IX), 36.5 m (area X), 32.9 m (area XI), 22.1 m (area XII), 15.8 m (area XIII), and 17.8 m (area XIV).

Burrows were counted for each meter of the transect. Every month the position of the transect was changed within each section, so that the entire 400 m of beach and dunes were covered during the study period (Turra et al. 2005). The upper level of dunes comprised the area occurring from the beginning of the dunes to the margin of the road. The lower level of the beach proper went from the water level to the lower border of the dunes. During the night, crabs were captured manually and with a net (metal hoop of 30 cm diameter, wood handle of 1.5 m length, and mesh of 5 mm); a gas lamp (with a directed light beam) and pocket lanterns were used as light sources. In parallel, we recorded the temperature of the air, and the temperature and salinity of the water.

Captured specimens were kept in plastic bags, refrigerated in isoprene boxes with ice, and transported to the laboratory. There, specimens were identified, sorted for maturation stage (juvenile/adult), and the adults were identified by sex (Taissoun 1969). Carapace width and length were determined with a vernier caliper (precision of 0.01 cm). Body weight was measured with a semianalytic top-loading balance (precision of 0.01 g).

In sequence, each stomach was removed, opened, and estimated regarding degree of repletion (Santos 1978). In the qualitative–quantitative analyses, the method of the frequency of points (i.e., relative volume) and the method of frequency of occurrence (FO) (Hynes 1950, Berg 1979, Hyslop 1980) were applied. The food items were identified, as far as possible to the lowest taxonomic level. Those undetermined items resulting from a high degree of digestion were grouped as nonidentified organic material (NIOM).

Seasons of the year were established as spring (October, November, and December), summer (January, February, and March), fall (April, May, and June), and winter (July, August, and September). The chi-square test was used to verify the possible differences in the sexual proportion of the population along the year (Vazzoler 1996), whereas the abundance in collection areas and station of the year was compared by 1-way analysis of variance (Sokal & Rohlf 1969). The relation between the weight and the width of the carapace of the crabs was adjusted by the method established in Santos (1978).

The regurgitated pellets of the ground-burrowing owl (*Speotyto cunicularia* Molina, 1782) were collected monthly in the immediacy of the burrows, kept in plastic bags, and identified in the laboratory. Prey present in the regurgitated pellets were identified to the lowest taxonomical level and separated. Their relative importance in the diet of the owl was estimated from the proportion of hard parts contained in the regurgitated pellets.

RESULTS

Environmental Variables

Median air and water temperatures fluctuated relatively uniformly according to the season, with highest water temperatures occurring between the months of January and March (26–27°C), and the lowest water temperatures occurring in August (16°C) and May (17°C). The highest air temperatures were obtained in February and March (25°C); and the lowest air temperatures were also obtained in August (13.5°C).

Median surface water salinity values maintained a tendency of seasonal fluctuation, with the highest values (measured using the Practical Salinity Scale) occurring between the months of September (27) and March (28), and the lowest between May and July (19).

Population Structure

During the study period, 649 specimens of *O. quadrata* were captured: 255 females (39%), 241 males (37%), and 153 juveniles of undetermined sex (24%). The highest frequencies of adults were observed in July and November, and the lowest in May and June 2003; whereas juveniles were more abundant in July, February, and May, and absent in December, January, April, and July (Fig. 2A). Females predominated significantly (χ^2, $P < 0.05$) during the months of August and May, and the males predominated in July. During the remaining months, the proportion was maintained around 1:1 (Fig. 2A).

The distribution of relative frequencies of juvenile crabs by classes of carapace widths presented an amplitude of 0.4–1.2 cm, with a peak in the class of 0.8 cm. In adults, it varied from 0.8–3.8 cm, with peaks in the classes of 1.4 cm and 2.6 cm (females), and in the classes of 1.2 cm and 2.4 cm (males; Fig. 2B). The chi-square test indicated significant differences in favor of females in the classes of 2.6 cm and 3.8 cm, and of males in the classes of 1.0 cm, with a 1:1 proportion between the sexes in the remaining classes (Fig. 2B).

Table 1A demonstrates the seasonal variation in the capture of crabs and indicates that significant differences do not occur among seasons of the year ($F_{3-8} = 0.40$; $P \geq 0.05$), with largest rates occurring during the spring months, followed by summer, winter, and fall months.

The median number of captured specimens was approximately equivalent among the seven sampled areas ($F_{6-98} = 0.46$; $P \geq 0.05$), with the highest annual rates occurring in areas II and VII, and the lowest rates occurring in areas I and III (Table 1B).
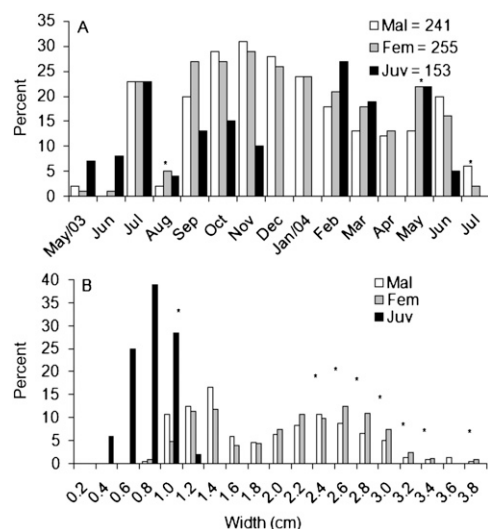

Figure 2. (A, B) Distribution in *Ocypode quadrata* frequency among females, males, and juveniles from May 2003 to July 2003 (A), and frequency of carapace width classes for females, males, and juveniles during the collecting period (B). *Significant difference at $P < 0.05$. fem, females; juv, juveniles; mal, males.

TABLE 1.

Mean number of captured crabs on the beach during the study period (A; *n* = 649) and total number of crabs captured on dunes during the study period (B; *n* = 649).

A, Beach

Months	I	II	III	IV	V	VI	VII	Beach	SD
May/03	8	5	6	6	2	4	4	5	0.723747
Jun/03	17	10	28	24	25	28	45	25.28571	4.104088
Jul/03	5	3	11	20	7	3	11	8.571429	2.287202
Aug/03	10	4	2	5	5	4	9	5.571429	1.087968
Sep/03	7	5	10	3	6	4	8	6.142857	0.911006
Oct/03	9	9	4	9	10	7	17	9.285714	1.491472
Nov/03	15	16	16	17	14	22	11	15.85714	1.26168
Dec/03	10	10	4	6	3	8	10	7.285714	1.127878
Jan/04	8	5	6	6	2	4	4	5	0.723747
Feb/04	9	10	7	10	9	9	5	8.428571	0.685119
Mar/04	5	2	9	4	13	9	3	6.428571	1.509606
Apr/04	5	3	5	1	4	2	2	3.142857	0.594762
May/04	6	10	8	7	19	5	12	9.571429	1.810777
Jun/04	5	6	8	2	7	10	10	6.857143	1.078548
Jul/04	18	6	9	6	9	2	9	8.428571	1.862629
Total	129	99	127	120	133	117	156		

B, Dunes

Months	VIII	IX	X	XI	XII	XIII	XIV	Dune	SD
May/03	1	3	14	5	16	11	6	8	2.160247
Jun/03	10	25	8	14	31	11	13	16	3.251373
Jul/03	3	11	8	31	17	12	13	13.57143	3.337073
Aug/03	12	28	7	12	23	19	6	15.28571	3.129843
Sep/03	8	2	1	2	2	8	10	4.714286	1.426188
Oct/03	1	3	14	5	16	11	6	8	2.160247
Nov/03	3	6	2	1	1	8	10	4.428571	1.360272
Dec/03	2	6	2	6	13	5	5	5.571429	1.39484
Jan/04	1	3	1	11	27	3	9	7.857143	3.514789
Feb/04	4	7	4	1	7	8	6	5.285714	0.918443
Mar/04	2	2	9	3	6	3	8	4.714286	1.106567
Apr/04	1	3	3	3	5	4	7	3.714286	0.714286
May/04	10	7	9	5	7	16	47	14.42857	5.588496
Jun/04	4	14	11	4	8	12	11	9.142857	1.486904
Jul/04	8	3	3	6	0	1	8	4.142857	1.223355
Total	69	120	82	104	163	121	159		

The weight-to-width proportion of the carapace of the sampled specimens presented a pattern of negative relative allometric growth (weight, 0.7134 g; width, 2.7983 cm), corroborated by the fit of points to the line and by the correlation coefficient ($r^2 = 0.9296$).

Number of Burrows

Of the 1,900 burrows of *O. quadrata* noted during the study period, 56.5% occurred in the lower level (beach) and 43.05% occurred in the upper level (dunes; Fig. 3A).

Significant differences were not seen in the number of burrows constructed on the beach ($F_{6-91} = 0.19$; $P \geq 0.05$), where the highest frequencies occurred in June and the lowest in April. Nor were they in the dunes ($F_{6-91} = 1.58$; $P \geq 0.05$), where the highest occurrences were between June 2003 and the lowest in April 2004 (Fig. 3A). Despite the absence of a significant difference in the number of burrows during the seasons of the year on the beach ($F_{3-8} = 0.97$; $P \geq 0.05$) and on the dunes
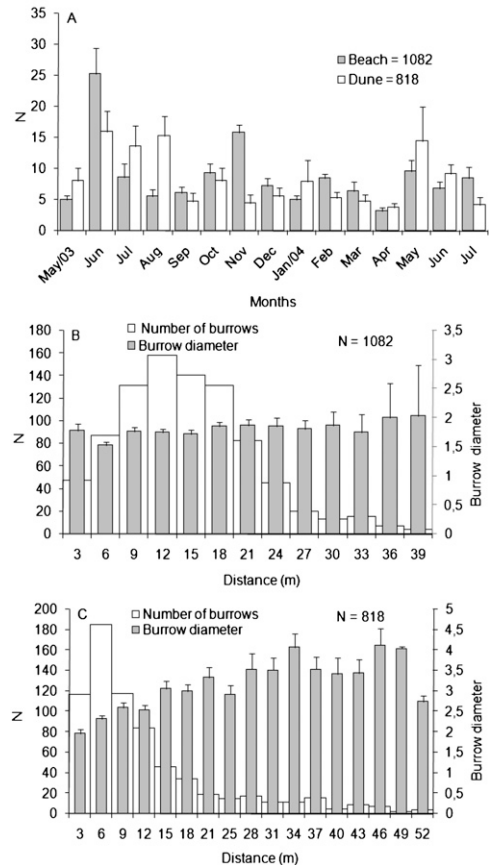

Figure 3. (A) Mean monthly frequency of burrows of *Ocypode quadrata* in the region of the beach (*n* = 1,082) and of the dunes (*n* = 818) from May 2003 to July 2004. **(B)** Distribution of mean diameter of burrows of crabs along the beach (lower level), measured from water line, from June 2003 to July 2004 (*n* = 818). **(C)** Distribution of mean diameter of burrows of crabs in dunes (upper level), measured from upper margin of beach, from June 2003 to July 2004 (*n* = 818).

($F_{3-8} = 1.93$; $P \geq 0.05$), in general the smallest values occurred during summer and fall months.

According to Figure 3B, the largest number of burrows on the beach occurred 12 m from the water level (*n* = 158). The median diameter in this region was estimated as 1.75 cm. The smallest number of burrows occurred 39 m from the water level (*n* = 4), with a median diameter of 2.02 cm. The largest incidence of burrows on the dunes was 6 m from the upper limit of the beach (*n* = 185), with a median diameter of 2.32 cm. The smallest densities of burrows on the dunes occurred 49 m from the lower limit of the dunes (*n* = 2), with a median diameter of 4.05 cm (Fig. 3C).

Feeding

Of the 449 stomachs analyzed, 202 were obtained from females, 83.7% of which had food; 187 were obtained from males, 80.2% of which contained some type of food; and 23 from juveniles, only 61.7% of which had food.

From the analyses of stomach content it was possible to identify 16 items composing the natural diet of *O. quadrata* (Table 2). The most important items in relative volume were *Apis* spp. (38.97%), nonidentified insects (12.21%), *Emerita*

TABLE 2.

Frequency of occurrence (FO) and percentage, and frequency of points (MP) and percentage of food items in the stomach content of *Ocypode quadrata* during May 2003 to June 2004.

Items	FO	%	MP	%
Plants	61	7.54	1,929	8.39
Macrophyta	1	0.12	5	0.02
Mollusca				
Gastropoda	5	0.62	14	0.06
Heliobia sp.	1	0.12	5	0.02
Polychaeta				
Calcareous spicule	11	1.36	62	0.27
Crustacea				
Callinectes sp.	26	3.21	273	1.19
Crustacean eggs	3	0.37	102	0.44
Penaeidae	3	0.37	160	0.70
Emerita brasilienses	36	4.45	1,973	8.58
Amphipoda	1	0.12	15	0.07
Insecta				
Apis spp.	139	17.18	8,963	38.97
Coleoptera	35	4.33	1,518	6.60
Nonidentified insects	77	9.52	2,809	12.21
Osteichthyes				
Nonidentified fish	9	1.11	62	0.27
NIOM	123	15.20	1,749	7.60
Sand	278	34.36	3,363	14.62
Total	809	100	23,002	100

NIOM, nonidentified organic matter.

brasilienses (8.58%), plants (8.39%), NIOM (7.60%), and coleoptera (6.60%). The remaining items represented less than 1.19% of the total (Table 2). Regarding frequency of occurrence, *Apis* spp. (17.18%) represented the most frequently consumed food item, followed by NIOM (15.20%), nonidentified insects (9.52%), plants (7.54%), *E. brasilienses* (4.45%), and coleoptera (4.33%; Table 2).

The 16 food items were grouped into 8 categories (Table 3), with Insecta the most important in frequency of occurrence (31.03%) and in frequency of points (57.78%). The second category was Crustacea, which represented 10.97% of the stomach volume, being present in 8.53% of the stomachs analyzed, followed by the categories plants, NIOM, Polychaeta, Ostheichthyes, and Mollusca. The category sand occurs in very significant quantities and frequencies, occupying 14.62% of the stomach volume and present in 34.36% of the stomachs analyzed. We assumed that sand represents an accidental item/category (Table 2).

Feeding of the Ground-Burrowing Owl

In the 82 regurgitated pellets collected near the burrows of the owl *S. cunicularia*, we identified 11 items grouped into 6 categories (Table 3). Rodent fragments represented 50.32% of the relative volume of consumed prey and were present in 35.88% of the analyzed pellets. The crab *O. quadrata* occupied the second position in volume, with 29.24% of the total, and was found in 22.52% of the regurgitated pellets, followed by Coleoptera and nonidentified insects.

Of the six food categories explored, Insecta contributed with three items; Mammalia, Crustacea, and plants with two, and

TABLE 3.

Frequency of occurrence (FO) and percentage, and frequency of points (MP) and percentage of prey in pellets regurgitated by *Speotyto cunicularia* from May 2003 to June 2004.

Items	FO	%	MP	%
Plants				
Macrophyta	11	4.20	115	1.49
Seeds	3	1.15	20	0.26
Crustacea				
Ocypode quadrata	59	22.52	2.260	29.24
Callinectes spp.	8	3.05	45	0.58
Insecta				
Nonidentified Insects	21	8.02	420	5.43
Coleoptera	50	19.08	845	10.93
Apis spp.	2	0.76	25	0.32
Amphibia				
Anurans	2	0.76	40	0.52
Birds				
Bird eggs	2	0.76	10	0.13
Mammalia				
Rodent remains	94	35.88	3,890	50.32
Bovine remains	10	3.82	60	0.78
Total	262	100.00	7,730	100.00

Anura and Aves with only one item (Table 3). The rodents (Mammalia) were the most important category in frequency of points (51.10%) and in frequency of occurrence (39.69%), whereas Crustacea represented 29.82% of the relative volume and were present in 25.57% of the regurgitates. Insecta contributed 16.69% of the total and were found in 27.86% of the pellets.

DISCUSSION

Air and water temperatures at Praia Brava followed the seasonal pattern of the region (Branco et al. 2002), directly lowering the mobility and activity of crabs in the range of 16.0–18.0°C during the winter months. This activity reduction was also observed along the coast of North America (Milne & Milne 1946, Haley 1972) and along the littoral of Rio Grande do Sul (Alberto & Fontoura 1999). The amplitude of salinity variation of the water remained within the tolerance range of *O. quadrata*, a species adapted to live in environments of both high and low salinity values (Santos et al. 1989).

Abundance peaks of crabs at Praia Brava recorded in the spring and summer months were also observed at beaches in Texas (Haley 1972), on the coast of São Paulo (Negreiros-Fransozo et al. 2002), and at beaches of Florianópolis, Santa Catarina (Blankensteyn 2006). Usually, crabs tend to reproduce continuously in tropical and subtropical regions, because of the favorable environmental conditions for availability of food, development of gonads, and liberation of larvae, whereas in temperate zones reproduction is restricted to the warm months (Costa & Negreiros-Fransozo 1998).

Considering the occurrence of egg-bearing females and juvenile crabs in the samples from Praia Brava, it is probable that the reproduction of *O. quadrata* occurs throughout the year, as also accounted for previously in the south and southeastern regions of Brazil (Alberto & Fontoura 1999, Negreiros-Fransozo et al. 2002, Blankensteyn 2006).

The available literature on sexual ratio in *O. quadrata* is limited. However, for the population of *O. gaudichaudii* Milne Edwards and Lucas, 1843, from Costa Rica, an equilibrium ratio of 1:1 was found (Trott 1998). For Praia Brava, this equilibrium tendency was maintained for the total number of captured specimens, but was altered during some months, with a predominance of females in August 2003 and May 2004, and with a preponderance of males in July 2004.

The largest sizes in carapace width obtained in the population of *O. quadrata* from Praia Brava remained around 3.8 cm, slightly below those recorded by Alberto and Fontoura (1999) and Negreiros-Fransozo et al. (2002), respectively, from the littoral of Rio Grande do Sul (3.97 cm) and São Paulo (4.07 cm), as well as from specimens sampled in the North Atlantic (4.8 cm and 5.35 cm) (Milne & Milne 1946, Haley 1972).

In general, male crabs tend to reach greater weight and larger size than females (Alberto & Fontoura 1999, Negreiros-Fransozo et al. 2002), with a negative (Branco & Lunardon-Branco 1993) or positive (Branco et al. 2002) pattern of relative allometric growth. A negative pattern is corroborated for the population of ghost crabs from Praia Brava.

At Praia Brava, as along the Brazilian coast, a tendency of reduction in the abundance of crabs in the direction of the dunes was seen, but with an increase in the median size of specimens (Alberto & Fontoura 1999, Turra et al. 2005, Blankensteyn 2006), demonstrating the preference of adult animals for regions more distant from the tidal level (Duncan 1986). On the other hand, the dispersion over the entire beach profile may be related to the food habits of these crabs, which are mostly nocturnal (Steiner & Leatherman 1981). Quijon et al. (2001) related the distribution and habitat structure of the Chilean ocypodid *O. gaudichaidii* H. Milne Edwards & Lucas, 1843, to behavioral rather than to purely physical causes.

In general, crustaceans represent the main food component in the diet of *O. quadrata* (Wolcott 1978). However, at Praia Brava, Insecta represents the most consumed item, particularly *Apis* spp. Insects are not frequent in the diet of Brachyura (Branco & Verani 1997), but the presence of insects and dead fish brought by the tide, in addition to molluscs from the beach, food remains from touristic activities, and the availability of prey from the dunes contributed to the ample feeding spectrum of this species.

A relatively high rate of empty stomachs suggests that obtaining food outside the burrows may involve a higher risk of predation by nocturnal predators than previously suspected. It may also be an indication of very flexible feeding habits of this single major inhabitant of supratidal beaches. These crabs are adapted to highly unstable conditions, requiring an ability to endure long periods of starvation (Wolcott 1978). In our study, the highest rates of empty stomachs were found in juveniles. Ghost crabs live for almost 3 y, taking 1 mo to become semiterrestrial and remaining as juveniles during their first year (Alberto & Fontoura 1999). Juveniles occur in the lowest intertidal levels of the species range along the beach. Ghost crabs do not need to leave their burrows to rehydrate, because they can extract the needed water from the damp sand of their burrow walls. In temperate climates they may remain underground for months at a time. Our data on food composition of *O. quadrata* (Table 2) confirm previous observations (Wolcott 1978) that most items correspond to animal protein, and only a fraction of less than 10% to plant matter. The conspicuous

fraction of sand grains is accidental. Sand grains are unlikely to be used like gizzard stones in birds, nor is it likely to come from deposit feeding, because ghost crabs prefer clean sands for burrowing and probably only deposit feed when there is rich, muddy sand nearby.

It has previously been observed that visual predators such as shore birds and gulls may be capable of exerting a considerable pressure on populations of this species (Blankensteyn 2006). The foraging behavior of the burrowing owl *S. cunicularia* has been studied in the state of São Paulo (Martins & Egler 1990). This owl is considered a generalist predator of arthropods, amphibians, reptiles, birds, and small mammals in South and Central America. However, in previous studies, only insects, rats, and lizards were identified in the regurgitated pellets (Martins & Egler 1990, Sick 1997). Gianuca (1997) actually mentioned predation on *O. quadrata* by owls in South Brazil. Our study indicates that the nocturnal crab *O. quadrata* is a frequent prey of the ground-burrowing owl *S. cunicularia* (Molina, 1782) on both dunes and beaches. The regurgitated pellets collected in the region of dunes at Praia Brava confirm the importance of rodents in the diet of this species (Bellocq 1987), and also of the crab *O. quadrata*, which occupied the 2nd position in volume and was found in 22.52% of the analyzed regurgitates.

We were unable to furnish an estimate of the predation pressure of owls on ghost crabs, but our data on prey items based on their frequency of occurrence and relative volume indicate that this predation pressure is significant.

More precise estimates of the population size of owls (How many owls are there? This was difficult to estimate because offspring of up to four young individuals do not usually leave their burrows.), of the turnover rate of owl pellets (Do they last for weeks of month?), and of the relative proportion between hard and soft parts of each prey item (Because only the indigestible hard parts remain in the pellets, and because this proportion is different for each prey item, the true biomass of prey can only be estimated from these relative amounts.) are still necessary to estimate how severe the predation pressure of owls is on ghost crabs.

The biological monitoring of sandy beaches using species sensitive to human impact is currently an important tool in the management and sustainability of tourist activities (Wolcott & Wolcott 1984). The periodic monitoring of the frequency of burrows of *O. quadrata* in the regions of the beach and dunes in the study area has been considered a reliable index of the impact of this activity during the summer months (Blankensteyn 2006, Neves & Bemvenuti 2006). Several experimental studies have attempted to show lethal effects of trampling and/or recreational use of beaches (Veloso et al. 2006). Although many anthropogenic influences, such as car driving on beaches, beach grooming, pollution, costal development, and sand removal may be stressful for crab populations, the fouling by organic detritus on beaches used for leisure may actually replenish a food resource for crab populations that may be limiting in pristine environments. Furthermore, predation pressure by owls represents an unaccounted nonanthropogenic pressure for ocypodid population dynamics, making the simple counting of burrows (Warren 1990) an imprecise or inadequate index of anthropogenic influence.

Our results indicate that the ghost crab is involved in more complex biotic interactions and trophic relations than previously reported. In comparison with the dominant role of the mud crab

N. granulata in mangroves and salt marshes, little is known of the interactions of *O. quadrata* with their main predator, the owl *S. cunicularia*, and with their main prey, such as bivalves, mole crabs, and the macroinfauna and meiofauna inhabiting sandy beaches.

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