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Cover photograph – "Little Ricky" - juvenile dolphin, San Salvador, Bahamas (courtesy of Sandra Voegeli, 2003)

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# GHOST CRAB BURROW CONSTRUCTION, PLACEMENT, AND LONGEVITY

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## ABSTRACT

The size of a ghost crab (*Ocypode quadrata*) burrow should be proportional to the size of the crab that constructs it, and the size of the crab (being a species with indeterminate growth) should in turn correspond to the age of the animal. Burrow size, therefore, can serve as a surrogate measure of the age structure of ghost crab populations, allowing easy monitoring of population dynamics. The construction of ghost crab burrows was examined by making plaster casts of burrows on Graham's Harbor beach. There was a strong correlation between hole size and mean diameter of the below ground burrow, although hole size overestimated burrow diameter. Burrow configuration varied from short, unbranched tunnels to long, branched structures with multiple entrances. The tendency to construct branched versus unbranched burrows was not related to crab (hole) size. Branched burrows tended to have a greater total length but the length of the main burrow did not differ significantly between branched and unbranched burrows, suggesting that burrow depth is more likely driven by characteristics of the environment (such as burrow placement relative to water table) than characteristics of the crab (such as age/size). For more complex burrows, construction appears to occur gradually; construction of the main burrow appears to occur first, with branches being added later. Most burrows are placed between the neap and spring high tide lines, although a small proportion of burrows are placed below the low high tide line or significantly above the highest high tide line. There is no correlation between crab (hole) size and distance from the high tide line, but the distribution of hole sizes differed below, between, and above high tide lines. Holes were distributed unevenly along the beach, with the highest densities apparently correlating with areas of greatest accretion. The abundance of holes varied across beaches and across years. Over a five-day period, the longest period of inactivity in a set of marked burrows was 96h. Patterns of burrow activity suggest that a significant proportion of the population may be made up of nomadic temporary burrowers, as compared with permanent burrow residents.

## INTRODUCTION

The ghost crab (*Ocypode quadrata*) is an inhabitant of the sandy intertidal along the eastern coasts of North, Central, and South America and among the islands of the western Atlantic Ocean and Caribbean Sea (Milne and Milne 1946). Their status as one of the fastest land animals has lead to many studies on locomotion (e.g. Weinstein 1995, 1998) and their ability to thrive in the transient and variable beachfront environment has given rise to examinations of their osmoregulatory capabilities (e.g. Wolcott 1984, Wolcott and Wolcott 1985). Despite their ubiquity and familiarity, information on their behavior is incomplete and information on their population dynamics is virtually non-existent.

Although ghost crabs are not threatened in any portion of their range, some studies have suggested that ghost crabs are sensitive to, and can be used as a measure of, human impact in beach environments (Steiner and Leatherman 1981, Wolcott and Wolcott 1984, Peterson et al. 2000, Barros 2001). In addition, ghost crabs have been shown to be predators on populations of endangered sea turtles and shorebirds (Arndt 1994, Loegering and Fraser 1995, however see also Wolcott and Wolcott 1999). Accurate monitoring of ghost crabs, therefore, can be a useful conservation tool.

Being largely nocturnal, direct census of ghost crab populations is not possible, but burrow openings can be used as an indirect measure of crab numbers. In addition, the size of a ghost crab burrow should be proportional to the size of the crab that constructs it, and the size of the crab (being a species with indeterminate growth) should correspond to the age of the animal. Burrow size, therefore, can potentially serve as a surrogate measure of the age structure of ghost crab populations, allowing easy monitoring of population dynamics.

Before accurate population modeling using burrow censuses is possible, many issues must be resolved, including: the relationship between crab size and hole size, longevity of burrows, rates of burrow occupancy, timing of crab activity, and the relationship between the physical environment and crab behavior. This study begins to investigate the accuracy of burrow censusing by examining burrow construction (size and configuration), placement (relative to tides and sand grain size), and longevity (frequency of crab activity).

## METHODS

### Burrow Construction

In 2001 and 2002, below ground burrow diameter was measured by making casts of ghost crab burrows. Burrow entrances were measured (side to side) to the nearest 0.1mm with dial calipers. Casts were made by pouring plaster (approximately 1:2 water and plaster) into burrow entrances and were allowed to dry for about 30 min. Casts were then excavated and the (side to side) diameter was measured every 5cm for the length of the cast to generate an average burrow diameter. Twelve casts were made each year. In 2001, casts were poured without regard to burrow placement relative to tide lines; in 2002, all casts poured were located above the high high tide line (HHT).

### Burrow Placement

From 2000-2002, burrows were censused at beaches around San Salvador to describe variation in crab abundance and crab size. Two beaches were selected at each of four compass directions: Graham's Harbor and Rice Bay to the north, Bonefish Bay and Long Bay to the west, Grotto and French Bay to the south, and Dim Bay and East Beach to the east. Burrows were censused for 150m (five 30m segments) along each beach. Graham's Harbor was censused starting at the government dock and moving west. Bonefish Bay was censused beginning at the gym and moving south. Long Bay was censused beginning at the monument and moving south. Grotto was censused beginning at its most eastern edge and moving west. French Bay was censused from the second road west of the public dock and moving west. Dim Bay was censused from just north of the cemetery and moving south. East Beach was censused from the road and moving south. The entire length of Rice Bay was censused as part of another project. Size of the burrow entrance was recorded to the nearest 0.1mm using dial calipers. In 1999 and 2000, the distance of each burrow from the strand line was measured at Rice Bay. In 2002, the general position of each burrow, above the high high tide line (HHT), between the high and low high tide lines (BHT), or below the low high tide line (LHT) was recorded at all beaches.

Sand samples were collected for sand grain size analysis from 2001-2003. In December 2001, three samples were taken at each beach adjacent to holes above HHT. In December 2002, two three-sample transects were made perpendicular to the beachfront (at HHT, BHT, and LHT); one transect collected samples adjacent to holes, one transect collected samples away from holes at the same position. In March 2003, a more intensive survey was conducted at Graham's Harbor from the Field Station dock to the west end of the beach. Samples were taken at HHT, BHT, and LHT every 15m. All samples were taken by pushing a 100ml plastic container into the sand to remove a core of approximately 5cm in diameter and 10cm in length. Samples were air dried and then shaken for 3 min on a sieve shaker. Fractions captured by 2.5, 1.0, 0.5, 0.25, 0.106, 0.053, 0.045micron screens were weighed to the nearest 0.01g.

### Burrow Longevity

Frequency of crab activity was monitored at individual burrows at Graham's Harbor in 2001 and 2003. All open burrows found on the first day were flagged and the size of the burrow entrance was measured as described above. In December 2001, flagged burrows were checked once each day for three days. The sand at each burrow entrance was smoothed after checking to identify new activity each day. In March 2003, burrows were checked three times a day for five days, but only covered after the morning check. New burrows were flagged as they appeared during all checks.

## RESULTS

### Burrow Construction

External hole size was positively correlated with mean internal burrow diameter ($r^2 = 0.44$, $P = 0.0008$; Figure 1).

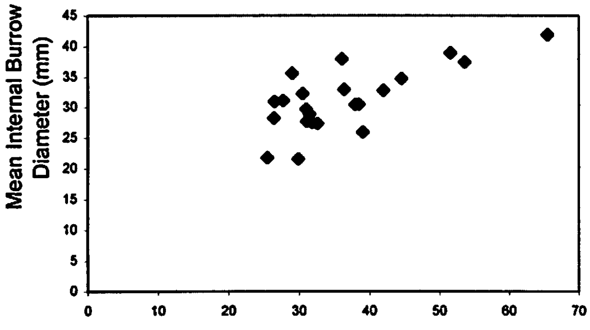

*Figure 1. Relation between internal and external measurements of burrow diameter.*

Hole size typically overestimated burrow diameter and the discrepancy between external hole size and mean internal burrow diameter increased with increasing hole size ($r^2 = 0.66$, $P = 0.0015$; Figure 2).

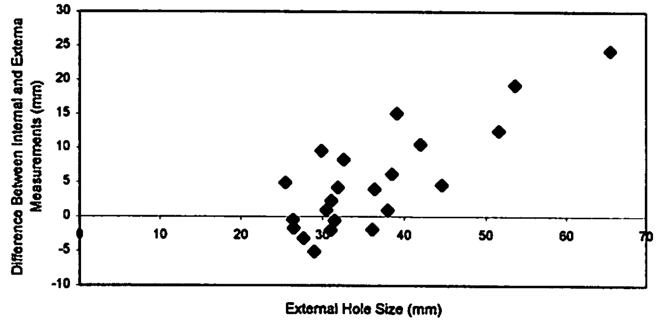

*Figure 2. Relation between hole size and measurement error.*

Excavated burrows could be classified into one of four configurations: an "I" shaped burrow that was relatively straight and unbranched, a "J" shaped burrow that was unbranched but recurved, a "W" shaped burrow that was recurved but branched, and a "Y" shaped burrow that was branched but relatively straight. "I" burrows were found LHT, BHT, and HHT but were the only type found LHT. The average proportion of burrows with secondary openings (branches that extended to the surface) was 6.75% (range 0-11.5%) in 2001 and 8.04% (range 0-20.7%) in 2002. Primary burrow openings were oriented towards the water while secondary burrow openings (when present) were oriented away from the water. Burrows with secondary openings were slightly larger than burrows with only one opening (one opening 31.5mm±11.0mm, two openings 35.5mm±13.0mm; $t = 2.9$, $P = 0.004$). Branch diameter was typically smaller than that of the main burrow (main 31.1±6.4mm, branch 27.6±5.0mm; $t = 2.20$, $P = 0.03$). Branched burrows had a greater total length than unbranched burrows (branched 73.8±17.6cm, unbranched 43.4±17.1cm; $t = 4.09$, $P = 0.0006$) but the length of the main tunnel was not significantly different between branched and unbranched burrows (branched 56.8+18.2cm, unbranched 43.4+17.1cm; $t = 1.78$, $P = 0.09$). There was no correlation between mean burrow diameter and total length of burrows ($r^2 = 0.11$, $P = 0.48$).

### Burrow Placement

The majority of burrows were located at or above the high tide line. There was no correlation between hole size and distance from the strand line (1999: $r^2 = 0.004$, $P = 0.53$; 2000: $r^2 = 0.002$, $P = 0.48$) nor was there any size difference among LHT, BHT, or HHT holes (2002: $F = 2.83$, $P = 0.06$). In 1999, however, burrows at Rice Bay were located significantly lower on the beach than in 2000 (1999: -2.3m±2.7m; 2000: 4.4m±3.3m; $t = 18.1$, $P < 0.00008$, where 0m = strand line). Burrows were not evenly distributed along the length of the beach. At both Rice Bay and western Graham's Harbor, where the most extensive surveys were conducted, burrow abundance was lowest near either end of the beach (Figure 3).

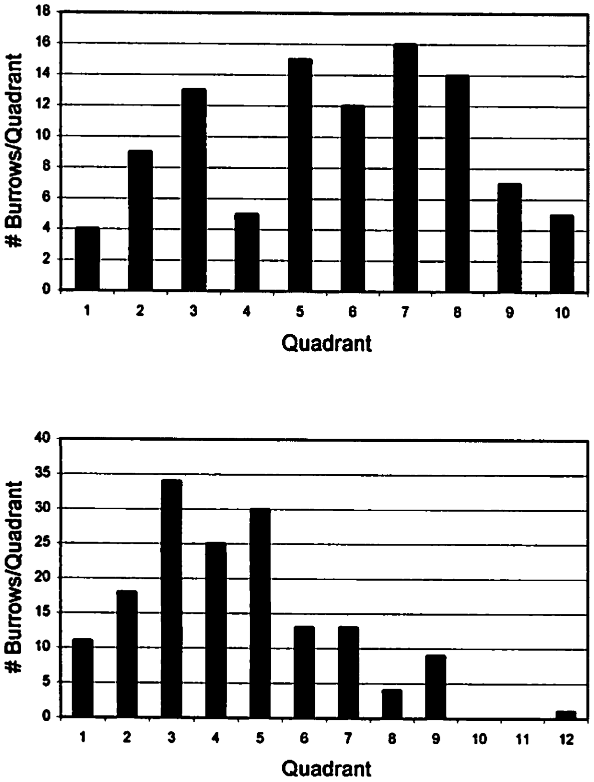

*Figure 3. Distribution of burrows along beach at W. Graham's Harbor (above) and Rice Bay (below).*

There was an inverse correlation between sand grain size and burrow abundance ($r^2 = 0.45$, $P = 0.033$, Figure 4). Although there was a marginally significant difference in sand grain size between samples taken adjacent to holes and samples taken randomly at the same position on the beach (hole: 18.1+1.94% 0.5mm sand; random: 16.1+1.88% 0.5mm sand; $t = 1.80$, $P = 0.492$), the direction of the difference was not consistent among paired samples; burrows were sometimes in coarser sand, sometimes in finer sand as compared with random samples.

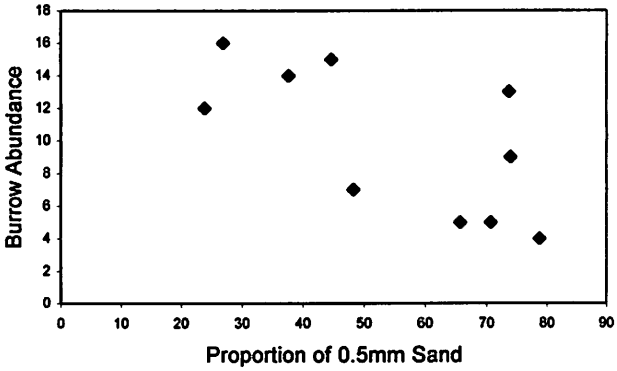

*Figure 4. Relation between burrow abundance and sand grain size.*

Sand grain size became slightly finer but more variable moving up the beach face from LHT to HHT, but differences in sand grain size perpendicular to the beach face were minor compared to the degree of variability found along (parallel to) the beach face (Table 1).

| | | **Position** | |
|---|---|---|---|
| **Quadrant** | **HHT** | **BHT** | **LHT** |
| 1 | 78.8 | 57.1 | 65.9 |
| 2 | 74 | 73.7 | 71.4 |
| 3 | 73.7 | 68.2 | 71.1 |
| 4 | 70.7 | 64.4 | 67.3 |
| 5 | 44.7 | 71.9 | 53.6 |
| 6 | 23.9 | 55.6 | 84.2 |
| 7 | 26.9 | 50.1 | 80 |
| 8 | 37.7 | 85.7 | 91.4 |
| 9 | 48.3 | 74.3 | 78.6 |
| 10 | 65.7 | 37.6 | 62.3 |
| mean | 54.44 | 63.86 | 72.58 |
| std dev | 20.66 | 13.98 | 11.11 |

*Table 1. Proportion of 0.5mm sand in different quadrants and at different heights on the beach.*

The number of burrows differed considerably among beaches and between years (Table 2). With the exception of East Beach and Grotto, burrow numbers were higher during 2002. Long Bay, Bonefish Bay, and East Beach had consistently low numbers of burrows. Rice Bay, Dim Bay, and Grotto had consistently high numbers of burrows. French Bay, however, increased the number of burrows by an order of magnitude between 2001 and 2002.

| | **Year** | |
|---|---|---|
| **Beach** | **2001** | **2002** |
| Graham's | 52 | -- |
| Bonefish | 11 | 29 |
| Long | 4 | 6 |
| Grotto | 86 | 52 |
| French | 10 | 165 |
| Dim | 61 | 118 |
| East | 30 | 19 |
| Rice | 97 | 165 |

*Table 2. Differences in burrow abundance between years and among beaches.*

With the exception of Grotto and Long Bay, average hole size was significantly higher in 2002 (t = 1.94, P = 0.025, Table 3).

| | **Year** | |
|---|---|---|
| **Beach** | **2001** | **2002** |
| Graham's | 29.1±9.3 | -- |
| Bonefish | 23.3±10.7 | 32.3±13.2 |
| Long | 28.8±10.9 | 28.5±7.5 |
| Grotto | 31.5±12.9 | 28.4±12.1 |
| French | 34.4±12.8 | 43.3±13.4 |
| Dim | 23.5±10.4 | 32.8±9.8 |
| East | 19.9±6.7 | 30.8±12.8 |
| Rice | 21.3±8.7 | 30.0±9.1 |

*Table 3. Differences in burrow size (mm) between years and among beaches.*

There were significant differences in average hole size among beaches in both years (2001: F =11.3, P < 0.0001; 2002: F=12.7, P <0.0001). In 2001, Bonefish, Dim, East, and Rice had smaller holes than Grotto, Long, French, and Graham's. In 2002, French Bay had significantly larger holes than all other beaches.

### Burrow Longevity

The average interval between periods of crab activity was greater during winter than spring (winter: 50.2h±21.8; spring: 35.4h±19.5h; t = 2.00, P = 0.011). The longest a crab stayed below ground before re-surfacing was 96h (n=1). The density of active crab burrows was also higher in spring than in winter (winter: 12/m, spring: 23/m). Average hole size was significantly smaller during spring (winter: 29.0±11.7mm, spring: 18.2+8.7mm, t = 1.97, P < 0.0001). During both seasons, the majority of flagged burrows (winter: 54.6%, spring: 34.4%) were not found to be active again during the observation period (Figure 5).

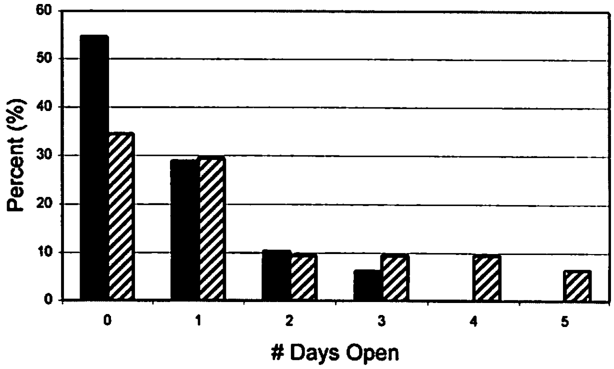

*Figure 5. Activity of burrows during December (solid bars) and March (hatched bars).*

The occurrence of these ephemeral burrows varied with placement. In LHT, 100% of burrows were ephemeral; in BHT, 43% of burrows were ephemeral; and in HHT, 18% of burrows were ephemeral. Ephemeral burrows were significantly larger than other burrows in spring (ephemeral: 25.6±6.1mm, non-ephemeral: 18.2±9.4mm, t = 2.05, P = 0.012) but not in winter (ephemeral: 28.8±11.7mm, non-ephemeral: 29.3±11.9mm, t = 1.99, P = 0.85). The number of new burrows flagged decreased over time, as did the number of active burrows, but five days after the observation period began, new burrows were still being found (Figure 6).

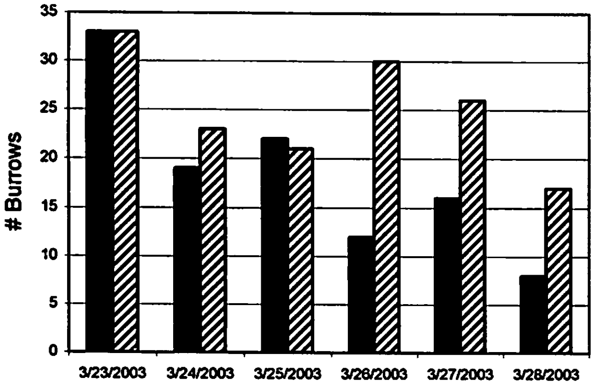

*Figure 6. Appearance of new burrows (solid bars) and active burrows (hatched bars) over time.*

## DISCUSSION

Hole diameter is a good indicator of internal burrow diameter, but there is also clearly a degree of error associated with measurement of burrow entrances. Larger holes are more difficult to measure accurately because the openings become more funnel-shaped as they increase in size and the jaws of the calipers are not long enough to reach the base of the opening. It should be possible to reduce the error associated with measuring burrow size by attaching an extension onto the jaws of the caliper. It would also be important to know, however, to what extent openings enlarge over time as a result of either crab activity or collapse as sand at the entrance dries. Hole size has been used as an indicator of the proportion of adults and juveniles in a population (Fisher and Tevesz 1979) because sexual maturity is typically obtained at a particular body size (25mm, Haley 1969). However, since burrows are typically smaller than openings, and the few measurements we have from crabs indicates that crabs are slightly smaller than their burrows, 30mm (hole diameter) may be a more suitable cut-off point for distinguishing juvenile burrows from adult burrows. It will be important to accurately describe the relationship between crab size and hole size before making inferences about population age structure.

Burrow configuration is consistent with main branches being constructed first. Above HHT we found long, straight burrows (Ys without branches) but never V-shaped burrows (Ys with branches but without the long main shaft). At BHT we found W-shaped burrows (Js with branches) but never U-shaped burrows (Js with branches but without a main shaft). Observation of captive crabs confirm that the main shaft is constructed first (Fellows 1966), but ghost crabs have also been documented to construct U-shaped burrows in some populations and in some habitats (Vannini 1980).

Branched burrows had almost twice the total length of unbranched burrows, and total burrow length can therefore be used as an indicator of burrow complexity. The absence of a relationship between burrow diameter and total length suggests that the configuration of burrows is not a function of size/age. This same conclusion was reached in a review of burrow construction within the genus as a whole (Vannini 1980). Burrow configuration was, however, related to the placement of burrows on the beach. Although ghost crabs do not necessarily burrow to the water table (Vannini 1980), experimental studies have shown that crabs are capable of fine distinctions in soil moisture content and will chose burrow sites based on moisture levels (Shuchman and Warburg 1978, Warburg and Shuchman 1979). Changes in burrow shape and length in this study are consistent with crabs burrowing to reach sand of a particular moisture content. Burrows dug below LHT were consistently short. Burrows slightly higher on the beach (BHT) tended to be longer and recurved. Burrows above HHT were longest and straight. Also, although the total length of branched and unbranched burrows is very different, the length of the main shaft of branched and unbranched burrows is not significantly different. This suggests that crabs burrowing at a particular position seek a particular depth. Other studies (Fellows 1966, Jones 1972, Vannini 1980) have not found a relationship between burrow shape and distance from the sea, but it should be noted that it is habitat and not distance per se that is important. On a beach backed by dunes, Chakrabarti (1981) found that burrows became progressively deeper away from the ocean, but on a beach backed by a marsh, burrows initially became deeper away from the ocean and then became shallow again as they approached the marsh.

Burrow configuration may also be a function of burrow longevity. Although the length and shape of the main shaft may be driven by conditions underground, the extent of branching may be related to the amount of time that the crab has inhabited the burrow. One burrow that was monitored over a 5-day period went from being a single hole to a twin hole, so clearly a branch had been added or extended. The amount of time spent burrowing may also come back to placement. The lower a hole is on the beach, the more likely it is to be filled by the tides. Crabs lower on the beach may therefore spend more time digging out and less time adding to an existing burrow. Time spent burrowing by crabs above the HHT is more likely to translate into greater burrow complexity. Above HHT, burrows with three openings were found in this study. Studies on timing of crab activity have shown that few new permanent burrows are constructed during spring tides when damage to burrows is most likely (Barrass 1963), suggesting that crabs may be conservative with regard to energy spent on burrowing. Short, straight burrows found higher on the beach may represent incomplete burrows or ephemeral ones. Monitoring of burrow fidelity would help to clarify the relationship among burrow placement, burrow longevity, and burrow configuration.

Several researchers (Frey and Mayou 1971, Fisher and Tevesz 1979, Chakrabarti 1981, Strachan et al. 1999) have documented a relationship between burrow size and burrow placement, with larger holes being located higher on the beach. The absence of such a relationship in this study may be related to beach width. During this study, beaches on San Salvador measured between 9-25m. Studies that found a relationship between burrow size and placement occurred on beaches 43-110m in width. Size stratification may simply not be an option on San Salvador where beaches are backed by beach rock (Long Bay), road (Graham's Harbor, Bonefish Bay), vertical banks (Rice Bay), or heavily vegetated dunes (Grotto, French Bay, Dim Bay, East Beach) that limit ghost crab habitat.

The inverse relationship between sand grain size and burrow abundance found in this study is more likely correlative than causal. Availability of ghost crab habitat varies considerably along the length of San Salvador's crescent-shaped beaches. At the head of a bay (upstream relative to the direction of drift) the beach is eroded away to bare limestone. Sediment from these points is deposited along the body of the crescent, and at the far end of the beach (relative to the direction of drift) the current again erodes the beach to reveal increasing amounts of beach rock. The same changes in current that create favorable habitat for burrowing also alter sediment size. Slower currents deposit finer sand, stronger currents transport it. The size of ghost crab populations are strongly driven by habitat suitability and may vary considerably depending on what portion of a beach is surveyed. The Long Bay transect, for example, is taken on an eroding portion of beach where beach rock dominates the HHT environment. It is not surprising that ghost crab populations in this area are consistently low. Transects on a different portion of this beach may yield very different results. Since it is generally not feasible to survey an entire beach, between-beach comparisons are best made using portions of beach with the greatest, or comparable, accretion.

Accretion, however, is not everything. The transect at Bonefish Bay occurs in an area that accumulates large quantities of sand. In 2001, much of this sand was transported to the inland side of the Queen's Highway as a result of Hurricane Michelle. The remaining sand was quite coarse and burrow counts were understandably low. The following year the character of the sand had changed to a very fine sand that created a hard packed beach, and although burrow counts were several times higher than 2001, they were still low. Whether hard-packed sand constitutes poor habitat for ghost crabs or whether recruitment at this site is low is not known. Presumably ghost crabs released as eggs at one site become recruits elsewhere as a result of drift, but nothing is known about the dispersal patterns of earlier life stages or even of the extent to which metamorphosed crabs range.

Annual changes in burrow abundance in this study were correlated with environmental change: beach sand was coarser and burrow abundance lower in 2001, which was a hurricane year, than in 2002, which was not a hurricane year. Changes in both sand grain size and burrow abundance could be attributed to changes in wave action associated with the hurricane. Average hole diameter was also significantly smaller in the hurricane year than in the non-hurricane year. The one beach (Grotto) that did not show an increase in hole size in the non-hurricane year also did not show an increase in burrow abundance (sample size at Long Bay is too small for reliable interpretation). The shift in hole size could be explained by depopulation during the hurricane followed by recruitment, resulting in a smaller average hole size in the months following the hurricane. Even in non-hurricane years, storms and currents can dramatically reshape beaches in ways that may impact crab populations. Generally speaking, crab populations will be as ephemeral or as stable as the beaches they inhabit. Furthermore, as a result of drift and dispersal, population dynamics in one area may be dependent upon the success and stability of crab populations in other areas.

Both the lower abundance of holes and the longer interval between emergences in December versus March suggests seasonality in crab activity. Temperature has been shown to influence activity levels; ghost crabs are not active below 12-15°C (Leber 1977) and at higher latitudes may remain below ground for months at a time (Leber 1982). Although average monthly temperatures do not fall below 20°C, and they are not significantly in December and March (Shaklee 1996), temperatures were higher in March 2003 than in December 2001 (pers. obs.). It should be noted, however, that the longer interval between emergences in December could also be a by-product of the shorter observation time (3d versus 5d). Activity is influenced by weather as well as climate. During days of high wind and surf, few crabs emerged; maximum time between emergences decreased to 48h in fair weather compared to 96h during rough weather. Since such weather is more common during winter than spring, this could result in longer intervals between emergences. Seasonal changes in emergence time could also be related to crab size, since hole size is larger during winter and it has been suggested that larger crabs can remain below ground for longer periods of time (Cowles 1908). Presumably, smaller hole size in spring is a function of more breeding and therefore more recruits of small crabs into the population.

At least a third of the population appeared to construct ephemeral burrows at Graham's Harbor. Such burrows have been described in *O. ceratophthalmus* (Barrass 1963) and burrows of similar construction (longevity unknown) have been documented in *O. quadrata* (Cowles 1908, Frey and Mayou 1971), though they have not been observed in all populations or species. This may be because not all species or populations construct them, or because surveys were conducted during higher tides or higher surf. Ephemeral burrows were most common low on the beach where burrows would be more likely to be damaged by incoming tides. Although average hole size (all burrows) changed seasonally, the size of ephemeral burrows did not. Ephemeral burrows were typically constructed by crabs of intermediate size, rather than by very small or very large crabs. Such crabs may be less in need of permanent burrows, being less vulnerable than young crabs, but not yet reproductive. The number of new burrows decreased over the observation period, consistent with an increasing proportion of individuals having emerged from permanent burrows. After five days, however, almost half of active burrows were previously undocumented, suggesting that a significant proportion of the population re-dug burrows on a daily basis. A longer term study is necessary to verify these observations, along with studies of burrow occupancy to relate burrow counts to true population size.

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