

FACTORS AFFECTING PREDATION OF MARINE TURTLE EGGS BY RACCOONS AND
GHOST CRABS ON CANAVERAL NATIONAL SEASHORE, FL

by

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ABSTRACT

Changes in abundance of interactive species can have cascading, community-wide effects (Soulé et al. 2003). Raccoons (*Procyon lotor*) prey on a competitor for marine turtle eggs, the Atlantic ghost crab (*Ocypode quadrata*). Conservation of marine turtles often includes managing raccoons—the most obvious egg predator—which may have broader ecological effects, and unknown effects on egg predation. Neither the relationship between raccoons and ghost crab density nor the effects of ghost crab density on egg predation are well understood. I studied raccoon-ghost crab interactions and the effects of environmental variation on their activity during the 2007 marine turtle nesting season on Canaveral National Seashore, FL. My goal was to model predator activity and identify efficient management strategies to reduce egg predation. Raccoon activity increased with increasing habitat diversity and edge of the dominant cover type, coastal strand. Raccoon activity increased locally and became less variable near segments of beach accessed for human recreation, but activity was greater on undeveloped beach, where habitat diversity and edge were greater. Ghost crab density and size were primarily affected by sand characteristics and recreation but decreased with increasing raccoon activity in June, which may have contributed to sustained declines in ghost crab density. Hatching success of marine turtles decreased with increasing ghost crab egg predation, suggesting ghost crabs are an important cause of egg mortality and not merely scavengers on unhatched eggs. Egg predation by ghost crabs was unrelated to ghost crab density or size, likely a result of monitoring limitations, but raccoon activity increased with increasing egg predation by ghost crabs, supporting previous research and experimental evidence suggesting ghost crabs can facilitate secondary nest predation by raccoons. This indirect interaction has strong implications for

marine turtle conservation, because its strength may increase with increasing ghost crab density, potentially negating the effects of raccoon removal.

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CHAPTER 1. ENVIRONMENTAL INFLUENCES ON ACTIVITY OF SEA TURTLE NEST PREDATORS & CONSEQUENCES FOR LOGGERHEAD SEA TURTLE HATCHING SUCCESS

Introduction

When predation affects species of conservation concern, such as marine turtles (Stancyk 1982), managers must identify the causes and consequences of changes in predator communities to avoid short-lived conservation benefits or unexpected, cascading negative effects (Soule et al. 2005). Predator replacement through immigration may require continuous predator removal, which has far-reaching effects on predator demographics (Barton and Roth 2007). Increased predation on sensitive species could result from increased density of intermediate predators, i.e., mesopredator release (Crooks and Soule 1999, Barton and Roth 2008). Scientific experiments that identify and mitigate factors affecting predator density (e.g., anthropogenic development and food subsidies) can improve the efficacy of conservation-oriented predator management (Boarman 2003).

Predation is one of the largest causes of egg mortality for marine turtles in North America (Stancyk 1982, Engeman et al. 2003). All four marine turtle species that nest on the Atlantic coast of the U.S. are listed as threatened or endangered under the Endangered Species Act of 1973 and endangered or critically endangered on the International Union for Conservation of Nature red list (2007), requiring management actions to mitigate egg loss to predators. Raccoons (*Procyon lotor*) are well-documented predators of marine turtle eggs, preying on >90% of nests on some U.S. beaches (Davis and Whiting 1977, Stancyk 1982, Engeman et al. 2005, Garmestani and Percival 2005). Common management strategies to reduce predation include removing raccoons and physically screening them from nests (Engeman et al. 2005, Garmestani and Percival 2005). Both methods effectively reduce nest predation by raccoons (Ratnaswamy et al.

1997, Engeman et al. 2005, Antworth et al. 2006) but even well-established practices can have unexpected results (Barton and Roth 2008) and the broader ecological effects of raccoon management are not well understood (Ratnaswamy and Warren 1998).

Predation of marine turtle eggs by ghost crabs (*Ocypode quadrata*) also can be substantial (Bouchard and Bjorndal 2000, Antworth et al. 2006, Barton and Roth 2008) and they may be the most important predators of marine turtle eggs on beaches where raccoon predation is controlled. Population densities of raccoons and ghost crabs are negatively correlated on sea turtle nesting beaches in Florida (Barton and Roth 2008), so raccoons may limit ghost crab populations and their impact on nesting turtles. Intraguild predation, where one predator preys on another that shares a common resource, is common in nature and important in structuring ecological communities (Polis and Holt 1992, Holt and Polis 1997, Arim and Marquet 2004). By selectively preying on large ghost crabs, which may be more effective egg predators (Barton and Roth 2008), raccoons could alter the size structure and reproduction of ghost crab populations, reducing egg predation by ghost crabs. Thus, the indirect negative effects of raccoon removal could outweigh the direct benefits for marine turtle hatching success.

The mesopredator release hypotheses states that removal of top predators can release intermediated-sized predators from predation and competition, resulting in greater predation on lower trophic levels (Crooks and Soule 1999). Mesopredator release often has been invoked over other explanations for increased predation and mesopredator density, such as changes in landscape characteristics that favor mesopredators but negatively affect their prey (see Litvaitis and Villafuerte 1996, Gehrt and Clark 2003, Gehrt and Prange 2007). Barton and Roth (2008) observed substantial predation of sea turtle nests even with low raccoon densities and suggested ghost crabs released from raccoon predation increased in density and size. Furthermore, they

suggested increased nest predation by ghost crabs increased the detectability of nests, facilitating predation by raccoons (Barton and Roth 2008). Thus, they explained high egg predation by both predators combined as arising through mesopredator release and an indirect behavioral interaction. However, potential confounding factors could contribute to differences in predator densities and predation among sites, including different levels of human development and recreation along east-central Florida beaches (Barton and Roth 2008).

Beach development and recreation may be favorable for raccoons, which often increase in density and alter their behavior in response to human activities (Prange et al. 2004) and increased landscape diversity (Oehler and Litvaitis 1996). Raccoon abundance and activity have been positively correlated with habitat edges (Danielson et al. 1997, Chamberlain et al. 2007) and proximity to aquatic habitats (Dijak and Thompson 2000, Chamberlain et al. 2007). Ghost crab abundance may be negatively affected by recreational activities due to habitat destruction (Barros 2001) or positively affected by food subsidy (Steiner and Leatherman 1981). Sediment composition also may influence ghost crab density, with lower abundance in poorly sorted (large standard deviation from mean grain size) sediments and smaller burrows in coarse-grained sand (Turra et al. 2005). Understanding how human activity and landscape diversity influence the dynamics of marine turtle nest predators is important for implementing the most effective strategy to reduce predation on sea turtle eggs.

All research was conducted in collaboration with James D. Roth, Research Faculty, Department of Biology, University of Central Florida. We measured the spatiotemporal effects of natural and human-influenced environmental variation on raccoon activity, ghost crab burrow density, and their subsequent effects on frequency of ghost crab predation on marine turtle eggs. We conducted research on Canaveral National Seashore, where all marine turtle nests were

screened to prevent nest predation by raccoons (Antworth et al. 2006). When raccoons prey on a turtle nest they generally eliminate all evidence of previous predation. Eliminating secondary nest predation by raccoons preserves evidence of primary predation and reduces the likelihood of underestimating egg predation by ghost crabs.

We tested the hypothesis that variation in marine turtle egg predation was primarily due to changes in ghost crab density, which is affected by turtle nest density, human recreational activities, sediment composition, and raccoon activity. We predicted ghost crab density would increase with increasing marine turtle nest density, decreasing human recreational activities, decreasing mean and standard deviation from mean (SD) sand grain size, and decreasing raccoon activity. We predicted raccoon activity would increase with increasing marine turtle nesting, human recreational activities, and habitat diversity. Finally, we predicted marine turtle egg predation would decrease with decreasing ghost crab density and increasing raccoon activity, due to direct effects on ghost crab numbers and indirect effects on their behavior.

Study Area

Canaveral National Seashore (CANA), located on central Florida's Atlantic coast, consists of 58,000 acres of barrier island, open lagoon, wetlands, coastal hammocks, and pine flatwoods managed by the National Park Service (NPS). The 38.4 km segment of barrier island varies widely in width, habitat composition and human recreational activity. The central 17.5 km (backcountry) has remained undeveloped, with public access restricted to permit holders on foot or horseback. The remaining 20.9 km includes the northern (Apollo Beach, ~11.7 km) and southern (Playalinda Beach, ~9.2 km) ends of the park. Apollo Beach is the widest portion of CANA's barrier island, with more road but fewer beach access points. Apollo Beach was bordered by the town of New Smyrna Beach and contained offices and buildings associated with

research and park management personnel. Playalinda Beach was bordered by relatively undeveloped beach and inland habitat managed by Kennedy Space Center and the U.S. Fish and Wildlife Service. Both beaches were accessible from parking lots distributed along primary access roads inland of the beach dunes. Each parking lot had a vault toilet and refuse cans in lidded enclosures, and garbage was relatively inaccessible to raccoons. The level of human disturbance varied across the landscape and differed between the two accessible segments of beach; Apollo Beach had fewer parking lots and visitors than Playalinda Beach.

Three species of marine turtle nest regularly on CANA: leatherback (*Dermochelys coriacea*), green (*Chelonia mydas*), and loggerhead (*Caretta caretta*). Loggerheads nest in the greatest abundance (Antworth et al. 2006) and Kemp's ridleys (*Lepidochelys kempii*) nest infrequently on CANA. The nesting season extends from April to September or October, but most nest deposition occurs from May to August. Nest density is generally higher in the southern region, but abundance varies greatly within areas (Antworth et al. 2006). The NPS screens > 90% of nests within 12 h of deposition to create a physical barrier to raccoon predation. Nests are marked with a single wooden stake and covered by a wire screen (2.25 m² with 5 cm x 10 cm mesh) impenetrable to most raccoons but not to ghost crabs (Antworth et al. 2006). Most raccoon predation occurs prior to screening, so screened nests allow unbiased assessment of egg predation by ghost crabs.

Methods

Predator Indices

We used passive tracking methods (Engeman et al. 2003, Barton and Roth 2008) to monitor raccoon and ghost crab activity from April to October 2007. Using a landscape rake, we smoothed 2 m wide transects from the dune edge to below the current high water mark and

marked the center of each transect with a single wooden stake at the dune edge. Transect area varied with beach slope and the tide cycle. We restricted measurements to the minimum distance on each transect unaffected by tide. Raccoons and ghost crabs are primarily nocturnal (Greenwood 1982, Valero-Pacheco et al. 2007) and human beach access was limited to daylight hours on CANA. To reduce human disturbance, we monitored transects from 1 h before sunset to 1 h after sunrise. We divided the beach into 24 sections and randomly selected four points spaced >100 m apart within each 1.6 km section. Thus, we sampled a total of 96 transects, each on two consecutive nights, bi-weekly; half the beach was sampled in a four day period, alternating which quarter was sampled first. To avoid any biases associated with rain, which washes away tracks, we sampled only in fair weather. We counted the number of raccoon tracks (a series of prints) intersecting each transect and total length (cm) of each raccoon track. We also counted the number of tracks of other mammals on the beach; armadillo (*Dasypus novemcinctus*), bobcat (*Lynx rufus*), and opossum (*Didelphis virginiana*). We counted all ghost crab burrows within transects, measured the diameter (mm) of each burrow (which correlates with carapace width; Turra et al. 2005) and considered ghost crab burrows ≥ 23 mm in diameter to reflect reproductive adults (Negreiros-Fransozo et al. 2002). At each sampling period we measured the length of each transect from dune to high tide mark in order to calculate burrow density.

Environmental Variables

We measured several environmental variables to determine their relationship to the distribution and abundance of raccoons and ghost crabs.

Nest Density.—We used a Garmin 12 Global Positioning System (GPS), accurate to 15 m, to gather locations of all marine turtle nests laid from April through July. We counted the cumulative number of nests laid within 100 m of each transect on each sampling day, as well as

the number of nests laid within the previous 2 d. Numbers of nests were averaged for all sampling days for each transect for spatial analyses and averaged for all sampling days within each month for temporal analyses.

Recreation.—We assumed the impact of human recreation on the beach would be related to distance to parking lots (which provide beach access with boardwalks over the dunes, thus acting as human recreation centers) and the relative use of parking lots by park visitors. We measured GPS locations of all beach access boardwalks associated with parking lots and measured the distance of each transect to the nearest boardwalk using ArcGIS 9.2. For each parking lot, we counted the cars on at least eight occasions between 1700 and 1730 h prior to clearing transects for sampling, then regressed the number of cars against the park entrance counts (collected by NPS at gate) for each day. We used the resulting linear equations to estimate the number of cars present in each parking lot on each sampling day. We averaged the estimated daily counts at the nearest parking lot across all sampling days for each transect.

Sand Composition.— To test the effect of sand composition on ghost crab activity, we collected sand from every fourth transect using a 2.5-cm diameter PVC pipe sunk 30 cm vertically into the sand, 5 m from the dune edge along the center of the transect. Sand was stored in plastic bags and later oven-dried for 24 h, then sifted using USA standard sieves ranging from 4750 to 63 μm . We decreased the mesh size of each sieve until all sand grains were categorized by size. We weighed the sand in each category using a scale accurate to 1 mg and used proportions of total sample weight in the program GRADISTAT (Blott and Pye 2001) to calculate mean sand grain size and sorting coefficient (SD) using the geometric graphical method described in Folk (1966).

Land Cover.—We used 2003 land cover maps created by Dynamac Corp., Kennedy Space Center, to quantify land cover variables. Edge delineation was accurate to within 5 m for gross land cover types (e.g., anthropogenic vs. natural cover edge) and to within 30 m for ecotones with gradual transitions (e.g., upland scrub to wetland scrub). Using ArcGIS 9.2, we created 200 m dia. buffers around each transect and calculated area and edge for each cover type, excluding beach and open ocean, within each buffer. We calculated several additional landscape variables that may be relevant for raccoons, including total edge (sum of the lengths of the edges between cover types within each buffer), coastal strand edge (sum of the lengths of the edges of coastal strand, the dominant land cover type), water edge (sum of the lengths of edges of all water cover types, excluding open ocean), edge/area (total edge divided by total area of all cover types), and habitat diversity (Shannon's Index): $H' = \sum \frac{n_i}{N} \ln \frac{N}{n_i}$, where n_i is the area of cover type i and N is total area (Morrison et al. 1998).

Nest Predation

To quantify egg predation we randomly selected 2 freshly deposited nests per 1.6 km section of beach during peak nesting in July 2007 (selected nests were >100 m apart). We located these nests during deposition (or the morning after deposition), excavated eggs to determine clutch size, and reburied each in its original nest chamber (Barton and Roth 2008). Egg fate is unaffected by this activity if eggs are handled within 12 h of deposition (Florida Fish and Wildlife Conservation Commission 2007). Some nests were washed out or marks were lost, so to supplement the sample size we selected the nearest nest to each transect laid between 15 July and 15 August, 2007. All nests selected were >100 m apart and within 100 m of a transect. We excavated nests after a 70-d incubation period or within one week of hatchling emergence, and

recorded the number of hatched and unhatched eggs and the number of eggs preyed on by each predator. Egg fates were determined using procedures described in Bouchard & Bjorndal (2000), and each egg was categorized as hatched (including hatchlings remaining in the nest), unhatched (including pipped), or preyed on by ghost crabs.

Data Analyses

We sampled the same transects throughout the nesting season. Thus, we used repeated measures analysis of variance (ANOVA) to test the effect of month on ghost crab burrow density and raccoon activity. When data failed to meet assumptions of sphericity, we adjusted degrees of freedom using the Greenhouse-Geisser correction (Keselman et al. 1996). We used univariate regression to compare ghost crab burrow density and raccoon activity to cumulative marine turtle nests each month. We also tested the relationships each month between ghost crab burrow diameter and raccoon activity, and raccoon activity and density of potentially hatching nests. We recorded ghost crab burrow density and diameter from Apr.-Oct., raccoon activity from May-Oct., and nest density from Apr.-July. Raccoon activity and ghost crab burrow density were square root transformed for analyses by month.

We compared habitat edge and diversity adjacent to the beach between areas developed for recreation and undeveloped backcountry using independent sample t-tests. For each transect we calculated mean ghost crab density, mean raccoon activity, and variance in raccoon activity over the entire season and compared mean predator activity (independent sample t-test) and variance in raccoon activity (Mann-Whitney U test) between developed and undeveloped beach.

We assessed alternative general linear models of the primary dependent variables (mean raccoon total track length, mean density of ghost crab burrows, mean ghost crab burrow diameter, ghost crab egg predation) and natural and anthropogenic habitat variables. Where

necessary, data were transformed to meet the assumptions of statistical tests. We excluded variables with correlations >0.60 to avoid collinearity. We used Akaike's Information Criterion (AIC) values to select the most informative general linear and multiple regression models (Burnham and Anderson 2002).

Ghost Crab Density.—We calculated density of ghost crab burrows (burrows/m²) on each transect for each subsampling event and averaged all subsamples. We tested relationships between ghost crab density and marine turtle nest density, distance to nearest boardwalk, mean and SD sand grain size (location), width of the beach above high tide mark (beach width), and raccoon activity.

Raccoon Activity.—Our index of raccoon activity was total raccoon track length (sum of lengths of all tracks on a transect), which did not require distinguishing among individual tracks present on transects. For each transect, we averaged total track length for each sampling period. We included location (distance along the beach from the northern park boundary) in all models to account for spatial autocorrelation among transects. The most complex model included location, coastal strand edge (log-transformed), habitat edge/area, habitat diversity (Shannon Index), and distance to nearest boardwalk. The full model was compared to models of lesser complexity created through stepwise exclusion of variables.

Nest Predation.—Using all nest data, we compared number of eggs preyed on by ghost crabs with number of hatched eggs and with number of unhatched eggs that were not preyed on. A negative relationship between number of hatched eggs and number consumed by ghost crabs could either mean that ghost crabs decreased hatching success (predation) or that when a greater number of eggs failed to hatch for other reasons, more of them were consumed by ghost crabs (scavenging). To test whether egg damage by ghost crabs indicated predation or scavenging, we

compared number of eggs that failed to hatch for any reason (undeveloped or preyed upon) with the proportion of those eggs preyed on by ghost crabs. Since nest predation by raccoons obscures predation by ghost crabs, we excluded nests affected by raccoons in analyses of egg predation by ghost crabs. To investigate other variables that may affect ghost crab predation, we used the nearest nests within 100 m of a transect where predator activity was monitored and averaged across the incubation period for each nest. We then tested the relationship between the number of eggs preyed on by ghost crabs and ghost crab density, density of adult ghost crab burrows (>23 mm diameter), and raccoon activity on the nearest transect during the incubation period for each nest.

We assumed a significance level of $\alpha = 0.05$. Results are presented as mean \pm SE.

Results

Marine turtles laid 3,627 nests on CANA from April-October, 2007, with an average of 584.1 ± 220.8 nests/month. Peak nesting occurred in July (1496 nests). Likewise, activity of both predators varied temporally (Figure 1.1) and spatially (Figure 1.2). Raccoons were much more abundant than any other mammal recorded (Figure 1.3).

Ghost Crab Burrow Density and Size

Ghost crab burrow density differed significantly among months (repeated measures ANOVA, $F_{4,4,362.4} = 47.64$, $P < 0.001$) and was best described by a cubic model ($F_{1,82} = 111.75$, $P < 0.001$). Ghost crabs were most abundant in April and May, declined from May – August, and increased slightly at the end (Figure 1.1). Ghost crab burrow density decreased with increasing raccoon activity only in June (Figure 1.4; $F_{1,94} = 28.67$, $P < 0.001$); burrow density was unrelated to raccoon activity in May ($F_{1,94} = 0.01$, $P = 0.91$), July ($F_{1,94} = 0.34$, $P = 0.56$), August ($F_{1,94} = 0.62$, $P = 0.43$), September ($F_{1,81} = 0.35$, $P = 0.56$), and October ($F_{1,94} = 0.14$, $P = 0.71$). Ghost

crab density was also unrelated to marine turtle nest density each month: April ($F_{1,91} = 0.17$, $P = 0.68$), May ($F_{1,94} = 2.60$, $P = 0.11$), June ($F_{1,94} = 0.49$, $P = 0.49$), and July ($F_{1,94} = 0.53$, $P = 0.47$).

Density of adult ghost crab burrows (≥ 23 mm) also differed significantly among months ($F_{1,82} = 24.121$, $P < 0.001$). Adult ghost crab density decreased with increasing raccoon activity in June ($r^2 = 0.106$, $F_{1,94} = 11.11$, $P = 0.001$), increased with increasing raccoon activity in September ($r^2 = 0.058$, $F_{1,79} = 11.11$, $P = 0.001$), and was unrelated to raccoon activity in May ($r^2 = 0.0$, $F_{1,94} = 0.15$, $P = 0.90$), July ($r^2 = 0.002$, $F_{1,94} = 0.22$, $P = 0.64$), August ($r^2 = 0.0$, $F_{1,94} = 0.39$, $P = 0.53$), and October ($r^2 = 0.01$, $F_{1,94} = 1.08$, $P = 0.30$). Ghost crab burrow diameter differed significantly among months ($F_{4.4,363.7} = 5.679$, $P < 0.001$), decreasing linearly ($F_{1,82} = 16.579$, $P < 0.001$). When we analyzed separately each month using linear regression, mean burrow diameter increased with increasing raccoon activity in September ($r^2 = 0.096$, $F_{1,79} = 8.39$, $P = 0.005$), but they were unrelated in May ($r^2 = 0.0$, $F_{1,94} = 0.17$, $P = 0.90$), June ($r^2 = 0.006$, $F_{1,94} = 0.60$, $P = 0.44$), July ($r^2 = 0.009$, $F_{1,94} = 0.81$, $P = 0.37$), August ($r^2 = 0.007$, $F_{1,94} = 0.69$, $P = 0.41$), or October ($r^2 = 0.015$, $F_{1,94} = 1.39$, $P = 0.24$).

To determine spatial effects on ghost crab density, we averaged burrow densities on each transect across all sampling days. Ghost crab burrow density was unrelated to number of marine turtle nests ($r^2 = 0.013$, $F_{2,94} = 1.24$, $P = 0.27$), loggerhead nests ($r^2 = 0.020$, $F_{2,94} = 1.90$, $P = 0.171$), nests laid within the two previous nights (new nests) ($r^2 = 0.018$, $F_{2,94} = 1.70$, $P = 0.20$), or new loggerhead nests ($r^2 = 0.012$, $F_{2,94} = 1.13$, $P = 0.29$). Ghost crab burrow density was related quadratically to distance to nearest boardwalk ($F_{3,93} = 6.49$, $P < 0.002$; Figure 1.5a, Table 1.1). Splitting the analysis between transects in the north and south end of CANA highlighted a potential interaction between location and distance to boardwalk. Ghost crab burrow density

increased quadratically with increasing distance from boardwalks in the north ($F_{3,45} = 19.86$, $P < 0.001$; Figure 1.5b) and decreased quadratically with distance to boardwalks in the south ($F_{3,45} = 10.33$, $P < 0.001$, Figure 1.5c).

Ghost crab burrow density decreased logarithmically as sand became less sorted ($r^2 = 0.285$, $F_{2,22} = 8.78$, $P = 0.007$) and decreased with increasing grain size ($F_{2,22} = 10.02$, $P = 0.004$; Figure 1.6). Sand grain size and sorting (σ) were correlated with each other ($r = 0.438$, $P = 0.032$) and location was highly correlated with both size ($r = -0.832$, $P < 0.001$) and sorting ($r = -0.774$, $P < 0.001$; Figure 1.7). Thus, we included location in model selection as a proxy for sand characteristics. Ghost crab burrow density increased with location (distance from the northern park boundary) ($F_{2,94} = 87.38$, $P < 0.001$; Figure 1.8a). The same pattern was observed in adult (≥ 23 mm burrow width) ($r^2 = 0.206$, $F_{2,94} = 24.45$, $P < 0.001$) and juvenile ghost crabs ($r^2 = 0.483$, $F_{2,94} = 87.95$, $P < 0.001$). The relationship between ghost crab burrow density and beach width was described best by a quadratic function ($F_{3,93} = 7.39$, $P = 0.001$; Figure 1.8b, Table 1.1). Beach width was correlated with location ($r = -0.205$, $P = 0.045$) and distance to boardwalk ($r = -0.302$, $P = 0.003$). Ghost crab burrow density was unrelated to raccoon activity ($F_{2,94} = 3.35$, $P = 0.070$; Figure 1.9a) but density of reproductive ghost crabs (≥ 23 mm) decreased with increasing raccoon activity ($F_{2,94} = 4.16$, $P = 0.044$; Figure 1.9b). Mean ghost crab burrow density was best explained by the overall multiple regression model including location, distance to nearest boardwalk (quadratic), and raccoon activity as independent variables ($F_{4,91} = 33.00$, $P < 0.001$; Table 1.2). This model was better than all other models, including those that included an interaction between location and distance to boardwalk (Table 1.2).

We also assessed models to explain ghost crab burrow density in June, the only month in which burrow density was negatively related to raccoon activity. June ghost crab burrow density

increased with increasing distance from the northern park boundary (location; $r^2 = 0.489$, $F_{2,94} = 90.00$, $P < 0.001$, $\beta_0 = 0.153$, $\beta_1 = 9.4 \times 10^{-6}$), had a quadratic relationship with beach width ($r^2 = 0.145$, $F_{2,94} = 7.90$, $P = 0.001$, $\beta_0 = -0.152$, $\beta_1 = 0.092$, $\beta_2 = -0.004$), and increased with increasing distance to the nearest boardwalk ($r^2 = 0.150$, $F_{2,94} = 16.53$, $P < 0.001$, $\beta_0 = 0.280$, $\beta_1 = 1.9 \times 10^{-5}$). June ghost crab burrow density was best explained by the overall multiple regression model that included location, beach width, distance to nearest boardwalk, and mean raccoon activity ($F_{5,90} = 41.53$, $P < 0.001$; Table 1.3). The contribution of raccoon activity to the model was nearly as great as that of location and distance to boardwalk, the two most important variables in the overall model for ghost crab density (Tables 1.2, 1.3).

Mean ghost crab burrow diameter increased significantly with increasing distance from the northern park boundary (i.e., decreasing mean and SD sand grain size; $F_{2,94} = 16.27$, $P < 0.001$; Figure 1.10) but was not related to beach width ($r^2 = 0.000$, $F_{2,94} = 0.04$, $P = 0.84$), distance to the nearest boardwalk ($r^2 = 0.002$, $F_{2,94} = 0.22$, $P = 0.62$), or raccoon activity ($r^2 = 0.000$, $F_{2,94} = 0.02$, $P = 0.86$). Burrow diameter was positively correlated with ghost crab burrow density ($r = 0.440$, $P < 0.001$).

Raccoon Activity

Raccoon activity (total track length) increased through most of the nesting season and decreased at the end, and differed significantly among months ($F_{3,9,317.7} = 33.822$, $P < 0.001$), with a relationship best described by a quadratic function ($F_{1,82} = 156.461$, $P < 0.001$; Figure 1.1). To examine the effect of marine turtle nesting activity on raccoon activity over time, we used univariate regression to compare mean monthly raccoon activity to cumulative nests per transect per month. Raccoon activity was unrelated to the number of marine turtle nests in May ($r^2 = 0.002$, $F_{1,94} = 0.15$, $P = 0.70$), June ($r^2 = 0.003$, $F_{1,94} = 0.25$, $P = 0.62$), or July ($r^2 = 0.035$,

$F_{1,94} = 3.44$, $P = 0.07$). Raccoon activity peaked near the approximate peak in hatching for all marine turtle nests (Figure 1.1), but was unrelated to density of potentially hatching nests (2 mo. lag time) in July ($r^2 = 0.018$, $F_{1,94} = 1.74$, $P = 0.19$), August ($r^2 = 0.01$, $F_{1,94} = 0.91$, $P = 0.34$), or September ($r^2 = 0.037$, $F_{1,94} = 3.09$, $P = 0.08$). Few nests were laid in April so data did not meet assumptions of normality.

To determine spatial effects on raccoon activity, we averaged raccoon total track length on each transect across all sampling days. Raccoon activity was not related to number of marine turtle nests ($r^2 = 0.022$, $F_{94} = 2.07$, $P = 0.15$), loggerhead nests ($r^2 = 0.001$, $F_{94} = 0.13$, $P = 0.72$), new nests ($r^2 = 0.019$, $F_{94} = 1.80$, $P = 0.18$), or new loggerhead nests ($r^2 = 0.000$, $F_{94} = 0.02$, $P = 0.90$). Based on the distribution of mean number of cars in the parking lot nearest to each transect (Figure 1.11), we split analyses of the effects of distance to nearest boardwalk into two categories: at parking lots with <10 or >10 cars. At parking lots with <10 cars, raccoon activity decreased exponentially with increasing distance to nearest boardwalk ($F_{2,39} = 13.27$, $P = 0.001$; Figure 1.12a). At parking lots with >10 cars, raccoon activity was best explained by a cubic function of distance to nearest boardwalk ($F_{4,51} = 12.43$, $P < 0.001$; Figure 1.12b). There was little overlap in distance to nearest boardwalk between the two categories, however, so we excluded the categorization in the overall spatial relationship between raccoon activity and recreation. This relationship was best described by a cubic function relating raccoon activity to distance to the nearest boardwalk ($F_{4,92} = 7.67$, $P < 0.001$), which was selected over competing models using AIC (Table 1.1). Raccoon activity decreased up to about 2 km from the nearest boardwalk and then started to increase (Figure 1.12c). Overall raccoon activity was greater on transects >2000 m from the nearest boardwalk ($t'_{93,2} = -2.98$, $P = 0.004$; Figure 1.13). Variance

in raccoon activity was also greater in the backcountry (median = 38.16) than on segments of beach developed for recreation (median = 15.43: *Mann-Whitney U* = 448.0, $P < 0.001$).

Raccoon activity (total track length) increased with increasing habitat edge ($r^2 = 0.134$, $F_{2,94} = 14.52$, $P < 0.001$, $\beta_0 = -12.558$, $\beta_1 = 2.056$), habitat edge/area ($F_{2,94} = 15.03$, $P < 0.001$), coastal strand edge ($F_{2,94} = 12.01$, $P = 0.001$), and habitat diversity (H') ($F_{2,94} = 5.34$, $P = 0.023$) (Figure 1.14). Raccoon activity was unrelated to water edge ($r^2 = 0.008$, $F_{2,94} = 0.72$, $P = 0.40$). Habitat edge ($t_{2,94} = -3.856$, $P < 0.001$), coastal strand edge ($t_{2,94} = -7.153$, $P < 0.001$), and edge/area ($t_{2,94} = -4.394$, $P < 0.001$) were significantly greater on transects >2000 m from recreation ($n = 43$) than on sections of beach developed for recreation. Habitat diversity followed the same trend but was not significant ($t'_{79,0} = -1.774$, $P = 0.080$). Distance to boardwalk was correlated with coastal strand edge ($r = 0.596$, $P < 0.001$). Habitat edge was correlated with edge/area ($r = 0.946$, $P < 0.001$), coastal strand edge ($r = 0.404$, $P < 0.001$), and habitat diversity ($r = 0.714$, $P < 0.001$). Edge/area was also correlated with coastal strand edge ($r = 0.498$, $P < 0.001$) and habitat diversity ($r = 0.560$, $P < 0.001$). Significant independent variables with correlations < 0.6 were retained in multiple regression models, i.e. distance to nearest boardwalk, edge/area, coastal strand edge, and habitat diversity. Overall raccoon activity was best explained by the multiple regression model including distance to boardwalk (cubic), coastal strand edge (ln), habitat diversity, and location ($F_{6,89} = 8.663$, $P < 0.001$; Table 1.4).

Loggerhead Hatching Success and Egg Predation

We monitored 102 loggerhead turtle nests, 25 of which washed out with high tides or lost their marks. Initial clutch sizes determined for 24 of these nests (counted immediately after laying) averaged 107.0 ± 4.8 eggs. After incubation, inventoried clutch size of these pre-counted nests was 100.3 ± 4.6 , with an average of 6.7 ± 1.8 eggs missing (max = 42), presumably removed by

ghost crabs. Two of these pre-counted nests were preyed on by ghost crabs within 12 h of deposition, and one pre-counted clutch was completely consumed by raccoons after partial predation by ghost crabs. Raccoon predation occurred in one previously unhandled nest where ghost crabs also had preyed on eggs. However, the order of predation was unknown.

Mean clutch size of unhandled nests (104.4 ± 2.9 , $n = 52$) did not differ significantly from pre-counted nests at inventory ($t_{74} = 0.762$, $P = 0.45$). Handled and unhandled nests did not differ in mean number of eggs that hatched ($t_{72} = 0.715$, $P = 0.64$), were preyed on by ghost crabs ($t_{72} = 0.459$, $P = 0.65$), or failed to hatch for any other reason ($t_{72} = 0.841$, $P = 0.40$), so all nests were pooled for further analyses. Average inventoried clutch size was 102.9 ± 2.5 ($n = 76$): 48.4 ± 3.6 eggs hatched, 46.1 ± 3.5 hatchlings successfully emerged from nests, 34.9 ± 3.1 eggs remained pipped or intact and unhatched, raccoons preyed on 1.3 ± 1.0 eggs. Ghost crabs preyed on 17.7 ± 2.1 eggs per nest ($n = 74$). In total, we recorded the fates of 7,837 eggs: 3,632 (0.463) hatched, 3,502 (0.447) produced hatchlings that emerged from nests, at least 1,390 (0.177) were preyed on by ghost crabs, and 101 (0.013) potentially were preyed on by raccoons (unknown previous predation by ghost crabs). The ratio of successfully hatched eggs to eggs preyed on by ghost crabs was $< 2.5:1$. With average clutch size estimated to be 102.9 eggs, 2572.5 (0.246) of the estimated 10,445.5 eggs monitored were washed out, which likely occurred before hatchling emergence. When washed out nests were taken into account, hatching success declined to 33.5%.

We assessed the relationships between egg fate and predator activity for 59 nests within 100 m of a transect. Two of these transects had two nests within 100 m, so data for those nests were averaged. Number of eggs preyed on by ghost crabs was not related to ghost crab burrow density ($r^2 = 0.008$, $F_{2,55} = 0.45$, $P = 0.51$) or reproductive ghost crab burrow density ($r^2 = 0.002$, $F_{2,55} = 0.09$, $P = 0.77$) during egg incubation. Number of hatched eggs decreased with increasing

number of eggs preyed on by ghost crabs ($F_{2,72} = 21.58, P < 0.001$; Figure 1.15a) but predation was unrelated to number of unhatched eggs ($F_{2,72} = 1.35, P = 0.25$; Figure 1.15b). Likewise, the proportion of unsuccessfully hatched eggs preyed on by ghost crabs was unrelated to the number of all eggs that did not hatch ($F_{2,72} = 0.76, P = 0.36$; Figure 1.15c). When averaged across egg incubation, raccoon activity increased marginally with increasing number of eggs preyed on by ghost crabs ($F_{2,72} = 3.76, P = 0.058$; Figure 1.16).

Discussion

Ghost crab activity was primarily affected by human recreational activity and location (sand grain characteristics), and including raccoon activity improved the overall model explaining ghost crab activity. Raccoon activity was affected by human recreational activity, habitat diversity (H'), and length of coastal strand edge. Neither ghost crabs nor raccoons responded to spatial variation in marine turtle nesting activity, but raccoon activity tended to increase with increasing egg predation by ghost crabs (see Figure 1.17, path of coefficients among all variables).

Although we failed to support our overall hypothesis that loggerhead egg predation was primarily affected by changes in ghost crab density, monitoring limitations may have affected our ability to detect a relationship between ghost crab density and predation. Ghost crab densities on transects up to 100 m away may not be relevant to predation rates in individual nests, because we observed high local variation in density. Also, we had very few samples of ghost crab density during the incubation period of some nests. However, large ghost crabs feed at a higher trophic level than small crabs, suggesting large crabs consume more marine turtle eggs (Barton and Roth 2007) and on CANA ghost crab burrow diameter increased with increasing burrow density. Thus, more refined monitoring may find that egg predation is density dependent.

Through our analysis of egg predation we were able to clarify the effect of ghost crabs on loggerhead hatching success. We found a negative relationship between the number of eggs destroyed or consumed by ghost crabs and the number of hatched eggs. If ghost crab activity were primarily compensatory, we would expect to find a positive relationship between the proportion of unhatched eggs affected by ghost crabs and the total number of unhatched eggs (undeveloped or preyed on by ghost crabs). We found no such association, which suggests ghost crabs are predators of potentially viable eggs. This evidence is supported by the detection of ghost crab predation in freshly laid nests.

Interestingly, we did find a relationship between raccoon activity and egg predation, but it was not the indirect negative relationship we predicted. Raccoon activity increased with increasing egg predation, suggesting raccoons are attracted to nests preyed on by ghost crabs, particularly nests with high rates of egg predation. This finding supports the prediction that ghost crabs facilitate egg predation by raccoons (Barton and Roth 2008) and is supported by experimental data (see Chapter 2).

Although egg predation by raccoons was rare among the nests we inventoried (2/76 nests), we only selected nests screened before raccoon predation occurred. Interestingly, the two screened nests preyed on by raccoons were also preyed on by ghost crabs, and in one case raccoon predation was definitely secondary. Egg predation by raccoons is common in the United States and has resulted in the loss of up to 95% of nests on some beaches (Stancyk 1982). Our data suggest ghost crabs contribute substantially to egg predation, even when densities are potentially depressed by raccoons, and their effects may have been underestimated previously (Bouchard and Bjorndal 2000, Barton and Roth 2008) when nests were secondarily preyed on by raccoons. When we inventoried nests to determine egg fates in clutches of known size, we

discovered that some eggs were often missing (max = 42), which suggests they were removed by predators. We often observed egg shells removed from incubating nests when the only apparent predator sign was ghost crab burrows, but egg shells are often scattered before nests are inventoried. Ghost crab behavior, coupled with nest monitoring limitations, may further contribute to underestimation of their egg predation. We determined that counting eggs within 12 h of clutch deposition had no effect on loggerhead hatching success and knowledge of initial clutch size is necessary for accurately estimating egg predation by ghost crabs.

Although we found no relationship between ghost crab density and egg predation, we were able to construct simple models describing the activity of marine turtle egg predators. These models could help improve the efficiency of marine turtle management by identifying landscape characteristics and environmental features that potentially alter the susceptibility of eggs to predation. The spatial distribution of ghost crabs was affected primarily by human recreational activity and sand characteristics. The effect of recreation appeared to be mediated by location, since ghost crab density in the southern half of CANA responded positively to proximity to boardwalks, while the response in the north was negative (Figure 1.10). Although the interaction between distance to nearest boardwalk and location explained nearly as much variation in ghost crab burrow density as did raccoon activity, it did not improve the overall model (Table 1.2). Ghost crab density initially decreased with increasing distance to recreation, suggesting a positive effect of recreation, but it then increased, suggesting recreation has localized effects that may be outweighed by underlying environmental variation (i.e., sand characteristics).

Ghost crab density increased with increasing distance from the northern park boundary, as mean and SD sand grain size decreased. Turra et al. (2005) associated fine sands and poor sorting with low densities of ghost crabs, but their findings were confounded by recreational

activities. Similarly, we found higher ghost crab densities in well-sorted sands, but accompanied by small mean grain size. Turra et al. (2005) associated smaller burrows with coarse sand and we found smaller mean diameters in coarse sand, but we found higher densities of adult and juvenile ghost crab burrows in fine sand. Ghost crabs feed primarily on filter-feeders (Wolcott and Wolcott 1984) and likely derive little benefit from unpredictable human resources on the beach. Sand characteristics likely directly affect ghost crab density and are good indicators of tidal characteristics that affect ghost crabs and their prey.

While sand characteristics and recreation were consistently strong factors affecting ghost crab density, beach width and raccoon activity were more limited, with strong effects only in June. The differences between the overall ghost crab model (Table 1.2) and the model for burrow density in June (Table 1.3) likely indicate important temporal variation in predator behavior and environmental variables such as tides. In June, ghost crabs initially increased in density as the beach became wider, but eventually decreased with wider beaches. Narrow beaches are an unstable environment, subject to erosion and high tides, both potentially detrimental to crabs. Ghost crabs prefer to burrow in moist sand near the high tide mark to retain gill water (Valero-Pacheco et al. 2007). Thus, lower densities on wide beaches may result from patterns in burrow selection due to the disproportionately large amount of dry sand.

Ghost crab burrow density declined sharply between May and July (Figure 1.1) and was strongly affected by raccoons in June (Figure 1.8). Raccoon activity in June affected ghost crab density nearly as much as location and recreation, the two most important variables in the overall spatial model (Table 1.2). Raccoons also appeared to target large ghost crabs in June, which may have contributed to suppressing overall ghost crab density by reducing reproduction. We observed raccoons hunting ghost crabs and evidence of hunting (i.e., chases, dug up sand or

burrows, partially eaten ghost crabs) early in the marine turtle nesting season, but rarely later, which suggests raccoons might switch to more abundant prey. Although the interaction was weak at the transect level, the temporal relationship between raccoon activity and ghost crab density appeared to be strong and negative when averaged across the entire beach (Figure 1.1).

It can be difficult to determine how landscape variables affect the distribution of generalist consumers like raccoons (Crooks 2002) but raccoon activity in our study was clearly related to recreation, habitat diversity, and edge of the dominant cover, coastal strand. These relationships were not surprising, because raccoons are often associated with human food sources (Prange et al. 2004), habitat edges, or diverse cover (Oehler and Litvaitis 1996, Dijak and Thompson 2000, Barding and Nelson 2008).

The lower inflection point in the cubic relationship between raccoon activity and distance to nearest boardwalk was approximately 2000 m, which corresponded closely with the division between segments of developed beach, fully-accessible to recreation, and undeveloped beach only accessible to permit-holders. Both mean and variance of raccoon activity were lower near low diversity cover and centers of human recreation, suggesting these segments of beach provided more stable, but lower quality resources than those found near diverse natural cover. Raccoon activity was concentrated near recreation access points, suggesting raccoons were drawn to human-subsidized resources. However, these resources were not of great enough value to stimulate a numerical response in the population. Trash on CANA is disposed of in lidded containers inaccessible to raccoons except on high use days when they are overflowing, so raccoon typically only consume trash or fishing bait left on the beach. Mean and variance in raccoon activity were greater on undeveloped beach and increased with increasing habitat

diversity and length of coastal strand edge. Increased variance in activity on undeveloped beach likely reflected opportunistic foraging in a higher density segment of the population.

Although raccoons did not respond numerically to human recreational activity, their activity was concentrated and less variable near recreation areas, so nests and hatchlings near boardwalks may be more vulnerable to predation. We did observe hatchlings preyed on by raccoons near boardwalks on Playalinda Beach. Neither predator altered activity in response to marine turtle nesting activity, but when averaged for the entire beach, raccoon activity increased with increasing nesting activity, with a lag the approximate length of egg incubation. We observed no relationship between raccoon activity and estimated density of hatching nests on individual transects in repeated measures analysis. However, incubation is highly variable and the presence of hatchlings is ephemeral, so hatching activity was not likely to have strong effects on raccoon activity on individual transects, particularly since activity was averaged for each month. Despite being screened from eggs, raccoon activity increased on the beach during peak hatch, increasing the likelihood of encountering hatchlings.

Management Implications

Raccoon activity and ghost crab density can be coarsely predicted using simple models constructed from easily attainable environmental measurements. Once developed, these models may reduce the effort necessary to continuously monitor predator activity and can aid managers in focusing predator monitoring or removal efforts to increase the efficiency of costly management. These models may be particularly beneficial in more heterogeneous environments with more anthropogenic influence. Our data suggest there is important temporal variation in the environmental factors affecting predators and the strength of predator-predator interactions. For example, ghost crabs were strongly affected by raccoon activity and beach width in June, but

neither was significant in the overall spatial model. Ghost crabs and raccoons are substantial egg predators independently, but their combined predation may be enhanced by indirect, facilitated predation. Therefore, managers should focus on strategies to reduce the direct effects of both predators while simultaneously reducing the effect of indirect interactions. Managers interested in efficiently minimizing marine turtle egg predation should time raccoon removal efforts so raccoons can control ghost crab density.

Screening nests is likely an effective method to reduce egg predation by raccoons on CANA, because observed rates of nest predation were quite small. However, the effect of unmanaged raccoon populations on hatchlings remains unclear and screened nests laid during the peak in nesting activity from July to August were strongly affected by high tides. A larger proportion of eggs were washed out by high tides than were destroyed by either predator, and the proportion of eggs that washed out was only exceeded by the proportion of eggs that did not hatch due to reasons other than raccoon or ghost crab predation. A portion of the remaining eggs did not hatch due to tidal inundation, further increasing the effect of tides. Screening and marking nests could increase the likelihood of washout by increasing water turbulence and sand erosion. Screening may be innocuous, but given the high proportion of washed out nests on CANA, the assumption should be validated experimentally. Screens not only affect the interaction between nests and predators, but nests and the physical environment, which may have stronger effects on hatching success than predation.

Ghost crab density declined through the majority of the 2007 nesting season on Canaveral National Seashore (CANA). Off-road vehicles (ORVs) may have strong effects on density of ghost crabs and other intertidal invertebrates, particularly if used in the intertidal zone at night (Wolcott and Wolcott 1984), and may have broader community effects (Schlacher et al. 2008).

Marine turtle management activities on CANA required nightly use of ORVs, which was primarily restricted to the high intertidal to avoid dune erosion and disturbance of nesting birds (pers. comm., J. Stiner, NPS, Canaveral National Seashore), but ghost crabs were often inadvertently killed (pers. obs.). The upper intertidal zone is used extensively by ghost crabs, particularly adults (Turra et al. 2005, Valero-Pacheco et al. 2007), so while screening nests may reduce egg predation by raccoons, managers are indirectly reducing ghost crab density by maintaining raccoon populations and directly manipulating ghost crab density through nighttime ORV use. The effects may be sustained outside the nesting season due to increased predation and inadvertent killing of potentially reproductive crabs.

We found substantial egg predation by ghost crabs, but our results do not suggest marine turtle egg predation would be mitigated by reducing ghost crab density. We have no ecological explanation for the lack of a relationship between egg predation and ghost crab density, so it may be a result of monitoring limitations. However, ghost crabs are top predators in a filter-feeding food chain (Wolcott 1978) and are preyed on by birds and mammals. Thus, changes in ghost crab density could have cascading effects in the intertidal community (Schlacher et al. 2008), and potential effects in terrestrial communities. Although ghost crabs are substantial predators of marine turtle eggs, the consequences of changes in ghost crab density are unknown, so further experimentation and observational studies are necessary to inform effective ghost crab and marine turtle management.

Marine turtles have delayed sexual maturity (Parham and Zug 1997), so the effects of management activities on nesting beaches may not be observed for decades. Therefore, it is critically important to minimize the broader ecological consequences of marine turtle

management, by adapting management based on the results of experiments with a community emphasis (Ratnaswamy and Warren 1998).

Literature Cited

- Antworth, R. L., D. A. Pike, and J. C. Stiner. 2006. Nesting ecology, current status, and conservation of sea turtles on an uninhabited beach in Florida, USA. *Biological Conservation* **130**:10-15.
- Arim, M. and P. A. Marquet. 2004. Intraguild predation: a widespread interaction related to species biology. *Ecology Letters* **7**:557-564.
- Barding, E. E. and T. A. Nelson. 2008. Raccoons use habitat edges in northern Illinois. *American Midland Naturalist* **159**:394-402.
- Barros, F. 2001. Ghost crabs as a tool for rapid assessment of human impacts on exposed sandy beaches. *Biological Conservation* **97**:399-404.
- Barton, B. T. and J. D. Roth. 2007. Raccoon removal on sea turtle nesting beaches. *Journal of Wildlife Management* **71**:1234-1237.
- Barton, B. T. and J. D. Roth. 2008. Implication of intraguild predation for sea turtle nest protection. *Biological Conservation*. doi:10.1016/j.biocon.2008.06.013
- Blott, S. J. and K. Pye. 2001. GRADISTAT: A grain size distribution and statistics package for the analysis of unconsolidated sediments. *Earth Surface Processes and Landforms* **26**:1237-1248.
- Boarman, W. I. 2003. Managing a subsidized predator population: Reducing common raven predation on desert tortoises. *Environmental Management* **32**:205-217.
- Bouchard, S. S. and K. A. Bjorndal. 2000. Sea turtles as biological transporters of nutrients and energy from marine to terrestrial ecosystems. *Ecology* **81**:2305-2313.
- Burnham, K. P. and D. R. Anderson. 2002. Model selection and multimodel inference : a practical information-theoretic approach. 2nd edition. Springer, New York.
- Carthy, R. R., A. M. Foley, and Y. Matsuzawa. 2003. Incubation environment of loggerhead turtle nests: effects on hatching success and hatchling characteristics. Pages 144-153 in A. B. Bolten and B. E. Witherington, editors. *Loggerhead Sea Turtles*. Smithsonian Institution, Washington, D.C.
- Chamberlain, M. J., J. Austin, B. D. Leopold, and L. W. Burger. 2007. Effects of landscape composition and structure on core use areas of raccoons (*Procyon lotor*) in a prairie landscape. *American Midland Naturalist* **158**:113-122.
- Chan, B. K. K., K. K. Y. Chan, and P. C. M. Leung. 2006. Burrow architecture of the ghost crab *Ocypode ceratophthalma* on a sandy shore in Hong Kong. *Hydrobiologia* **560**:43-49.
- Crooks, K. R. 2002. Relative sensitivities of mammalian carnivores to habitat fragmentation. *Conservation Biology* **16**:488-502.
- Crooks, K. R. and M. E. Soule. 1999. Mesopredator release and avifaunal extinctions in a fragmented system. *Nature* **400**:563-566.
- Danielson, W. R., R. M. DeGraaf, and T. K. Fuller. 1997. Rural and suburban forest edges: effect on egg predators and nest predation rates. *Landscape and Urban Planning* **38**:25-36.

- Davis, G. E., and Whiting, M.C. 1977. Loggerhead sea turtle nesting in Everglades National Park, Florida, USA. *Herpetologica* **33**:18-28.
- Dijak, W. D. and F. R. Thompson. 2000. Landscape and edge effects on the distribution of mammalian predators in Missouri. *Journal of Wildlife Management* **64**:209-216.
- Engeman, R. M., R. E. Martin, B. Constantin, R. Noel, and J. Woolard. 2003. Monitoring predators to optimize their management for marine turtle nest protection. *Biological Conservation* **113**:171-178.
- Engeman, R. M., R. E. Martin, H. T. Smith, J. Woolard, C. K. Crady, S. A. Shwiff, B. Constantin, M. Stahl, and J. Griner. 2005. Dramatic reduction in predation on marine turtle nests through improved predator monitoring and management. *Oryx* **39**:318-326
- Florida Fish and Wildlife Conservation Commission. Nov. 2007. *Marine turtle conservation guidelines*. Florida Fish and Wildlife Conservation Commission, Tallahassee, FL.
- Folk, R. L. 1966. A review of grain-size parameters. *Sedimentology* **6**: 73-93
- Garmestani, A. S. and H. F. Percival. 2005. Raccoon removal reduces sea turtle nest depredation in the ten thousand islands of Florida. *Southeastern Naturalist* **4**:469-472.
- Gehrt, S. D. and W. R. Clark. 2003. Raccoons, coyotes, and reflections on the mesopredator release hypothesis. *Wildlife Society Bulletin* **31**:836-842.
- Gehrt, S. D. and S. Prange. 2007. Interference competition between coyotes and raccoons: a test of the mesopredator release hypothesis. *Behavioral Ecology* **18**:204-214.
- Greenwood, R. J. 1982. Nocturnal activity and foraging of prairie raccoons (*Procyon lotor*) in North Dakota. *American Midland Naturalist* **107**(2):238-243.
- Hannan, L. B., J. D. Roth, L. M. Ehrhart, and J. F. Weishampel. 2007. Dune vegetation fertilization by nesting sea turtles. *Ecology* **88**:1053-1058.
- Holt, R. D. and G. A. Polis. 1997. A theoretical framework for intraguild predation. *American Naturalist* **149**:745-764.
- Keselman, J. C., L. M. Lix, and H. J. Keselman. 1996. The analysis of repeated measurements: A quantitative research synthesis. *British Journal of Mathematical & Statistical Psychology* **49**:275-298.
- Litvaitis, J. A. and R. Villafuerte. 1996. Intraguild predation, mesopredator release, and prey stability. *Conservation Biology* **10**:676-677.
- Morrison, M. L., B. G. Marcot, and R. W. Mannan. 1998. *Wildlife-habitat relationships: concepts & applications*. 2nd edition. University of Wisconsin Press, Madison, WI, USA.
- Negreiros-Fransozo, M. L., A. Fransozo, and G. Bertini. 2002. Reproductive cycle and recruitment period of *Ocypode quadrata* (Decapoda, Ocypodidae) at a sandy beach in southeastern Brazil. *Journal of Crustacean Biology* **22**:157-161.
- Oehler, J. D. and J. A. Litvaitis. 1996. The role of spatial scale in understanding responses of medium-sized carnivores to forest fragmentation. *Canadian Journal of Zoology-Revue Canadienne De Zoologie* **74**:2070-2079.
- Parham, J. F. and G. R. Zug. 1997. Age and growth of loggerhead sea turtles (*Caretta caretta*) of coastal Georgia: An assessment of skeletochronological age-estimates. *Bulletin of Marine Science* **61**:287-304.
- Polis, G. A. and R. D. Holt. 1992. Intraguild Predation - the Dynamics of Complex Trophic Interactions. *Trends in Ecology & Evolution* **7**:151-154.

- Prange, S., S. D. Gehrt, and E. P. Wiggers. 2004. Influences of anthropogenic resources on raccoon (*Procyon lotor*) movements and spatial distribution. *Journal of Mammalogy* **85**:483-490.
- R Development Core Team. 2006. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL <http://www.R-project.org>.
- Ratnaswamy, M. J. and R. J. Warren. 1998. Removing raccoons to protect sea turtle nests: are there implications for ecosystem management? *Wildlife Society Bulletin* **26**:846-850.
- Ratnaswamy, M. J., R. J. Warren, M. T. Kramer, and M. D. Adam. 1997. Comparisons of lethal and nonlethal techniques to reduce raccoon depredation of sea turtle nests. *Journal of Wildlife Management* **61**:368-376.
- Schlacher, T. A., D. Richardson, and I. McLean. 2008. Impacts of off-road vehicles (ORVs) on macrobenthic assemblages on sandy beaches. *Environmental Management* **41**:878-892.
- Soule, M. E., J. A. Estes, J. Berger, and C. M. Del Rio. 2003. Ecological effectiveness: Conservation goals for interactive species. *Conservation Biology* **17**:1238-1250.
- Soule, M. E., J. A. Estes, B. Miller, and D. L. Honnold. 2005. Strongly interacting species. conservation policy, management, and ethics. *Bioscience* **55**:168-176.
- Stancyk, S. E. 1982. Non-human predators of sea turtles and their control. Pages 139-152 in K. A. Bjorndal, editor. *Biology and conservation of sea turtles*. Smithsonian Institution Press, Washington, D.C.
- Steiner, A.J. and Leatherman, S.P., 1981. Recreational impacts on the distribution of ghost crabs *Ocypode quadrata* Fab. *Biological Conservation* **20**, pp. 111–122
- Strachan, P. H., R. C. Smith, D. A. B. Hamilton, A. C. Taylor, and R. J. A. Atkinson. 1999. Studies on the ecology and behaviour of the ghost crab, *Ocypode cursor* (L.) in northern Cyprus. *Scientia Marina* **63**:51-60.
- Turra, A., M. A. O. Goncalves, and M. R. Denadai. 2005. Spatial distribution of the ghost crab *Ocypode quadrata* in low-energy tide-dominated sandy beaches. *Journal of Natural History* **39**:2163-2177.
- Valero-Pacheco, E., F. Alvarez, L. G. Abarca-Arenas, and M. Escobar. 2007. Population density and activity pattern of the ghost crab, *Ocypode quadrata*, in Veracruz, Mexico. *Crustaceana* **80**:313-325.
- Wolcott, T. G. 1978. Ecological role of ghost crabs, *Ocypode qadrata* (Fabricus), on an ocean beach - scavengers or predators. *Journal of Experimental Marine Biology and Ecology* **31**:67-82.
- Wolcott, T. G. and D. L. Wolcott. 1984. Impact of off-road vehicles on macroinvertebrates of a mid-atlantic beach. *Biological Conservation* **29**:217-240.

Table 1.1 Univariate regression model selection using Akaike's Information Criterion (AIC); RSS is residual sum of squares, K is number of parameters, Δ AIC is the difference between each model and the best model, and AIC weight is relative information content. N = 96

Model: Ghost crab density	RSS	K	AIC	ΔAIC	AIC Weights
Distance to boardwalk					
quadratic	0.416	4	-241.95	0.00	0.66
cubic	0.414	5	-240.39	1.56	0.30
linear	0.451	3	-236.14	5.82	0.04
logarithmic	0.470	3	-232.32	9.63	0.01
exponential	0.479	3	-230.33	11.63	0.00
Beach width					
quadratic	0.409	4	-243.57	0.00	0.62
cubic	0.406	5	-242.34	1.23	0.34
linear	0.446	3	-237.29	6.27	0.03
logarithmic	0.455	3	-235.36	8.20	0.01
exponential	0.493	3	-227.54	16.02	0.00
Model: Ghost crab density (June)					
Beach width					
quadratic	1.843	4	-99.04	0.00	0.60
cubic	1.822	5	-98.14	0.90	0.38
linear	2.025	3	-92.02	7.02	0.02
logarithmic	2.067	3	-90.02	9.02	0.01
Model: Raccoon track length					
Distance to boardwalk					
cubic	5.858	5	13.97	0.00	0.64
quadratic	6.079	4	15.52	1.56	0.29
linear	6.394	3	18.38	4.41	0.07
logarithmic	7.036	3	27.56	13.59	0.00

*Ghost crab density = mean ghost crab burrows m^{-2} , raccoon track length = mean raccoon total track length (m), distance to boardwalk = distance to the nearest recreational boardwalk (m), beach width = mean beach width above high tide mark

Table 1.2 Comparison of best models describing ghost crab burrow density (averaged across the 2007 marine turtle nesting season), with models including the interaction between distance to recreation and location. Model selection used Akaike’s Information Criterion (AIC); RSS is residual sum of squares, K is number of parameters, Δ AIC is the difference between each model and the best model, and AIC weight is relative information content. Below are descriptive statistics for the best model and its variable components: P is the statistical significance of the model, parameter estimates are slopes, P_i is the statistical significance of variable i . We summed AIC weights across all models containing an individual variable (i.e., the weight of each variable, given these models). $N = 96$

Model: Ghost Crab Burrows m⁻²	RSS	K	R²	Adj.R²	AIC	ΔAIC	AIC Weights
Competing Models							
location + recreation + raccoon	0.19	6	0.592	0.574	-311.45	0.00	0.244
location + recreation	0.20	5	0.583	0.569	-311.37	0.08	0.234
location + recreation + rec:loc	0.19	6	0.591	0.573	-311.11	0.34	0.205
location + recreation + raccoon + rec:loc	0.19	7	0.595	0.573	-310.18	1.27	0.129
location + recreation + width	0.20	7	0.588	0.566	-308.62	2.83	0.059
location + recreation + raccoon + width	0.19	8	0.596	0.569	-308.47	2.99	0.055
location + recreation + rec:loc + width	0.19	8	0.594	0.567	-308.03	3.42	0.044
location + recreation + raccoon + rec:loc + width	0.19	9	0.599	0.567	-307.17	4.28	0.029
location + raccoon + rec:loc	0.23	5	0.516	0.501	-297.13	14.32	0.000
location + rec:loc	0.24	4	0.503	0.493	-296.60	14.85	0.000
location + raccoon	0.24	4	0.502	0.491	-296.29	15.16	0.000
location	0.25	3	0.482	0.476	-294.51	16.95	0.000
location + raccoon + rec:loc + width	0.23	7	0.522	0.495	-294.23	17.23	0.000
location + raccoon + width	0.23	6	0.507	0.486	-293.35	18.11	0.000
Best Model	R²	P	Parameter Estimate	P_i	Σ AIC Weights		
	0.592	<0.001					
location			$\beta_1=4.376 \times 10^{-6}$	<0.001	1.0000		
recreation			$\beta_1=-1.836 \times 10^{-5}$	0.001	0.9994		
			$\beta_2=2.582 \times 10^{-9}$	<0.001			
raccoon			$\beta_1=-3.904 \times 10^{-3}$	0.16	0.4568		
Excluded Variables							
rec:loc					0.4076		
width					0.1926		

*location = distance from northern park boundary (m), recreation = distance to nearest recreation access boardwalk (m), raccoon = ln mean raccoon total track length (m), rec:loc = interaction between recreation and location, width = mean beach width above high tide mark (m)

Table 1.3 Comparison of models describing ghost crab burrow density (averaged in June). Model selection used Akaike's Information Criterion (AIC); RSS is residual sum of squares, K is number of parameters, Δ AIC is the difference between each model and the best model, and AIC weight is relative information content. Below are descriptive statistics for the best model and its variable components: P is the statistical significance of the model, parameter estimates are slopes, P_i is the statistical significance of variable i . We summed AIC weights across all models containing an individual variable (i.e., the weight of each variable, given these models). $N = 96$

Model: Ghost Crab Density (June)	RSS	K	R^2	Adj.R^2	AIC	ΔAIC	AIC Weights
Competing Models							
location + recreation + raccoon + width	0.65	7	0.698	0.681	-192.82	0.00	0.937
location + recreation + raccoon	0.72	5	0.667	0.656	-187.40	5.41	0.063
location + recreation	0.86	4	0.602	0.593	-172.38	20.44	0.000
location + recreation + width	0.84	6	0.609	0.592	-170.16	22.66	0.000
location + raccoon + width	0.85	6	0.605	0.588	-169.25	23.57	0.000
location + raccoon	0.90	4	0.581	0.572	-167.58	25.23	0.000
location	1.10	3	0.489	0.482	-150.46	42.35	0.000
location + width	1.09	5	0.496	0.480	-147.81	45.01	0.000
recreation + raccoon + width	1.33	6	0.382	0.355	-126.17	66.64	0.000
raccoon + width	1.47	5	0.317	0.295	-118.56	74.25	0.000
recreation + raccoon	1.53	4	0.291	0.276	-116.98	75.84	0.000
recreation + width	1.66	5	0.230	0.205	-107.08	85.73	0.000
raccoon	1.75	3	0.190	0.181	-106.16	86.65	0.000
recreation	1.83	3	0.150	0.141	-101.54	91.28	0.000
width	1.84	4	0.145	0.127	-99.04	93.78	0.000
Best Model	R^2	P	Parameter Estimate	P_i	Σ AIC Weights		
	0.698	<0.001					
location			$\beta_1=8.605 \times 10^{-6}$	<0.001	1.00000		
recreation			$\beta_1=1.567 \times 10^{-5}$	<0.001	0.99999		
raccoon			$\beta_1=-7.167 \times 10^{-2}$	<0.001	0.99995		
width			$\beta_1=4.342 \times 10^{-2}$	0.066	0.93738		
			$\beta_2=-1.345 \times 10^{-3}$	0.15			

*location = distance from northern park boundary (m), recreation = distance to nearest recreation access boardwalk (m), raccoon = ln mean raccoon total track length (m), width = mean beach width above high tide mark (m)

Table 1.4 Comparison of models describing raccoon activity (total track length averaged across the 2007 marine turtle nesting season). Model selection used Akaike's Information Criterion (AIC); RSS is residual sum of squares, K is number of parameters, Δ AIC is the difference between each model and the best model, and AIC weight is relative information content. Below are AIC weights summed across all models containing an individual variable (i.e., the weight of each variable, given these models). N = 96

Model: Raccoon Track Length	RSS	K	R²	Adj. R²	AIC	ΔAIC	AIC Weights
Competing Models							
location + recreation + H' + strand	192.00	8	0.369	0.326	354.98	0.00	0.542
location + recreation + H' + strand + edge/area	191.97	9	0.369	0.319	356.96	1.98	0.201
location + recreation + H'	201.89	7	0.336	0.299	357.80	2.83	0.132
location + recreation + H' + edge/area	198.86	8	0.346	0.302	358.35	3.37	0.100
location + recreation + edge/area	213.22	7	0.299	0.260	363.04	8.07	0.010
location + H' + strand	224.73	5	0.261	0.237	364.09	9.11	0.006
location + recreation + strand	216.26	7	0.289	0.249	364.40	9.42	0.005
location + H' + strand + edge/area	224.61	6	0.261	0.229	366.04	11.06	0.002
location + H' + edge/area	231.75	5	0.238	0.213	367.04	12.06	0.001
location + recreation	234.34	6	0.229	0.196	370.11	15.13	0.000
location + edge/area	252.80	4	0.169	0.151	373.39	18.41	0.000
location + strand + edge/area	251.12	5	0.174	0.147	374.75	19.77	0.000
location + strand	269.58	4	0.114	0.095	379.56	24.58	0.000
location	299.31	3	0.016	0.005	387.60	32.62	0.000
Best Model	R²	P	Parameter Estimate		P_i	Σ AIC Weights	
	0.369	<0.001					
location			$\beta_1 = -6.461 \times 10^{-5}$		0.006	-	
recreation			$\beta_1 = -1.512 \times 10^{-3}$		0.001	0.991	
			$\beta_2 = 4.565 \times 10^{-7}$		<0.001		
			$\beta_3 = -3.274 \times 10^{-11}$		<0.001		
H'			$\beta_1 = 1.937$		0.001	0.985	
strand			$\beta_1 = 1.628$		0.035	0.756	
Excluded Variables							
edge/area						0.315	

* location = distance from northern park boundary (m), recreation = distance to nearest recreation access boardwalk (m), H' = Shannon Index (diversity of cover by area), strand = ln coastal strand edge (m)/200 m buffer, ege/area = habitat edge / habitat area in 200 m buffers

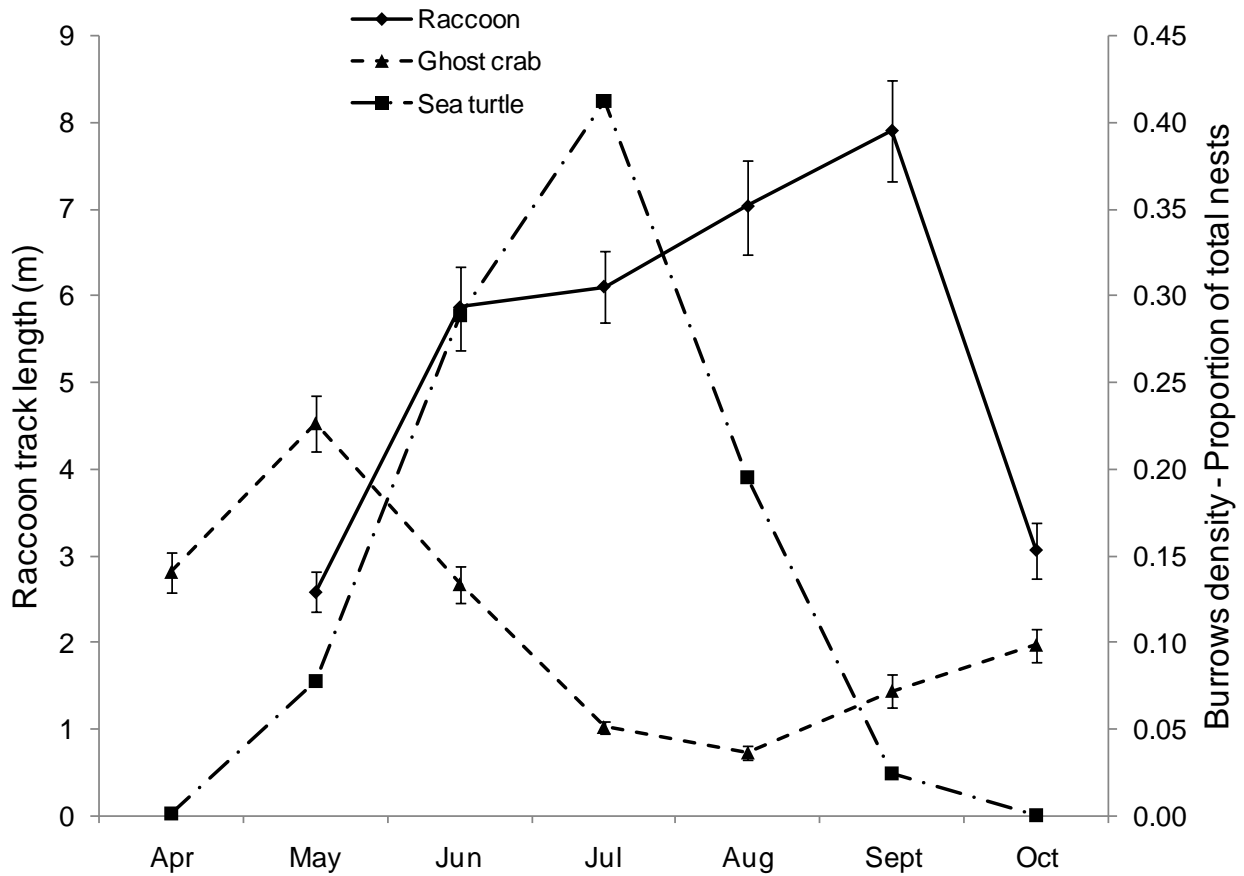


Figure 1.1 Monthly variation in marine turtle nesting and predator activity on Canaveral National Seashore, 2007. Turtle nests are the proportion of all nests laid that season (N=3627) by all three turtle species. Raccoon activity is total track length (m) and ghost crab activity is the mean density of ghost crab burrows, averaged across all transects (error bars are ± 1 SE).

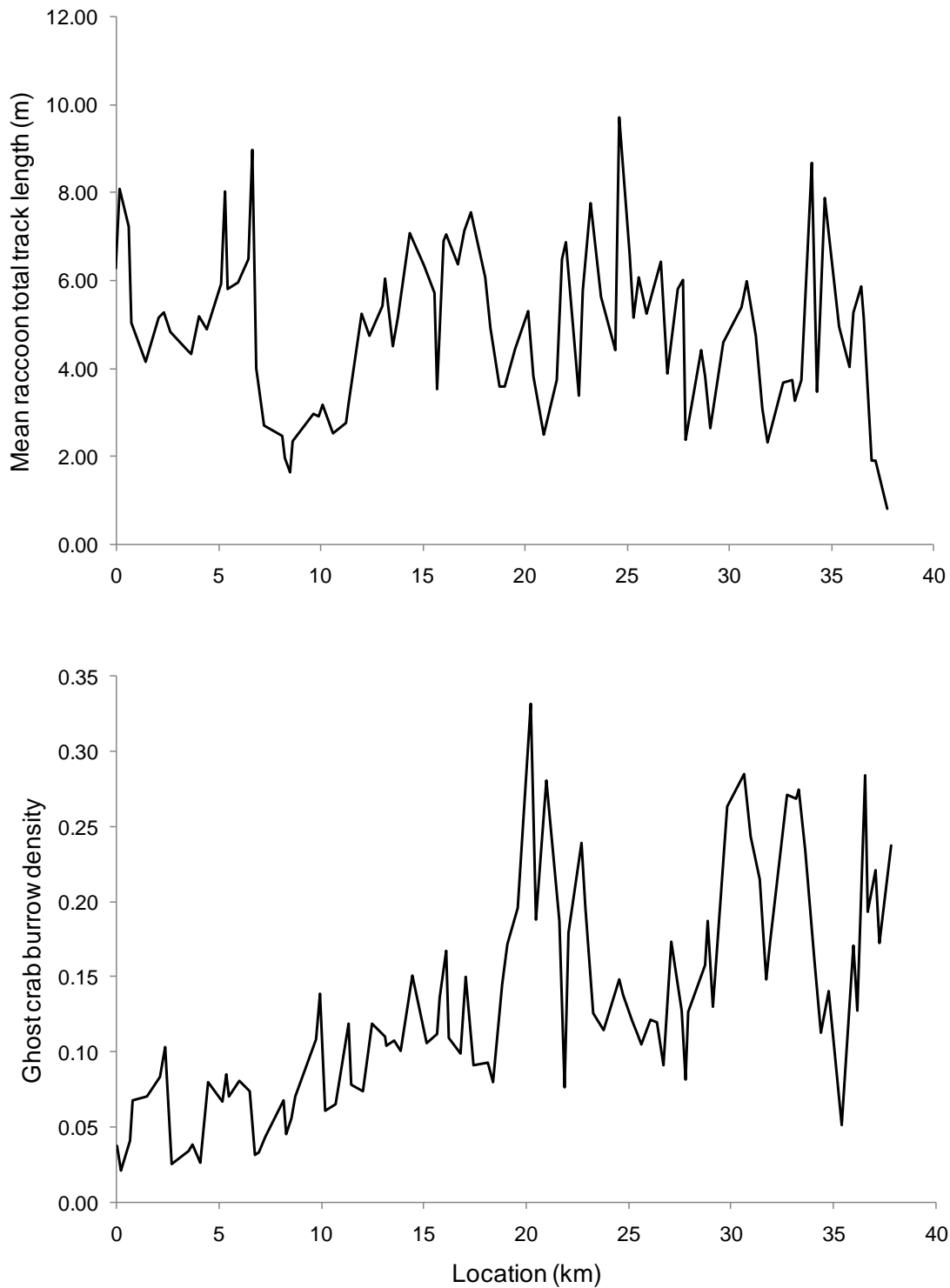


Figure 1.2 Spatial distribution of marine turtle egg predator activity on Canaveral National Seashore during the 2007 nesting season. Predator indices were averaged across all sampling dates for each location (distance from the northern park boundary).

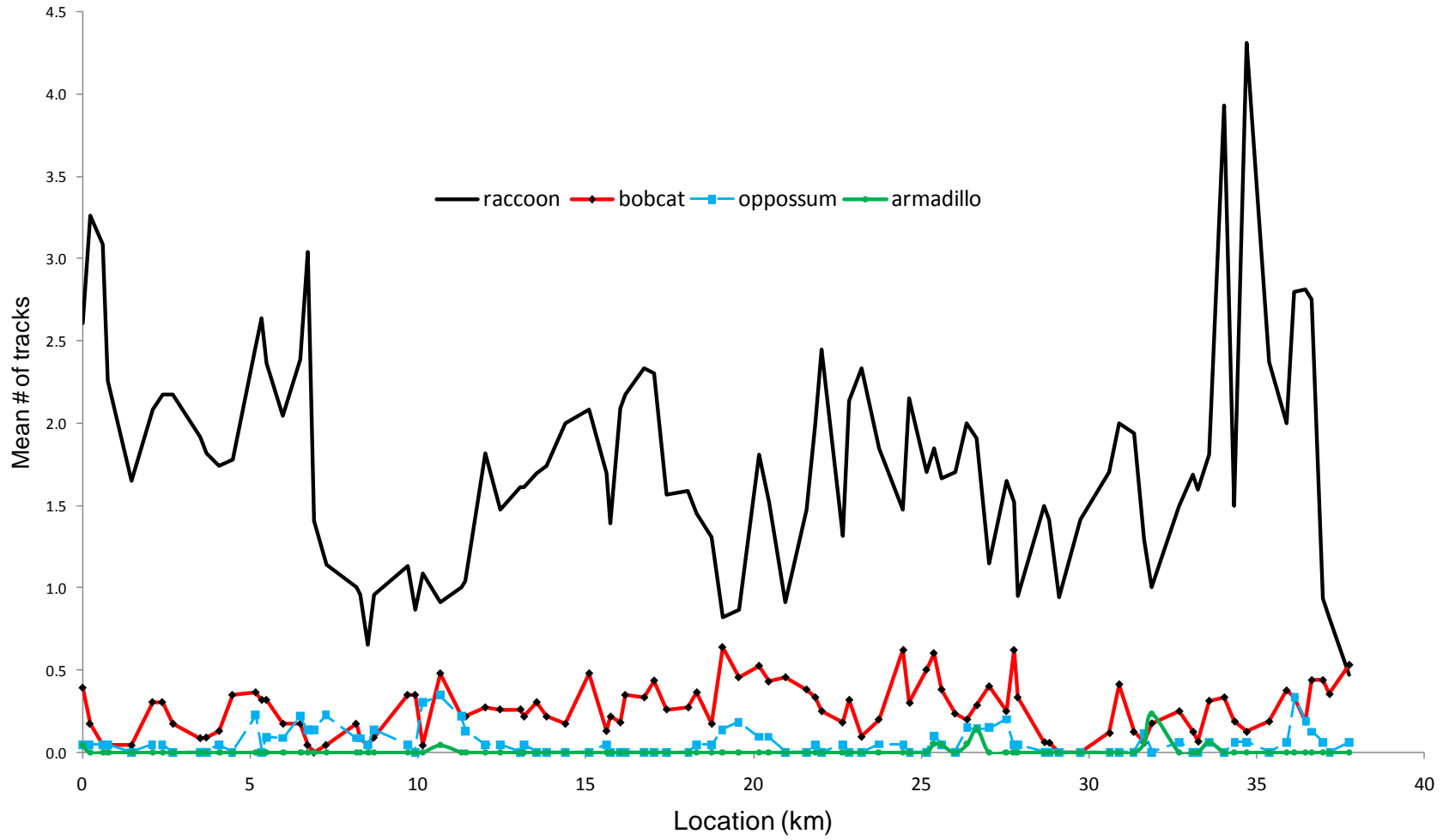


Figure 1.3 Number of tracks recorded for all mammalian predators (tracks/plot/night averaged over the 2007 marine turtle nesting season on Canaveral National Seashore).

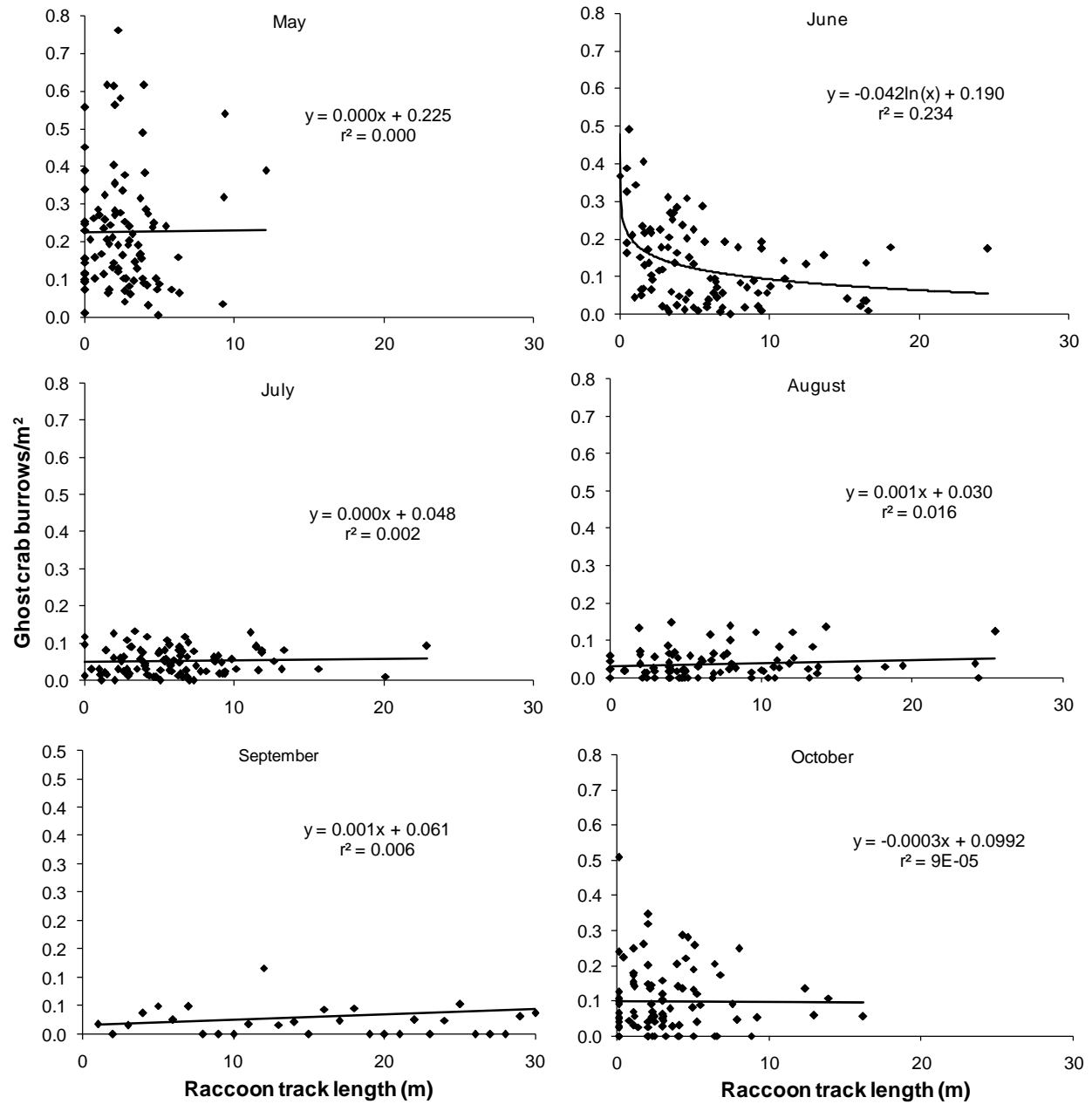


Figure 1.4 Temporal changes in response of ghost crab burrow density to raccoon activity (total track length, m) on Canaveral National Seashore, 2007 (N=96). Only June was significant ($P < 0.001$)

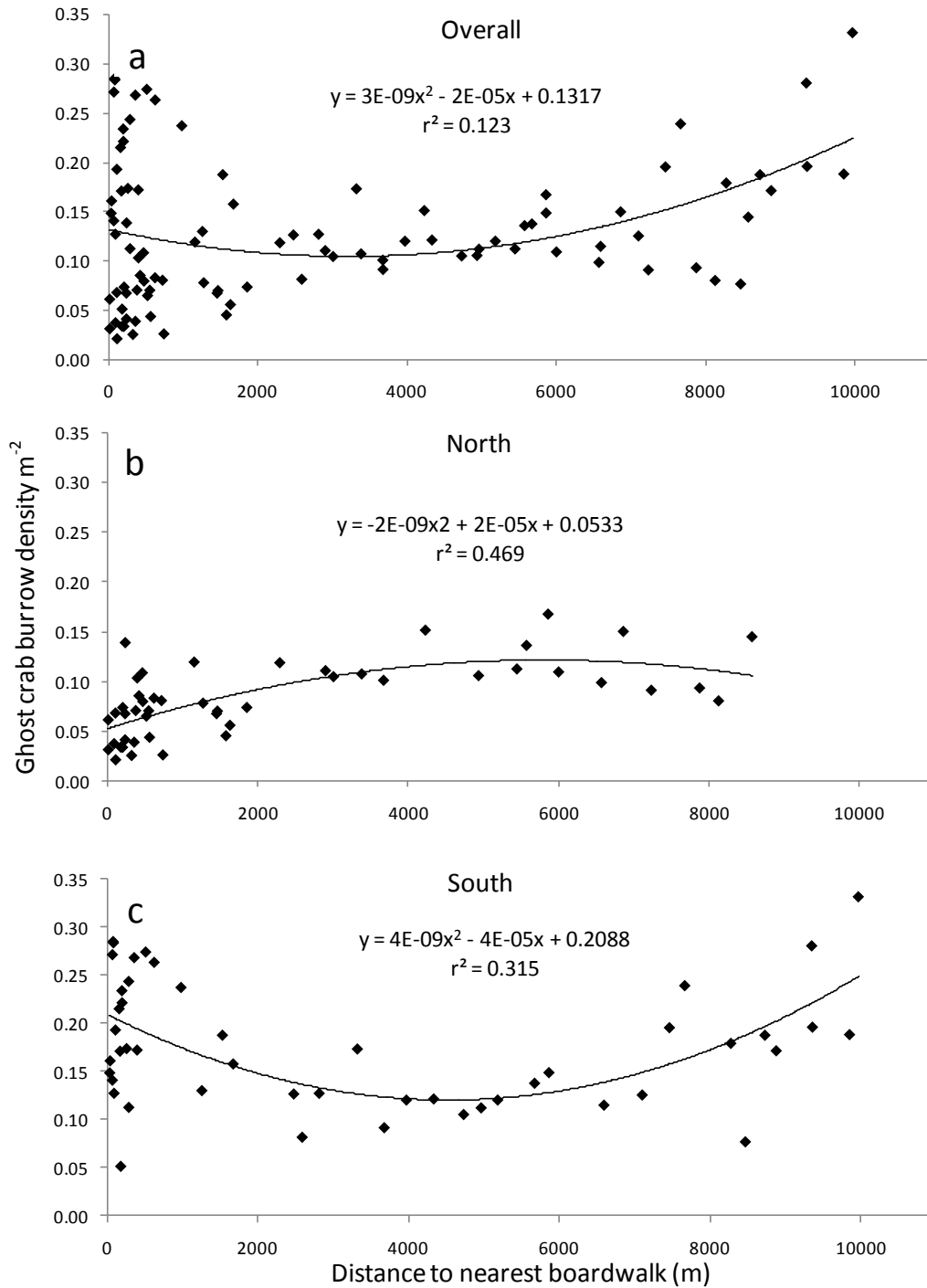


Figure 1.5 Relationship between ghost crab burrow density and distance to nearest boardwalk on Canaveral National Seashore, 2007, for (a) all transects, (b) transects in the north half of the beach, and (c) transects in the south half of the beach. Response to recreation appears to depend on location.

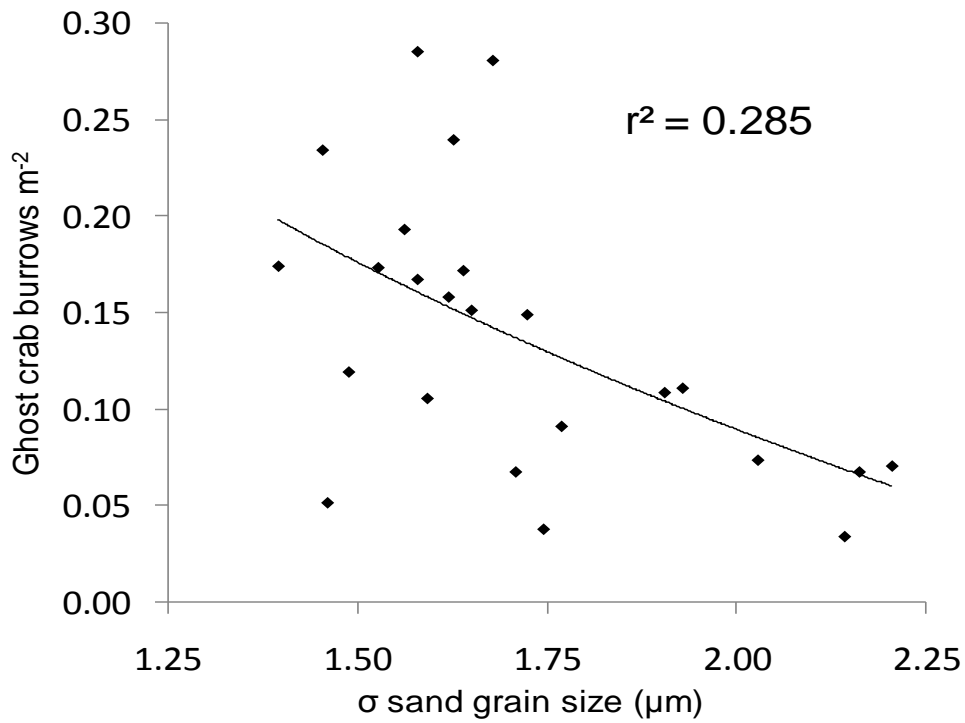
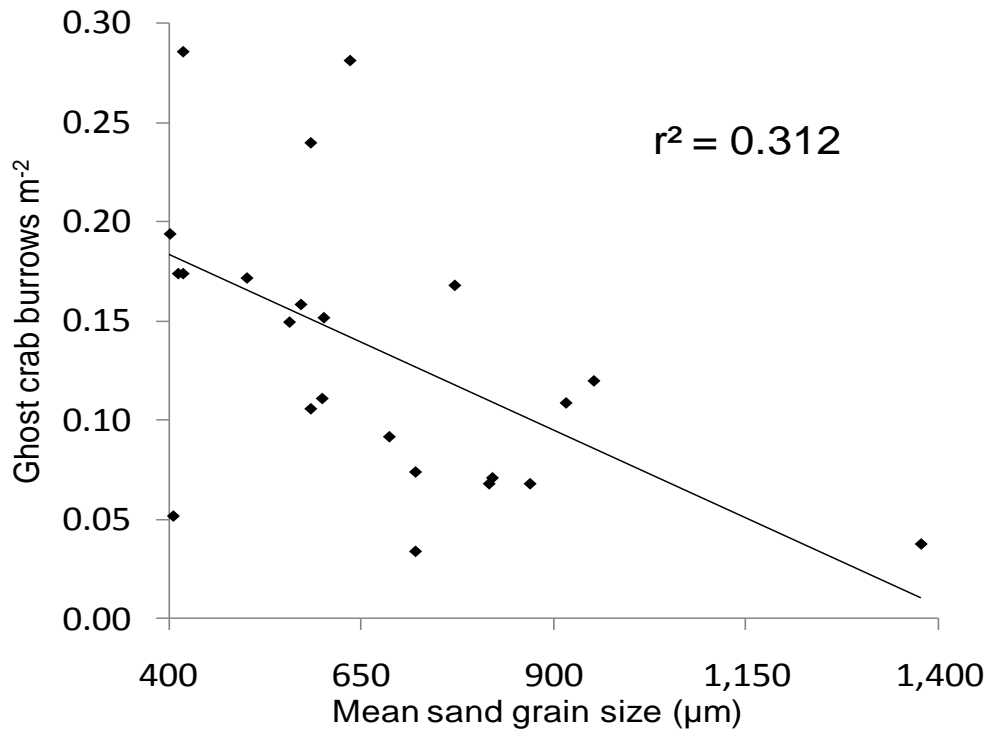


Figure 1.6 Relationship between ghost crab burrow density and sand characteristics on Canaveral National Seashore, 2007.

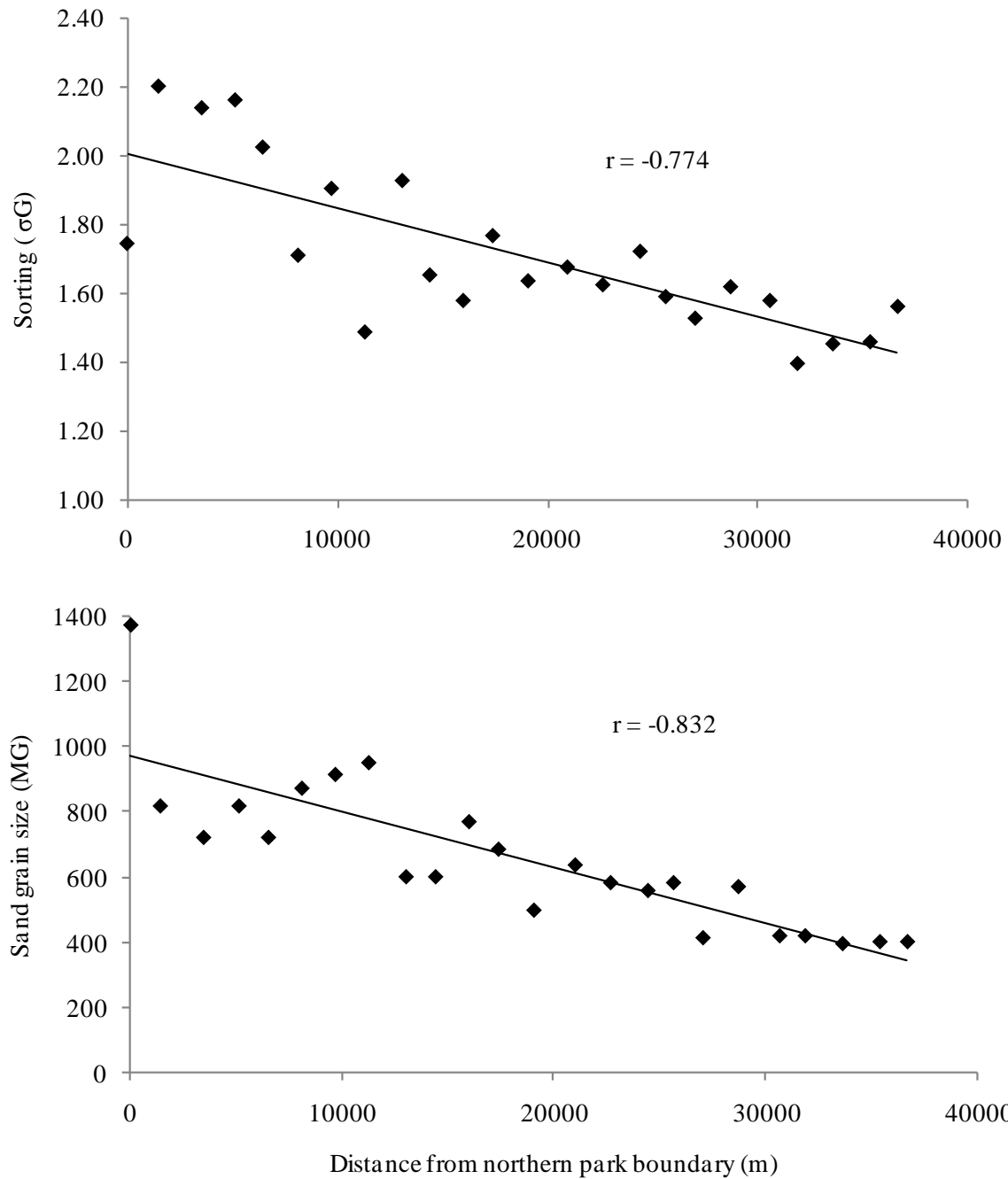


Figure 1.7 Relationship between location along the beach and sand characteristics on Canaveral National Seashore, 2007.

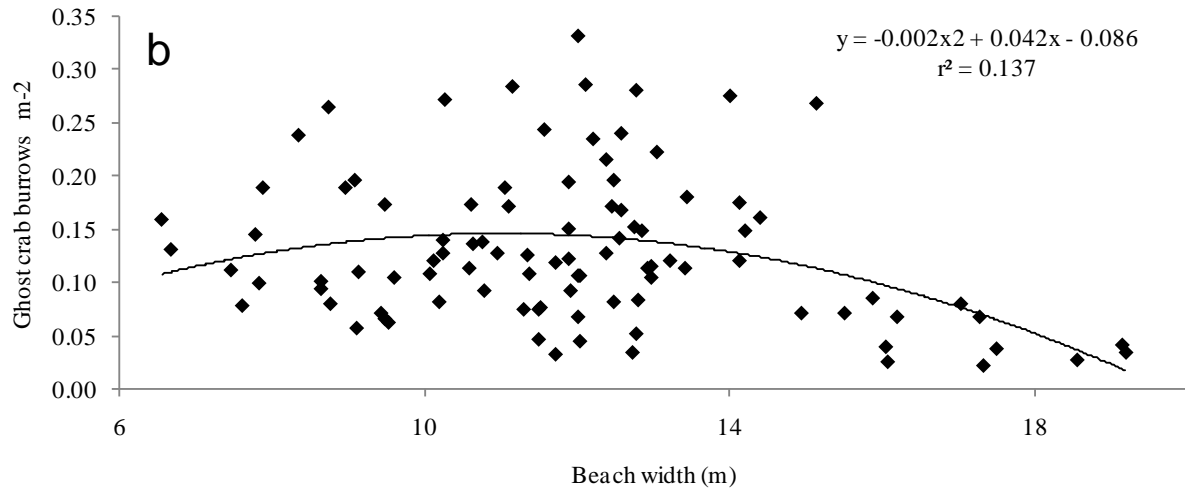
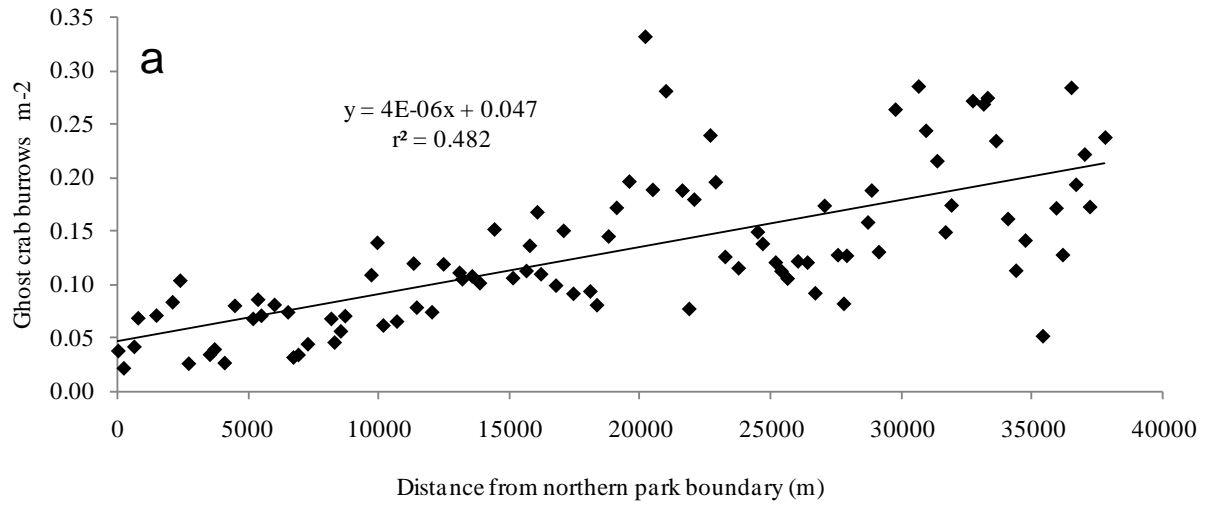


Figure 1.8 Responses of ghost crab burrow density to environmental variables on Canaveral National Seashore, 2007 (N=96).

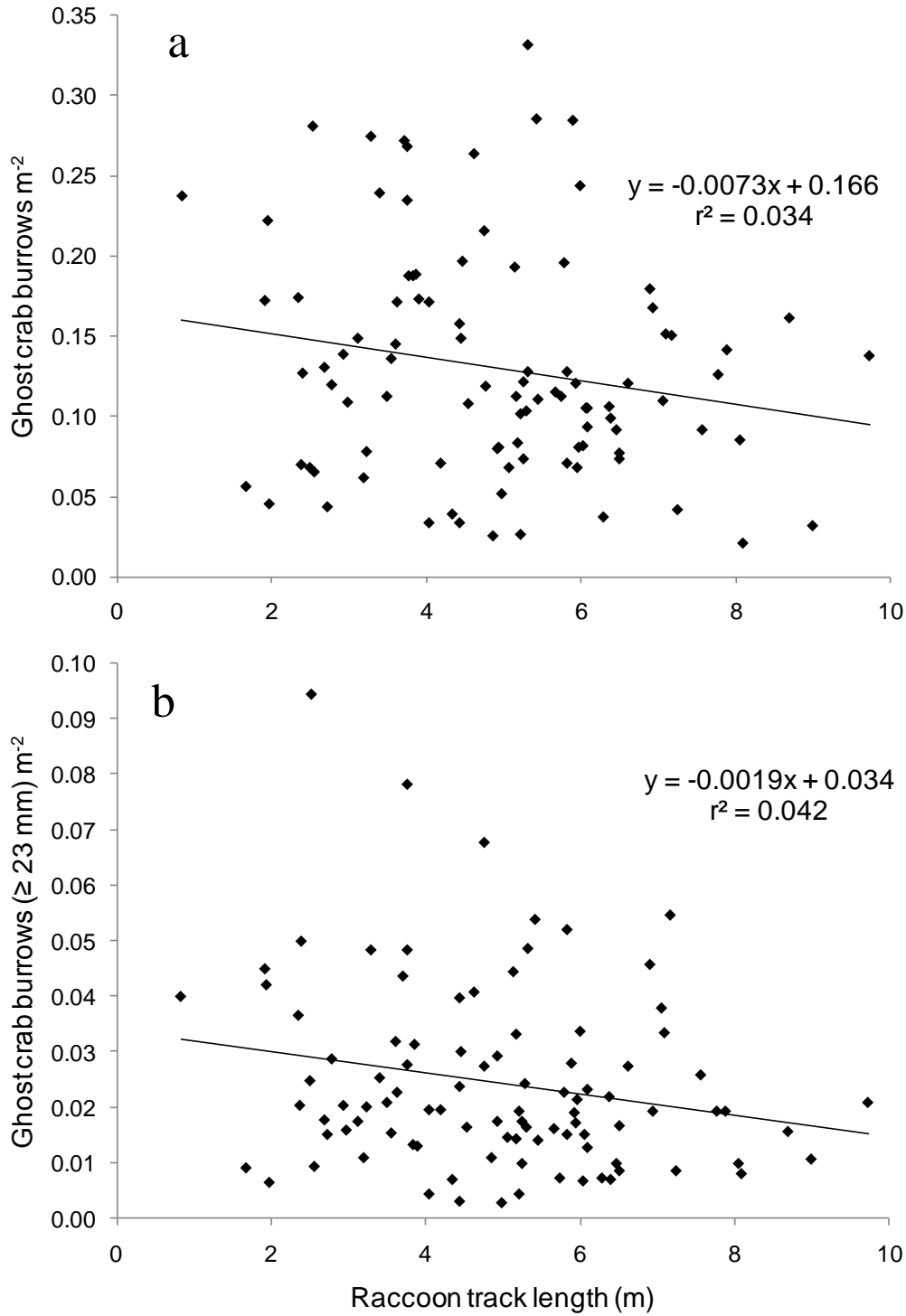


Figure 1.9 Effect of raccoon activity (total track length $plot^{-1} night^{-1}$) on (a) ghost crab burrow density and (b) reproductive (≥ 23 mm diameter) ghost crab burrow density on Canaveral National Seashore, 2007.

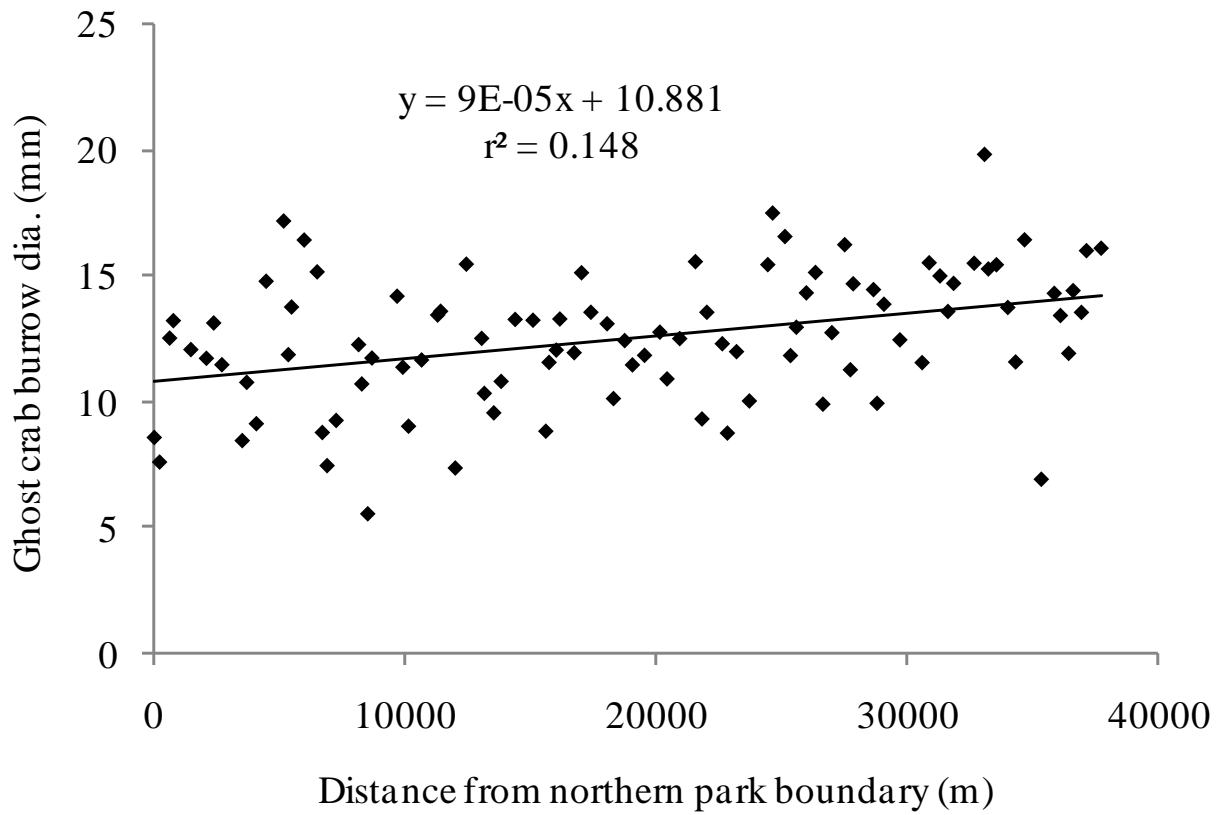


Figure 1.10 Relationship between mean ghost crab burrow diameter and location on Canaveral National Seashore, 2007 (N=96).

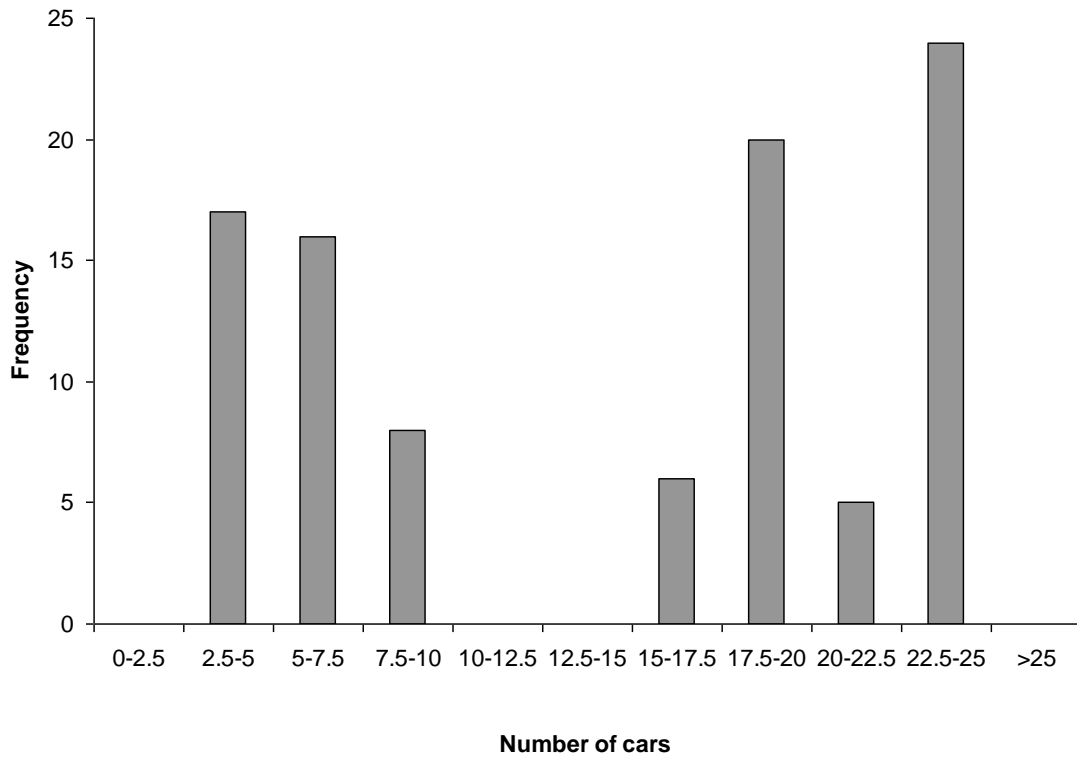


Figure 1.11 Histogram of the number of cars per parking lot at Canaveral National Seashore, 2007, averaged by transect for all sampling dates (96 transects). For analyses of the differential effects of recreation, analyses were split by parking lots with ≤ 10 or > 10 cars.

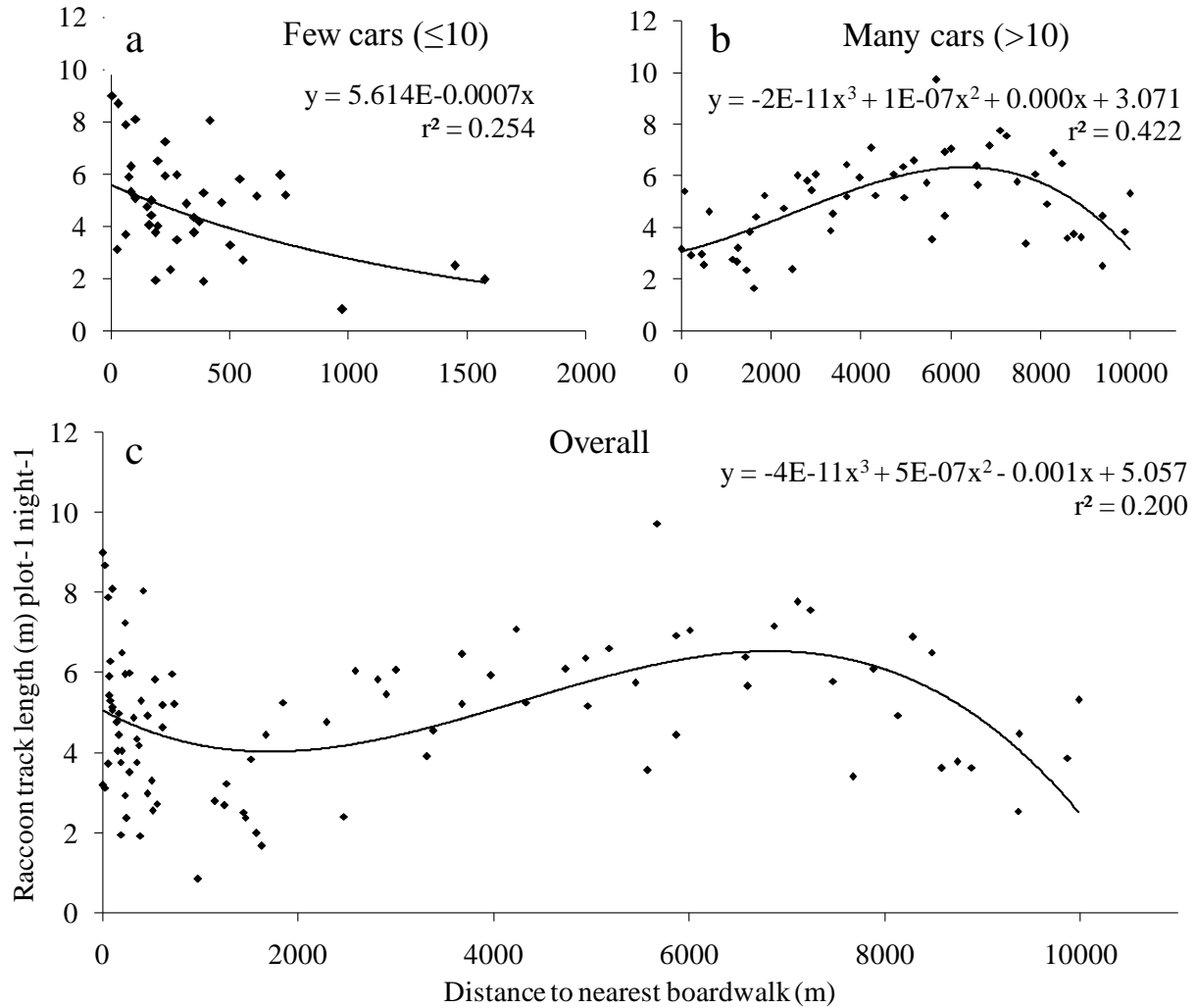


Figure 1.12 Relationship between raccoon activity and distance to recreational access points on Canaveral National Seashore, 2007, where the nearest parking lot had (a) ≤ 10 cars (N=41) or (b) > 10 cars (N=55), or (c) number of cars was excluded.

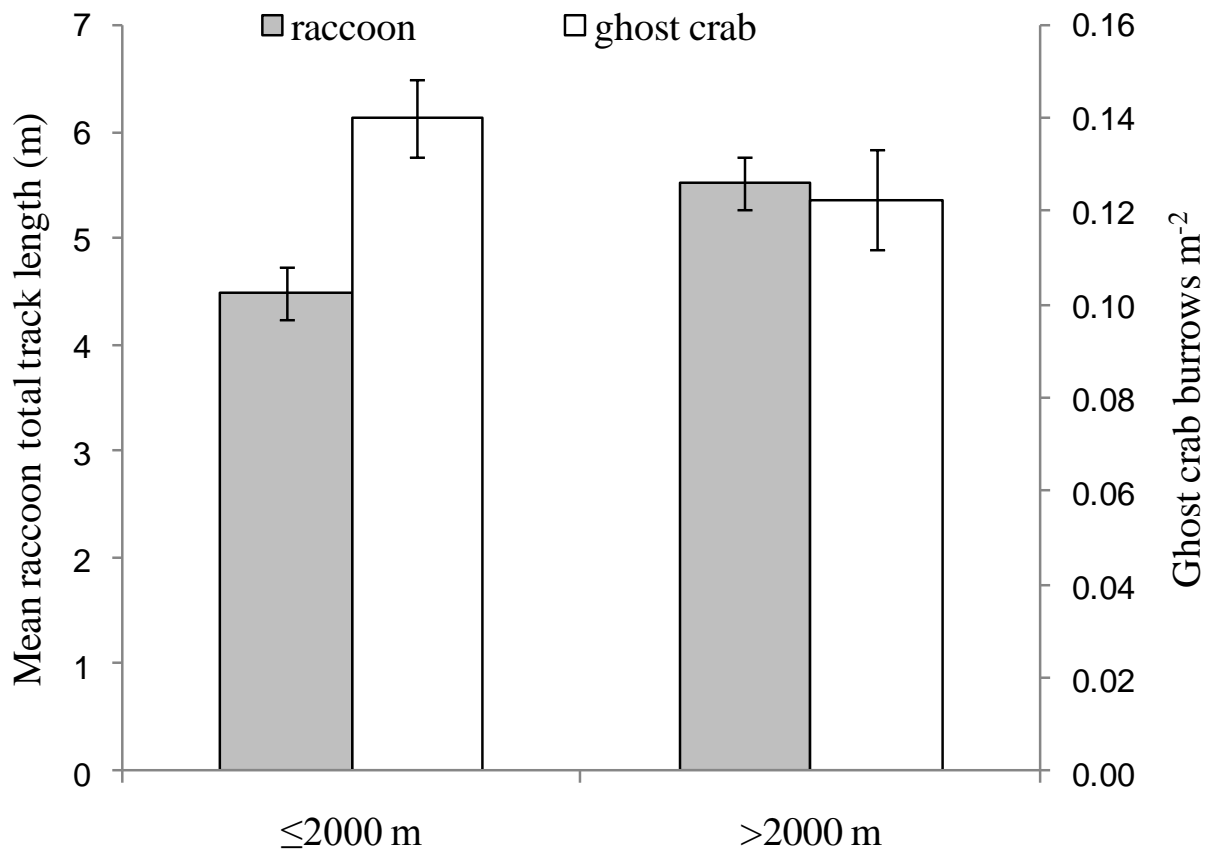


Figure 1.13 Predator activity (mean \pm SE) on recreation-accessible beach (≤ 2000 m from the nearest boardwalk) and backcountry beach (> 2000 m) on Canaveral National Seashore, 2007. Both raccoon activity (total track length, m) and ghost crab density (burrows m⁻²) were higher in areas far from recreation centers (N = 43 transects) than near (N = 53).

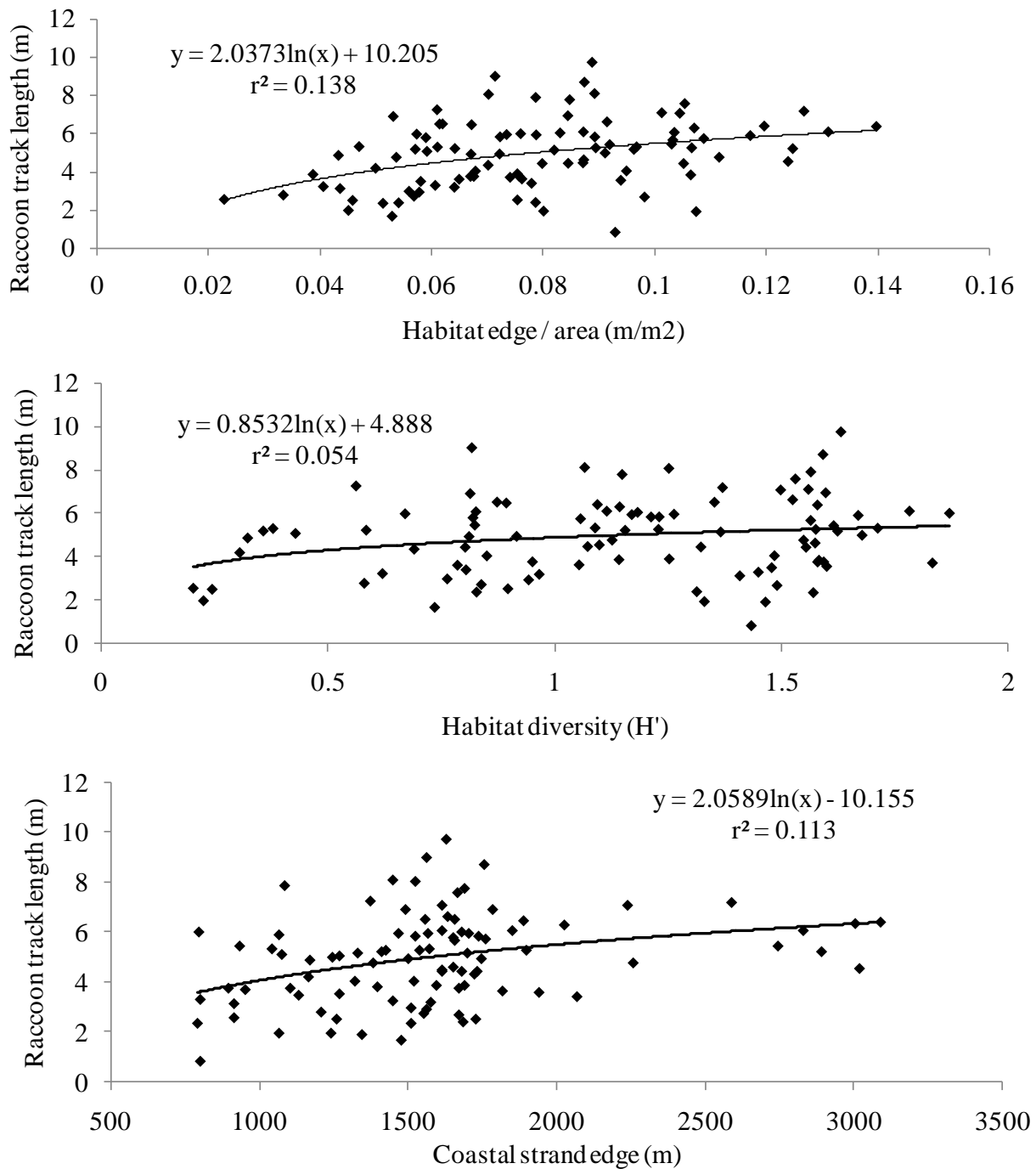


Figure 1.14 Response of mean raccoon activity (total track length (m) plot⁻¹ night⁻¹) to habitat variables on Canaveral National Seashore, 2007. Measurements were taken in 200 m buffers centered on each sampling transect (N=96). Habitat diversity was calculated using Shannon's Index (Morrison et al. 1998).

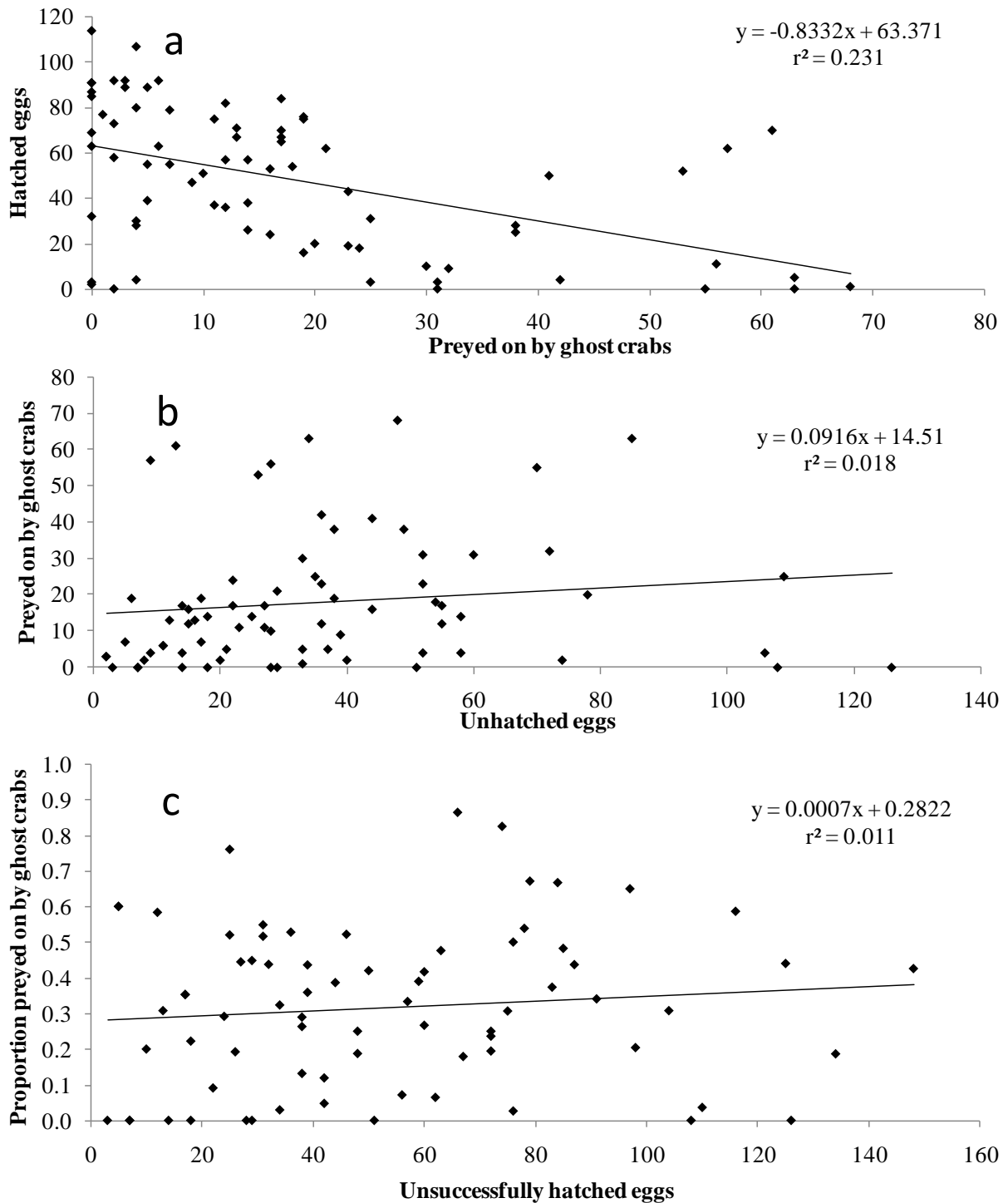


Figure 1.15 Relationship between a) number of eggs preyed on by ghost crabs and hatched eggs, and b) eggs preyed on by ghost crabs and unhatched eggs that were not preyed on, and c) all eggs that did not hatch (undeveloped and preyed on) and the proportion of those preyed on by ghost crabs. Each point represents a separate nest. Only the top relationship was significant ($p < 0.001$) ($N=74$)

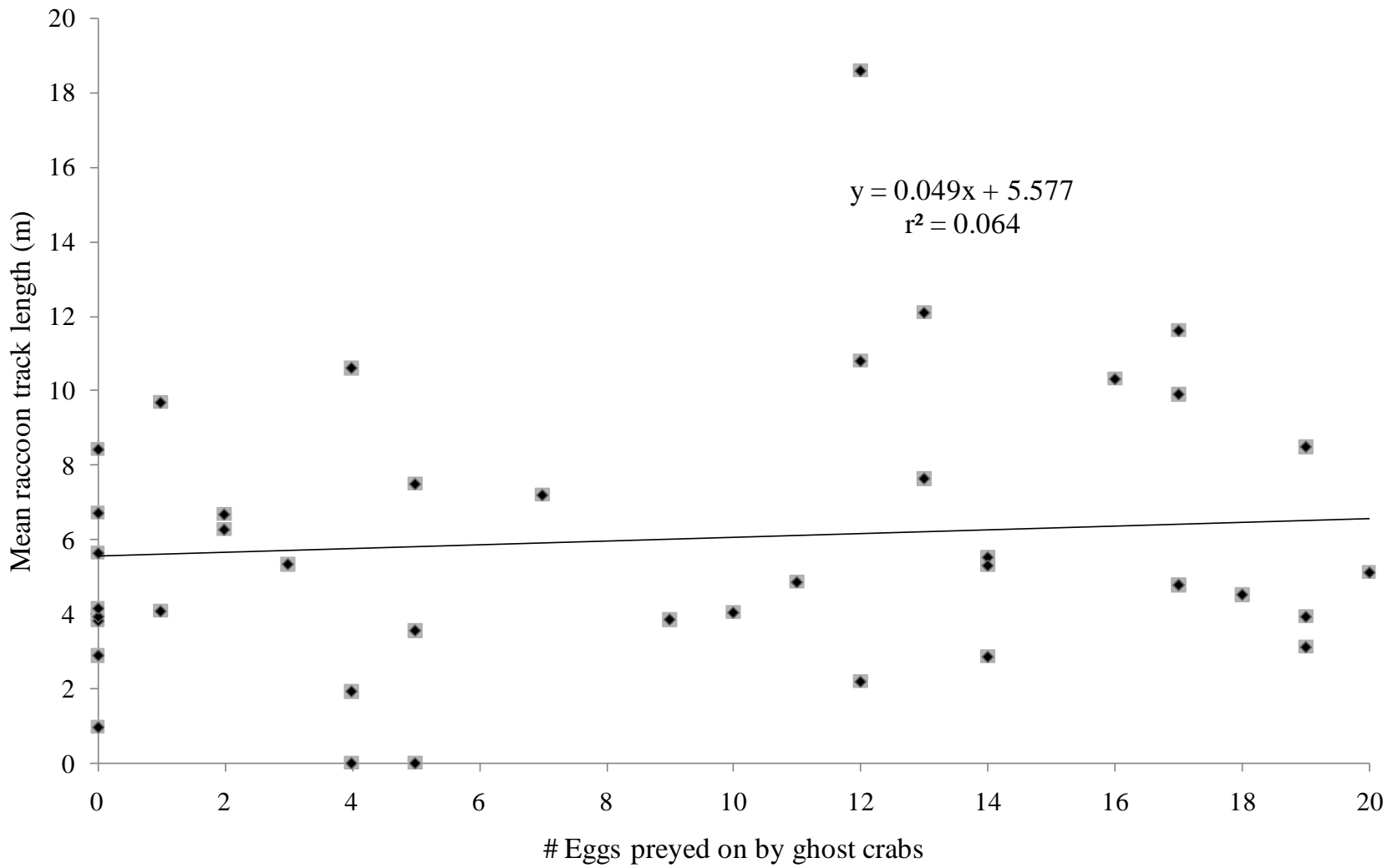


Figure 1.16 Response of raccoon activity during nest incubation to number of loggerhead sea turtle eggs/nest preyed on by ghost crabs on Canaveral National Seashore, 2007 (N=74).

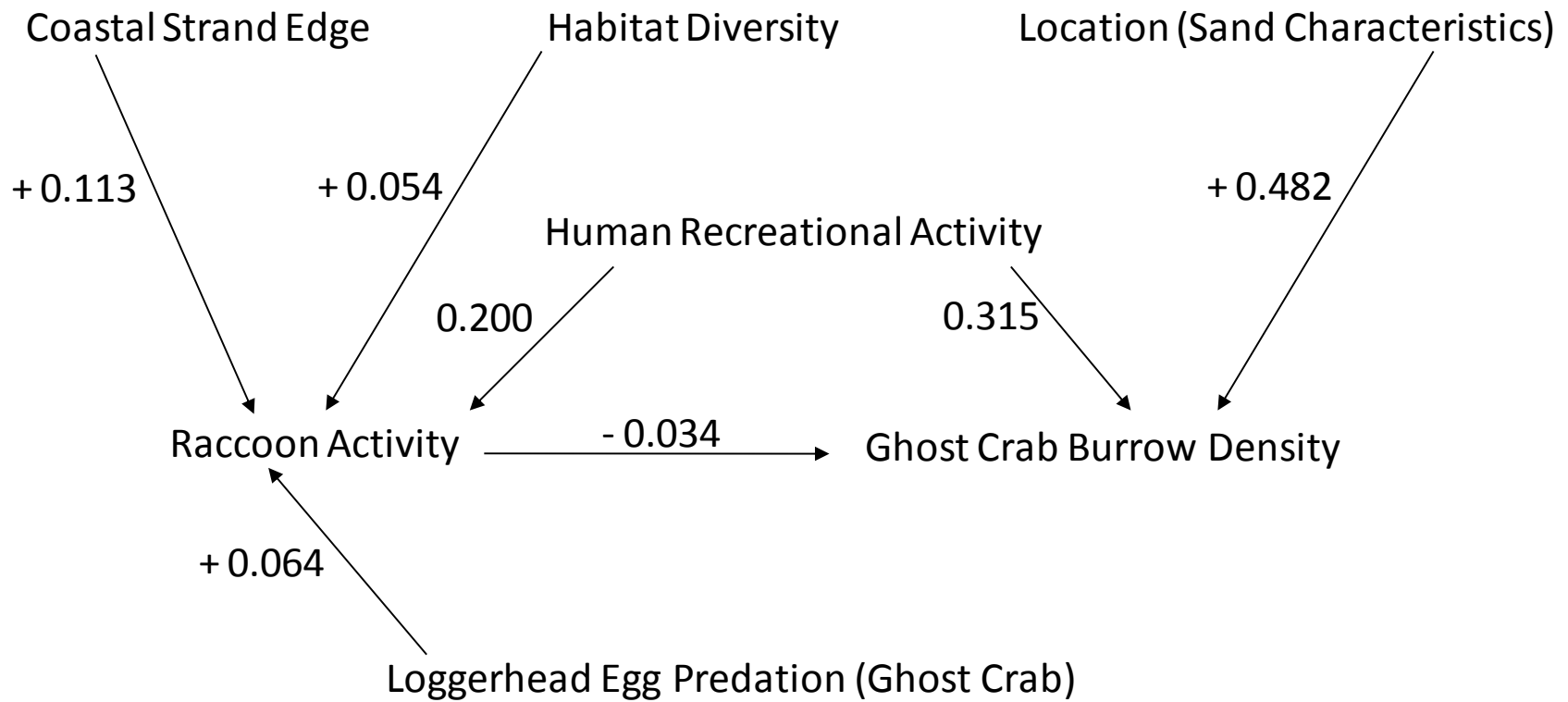


Figure 1.17 Observed causal relationships (r^2) among variables significant in spatial models and univariate analyses of egg predation. Both predators displayed non-linear relationships with human recreational activity, but both displayed positive relationships within approximately 2000 m of human recreational beach access. The dependent variables are at the end points of arrows and the slopes of relationships are indicated by + or - symbols.

CHAPTER 2. SYNERGISTIC INTERACTIONS BETWEEN INTRAGUILD PREDATORS: IMPLICATIONS FOR MARINE TURTLE NEST PROTECTION

Introduction

Interactions between predators take on many forms but typically fall into one of two categories: antagonistic or synergistic (Losey and Denno 1998). These two types of interactions differ in their net effect on shared prey. Antagonistic interactions between predators include intraguild predation (IGP), wherein one predator preys on its competitor (Polis et al. 1989). Early IGP models exploring the three-species interaction found coexistence of the two predators required a competitive advantage in the intermediate predator and significant benefit to the top predator derived from consuming its competitor (Holt and Polis 1997). If the interaction between predators is strong, the top predator may provide a net benefit to the basal resource by limiting predation by the more efficient intermediate predator (Holt and Polis 1997; Figure 2.1a).

Synergistic interactions, on the other hand, occur when one predator increases the susceptibility of a prey species to another predator, often by modifying the behavior of the prey (Charnov et al. 1976). The combined effect of both predators on the prey, given the interaction, is greater than the sum of the individual effects alone (Soluk 1993, Sih et al. 1998; Figure 2.1b)

A more complex interaction could combine IGP with facilitated predation. If predation on the basal resource by the top predator is facilitated by the intermediate predator in an IGP relationship, the top predator may no longer gain by preying on the intermediate predator. If predation on the intermediate predator is strong, the relationship between predators may be primarily antagonistic and provide net benefit to the prey. However, if the direct interaction between predators is relatively weak, the relationship could be synergistic, with amplified negative effects on the basal resource.

Raccoons (*Procyon lotor*) prey on ghost crabs (*Ocypode quadrata*) and appear to limit their populations (Barton and Roth 2008). Both predators consume eggs of threatened and endangered marine turtles (Bouchard and Bjørndal 2000, Antworth et al. 2006, Barton and Roth 2008). Given the assumptions of simple intraguild predation models, raccoons could reduce competition for eggs by eating ghost crabs. However, egg predation rates appear to be independent of raccoon density (Barton and Roth 2008), suggesting exploitative competition between these nest predators may be weak. Furthermore, the highest combined egg predation rates occurred at the study site where raccoons were least and ghost crabs were most abundant; thus nest predation by ghost crabs may facilitate secondary nest predation by raccoons by releasing olfactory cues through burrows into nests (Barton and Roth 2008). Facilitation by ghost crabs may decrease raccoon search time for nests, thereby increasing efficiency. Thus, the cost of preying on ghost crabs may outweigh the benefit to raccoons if the synergistic behavioral interaction is suppressed at low ghost crab densities.

To understand the net effect of the interaction between these predators on hatching success of marine turtle nests, the apparent facilitation of raccoon nest predation by ghost crabs must be verified. Therefore, we tested whether raccoons are attracted to simulated nest predation by ghost crabs. If this synergistic interaction occurs but densities of raccoons and ghost crabs are negatively correlated, marine turtle eggs may benefit from the negative interaction between their two most important predators.

Methods

Study Site

We conducted research on Canaveral National Seashore (CANA), on the east-central Florida coast. Canaveral National Seashore has 17.5 km of undeveloped beach rarely accessed for

recreation, which reduced any bias associated with human activity (see Ch. 1). Both raccoons and ghost crabs prey on marine turtle eggs laid on this beach (Antworth et al. 2006). We conducted research from 21-29 October, 2006, near the end of the marine turtle nesting season, to reduce potential effects of increased raccoon activity on nest predation due to our study.

Simulated Nests and Burrows

To simulate turtle nests we dug holes approximately 35 cm deep, corresponding with the average depth of loggerhead nests on CANA (Carthy et al. 2003). We placed one can of cat food (Purina Friskies ocean whitefish) in the bottom of each simulated nest and placed a 38 cm long, 2.5 cm dia. polyvinyl chloride (PVC) pipe into nests at an angle roughly 73° relative to the beach surface, corresponding with ghost crab burrow architecture (Chan et al. 2006). We placed one end into the attractant and the other end extended out to the beach surface.

At each site we paired a treatment and control nest spaced 10 m apart, parallel to the dune. Control pipes were filled with sand but treatment pipes were left open. During each sampling period, we installed nests at twenty sites with 100 m interspersion. We placed all nests 5 m from a relocation stake at the beach-dune edge. To avoid human disturbance, we installed nests within 1 h of sunset and checked nests within 1 h of sunrise the following two mornings. We smoothed sand within 1 m of each pipe during nest installation and the first morning. Each morning we recorded the occurrence of predation or predator tracks ≤ 20 cm from each simulated burrow. We considered this assessment of predator attraction conservative, because some tracks within this distance simply intersected plots with no evidence the predator investigated burrows. One two-night sampling period constituted an event for each nest. One week after sampling the first twenty sites we established another 20 pairs of nests (treatment and control) in an adjacent section of beach that was previously unsampled and followed the same procedures for estimating

predator attraction. We tested for a significant difference between visits to treatment and control nests using a one-tailed Fisher's exact test.

Results

One treatment and three control nests were preyed on by ghost crabs, which reduced the sample size to 39 treatments and 37 controls. Raccoons visited significantly more treatment than control nests (25.6% and 2.7%, respectively, $P = 0.004$, FET; Table 2.1). All control nests preyed on by ghost crabs attracted raccoons. No other mammalian predators visited the artificial nests.

Discussion

Our results support the presence of a predator-predator interaction not previously described, which combines intraguild predation and facilitated predation. The effects of facilitated predation on the basal prey likely result from the strength of the numerical relationship between intraguild predators. If top-down predation is strong, as it appears to be between raccoons and ghost crabs (Barton and Roth 2008), then the synergistic interaction may be weak and the predator-predator interaction will remain antagonistic. However, if the numerical relationship between predator species is weak, then the interaction could be primarily synergistic, increasing net predation on the basal prey.

Raccoons are commonly removed from marine turtle nesting beaches to mitigate egg loss from predation (Engeman et al. 2005, Garmestani and Percival 2005), and removal has effectively reduced egg loss when predation rates were very high. However, raccoons can limit ghost crab density and our data suggest raccoons are attracted to nests preyed on by ghost crabs (Chapter 1, Barton and Roth 2008), so raccoon removal could have unexpected results due to facilitated predation. Even raccoons at low density that have limited experience with marine resources could have substantial effects on egg mortality (Barton and Roth 2007, 2008).

The direct effects of raccoons on ghost crab density and marine turtle egg predation may change seasonally or spatially with variation in resources (Chapter 1), altering the effect of facilitated predation on net predation. Managers should assess the strength of direct predator-predator and predator-prey interactions before assuming a management strategy used effectively elsewhere will have the same net effect in a different location. If egg predation by raccoons is very strong, then reducing raccoon densities may have a greater benefit than the potential costs of increased synergism. If nest predation by raccoons is not strong and there is a strong numerical relationship between raccoons and ghost crabs, then removing raccoons may have counterproductive results.

Raccoon and ghost crab activity can be predicted using simple spatial models (Chapter 1) and likely would be better described with spatiotemporal models. Future research could combine experiments designed to characterize predator activity with predator exclusion treatments to better understand the independent and indirect effects of both predators on egg predation. It may be beneficial to construct a simple three-species IGP model with facilitated predation to explore the effect of varying the numerical relationship between predators on basal prey stability. More complex models with spatial and temporal heterogeneity in predator-predator and predator-prey interactions may help generate predictions of the effects of predator manipulation in different environments.

Literature Cited

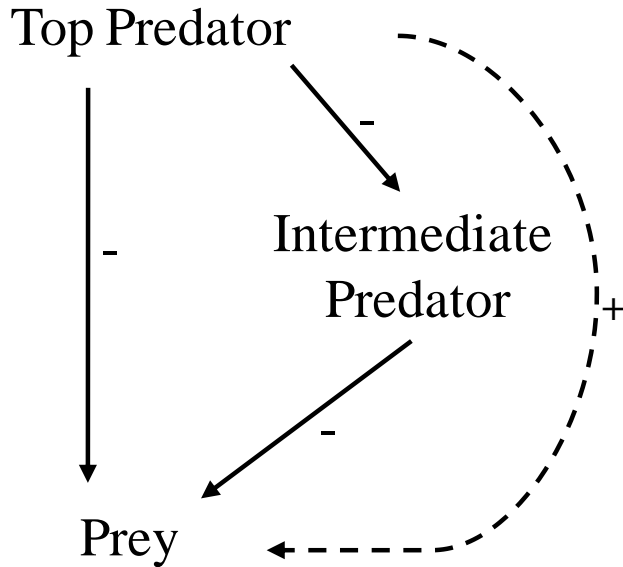
- Antworth, R. L., D. A. Pike, and J. C. Stiner. 2006. Nesting ecology, current status, and conservation of sea turtles on an uninhabited beach in Florida, USA. *Biological Conservation* **130**:10-15.
- Barton, B. T. and J. D. Roth. 2007. Raccoon removal on sea turtle nesting beaches. *Journal of Wildlife Management* **71**:1234-1237.
- Barton, B. T. and J. D. Roth. 2008. Implication of intraguild predation for sea turtle nest protection. *Biological Conservation*. doi:10.1016/j.biocon.2008.06.013.

- Bouchard, S. S. and K. A. Bjorndal. 2000. Sea turtles as biological transporters of nutrients and energy from marine to terrestrial ecosystems. *Ecology* **81**:2305-2313.
- Carthy, R. R., A. M. Foley, and Y. Matsuzawa. 2003. Incubation environment of loggerhead turtle nests: effects on hatching success and hatchling characteristics. Pages 144-153 in A. B. Bolten and B. E. Witherington, editors. *Loggerhead Sea Turtles*. Smithsonian Institution, Washington, D.C.
- Chan, B. K. K., K. K. Y. Chan, and P. C. M. Leung. 2006. Burrow architecture of the ghost crab *Ocypode ceratophthalma* on a sandy shore in Hong Kong. *Hydrobiologia* **560**:43-49.
- Charnov, E. L., G. H. Orians, and K. Hyatt. 1976. Ecological implications of resource depression. *American Naturalist* **110**:247-259.
- Engeman, R. M., R. E. Martin, H. T. Smith, J. Woolard, C. K. Crady, S. A. Shwiff, B. Constantin, M. Stahl, and J. Griner. 2005. Dramatic reduction in predation on marine turtle nests through improved predator monitoring and management. *Oryx* **39**:318-326.
- Garmestani, A. S. and H. F. Percival. 2005. Raccoon removal reduces sea turtle nest depredation in the ten thousand islands of Florida. *Southeastern Naturalist* **4**:469-472.
- Holt, R. D. and G. A. Polis. 1997. A theoretical framework for intraguild predation. *American Naturalist* **149**:745-764.
- Losey, J. E. and R. F. Denno. 1998. Positive predator-predator interactions: Enhanced predation rates and synergistic suppression of aphid populations. *Ecology* **79**:2143-2152.
- Polis, G. A., C. A. Myers, and R. D. Holt. 1989. The ecology and evolution of intraguild predation – potential competitors that eat each other. *Annual Review of Ecology and Systematics* **20**:297-330.
- Sih, A, G. Englund and D. Wooster. 1998. Emergent impacts of multiple predators on prey. *Trends in Ecology and Evolution* **13**(9):350-355.
- Soluk, D. A. 1993. Multiple predator effects – predicting combined functional-response of stream fish and invertebrate predators. *Ecology* **74**:219-225.

Table 2.1 Raccoon attraction to simulated egg predation by ghost crabs. Tracks ≤ 20 cm from burrows were treated as attraction.

	Treatment	Control	Total
Attraction	10	1	11
Non-attraction	29	36	65
Total	39	37	76

a) Antagonistic Interaction



b) Synergistic Interaction

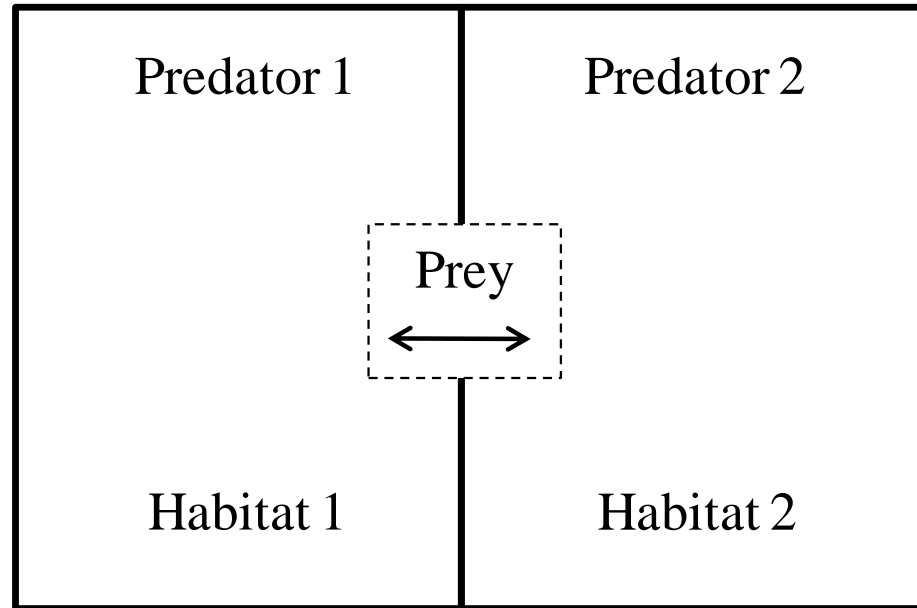


Figure 2.1 In the example of an antagonistic interaction (a) the predators compete for prey, but the top predator preys on the intermediate predator, which preys more efficiently on the basal prey. The interaction between predators has an indirect (dashed line) and net positive effect on the basal prey. In the synergistic example (b) the predators prefer different habitats, and avoiding one predator increases the prey's likelihood of being preyed on by the other predator. Thus, the interaction has a net negative effect on the prey.

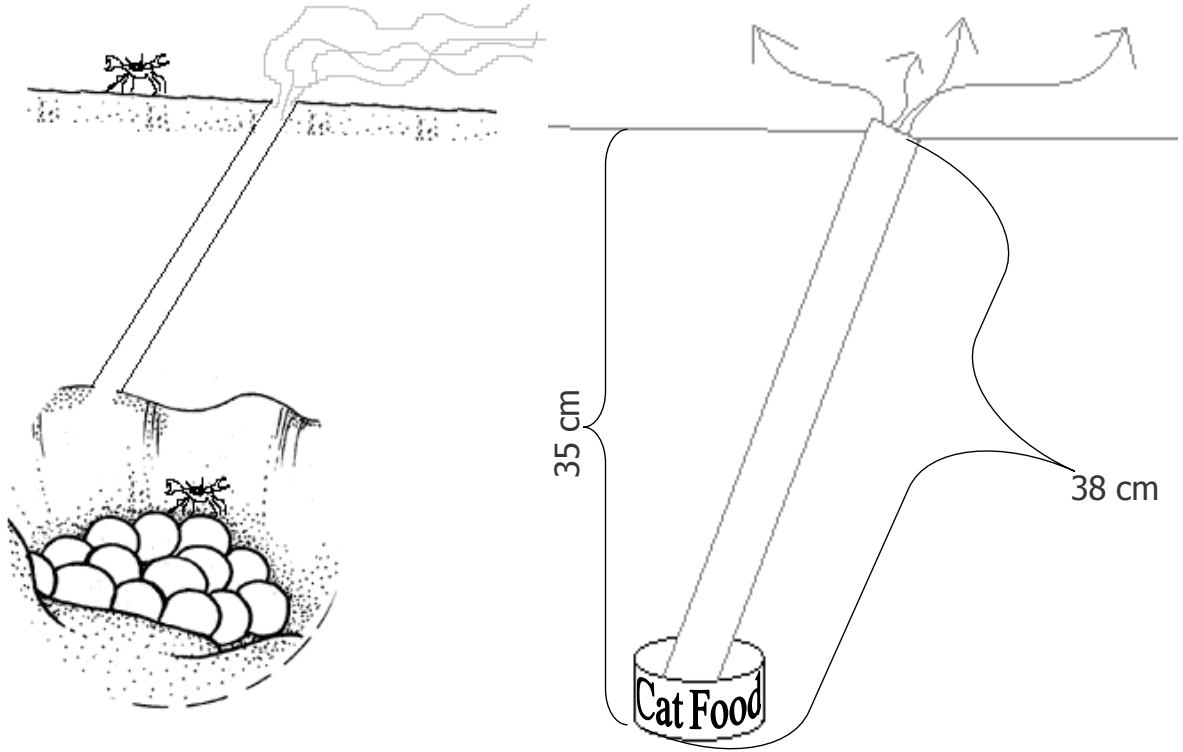


Figure 2.2 Simulated ghost crab burrow in a loggerhead turtle nest.