

Cascading Effects Of Predator Removal On The Ecology Of Sea Turtle Nesting Beaches

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CASCADING EFFECTS OF PREDATOR REMOVAL
ON THE ECOLOGY OF SEA TURTLE NESTING BEACHES

by

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B.S. University of Idaho, 2003

A thesis submitted in partial fulfillment of the requirements
for the degree of Master of Science
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in the College of Arts and Sciences
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ABSTRACT

Traditional views of food web dynamics have characterized species interactions as linear and direct. However, modern food web theory suggests that interactions can also be nonlinear and indirect, so that disturbance at one trophic level is transmitted throughout the community. Many previous studies have demonstrated that the removal of top predators from terrestrial ecosystems can have broad-scale impacts on community ecology. I examined the direct and indirect effects of raccoon removal from sea turtle nesting beaches in east-central Florida during the summers of 2003 and 2004. Raccoon and ghost crab predation are among the highest causes of egg mortality for sea turtles in Florida and raccoons are intraguild predators of ghost crabs. Because of the damage done to sea turtle nests, raccoons have been removed from some beaches during the sea turtle nesting season. I compared the diet and demography of a raccoon population that had experienced two decades of raccoon removal to a population that had previously been unmanipulated. I found that long-term raccoon removal had created a significantly male-biased sex ratio in that population. I also examined the indirect effects of raccoon removal by comparing the abundances of raccoons and ghost crabs at four study sites using passive tracking plots. My data suggest intraguild predation by raccoons limits ghost crab abundance and that reduced raccoon abundance allowed ghost crab abundance to increase, resulting in a net increase in sea turtle egg predation. These results support my hypothesis that intraguild predation of ghost crabs by raccoons is an influential interaction on sea turtle nesting beach community dynamics.

This is dedicated to Grandma, who put the first fishing pole in my hand
and consequently, a love for the outdoors in my heart

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LIST OF ACRONYMS/ABBREVIATIONS

ACNWR	Archie Carr National Wildlife Refuge
ACNWR-N	Archie Carr National Wildlife Refuge Northern Site
ACNWR-S	Archie Carr National Wildlife Refuge Southern Site
CANA	Canaveral National Seashore
IGP	Intraguild predation
MINWR	Merritt Island National Wildlife Refuge
MPR	Mesopredator release
UCF	University of Central Florida
UCFMTRG	University of Central Florida Marine Turtle Research Group

CHAPTER ONE: INTRODUCTION

The cascading affects of removing predators from ecosystems have been well demonstrated in the scientific literature. Paine's (1969) research with the predatory starfish *Pisaster ochraceous* is the classical example of the importance of top-down regulation in ecosystems. Removing *Pisaster* from intertidal ecosystems reduced the overall biodiversity of the community. The mussel *Mytilus californianus*, a natural prey of *Pisaster*, out-competed and displaced other species in the community. Henke (1992) described a similar situation in a terrestrial ecosystem. Following removal of coyotes (*Canis latrans*), a single rodent species out-competed all others, resulting in decreased rodent species diversity.

The absence of top predators does not always result in reduced predation and can produce increased mortality on prey species. Soulé et al. (1988) coined the term "mesopredator release" to explain the increased abundance of smaller predators (striped skunk, raccoon and grey fox) when top predators (coyote) were absent and the corresponding negative impact on prey (scrub-breeding birds). This theory has been tested with a variety of taxa and supports the tenet that predators are important components in maintaining community structure and composition (Palomares et al. 1995, Rogers and Caro 1998, Courchamp et al. 1999, Crooks and Soulé 1999, Schmidt 2003).

The theory of mesopredator release suggests linear interactions among trophic levels. However, food webs are rarely linear and interactions often occur within trophic levels. Intraguild predation (the killing and eating of potential resource competitors) is a widespread interaction (Arim and Marquet 2004). Because intraguild predation involves direct mortality and reduced competition, it has the potential to significantly affect communities (Polis et al. 1989).

Stapp (1997) experimentally showed that intraguild predation limited species diversity in shortgrass-prairie rodents. Similarly, Fedriani and Fuller (2000) showed that coyotes were intraguild predators on gray foxes and that this interaction produced a competitive advantage that allowed coyotes to be more abundant.

My research addresses the theories of mesopredator release and intraguild predation on sea turtle nesting beaches in east-central Florida by examining the interactions between two sea turtle egg predators: raccoons and ghost crabs. However, the project was initiated by the analysis of intraspecific effects of raccoon removal when a predator removal program was implemented at Archie Carr National Wildlife Refuge (ACNWR) in 2003. That year was the first time the US Fish and Wildlife Service removed raccoons from ACNWR, although raccoons have been removed from Merritt Island National Wildlife Refuge (MINWR) since 1979. By comparing raccoons removed from ACNWR and MINWR, I was able to assess the effects of long-term removal on the raccoon population (Chapter 2).

Many factors, including predator removal and urbanization, have contributed to a mosaic pattern of raccoon density along Florida's east coast, which I studied at four sites (Figure 1.1). I used the variability of raccoon abundance as an experimental treatment to determine if raccoons limited the abundance of ghost crabs and examined how these two predators contributed to sea turtle egg mortality (Chapter 3). My results have important implications for resource managers interested in increasing sea turtle hatching success.

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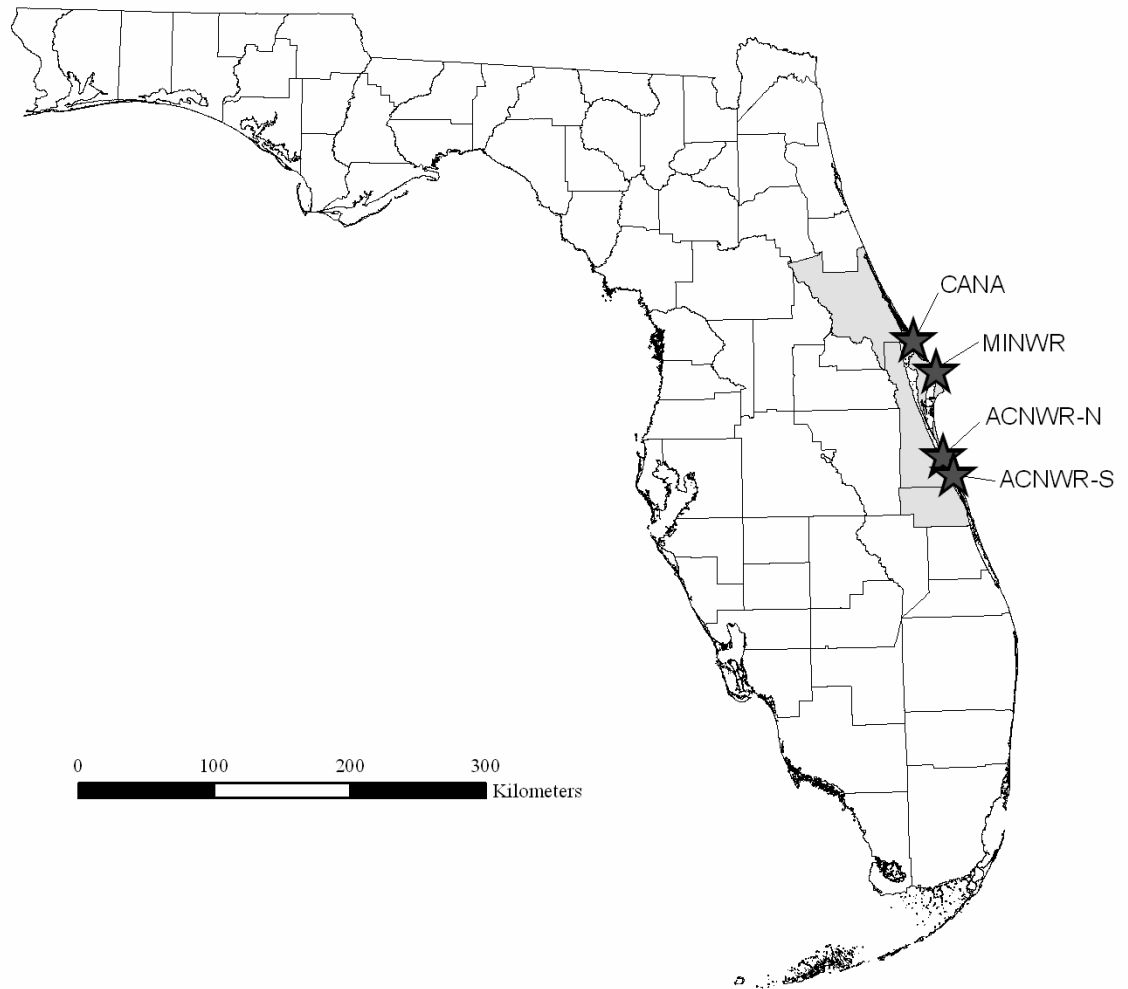


Figure 1. 1. Location of four study sites in east-central Florida.

CHAPTER TWO: INTRASPECIFIC EFFECTS OF RACCOON REMOVAL ON SEA TURTLE NESTING BEACHES

Raccoon (*Procyon lotor*) predation is one of the highest causes of egg mortality for sea turtles, with nearly 90% of the nests on some beaches in the southeastern United States suffering predation (Davis & Whiting 1977, Stancyk 1982). All four species of sea turtles that nest along the Atlantic coast of the United States are listed as threatened or endangered under the Endangered Species Act of 1973, requiring actions to protect and restore these species. Several management strategies have been employed to counteract the loss of eggs to predation, including screening nests with wire mesh and removing raccoons from nesting beaches (Ratnaswamy et al. 1997). Control of raccoons by trapping or shooting has been particularly effective at lowering sea turtle nest predation (Stancyk 1982).

Because of the damage done to sea turtle nests, raccoons have been removed from nesting beaches at the Merritt Island National Wildlife Refuge (MINWR) during the sea turtle nesting season since 1978 (Schroeder 1981, Ratnaswamy et al. 1997). These control measures have been quite effective at decreasing egg mortality caused by raccoon predation. In 1980, sea turtle nest predation was significantly lower in areas of beach where raccoons were removed (25%) compared to unmanipulated control areas (72%; Schroeder 1981). Overall, the rate of nest predation has decreased from over 90% prior to the implementation of control measures to less than 10% in recent years (Popotnik and Epstein 2002). In order to retain their effectiveness, the intensive removals have continued each year, since immigrants can quickly replace removed raccoons (Stancyk 1982).

Although removing predators is often a crucial for the conservation of threatened and endangered species (Stancyk 1982, Palorares et al. 1995), removing predators from ecosystems

can have dramatic consequences (Sih et al. 1985, Crooks & Soule 1999). I compared demographic characters and diet of raccoons removed from sea turtle nesting beaches to examine the intraspecific effects of raccoon removal. An analysis of raccoon populations on sea turtle nesting beaches was fundamental to understanding the cascading effects of raccoon removal throughout the community (Chapter 3). I compared the age structure, sex ratio, reproductive status and diet of raccoons captured on the nesting beach at MINWR and Archie Carr National Wildlife Refuge (ACNWR). This was the first year raccoons were removed from ACNWR, where levels of sea turtle nest depredation by raccoons have traditionally been around 70% on some stretches of beach (L. Ehrhart, University of Central Florida, unpublished data). The demographic characteristics of this historically unmanaged population provide a basis for comparison to the raccoon population that has been managed to control sea turtle nest predation at MINWR. These comparisons were intended to determine some of the intraspecific effects associated with predator removal.

I predicted that raccoon removal would create a population sink which would be filled by dispersing individuals. Male raccoons have larger home ranges and the tendency to move longer distances than females (Greenwood 1982, Walker and Sunkist 1997), therefore I predicted that the sex ratio of the managed population would be male-biased. I predicted that the age structure of the managed population would be skewed towards younger animals, due to natal dispersal (Stevens et al. 1995, Gehrt and Fritzell 1998). I also predicted that the body condition of raccoons from the managed population would be lower on average because they are recent dispersers to the area.

Methods

This study was conducted in east-central Florida on two study sites approximately 60 km apart. Raccoons were trapped and removed from the nesting beach at MINWR (28° 34' 57" N, -80° 34' 27" W) and ACNWR (27° 53' 40" N, -80° 27' 56" W) by U.S. Fish and Wildlife Service personnel as part of their management activities to enhance sea turtle nesting success. Raccoons were also removed from an Indian River County beach south of ACNWR, which, due to its close proximity, was included in the ACNWR data. Road-kill raccoons within ACNWR were collected along Highway A1A, all of which were within 100 m of the beach.

I determined body mass, body length, total length, hind foot length, sex and reproductive condition of each raccoon. Females were identified as reproductive by the presence of fetuses or swollen nipples. The lower mandible of each animal was removed behind the first molar and used to determine the age of individuals (Fancy 1980). Mandibles were x-rayed at the University of Central Florida Radiological Sciences Laboratory. I viewed backlit radiographs to determine the size of the pulp cavity of each incisor. Juveniles (< 1 year) were distinguished from adults (>1 year) by their open root canals compared to the partially or completely closed root canal of adults (Grue and Jensen 1976, Kuehn and Berg 1981).

I removed the stomach of each individual and quantified diets by examining the stomach contents from each raccoon to determine the specific foods ingested and the frequency of occurrence of foods (see Anthony et al. 2000). Food items were stored in 90% ethanol. Parasites within stomachs were also recorded and frozen. Organismal stomach contents were identified to the lowest possible taxonomic level.

I compared several characteristics of raccoons removed from the two beaches, including capture date, sex ratio, age structure, morphology and diet. An index of body condition was calculated by dividing body mass by hind foot length (Krebs and Singleton 1993). Body mass

and length were log-transformed prior to statistical analyses. Frequencies of diet categories were compared using Chi-square analysis for common food types, or the Fisher Exact Test when expected frequencies were less than five (Zar 1999).

Results

I sampled 58 raccoons that were collected between April and October 2003. Twenty-three raccoons were collected from MINWR and 35 from ACNWR (including six road-killed individuals). Comparing road killed to beach-trapped animals from ACNWR, there were no differences in mass ($t_{31} = 0.80$, $p = 0.43$), sex (Fisher Exact Test, $p=0.70$), age (Fisher Exact Test, $p = 0.50$), date of collection ($t_{31} = 0.46$, $p = 0.65$), or latitudinal location ($t_{30} = 0.996$, $p = 0.33$), so road kill animals were included in the ACNWR data.

Capture dates differed between the two beaches ($t_{54} = 4.8$, $p < 0.001$; Figure 2.1). There was a significant difference in sex ratio of raccoons captured at the two beaches ($\chi^2 = 10.02$, $p = 0.0015$). The difference in adult sex ratio was even greater ($\chi^2 = 10.67$, $p = 0.0011$), with females dominating the adult captures at ACNWR and males dominating the captures at MINWR (Figure 2.2). No juvenile females were captured at either beach. The ratio of juveniles to adults did not differ between the beaches, either overall ($\chi^2 = 0.09$, $p = 0.76$) or just within males ($\chi^2 = 1.57$, $p = 0.21$). Six of the 17 females captured in ACNWR were pregnant or lactating, while neither of the two MINWR females were pregnant or lactating.

Physical properties (mass, body length, body condition) of raccoons captured on the two beaches did not differ (Figure 2.3; mass $F_{1,54} = 0.67$, $p = 0.42$; length $F_{1,55} = 0.85$, $p = 0.36$; condition $F_{1,54} = 0.77$, $p = 0.38$), nor were there significant differences between males and females (mass $F_{1,54} = 0.003$, $p = 0.96$; length $F_{1,55} = 0.046$, $p = 0.83$; condition $F_{1,56} = 0.401$, $p =$

0.53). The reproductive condition (gestating or lactating vs. non-reproductive) of adult females did not affect mass ($F_{1,14} = 2.42$, $p = 0.14$) or body condition ($F_{1,14} = 1.24$, $p = 0.28$), but the body length of reproductive females was longer ($F_{1,15} = 6.17$, $p = 0.025$).

The stomach contents for 55 raccoons (ACNWR, $n = 32$; MINWR, $n = 23$) are summarized in Table 2.1. Hair, fruits and vegetation had the highest frequency of occurrence in the stomachs of both populations (Figure 2.4). There were no significant differences among the beaches in the occurrence of remains of turtle (Fisher Exact Test, $p = 0.19$), crustacean ($p = 0.38$), insect/arachnid ($p = 0.57$), lizard ($p = 0.59$), stomach parasites ($\chi^2 = 1.81$, $p = 0.18$), or empty stomachs ($p = 0.14$). Plant matter (berries, seeds and other vegetation) was found more often in ACNWR raccoons ($\chi^2 = 10.47$, $p = 0.001$), although occurrence of animal matter did not differ between the beaches ($\chi^2 = 2.67$, $p = 0.10$). At ACNWR, road-killed raccoons had a significantly higher proportion of empty stomachs compared to beach-trapped animals ($\chi^2 = 9.07$, $p = 0.003$). Among beach-trapped raccoons, raccoons at MINWR had a significantly higher proportion of empty stomachs compared to raccoons from ACNWR ($\chi^2 = 6.32$, $p = 0.012$).

Discussion

Differences in the distribution of capture dates between the two beaches (Figure 2.1) may reflect differences in the trapping strategies employed. At MINWR, traps were set every night throughout the sea turtle nesting season, one trap per km along the entire 10 km stretch of beach. At ACNWR, traps were usually set in areas where nest depredations had started to occur, after being identified as problem areas by personnel monitoring turtle nesting activity. Thus, the preventative management strategy at MINWR focused captures at the beginning of the nesting season, prior to raccoons having the opportunity to inflict damage on turtle nests. The responsive

management strategy at ACNWR tracked depredation events, which are related to nesting activity, and therefore raccoon captures followed nesting activity patterns more closely, with a short lag until depredation rates increased (peak loggerhead turtle nesting occurs in late June; Weishampel et al. 2004).

The frequency of occurrence of turtle eggs and hatchlings consumed on the two beaches was statistically indistinguishable, which may imply that both strategies were equally effective. However, nest fates (proportion of eggs consumed by predators) may better reflect the effectiveness of these management strategies (see Chapter 3).

The observed male-biased sex ratio in the MINWR population was a predicted result of long-term raccoon removal, which likely has removed all resident raccoons within close proximity of the beach. Males typically have larger home ranges and move farther than females (Walker and Sunkist 1997), so it is likely that the raccoons found on the beach at MINWR are recent immigrants into the area. The greater frequency of empty stomachs at MINWR also suggests these raccoons had recently dispersed into the area. I expected the age structure at MINWR to be skewed toward younger animals, which disperse from natal areas and are displaced to less desirable habitat by mature individuals (Gehrt and Fritzell 1998). Analysis of the population's age structure did not show any significant differences when raccoons were grouped into two groups, juvenile and adult (Figure 2.2).

The high percentage of adult females, many of which were reproductive, captured at ACNWR may be due to the high protein and energy requirements of gestation and lactation (McLean 1999). Beaches receive large quantities of animal matter and carrion from the ocean (Polis and Hurd 1996) and reproductive females may prefer to forage in such habitats where they are more likely to meet their inflated nutritional demands. Ratnaswamy (1995) found that female

raccoons in Canaveral National Seashore increased their use of beach habitat during the sea turtle nesting season in one of two years. However, she did not compare reproductive females with non-reproductive females or males with females, and concluded that the raccoon population did not respond to the seasonal availability of sea turtle eggs with any dramatic shifts in use of beach habitat or changes in home ranges.

The highway on which road kills were collected (Highway A1A) divides ACNWR into two sections, beach habitat and inland habitat, and raccoons found on the highway were crossing from one habitat to the other. The absence of food in the stomachs of two-thirds of those animals suggests they did not forage in the habitat from which they were leaving. However, virtually all (96%) beach-caught raccoons had foraged recently, suggesting the road-killed raccoons were probably moving from the inland habitat to the beach to forage. This difference may indicate that the beach has greater foraging value or opportunities than the inland habitat.

My analysis of the raccoons within ACNWR and MINWR revealed much similarity in diet. The only documented difference in diet between the two populations was the increased occurrence of plant matter at ACNWR raccoons. This may be due in part to the higher degree of urbanization on the ACNWR in comparison to MINWR that may have resulted in a higher availability of more ornamental and fruit-producing plants.

The comparison between MINWR and ACNWR is confounded by the lack of replication since management activities are not the only factors that differ between the beaches and can impact the raccoon populations (e.g., food availability, human influence). However, any information on the diet of these animals or the effects of management on the population structure could be useful for developing management strategies involving this important predator.

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Table 2. 1. Stomach contents of raccoons removed from MINWR (n=23) and ACNWR (n=32). Values are total number of stomachs with food types present.

Food Category	MINWR	ACNWR
Hair/fur	10	16
Fruit/seed/berry	6	16
Brazilian pepper (<i>Schinus terebinthifolius</i>)		
Saw palmetto (<i>Serona repens</i>)		
Sand bean (<i>Strophostyles helvula</i>)		
Gallberry Holly (<i>Ilex glabra</i>)		
Greenbrier (<i>Smilax sp.</i>)		
Grapevine (<i>Vitis sp.</i>)		
Other vegetation	6	16
Turtle	1	5
Crustacean	2	1
Ghost crab (<i>Ocypode quadrata</i>)		
Reptile	0	1
Brown Anole (<i>Anolis sagrei</i>)		
Other Invertebrates	5	6
Roaches (Order: Blatara)		
Blue Dasher (<i>Pachydiplax longipennis</i>)		
Carolina Saddlebags Dragonfly (<i>Tramea carolina</i>)		
Orb weavers (Family: Araneidae)		
Beetles (Family: Carabidae)		
Giant Water Bug (Family: Belostomitidae)		
Grasshoppers (Family: Acrididae)		
Chafers (<i>Anomala sp.</i>)		
Garbage	1	4
Plastic		
Paper		
Empty stomachs	7	5

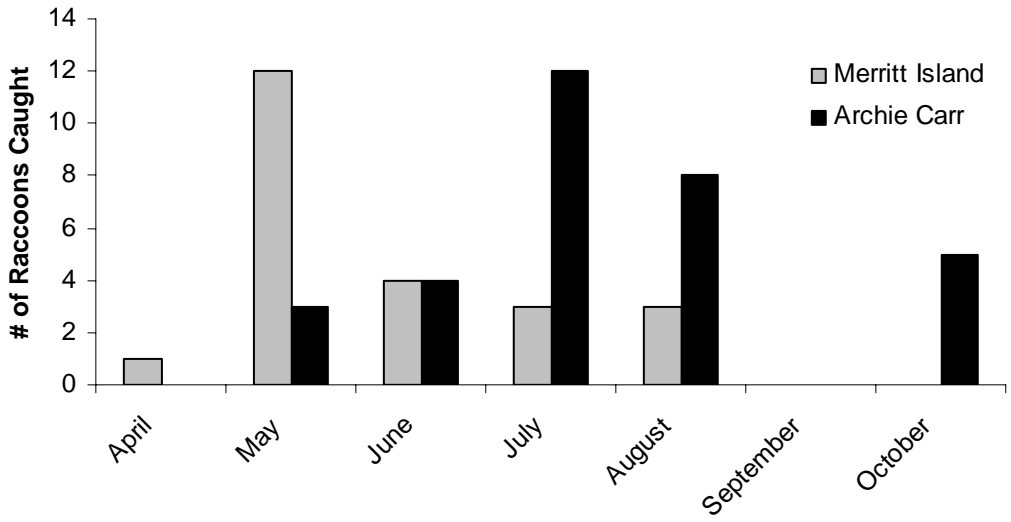


Figure 2. 1. Monthly captures of raccoons removed from ACNWR and MINWR in 2003.

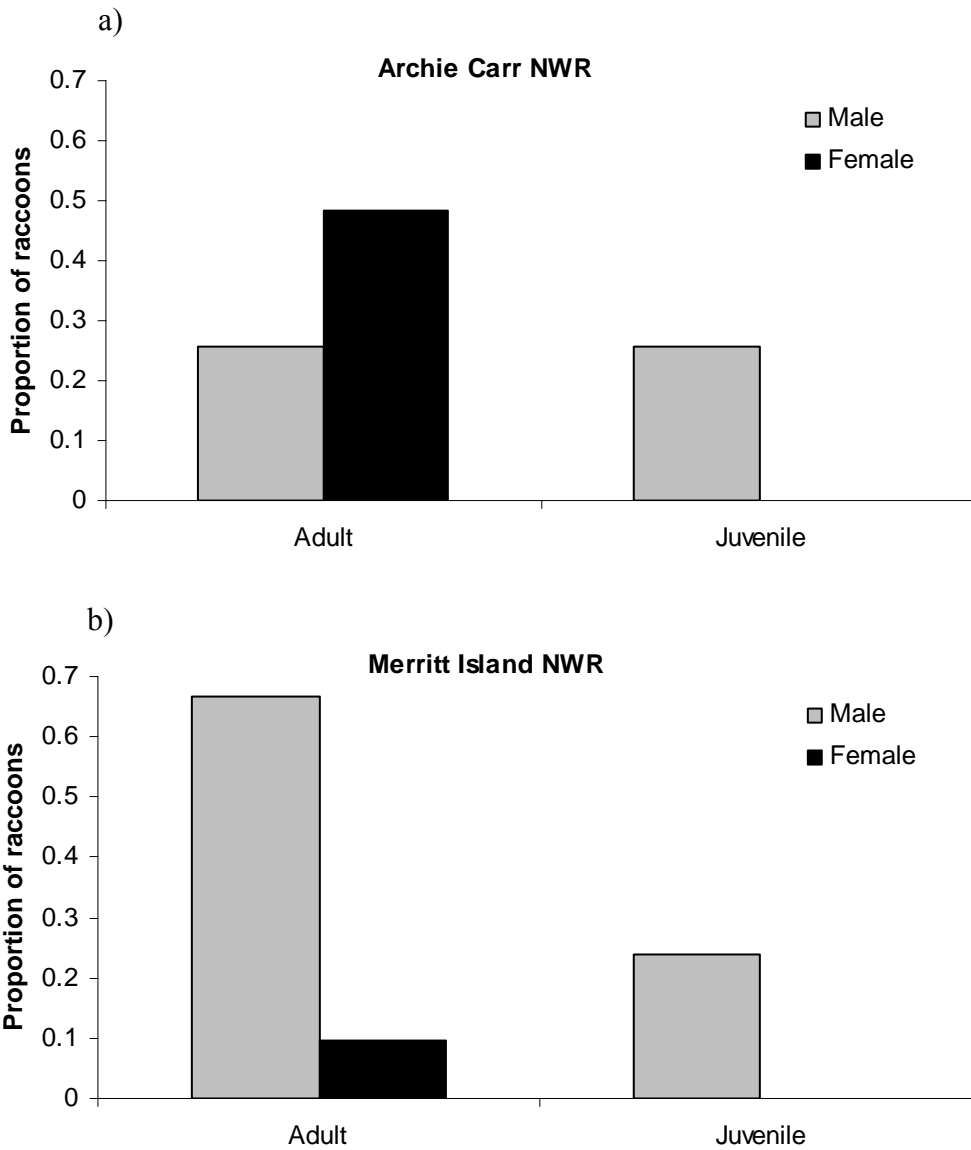


Figure 2. 2. Proportion of raccoons in each age/sex class captured at ACNWR (a, n = 29) and MINWR (b, n = 21).

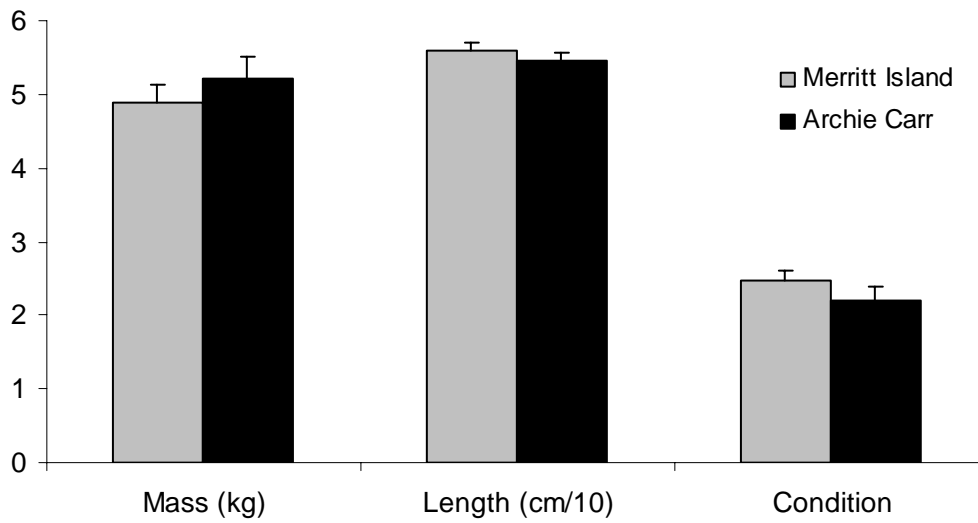


Figure 2. 3. Morphological characteristics of raccoons captured at ACNWR (n = 35) and MINWR (n = 23). Body length was divided by 10 for display purposes. Body condition was calculated as hind foot length (cm) divided by body mass (kg).

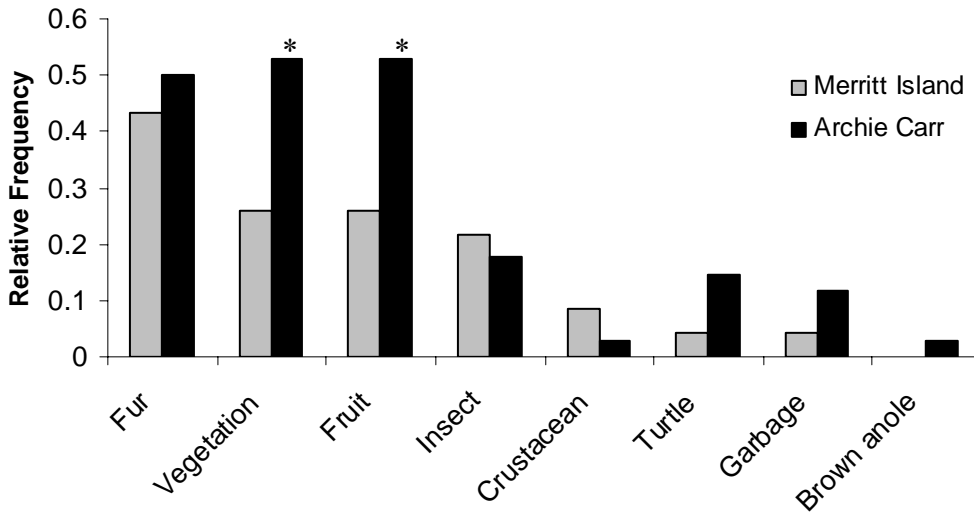


Figure 2. 4. Stomach contents of raccoons captured at ACNWR (n= 32) and MINWR (n = 23). Values were calculated as the proportion of raccoons with that food type present in the stomach. * indicates stomach contents which differ significantly between study sites.

CHAPTER THREE: CASCADING EFFECTS OF RACCOON REMOVAL ON SEA TURTLE NESTING BEACHES

Intraguild predation (IGP) is the killing and eating of one species by a potential resource competitor (Polis and Holt 1992). Thus, the benefits of IGP to the predator are two-fold—the nutritional benefit from consumption and increased resource availability due to reduced competition (Polis et al. 1989, Gerber and Echternacht 2000). This dual interaction can strongly affect community structure and composition (e.g., Palomares et al. 1995, Stapp 1997, Fedriani and Fuller 2000, Roemer et al. 2002). IGP is widespread in ecological communities (Arim and Marquet 2004) and among a diverse array of taxa, including arachnids (Polis and McCormick 1986), insects (Sato et al. 2003), amphibians (Cortwright 1988), reptiles (Gerber and Echternacht 2000) and mammals (Doncaster 1992). However, IGP is most frequent among size-structured populations with generalist predators and is virtually ubiquitous when smaller predators are present (Polis et al. 1989).

The theory of mesopredator release (MPR) is useful in explaining cascading, indirect interactions among top predators, secondary predators and prey species (Soulé et al. 1988, Terborgh et al. 1999). Mesopredators are typically medium-sized omnivores and nest predators (Rogers and Caro 1998), but a species may be considered a mesopredator in one system and the top predator in another (see: Courchamp et al. 1999, Crooks and Soulé 1999). MPR involves the increased abundance of mesopredators following the decline of top predators and results in increased exploitation of species at lower trophic levels (Palomares et al. 1995, Crooks and Soulé 1999, Schmidt 2003). MPR explains numerical relationships in species abundance, however does not make assumptions about the mechanism by which top predators influence mesopredators. Top predators can limit mesopredator abundance directly (interference

competition and predation) or indirectly (behavioral avoidance and displacement). MPR can be the result of IGP, however both theories can exist independently.

According to MPR theory, top predators are integral for management and conservation of prey species. Palomares et al. (1995) argued that Iberian lynx (*Felis pardina*) limited mongoose (*Herpestes ichneumon*) densities, which benefited rabbit (*Oryctolagus cuniculus*) populations. Courchamp et al. (1999) demonstrated the conservation value of feral cats (*Felis catus*) to the endangered kakapo (*Strigops habroptilus*) by controlling exotic mesopredator rodents (*Rattus* sp.).

The theories of IGP and MPR have reshaped the way ecologists examine trophic interactions within communities. These two theories suggest that trophic interactions can be indirect (Soulé et al. 1988) and nonlinear (Polis et al. 1989). The combined effects of IGP and MPR can amplify the impacts of multispecies interactions on the community. Although most research to date has examined IGP and MPR independently, the inclusion of both theories is necessary to understand some predator-prey systems (e.g., Palomares et al. 1995). In such a system, top predators are limited by competition, mesopredators are limited by predation and competition, and prey species are limited by predation from both predators. I report another example of the effects and implications of IGP and MPR in a raccoon (*Procyon lotor*), ghost crab (*Ocypode quadrata*), and sea turtle system on east-central Florida beaches.

Egg predation by raccoons and ghost crabs accounts for nearly all loggerhead turtle (*Carretta caretta*) depredations in the United States (Davis and Whiting 1977, Stancyk 1982, Osegovic 2001). All four species of sea turtles that nest along the Atlantic coast of the United States are listed as threatened or endangered under the Endangered Species Act of 1973, requiring actions to protect and restore these species. Several management techniques have been

implemented to decrease raccoon depredation on sea turtle nests, including lethal removal of raccoons from sea turtle nesting beaches (Stancyk 1982). Ratnaswamy and Warren (1998) hypothesized that the indirect effects of raccoon removal could result in increased ghost crab abundance, adversely affecting sea turtle conservation.

I compared the abundance of raccoons and ghost crabs on four east-central Florida sea turtle nesting beaches to better understand the relationship between these two predators and the implications of this interaction for sea turtle conservation. Because ghost crabs can reach high densities in the absence of heavy predation (Burggren and McMahon 1988) and raccoons are ghost crab predators (Tyson 1950, Ratnaswamy et al. 1997), I predicted that raccoon and ghost crab abundance would be inversely related. Optimal foraging theory (Křivan 1996) and personal observations from raccoon stomach contents and kill sites suggests raccoons selectively forage on larger ghost crabs. Accordingly, I predicted that when raccoon abundance was low, an increased abundance of large ghost crabs would result in higher net sea turtle egg loss (combined mortality due to raccoons and ghost crabs). My results demonstrate the complexity of trophic interactions on sea turtle nesting beaches and have direct implications for sea turtle conservation.

Methods

Study sites

I conducted this study at four sites along Florida's east coast. The field season began on 1 May 2004 and ended on 30 August 2004. I established one study site at Canaveral National Seashore (CANA), one study at Merritt Island National Wildlife Refuge (MINWR) and two sites at Archie Carr National Wildlife Refuge that were separated by 13.5 km (ACNWR-N and ACNWR-S). Predator management strategies differed among these sites during the 2004 study

period in terms of the removal of raccoons and the placing of wire mesh screens over nests to deter raccoon predation. At CANA, managers did not remove raccoons but did screen sea turtle nests (described below). At MINWR, raccoons were removed and nests were not screened and at ACNWR (North and South) raccoons were not removed and nests were not screened (although a single year of trapping had been conducted in 2003).

Tracking plots

I estimated raccoon and ghost crab abundance at each site with passive tracking methodology similar to Engeman et al. (2003). Each site contained 11 tracking plots spaced at 200 meter intervals. A single wooden stake was placed at the dune-beach boundary to denote the center of each tracking plot and ensure consistent sampling. Plots were constructed within one hour of sunset by raking a two-meter wide strip of smoothed sand, extending from dune base to below the current water level. As high tide approached, the water would erase the bottom of the plot so that I could easily determine the high tide line for that night. The time at which high tide occurred varied nightly, therefore I did not count any tracks or ghost crab burrows below high tide. I returned to the site within one hour of sunrise the following morning to record the total number and species of any tracks that crossed each plot. I recorded the distance from the dune to the high tide line (to determine plot area and available beach habitat) and dune to any tracks or burrows present. I recorded the total number and diameter of ghost crab burrows that were constructed within each plot during the night. Burrow diameter is approximately equal to carapace width (Fisher and Tevesz 1979) and therefore was used to determine mean ghost crab size at each site. I calculated predator abundance as the mean number of tracks or burrows per plot per night, and ghost crab density as the number of burrows per plot divided by plot area.

All tracks and burrows were erased by raking the plot and sampled for two consecutive nights. I sampled two sites each week and returned to sites on alternating weeks between May and August. The only exception to this schedule was failing to sample during one period (27–28 July 2004) at MINWR because beach access was restricted due to Kennedy Space Center activities. For all variables investigated, I calculated the mean for the sampling period and finally the mean for each month (May—August).

Sample Nests

Loggerhead nest depredation rates were determined by sampling a subset of nests laid at each site. Newly laid nests were located while the turtle was nesting or the following morning during daily surveys of nesting activity. Egg chambers were located by digging into the nest by hand, and were marked with wooden stakes. Clutches at CANA were then covered with a wire screen (approximately 1m x 1m with 15cm x 15cm mesh) secured with metal stakes at each corner and covered with sand so that the screen was not visible. At ACNWR, clutch size was determined by removing each egg from the egg chamber and counting the total number of eggs laid. This process does not affect egg fate if conducted within 12 hrs of egg deposition (L. M. Ehrhart, personal communication). Extreme care was taken to prevent injury to the eggs while counting. Nests were monitored on daily morning surveys and depredations were noted.

Determining depredation rates

I determined egg fate in each nest after an incubation period of 70 days, or within one week of hatchling emergence. The number of eggs hatched, unhatched and depredated by each predator was determined by examining the remains of each nest (Table 3.1). I calculated total clutch size as the sum of these values. I marked 25 loggerhead nests at each study site, but significant beach erosion and destruction of many of my study nests during the hurricane season

reduced sample sizes at all sites. Differences in protocols for determining egg fates prohibited using data collected by agency personnel at CANA and MINWR to increase my sample size, but the protocol used by UCFMTRG at ACNWR was identical to ours. I incorporated data from sea turtle nests sampled by UCFMTRG one kilometer north and south of my study sites to increase my samples size (CANA: $n = 14$; MINWR: $n = 10$; ACNWR-N: $n = 20$; ACNWR-S: $n = 10$).

I calculated two measures of predator depredation: nest depredation rate and egg depredation rate. Nest depredation rates were calculated by dividing the number of depredated nests by the total number of nests. Egg depredation rates in nests with a predetermined clutch total were calculated by dividing the number of depredated eggs by the total clutch size. For nests without a predetermined clutch size, the total number of depredated eggs could not be determined directly because raccoons usually remove the shells of consumed eggs. However, over the last 18 years at ACNWR, the proportion of eggs removed from raccoon depredated nests averaged 0.757 (± 0.021 SE, $n = 247$, L. M. Ehrhart, unpublished data). Therefore, I assumed 75% egg depredation for nests depredated by raccoons when clutch size had not been predetermined.

Statistical analysis

Raccoon abundance, ghost crab abundance, ghost crab density, ghost crab size, raccoon track distance to the dune, ghost crab burrow distance to the dune, and high tide distance to the dune were compared among sites using a repeated measures analysis of variance and a Tukey HSD post hoc test. The proportion of sampling periods when raccoons were present was compared among sites with a Fisher exact test. I also used a Fisher exact test to compare the proportion of nests depredated by each predator among sites. The Fisher exact test allows for more accurate comparisons than a chi-square analysis, especially when frequencies are small

(Zar 1999). Egg depredation rates were compared among sites with an analysis of variance and Tukey HSD post hoc test. I examined the relationships between raccoon abundance, ghost crab abundance, density and size, raccoon and ghost crab distance to the dune, high tide to the dune and depredation rates using Spearman's rho correlation. All analyses were considered significant at $\alpha = 0.05$.

Results

Tracking plots

I recorded a diverse array of potential sea turtle nest predators at my study sites (Table 3.2). The diversity and overall abundance of mammalian nest predators was highest at CANA and MINWR, and lowest at the two ACNWR sites. Raccoon abundance increased over time at CANA, ACNWR-N, and ACNWR-S (Figure 3.1a; $r_s = 1.00$, $n = 4$, $p = 0.01$), but not at MINWR ($r_s = -0.738$, $n = 4$, $p < 0.262$). Ghost crab density decreased over time at CANA (Figure 3.1b; $r_s = -1.00$, $n = 4$, $p < 0.001$), but not at MINWR ($r_s = 0.60$, $n = 4$, $p = 0.40$), ACNWR-N ($r_s = -0.80$, $n = 4$, $p = 0.20$), or ACNWR-S ($r_s = -0.80$, $n = 4$, $p = 0.20$). Raccoon abundance differed significantly among sites (Figure 3.2a; $F_{3,40} = 6.02$, $p = 0.002$). MINWR had the lowest mean raccoon abundance but differed significantly only from ACNWR-S (Tukey HSD, $p < 0.001$). Raccoons were present during every sampling period at CANA and ACNWR-S, 88% of the sampling periods at ACNWR-N and 57% of sampling periods at MINWR (Table 3.3). The proportion of sampling periods with raccoons present did not differ among sites (Figure 3.2b; Fisher exact test, $p \geq 0.063$), but raccoons tended to be present less frequently at MINWR than at CANA (Fisher exact test, $p = 0.077$) and ACNWR-S (Fisher exact test, $p = 0.063$).

Ghost crab abundance differed among sites (Figure 3.3a; $F_{3,40} = 77.33$, $p < 0.001$). Ghost crabs were most abundant at MINWR (Tukey HSD, $p < 0.001$), but did not differ among the other sites (Tukey HSD, $p \geq 0.182$). The density of ghost crabs differed among sites (Figure 3.3b; $F_{3,40} = 17.72$, $p < 0.001$). Ghost crab density was highest at MINWR (Tukey HSD, $p < 0.001$) and lowest at ACNWR-S (Tukey HSD, $p \leq 0.031$). Ghost crab burrow diameter was largest at MINWR (Figure 3.4; $F_{3,39} = 51.88$, $p < 0.001$; Tukey HSD, $p < 0.001$).

The distance from the dune to high tide line differed among sites (Figure 3.5a; $F_{3,40} = 53.80$, $p < 0.001$). The mean distance of ghost crab burrows to the dune differed among sites (Figure 3.5b; $F_{3,39} = 23.84$, $p < 0.001$), however the mean distance of raccoon tracks to the dune did not ($F_{2,3} = 6.13$, $p = 0.87$).

Raccoon abundance was inversely correlated with ghost crab abundance (Figure 3.6a; $r_s = -1.00$, $n = 4$, $p < 0.001$) and ghost crab density (Figure 3.6b; $r_s = -1.00$, $n = 4$, $p < 0.001$). Ghost crab size was not correlated with raccoon abundance (Figure 3.7; $r_s = -0.20$, $n = 4$, $p = 0.80$), ghost crab abundance ($r_s = 0.20$, $n = 4$, $p = 0.80$), or ghost crab density ($r_s = 0.20$, $n = 4$, $p = 0.80$). Beach width (distance from dune to high tide) was not correlated with raccoon abundance ($r_s = -0.40$, $n = 4$, $p = 0.60$), ghost crab abundance ($r_s = 0.40$, $n = 4$, $p = 0.60$) or ghost crab density ($r_s = 0.40$, $n = 4$, $p = 0.60$).

Depredation rates

The proportion of nests depredated by raccoons differed between MINWR and ACNWR-N (Figure 3.8a; Fisher exact test, $p = 0.03$) and tended to differ between MINWR and CANA (Fisher exact test, $p = 0.059$). The proportion of nests depredated by ghost crabs did not differ among sites (Fisher exact test, $p \geq 0.62$), except ACNWR-N tended to have more ghost crab depredated nests than CANA (Fisher exact test, $p = 0.08$). The proportion of eggs depredated by

raccoons differed among sites (Figure 3.8b; $F_{3, 50} = 3.74$, $p = 0.017$), with raccoon egg depredation at MINWR significantly higher than at CANA (Tukey HSD, $p = 0.037$) and ACNWR-N (Tukey HSD $p = 0.037$; no other pairwise comparisons were significant, Tukey HSD, $p > 0.41$). The proportion of eggs depredated by ghost crabs did not differ among sites ($F_{3, 47} = 2.07$, $p = 0.118$). The proportion of eggs depredated by raccoons and ghost crabs combined tended to differ among sites ($F_{3, 50} = 2.72$, $p = 0.055$), with MINWR suffering higher overall egg depredation rates than CANA (Tukey HSD, $p = 0.038$).

I compared egg depredation rates with mean predator abundance at each site and found no relationship between raccoon abundance and the proportion of eggs depredated by raccoons ($r_s = -0.316$, $n = 4$, $p = 0.68$), the proportion of eggs depredated by ghost crabs ($r_s = 0.00$, $n = 4$, $p = 1.00$), or net egg depredation ($r_s = -0.200$, $n = 4$, $p = 0.80$). Likewise, I found no relationship between ghost crab abundance and the proportion of eggs depredated by raccoons ($r_s = 0.316$, $n = 4$, $p = 0.68$), the proportion of eggs depredated by ghost crabs ($r = 0.00$, $n = 4$, $p = 1.00$), or net egg depredation ($r_s = 0.20$, $n = 4$, $p = 0.80$). I found no relationship between ghost crab density and the proportion of eggs depredated by raccoons ($r_s = 0.316$, $n = 4$, $p = 0.68$), the proportion of eggs depredated by ghost crabs ($r = 0.00$, $n = 4$, $p = 1.00$), or net egg depredation ($r_s = 0.20$, $n = 4$, $p = 0.80$). However, net egg depredation increased with ghost crab size (Figure 3.9; $r_s = 1.00$, $n = 4$, $p = 0.01$). Although ghost crab egg depredation and ghost crab size were unrelated ($r_s = 0.40$, $n = 4$, $p = 0.60$), egg depredation by raccoons tended to increase with ghost crab size ($r_s = 0.949$, $n = 4$, $p = 0.051$).

Discussion

My results suggest that raccoons can limit the abundance of ghost crabs on sea turtle nesting beaches where they co-occur. As predicted, raccoon and ghost crab abundances were negatively correlated (Figure 3.6a). Although beach width (i.e., available habitat) did not affect ghost crab abundance, I calculated ghost crab density to control for the potential effects of beach width and found that raccoon abundance and ghost crab density were negatively correlated (Figure 3.6b).

Raccoons have previously been described as ghost crab predators elsewhere (Tyson 1950, Ratnaswamy et al. 1997). In my analysis of raccoon stomach contents at ACNWR and MINWR, ghost crab remains were present in 3.13% and 8.70% of stomachs, respectively (Figure 2.4). I have identified the remains of up to three ghost crabs depredated by a single raccoon in one night by tracking animals on the beach. Raccoons are indeed ghost crab predators, which is the causal element explaining the negative correlation in predator abundance, and it appears that raccoon predation indeed limited ghost crab abundance on my study sites.

The variation in raccoon abundance is probably the result of differing management strategies and levels of urbanization among sites. Raccoon abundance was higher at ACNWR-S than other sites, probably because human activity provides additional resources for them to exploit. Conversely, raccoon abundance was lowest at MINWR, where there is little evidence of urbanization and raccoons are trapped annually. Raccoon abundance is often inflated in urbanized areas (Engeman et al. 2003), but the effects of human disturbance on ghost crabs are debated. Barros (2001) concluded that ghost crab abundance was decreased at urban beaches, which is another hypothesis explaining the negative correlation between raccoon and ghost crab abundance. However, he defined urban beaches by the presence of a sea wall—a concrete wall above the dune that is usually constructed to protect buildings from erosion. Sea walls alter the

beach landscape and prohibit ghost crabs from accessing the dune. There were no sea walls present at any of my study sites, therefore the conclusions made by Barros (2001) are probably not applicable to my study. Most studies examining the affect of human activity on ghost crab abundance have found a positive correlation between these two variables (Steiner and Leatherman 1981, Strachan et al. 1999). Steiner and Leatherman (1981) reported ghost crab abundance was high on beaches with heavy pedestrian use and reduced in areas of high off-road vehicle traffic. They speculated that anthropogenic food sources maintain high ghost crab abundance. Although not quantified, off-road vehicle traffic (in the form of personal ATVs) appeared equivalent among my study sites and it is unlikely that direct human impact was responsible for the variation in ghost crab abundance that I observed.

My analysis of egg fates suggests ghost crabs are important sources of loggerhead egg mortality at all sites (Figure 3.8). Although I failed to detect a significant difference among egg or nest depredation rates by ghost crabs, this failure may be due to a small sample size. Interestingly, the site with the highest egg and nest depredation by raccoons also had the lowest raccoon abundance and highest ghost crab abundance and density. Previously research has suggested that ghost crab depredated nests are more likely to be depredated by raccoons (B. Witherington, unpublished data). Raccoons may be able to detect chemical cues from the eggs that are transmitted through ghost crab burrows to the beach surface. Inexperienced raccoons may learn to dig for sea turtle eggs through this mechanism (S. Murphy, South Carolina Department of Natural Resources, personal communication). Thus, ghost crabs may facilitate depredation by raccoons and appear to have increased the per capita rate of sea turtle nest and egg depredation rate by raccoons.

Mesopredator release theory predicts a negative relationship between top predator abundance and resource exploitation (Soulé et al. 1988, Palomares et al. 1995, Courchamp et al. 1999). My study sites did produce the pattern expected according to this theory: net egg depredation was highest where raccoon abundance was lowest. This observation has direct management implications since the goal of raccoon removal is to increase sea turtle hatching success by decreasing egg mortality. If ghost crab predation compensates for (or exceeds) raccoon depredation there is no net benefit to sea turtle conservation.

Anecdotal support of this relationship comes from ACNWR in the years preceding this study (L. Ehrhart, unpublished data). In 2002, raccoons depredated 3.3% of loggerhead eggs. Twenty-four raccoons were removed from ACNWR by the US Fish and Wildlife Service in 2003. The raccoon egg depredation rate decreased to 0.98% in 2004. However, egg depredation by ghost crabs increased from 3.4% in 2002 to 5.0% in 2004. The overall egg depredation rate after raccoon removal was not significantly different than before (6.0% and 6.7%; $F_{175, 768} = 1.058$, $p = 0.307$). Unfortunately, no data are available to determine if the increase in ghost crab depredation was the result of a numerical increase in ghost crab abundance or another mechanism such as reduced competition for eggs. Regardless of the mechanism, ghost crab induced egg mortality increased and compensated for reduced raccoon depredation and net egg depredation did not decrease.

The evidence presented here suggests intraguild predation by raccoons limits the abundance and density of ghost crabs and that raccoon removal can result in the release of ghost crabs and increase sea turtle egg mortality. I have examined only a small portion of the nesting beach food web. Raccoons have ecological connections with many components of coastal communities and their abundance may have diverse cascading effects beyond those explored in

this research (Ratnaswamy 1997). Ghost crabs are beach scavengers (Wellins et al. 1989), predators of small invertebrates and mollusks (Wolcott 1978) and shorebird eggs and chicks (Loegering et al. 1995, Watts and Bradshaw 1995). The interactions between raccoons and ghost crabs likely have additional consequences at other trophic levels that were not explored here.

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Table 3. 1. Description of characteristics used to distinguish sea turtle egg fates.

Egg fate	Description
Unhatched	Egg is whole and is not punctured
Hatched	Eggshell is empty/hollow and is dry, bright white or slightly gray in color, with a thin, paper-like consistency.
Broken	Eggshell has a thicker consistency than hatched eggs. Albumin residue remains on the inside of egg shell.
Ghost crab depredation	Egg appears hollow/desiccated, with an X- or box-shaped hole in eggshell. Albumin residue remains inside eggshell.
Raccoon depredation	The number of eggs missing from a nest that was previously identified as being depredated by raccoons (only possible if the total clutch size was determined before depredation).

Table 3. 2. Mean (+ SE) abundance of all potential sea turtle nest predators recorded at four east-central Florida beaches from May to August 2004. Mean abundance was calculated as predator tracks per night per site. "a" differs from "b" within rows (i.e., species) at $p < 0.05$.

	CANA	MINWR	ACNWR-N	ACNWR-S
Armadillo	0.01 ± 0.01^b	0.06 ± 0.03^a	0.0 ± 0.0^b	0.0 ± 0.0^b
Bobcat	0.37 ± 0.06^a	0.37 ± 0.07^a	0.01 ± 0.01^b	0.0 ± 0.0^b
Hog	0.0 ± 0.0^a	0.120 ± 0.121^a	0.0 ± 0.0^a	0.0 ± 0.0^a
Opposum	0.33 ± 0.08^a	0.18 ± 0.06^a	0.01 ± 0.01^b	0.0 ± 0.0^b
Raccoon	0.21 ± 0.04^a	0.12 ± 0.03^{ab}	0.27 ± 0.06^{ab}	0.46 ± 0.07^b
Skunk	0.0 ± 0.0^a	0.05 ± 0.02^a	0.0 ± 0.0^a	0.04 ± 0.02^a

Table 3. 3. Summary of data collected from four east-central Florida beaches from May to August 2004 (mean +SE).

	CANA	MINWR	ACNWR-N	ACNWR-S
Raccoon abundance (raccoon tracks per plot per night)	0.21 ± 0.04	0.12 ± 0.03	0.27 ± 0.06	0.46 ± 0.07
Proportion of sampling periods with raccoons present	1.00 (8/8)	0.57 (4/7)	0.88 (7/8)	1.00 (9/9)
Ghost crab abundance (burrows per plot per night)	3.46 ± 0.22	7.12 ± 0.58	2.83 ± 0.22	2.49 ± 0.15
Ghost crab density (ghost crab burrows m ²)	0.13 ± 0.01	0.19 ± 0.01	0.12 ± 0.01	0.09 ± 0.004
Ghost crab burrow size (cm)	1.47 ± 0.02	1.68 ± 0.05	1.48 ± 0.03	1.51 ± 0.03
Mean raccoon track distance from dune (m)	2.76 ± 0.28	3.19 ± 0.38	2.41 ± 0.29	2.40 ± 0.22
Mean ghost crab burrow distance from dune (m)	10.04 ± 1.15	19.67 ± 3.24	11.32 ± 1.83	12.01 ± 0.31
Mean high tide distance from dune (m)	14.22 ± 0.54	26.73 ± 1.19	13.93 ± 0.62	15.87 ± 0.41
Number of loggerhead nests sampled	14	10	20	10
Proportion of nests depredated by ghost crabs	0.36	0.71	0.70	0.50
Proportion of nests depredated by raccoons	0.00	0.20	0.00	0.20
Proportion of eggs depredated by ghost crabs	0.01 ± 0.01	0.12 ± 0.05	0.18 ± 0.06	0.07 ± 0.05
Proportion of eggs depredated by raccoons	0.00 ± 0.00	0.23 ± 0.12 ^a	0.00	0.12 ± 0.09
Total proportion of eggs depredated	0.01 ± 0.01	0.31 ± 0.10	0.18 ± 0.06	0.19 ± 0.10

^a Proportion of eggs depredated by raccoons was estimated as 75% of the total clutch (L. Ehrhart, unpublished data).

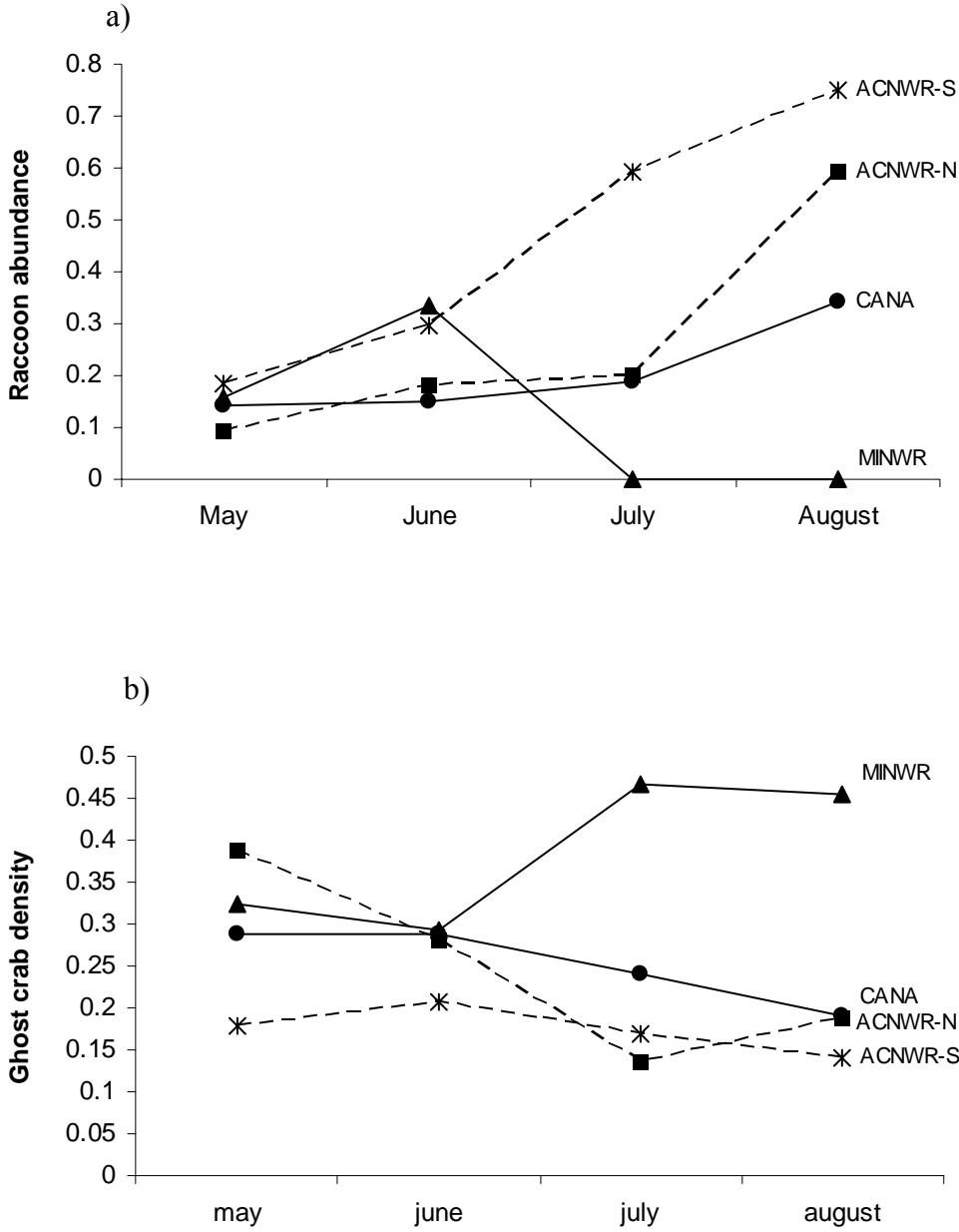


Figure 3. 1. Monthly mean raccoon abundance (a) and ghost crab density (b) at four east-central Florida beaches between May and August 2004. Raccoon abundance was calculated as the mean number of raccoon tracks per plot per sampling night. Ghost crab density was calculated as the mean number of ghost crab burrows per square meter.

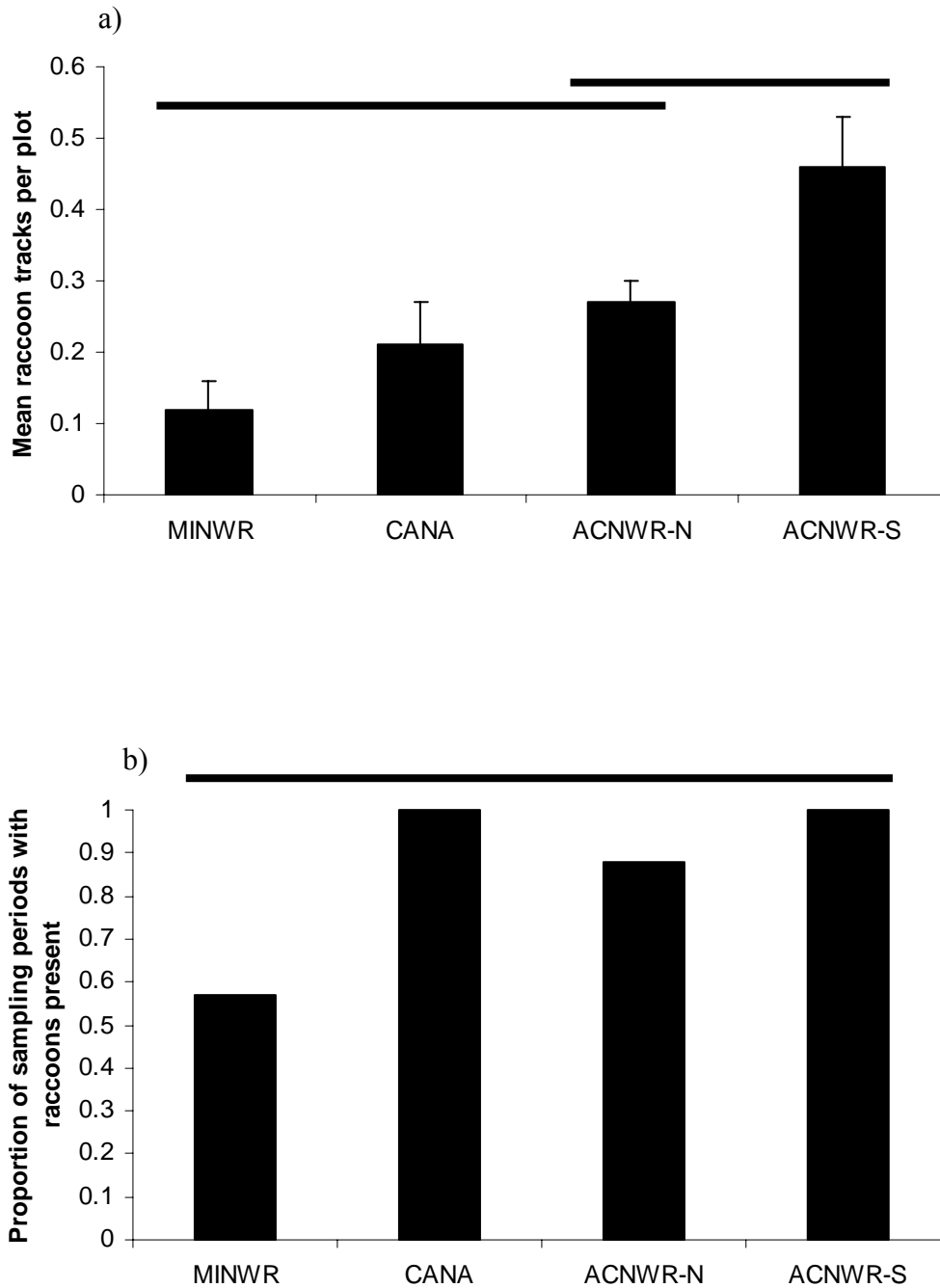


Figure 3. 2. Comparison of raccoon abundance (a) and frequency (b) at four east-central Florida beaches between May and August 2004. Abundance was calculated as the mean number of raccoon tracks per plot per sampling night. The solid horizontal bar denotes sites that are not significantly different at $p = 0.05$. Error bars represent standard error of the mean.

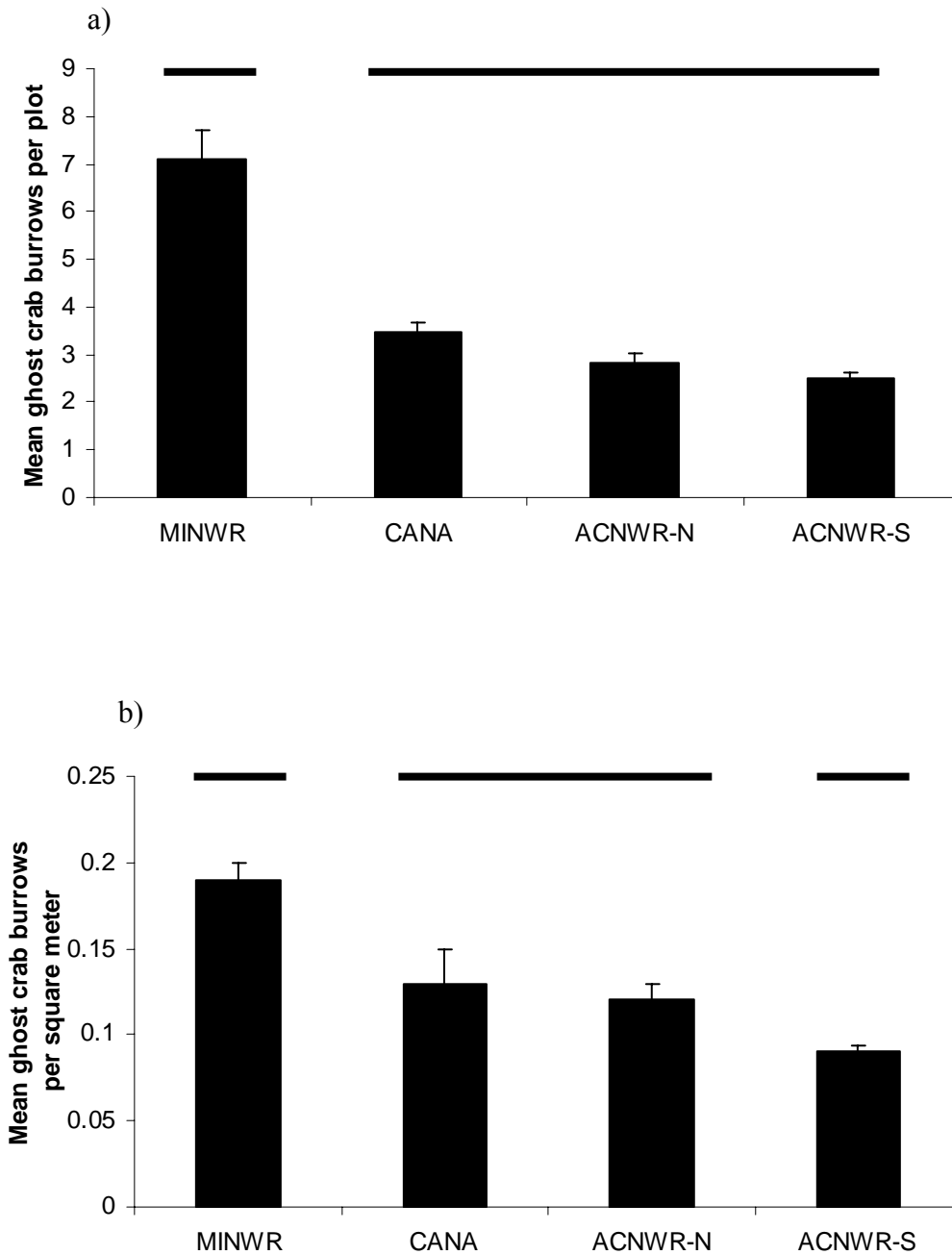


Figure 3. 3. Comparison of ghost crab abundance (a) and density (b) at four east-central Florida beaches between May and August 2004. Abundance was calculated as the mean number of ghost crab burrows per plot per sampling night. Density was calculated as the mean number of ghost crab burrows per square meter. The solid horizontal bar denotes which are not significantly different at $p = 0.05$. Error bars represent standard error of the mean.

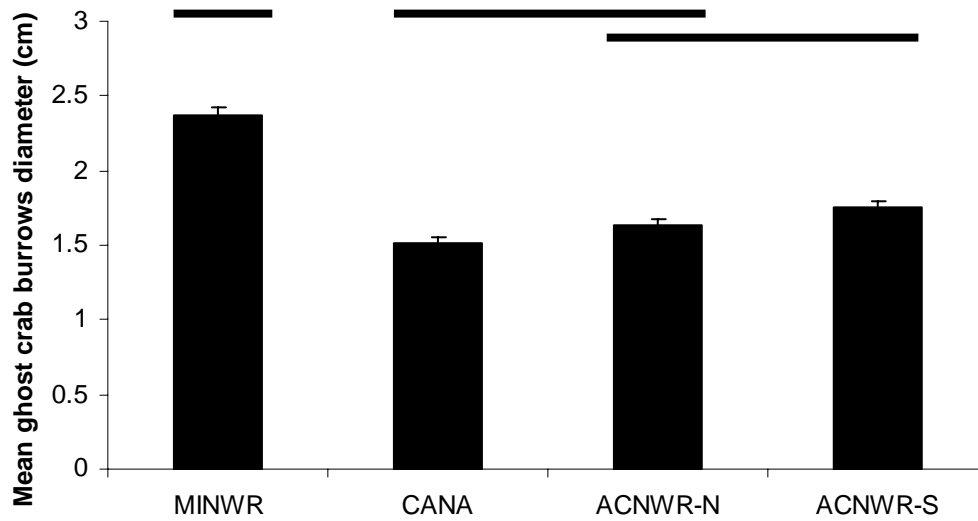


Figure 3. 4. Comparison of ghost crab burrow diameter at four east-central Florida beaches between May and August 2004. Burrow diameter is approximately equal to ghost crab carapace diameter, therefore was used to estimate ghost crab size. The solid horizontal bar denotes which are not significantly different at $p = 0.05$. Error bars represent standard error of the mean.

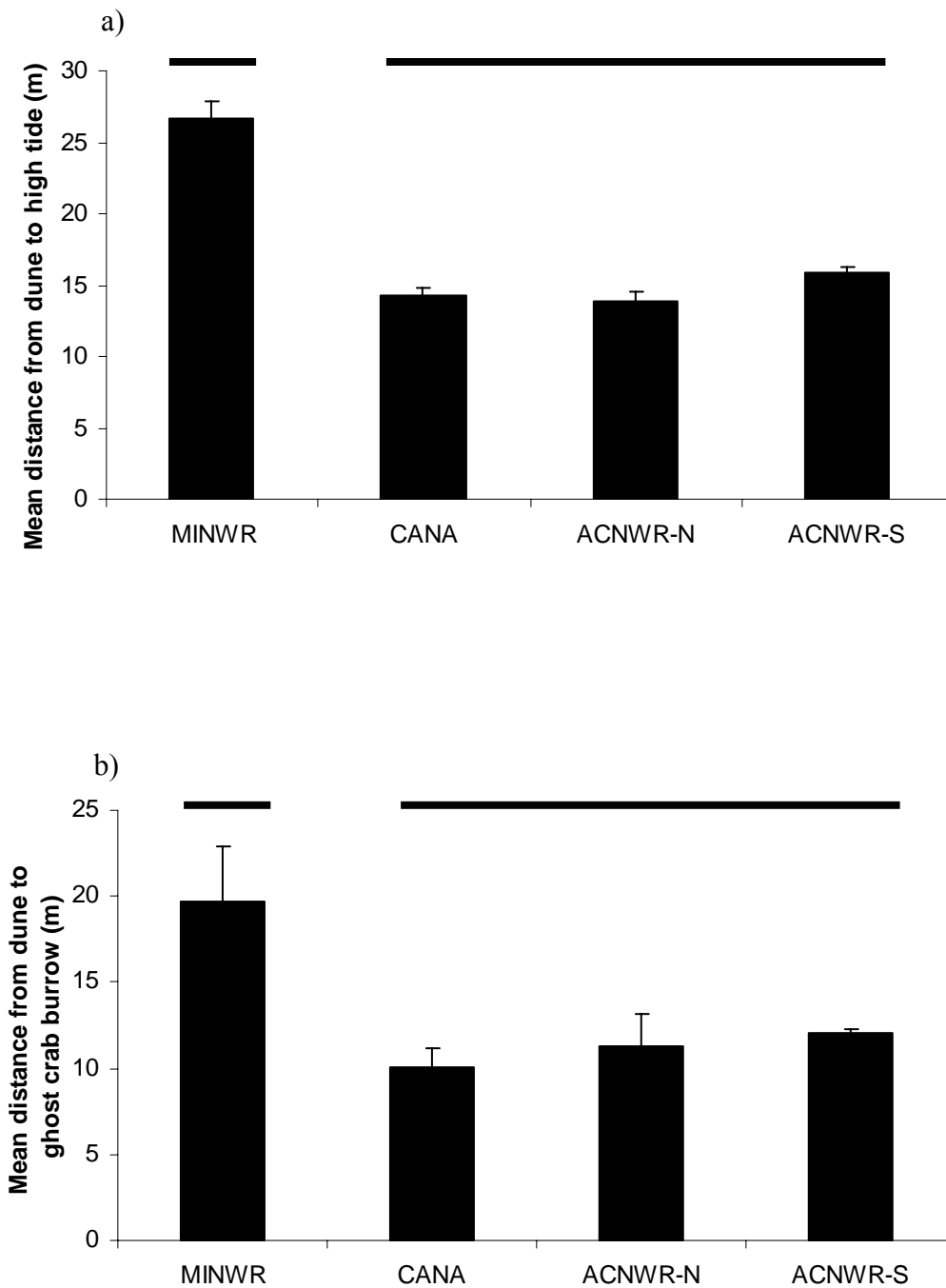


Figure 3. 5. Comparison of beach width (a) and ghost crab burrow distance from dune (b) at four east-central Florida beaches between May and August 2004. The solid horizontal bar denotes sites that are not significantly different at $p = 0.05$. Error bars represent standard error of the mean.

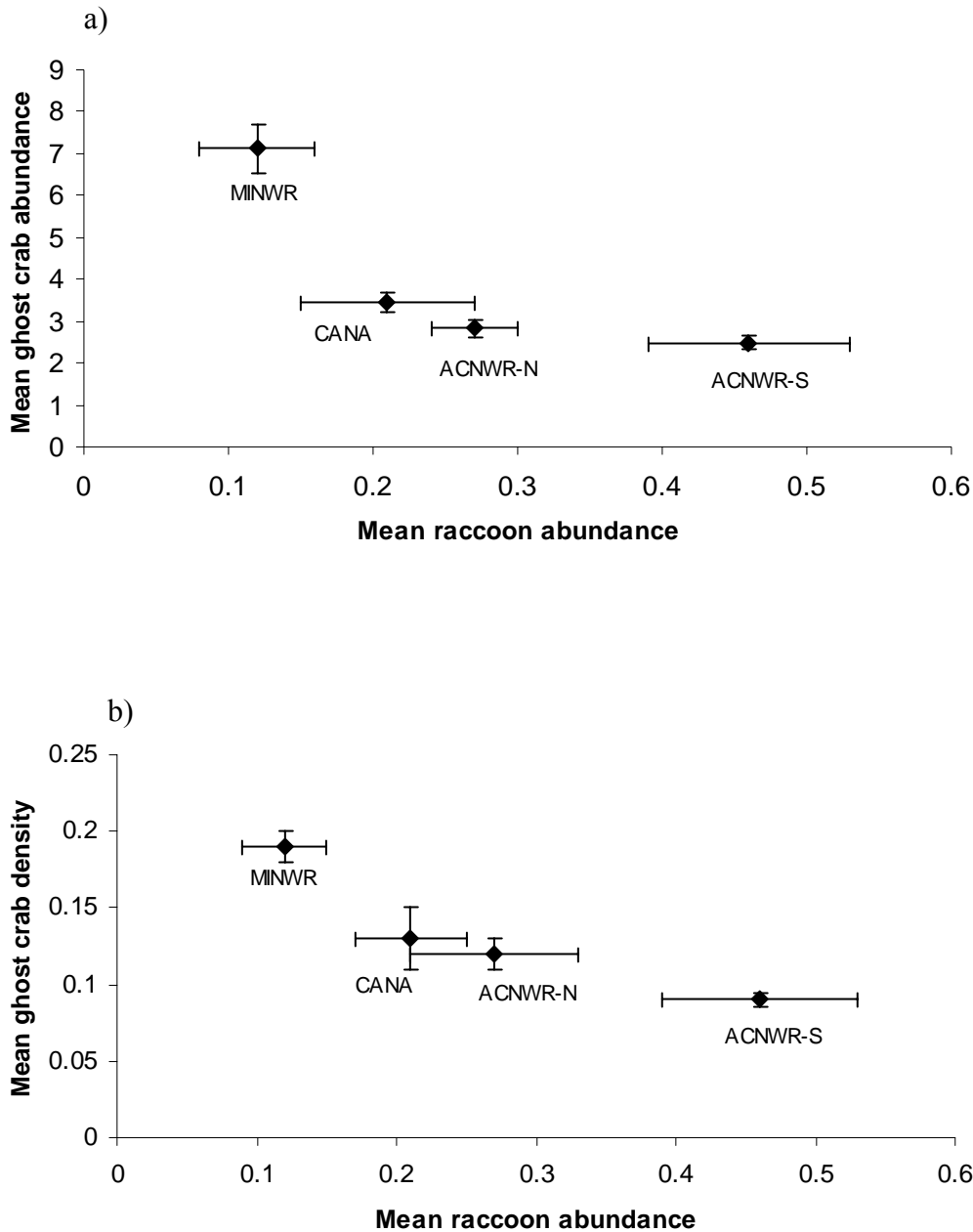


Figure 3. 6. Relationship of raccoon abundance to ghost crab abundance (a) and ghost crab density (b) at four east-central Florida beaches between May and August 2004. Burrow diameter reflects ghost crab size. Error bars represent standard error of the mean. The raccoon abundance was inversely related to ghost crab abundance ($r_s = -1.00$, $n = 4$, $p < 0.001$) and ghost crab density ($r_s = -1.00$, $n = 4$, $p < 0.001$).

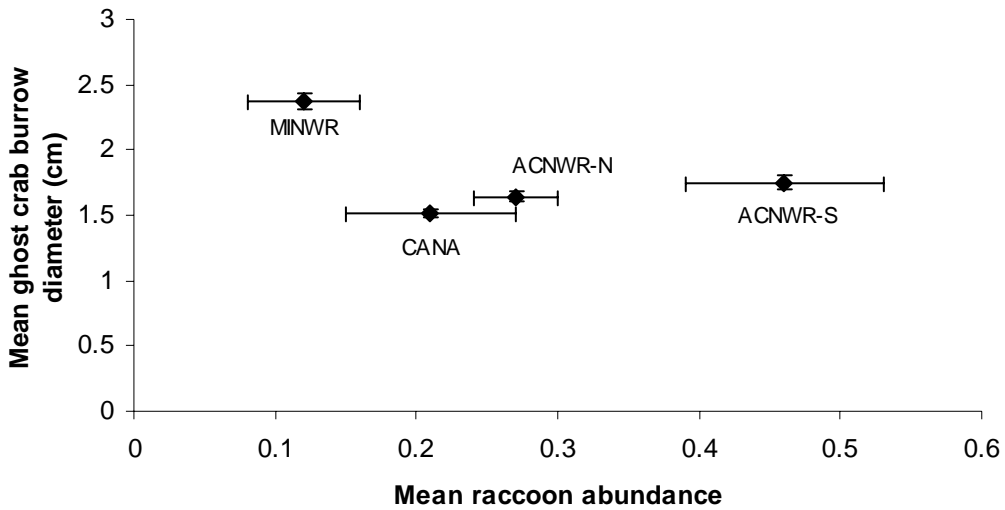


Figure 3. 7. Relationship of raccoon abundance and ghost crab burrow diameter at four east-central Florida beaches between May and August 2004. Burrow diameter reflects ghost crab size. Error bars represent standard error of the mean. Ghost crab size was not correlated with raccoon abundance ($r_s = -0.20$, $n = 4$, $p = 0.80$).

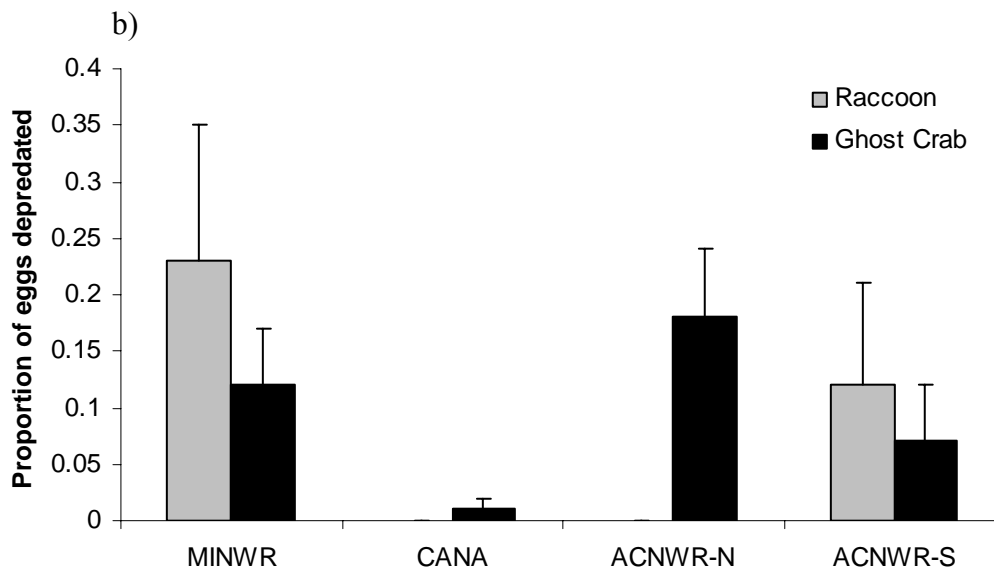
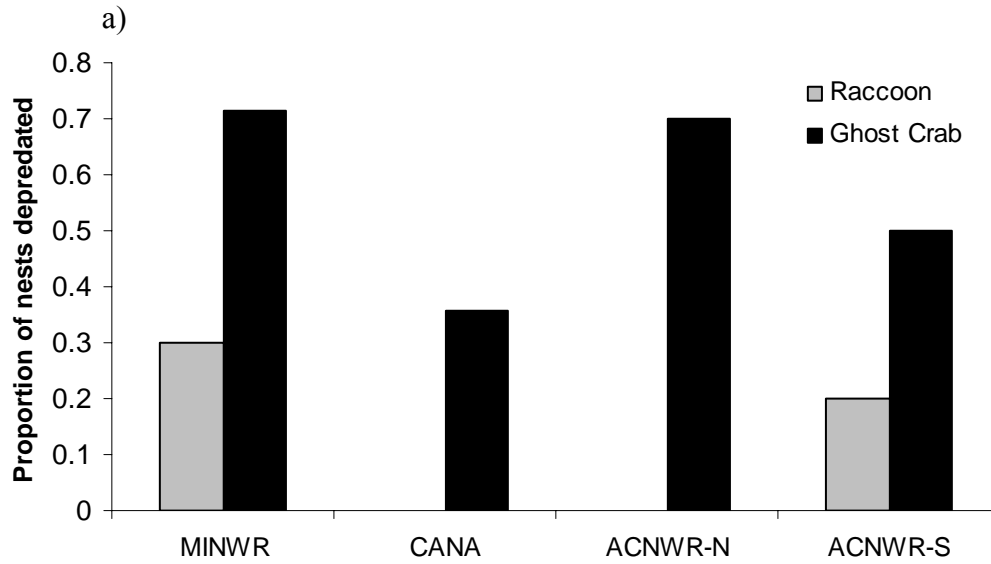


Figure 3. 8. Rates of nest depredation nest (a) and egg depredation (b) by raccoons and ghost crabs at four east-central Florida study sites during the 2004 sea turtle nesting season. Error bars represent standard error of the mean.

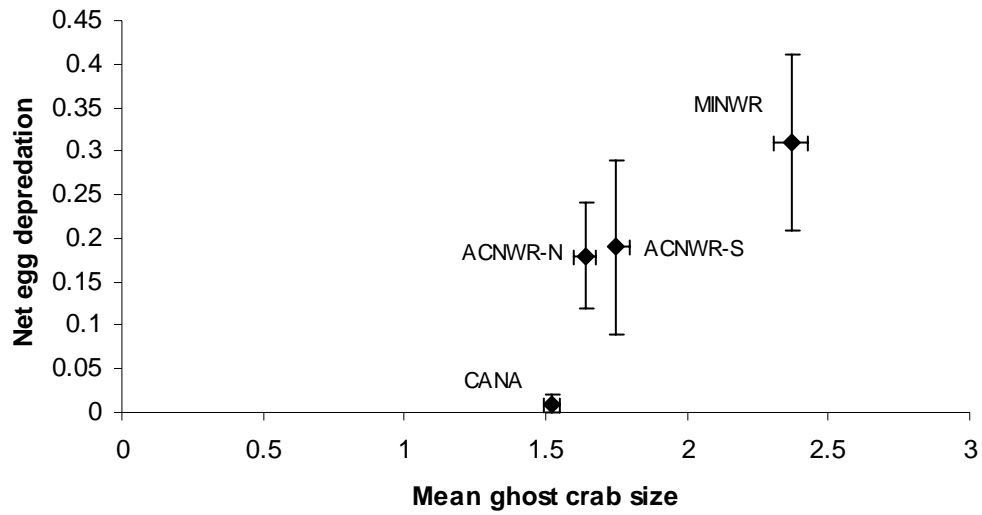


Figure 3. 9. Relationship of mean ghost crab size and net sea turtle egg depredation on four east-central Florida beaches between May and August 2004. Error bars represent standard error of the mean.

CHAPTER FOUR: CONCLUSIONS

My results complement the growing breadth of literature that suggests top-down regulation is an important process affecting terrestrial community ecology. My research suggests that raccoon removal directly affects raccoon populations (i.e., abundance and sex-ratio) and indirectly affects other members of the community (e.g., ghost crabs and sea turtles). Although I focused on three species in this study, the omnivorous diet of raccoons implies that this species has many ecological connections throughout the community (Ratnaswamy and Warren 1998). My research examined the role of raccoons as predators, yet it may be equally interesting to consider alternative interactions among raccoons and other species.

The diverse array of foods in the raccoon stomachs I examined attests to the ecological implications of raccoons as predators and herbivores. Seeds and berries were found frequently in the stomachs of raccoons, suggesting raccoons may facilitate plant dispersal. Brazilian pepper (*Schinus terebinthifolius*) is invasive to Florida and the fruits of this species were identified in the raccoon stomachs I examined. The interaction between raccoons and exotic plants may be of concern to natural resource managers interested in controlling invasive species.

The frequent occurrence of an unknown species of stomach parasite in the raccoons I examined may also have ecosystem-wide effects. One raccoon parasite, *Baylisascaris procyonis*, has been implicated as a threat to intermediate hosts and the prevalence of this parasite is directly related to raccoon abundance (LoGiudice 2003).

In addition to raccoons, I often recorded tracks from bobcats, armadillos, opossums and feral hogs on sea turtle nesting beaches, each of which are potential sea turtle egg and hatchling predators. Armadillos, opossums and feral hogs are common nest predators (Ratnaswamy and

Warren 1998) and I observed evidence of bobcats attacking newly emerged sea turtle hatchlings from a single nest. Competition between raccoons and opossums can affect the ecology of both species (Ginger et al. 2002) and it is likely that other interactions exist among these beach predators.

Predator removal is an important and effective part of management plans for many endangered, threatened, or protected species (Davis and Whiting 1977, Cote and Sutherland 1997, Sinclair et al. 1998, Banks 1999). Although predator removal can be effective in conserving prey species, unexpected consequences of reduced predator densities have been demonstrated in many studies (Soulé et al. 1988, Courchamp et al. 1999, Crooks and Soulé 1999, Schmidt 2003). I recommend that resource managers consider the direct and indirect effects of predator removal. Although raccoon removal has often been considered effective, the broad scale effects must be considered. I do not suggest less vigilance in management efforts to increase hatchling production on sea turtle nesting beaches. However, I do suggest that managers consider the community-wide implications of intensive predator removal and exploration of alternative control methods.

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