The impact of ghost crab predation on loggerhead sea turtles: environmental influences and management approaches

By

Rylie Hannah MacDonald

A Thesis submitted to the Faculty of Graduate Studies of

The University of Manitoba

In partial fulfilment of the requirements of the degree of

MASTER OF SCIENCE

Department of Biological Sciences

University of Manitoba

Winnipeg, MB

Copyright © 2025 by Rylie Hannah MacDonald

Abstract

Predation is one of the greatest threats to the eggs and hatchlings of threatened loggerhead sea turtles (*Caretta caretta)*. Management efforts tend to focus on removing mammalian predators, and invertebrate predators have largely been overlooked. Yet ghost crabs (*Ocypode spp.)* can become prolific predators of sea turtle eggs when they become abundant. Current methods used to quantify egg predation by crabs may underestimate predation, and nest-to-surf mortality of hatchlings rarely quantified. Additionally, ghost crab abundance is difficult to estimate due to their complex behavior shaped by environmental variables, but understanding these factors would aid in effective management. This study, conducted on the Atlantic coast of Florida from 2021 to 2023, explored the effects of environmental variables on ghost crab abundance and how ghost crab abundance affects egg and hatchling predation rates. We found that crabs predated 5-10% of all eggs and attacked 6-13% of hatchlings. Higher crab densities led to increased hatchling predation, particularly among disoriented hatchlings, but egg predation was unaffected by crab density. We quantified crab abundance using two methods, through visual surveys of live crabs and burrow counts. We explored the effects of environmental variables on these indices of crab abundance, and found interactive effects of temperature, moon luminosity, and ambient lighting. Our findings highlight the importance of considering multiple environmental variables when assessing ghost crab abundance and activity, because crab behavior, such as burrow construction and foraging activity, changes with these environmental variables. We found that these two indices were unrelated when comparisons included these other environmental variables, suggesting that it may not be appropriate to use them interchangeably. We attempted to reduce crab density through two methods, live capture and the use of a sod roller to dispatch crabs. While live capture did not significantly reduce crab abundance, the sod roller method had a significant impact, which lowered predation on hatchlings by 75%. Our study demonstrates the importance of invertebrate predators of sea turtle eggs and hatchlings, as well as the importance of including both eggs and hatchlings in predation estimates, when considering conservation strategies for this threatened species.

Contributions of Authors

Manuscript Authors: Rylie MacDonald, Brandon T. Barton, James D. Roth & Simona A. Ceriani

Both manuscript chapters (2 and 3) used methods and analyses designed by Rylie MacDonald, Brandon T. Barton, and James D. Roth to evaluate crab predation and abundance over three years on Cape Canaveral Space Force Station. Simona Ceriani assisted with the initiation and the conceptual design of the study. Rylie MacDonald has written these manuscripts with revisions from Brandon Barton, James Roth, and Simona Ceriani.

Permits:

Florida Fish and Wildlife Conservation Commission Marine Turtle Permits: 21-093, 22-093, 23-093

University of Manitoba Animal Care Protocol F21-009

U.S. Fish and Wildlife Service Biological Opinion, Service Consultation Code: 2023-0048449

Disclaimer

The conclusions in this manuscript are those of the authors and do not necessarily represent the views of the United States Fish and Wildlife Service or the United States Space Force.

Table of Contents

Chapter 1

Chapter 2

Chapter 3

Chapter 4

List of Figures

List of Tables

Acknowledgements

First, I would like to thank the United States Space Force (USSF) for funding the first two years of this study and the United States Fish and Wildlife Service (USFWS) for the third year. This study was a collective effort, and I am so grateful for the support over these last four years.

This project would not have been possible without Angy Chambers, Senior Wildlife Biologist with USSF who has worked on the Cape Canaveral Space Force Station (CCSFS) beach since 1991, and first noticed the increased ghost crab abundance and predation on the beach. Angy developed this project, secured the funding, and provided immense support throughout the three years of the study. Her work on CCSFS and her love of the wildlife there inspired me to continue my work with sea turtles on CCSFS and I hope to achieve as much in my career as she has. Thank you to Mike Blaylock, SLD 45 Environmental Chief who has been an advocate for me since I first began my project, supported me through consultations, coordinated with launch control and security to help me gain access to the beach and work around hazardous operations to prevent losing data, and rescued me off the beach with Patrick Stahl (USSF) multiple times after breaking down in UTVs and ATVs. Additional thanks to Megan Nicely (USSF) and Martha Carson (USSF) who checked my research nests for me so I could have some much-needed days off from the beach. In the four years I've spent working at CCSFS, I am continually awed by the resilience of the species present and the biologists who work there to protect them.

I am sincerely grateful to Dr. Robert Aldredge (USFWS) who wrote the Biological Opinion to make the third year of the study testing a novel method of ghost crab control possible. He helped me immensely through coding in R and gave invaluable advice on writing my thesis. This study led to my first full time job as a USFWS biologist, and I feel so lucky to have Rob as my now supervisor. Additional thanks to Mike Gillikin, Karen Frutchey, Lucas Davis, and Brendan Myers with USFWS for providing insight in the development of the Biological Opinion.

I am immensely appreciative of Marcus Jensen, United States Department of Agriculture (USDA), who spent late nights on the beach with me driving the UTV to count and remove ghost crabs during the removal experiment and he has been one of my greatest pillars of support in the last several years. Additional thanks to Parker Hall and Bryan Kluever with USDA Wildlife Services for helping to formulate our ghost crab removal methods and integrate ghost crab control into their nuisance wildlife control program for CCSFS in 2023.

I would also like to acknowledge my two advisors, Dr. Jim Roth and Dr. Brandon Barton, for spending countless hours meeting with me, helping me with analyses, and reviewing *many* drafts of this thesis to provide much-needed feedback, and my other committee members, Dr. Simona Ceriani and Dr. Patricia Ramey-Balci, for their insightful feedback and encouragement.

Finally, my sincere appreciation to my family in Florida, including my grandparents and my aunt Sue, who let me live with them so I could afford to do this project. Special thanks to the rest of my friends and family all over the country, especially my parents in Ohio, who encouraged and supported me for the last four years from a distance, and my two dogs, who always slept under my desk during late nights writing my thesis.

Chapter 1: Introduction

Apex predators demonstrate top-down control in marine, freshwater, and terrestrial ecosystems, and managing their numbers for conservation purposes may have cascading effects throughout the entire food web (Estes et al. 2011, Antiqueira et al. 2018, Edwards and Konar 2020, Leighton et al. 2023). Lethal mammalian predator removal is commonly used by natural resource managers to protect at-risk species. Removing predators changes community structures, which may lead to the release of mesopredators and changes in intraguild interactions (Soulé et al. 1988, Ritchie and Johnson 2009, Jachowski et al. 2020). The reduction of these top predators benefits secondary predators, which may inadvertently inflate total predation pressure on some prey species (Soulé et al. 1988, Barton and Roth 2008, Ritchie and Johnson 2009). The unintended consequences of managing one threat and exacerbating another is a familiar theme in conservation, and the resulting loss of the trophic cascade can be detrimental to species found in the lowest trophic levels (Barton and Roth 2008, Ripple et al. 2016, Jachowski et al. 2020).

The loggerhead sea turtle (*Caretta caretta)* is a species of conservation concern (Casale and Tucker 2015), facing a multitude of natural and anthropogenic threats. Due to their protected status, resource managers have an interest in reducing their mortality and increasing recruitment. Loggerheads use terrestrial, neritic, and oceanic ecosystems at various life stages, but spend most of their lives in the ocean (Hatase et al. 2002, Bolten 2003, Hawkes et al. 2006, McClellan and Read 2007). Only reproductive females, which reach sexual maturity around 30 years of age, come ashore to nest (NMFS and USFWS 2008). Each nest has roughly one hundred eggs, which are vulnerable to predation (Stancyk 1982, Antworth et al. 2006, Peterson et al. 2013, Engeman et al. 2014, Marco et al. 2015, Butler et al. 2020, Avenant et al. 2023), water inundation due to tidal changes (Gammon et al. 2023), temperature (Laloë et al. 2014, Reneker and Kamel 2016) and other environmental impacts during incubation. Hatchlings that emerge from nests are vulnerable to disorientation due to artificial lighting (Witherington et al. 2014) and terrestrial predators during their crawl to the ocean (Erb and Wyneken 2019 and Martins et al 2021). Resource managers tend to focus on these terrestrial life stages where threats can be more easily ameliorated (Crouse et al. 1987, Donlan et al. 2010).

Lethal mammalian predator removal has been employed for decades to remove native raccoons (*Procyon lotor)* to reduce mortality and increase recruitment for loggerhead turtles (Stancyk 1982, Ratnaswamy et al 1997 Engeman et al 2014, O'Connor et al 2017). Nests can also be screened or caged to protect against predators (Engeman et al. 2014, O'Connor et al. 2017, Pheasey et al. 2018) but the visual cues to predators created by this method may facilitate predation (Mroziak et al. 2000). Self-releasing screens and cages have openings large enough for hatchlings to emerge unaided, but do not protect the nest against smaller predators, such as the Atlantic ghost crab (*Ocypode quadrata*; Butler et al. 2020). Ghost crabs are another common predator of sea turtle eggs and hatchlings (Antworth et al. 2006, Peterson et al. 2013, Marco et al. 2015, Butler et al. 2020, Avenant et al. 2023), but management intervention primarily targets mammalian predators. Raccoons also consume ghost crabs and may limit their abundance and size (Barton and Roth 2008). By removing raccoons to protect sea turtle nests, management activities may increase ghost crab numbers, size and impact on sea turtle eggs and hatchlings.

Ghost crabs (*Ocypode spp*.) are abundant on sandy beaches worldwide (Lucrezi and Schlacher, 2014). With 22 subspecies variations globally, the Atlantic ghost crab (*O. quadrata*) is prevalent from Massachusetts to southern Brazil (Sakai and Türkay 2013, Lucrezi and Schlacher, 2014). Ghost crabs function as both scavengers and predators in the coastal ecosystem, feeding on a range of organic matter, including detritus, small invertebrates, carrion, and protected shorebird and sea turtle eggs and hatchlings (Branco et al. 2010).

In the Southeastern United States, annual estimates of egg predation by the ghost crab *O. quadrata* range from 1-18% of eggs (Schmidt and Burney 1997, Bouchard and Bjorndal 2000, Barton and Roth 2008). In Seychelles, ghost crabs *O. cordimanus* predation has been documented as high as 38.3% on Hawksbill (*Eretmochelys imbricata)* eggs (Hitchins et al. 2004). In Cabo Verde, *O. cursor* predation has been estimated as high as 70% egg mortality (Marco et al. 2015). The highest rates of egg predation by crabs have been reported in Gnaraloo Bay, Western Australia, where *O. convexa* and *O. ceratophthalma* crabs consume 78.5% of eggs (Avenant et al.2023). However, predation levels may be underestimated due to the methods of quantifying eggs damaged by crabs. The recommended method for evaluating eggs damaged by crabs is by using the presence of a “snip mark” left by crabs when opening eggs to consume their contents (Whitmore and Dutton 1985, Ali and Ibrahim 2002, Maros et al. 2003, Stokes et al. 2023). Yet eggs damaged by crabs may not always leave this sign (Brown 2009, Avenant et al. 2023). Further, ghost crabs can remove eggs from nest and consume them elsewhere (Marco et al. 2015, Avenant et al. 2023), and these unaccounted eggs may bias predation estimates (Ceriani et al. 2021).

While several studies have recognized the importance of assessing ghost crab egg predation, studies evaluating hatchling nest to surf mortality are more limited (Tomillo et al. 2010, Peterson et al. 2013, Erb and Wyneken, 2019, Martins et al. 2021 Avenant et al. 2023). During hatchling emergence, stimuli from artificial light sources can override the natural cues hatchlings rely on to orient to the ocean and disorient hatchlings (Witherington and Bjorndal 1991, Lorne and Salmon 2007, Witherington et al. 2014). Disorientation causes hatchlings to crawl in the wrong direction and increases their time spent on the beach and thus their exposure to predators. Disorientation is often cited as increasing hatchling predation risk (Witherington et al. 2014) but the rate of increase due to disorientation has not been quantified. Erb and Wyneken (2019) found that disorientation and ghost crabs were the two greatest threats to hatchling mortality but did not examine their interactive effects. Ghost crabs are hypersensitive to light (Rosenberg and Langer, 2001) and attracted to lighting of various wavelengths (Silva et al. 2017). The attraction of both crabs and turtles to artificial lighting may inadvertently increase predation pressure for hatchlings (Silva et al. 2017).

Understanding what drives predator population dynamics can aid in effective management. As a fossorial species, ghost crab density can be difficult to quantify. Burrow density is most commonly used to represent crab density (Schlacher et al. 2016), although the validity of this method has been debated in the literature. Burrow density may more appropriately be viewed as a metric of crab activity rather than crab abundance (Call et al. 2024). Crab burrow abundance can be used as a metric of beach condition and anthropogenic change (Lucrezi et al. 2009, Pombo and Turra 2013, Schlacher et al. 2016, Gül and Griffen 2018), and higher ghost crab densities are typically observed on low-disturbance beaches (Barros, 2001). Burrow fidelity and longevity is highest on beaches with low human impact, and weaker at more pristine sites (Gül and Griffen 2019).

Temperature, moon phase, and sand characteristics are additional environmental variables that affect ghost crabs. Ghost crabs are ectothermic, and temperature plays a key role in crab activity and metabolic processes (Vernberg and Vernberg, 1968, Weinstein and Full 1994). The abundance of crabs and their burrows varies seasonally, with the highest numbers observed in the summer (Tiralongo et al. 2020). Lunar cycles also influence crab activity and burrow distribution, and crab reproductive behavior follows a lunar periodicity, peaking near new and full moons (Fortaleza et al. 2020). Beach substrate features, such as sand characteristics, influence the abundance of crabs and their burrows, and finer-grain sands are associated with higher densities (Turra et al. 2005, Brown 2009, Lucrezi 2015, Jonah et al. 2015, Pombo et al. 2017). Beaches that perform nourishment activities, which involves depositing sediment to the beach to counteract erosion, observe suppressed abundance of ghost crabs and other invertebrates (Peterson et al. 2000).

Overall, Florida beaches account for 89 percent of Atlantic loggerhead nests, and the beaches at Cape Canaveral Space Force Station (CCSFS) are part of a primary rookery in the southeast for loggerheads (Provancha and Ehrhart 1987, NMFS and USFWS 2008, Ceriani et al. 2019). On average, CCSFS is the site of thousands of sea turtle nests each year and comprises approximately 5% of the total loggerhead nests in Florida (Space Launch Delta 45, 2022). While most of the Florida coastline has been impacted by human development and a growth in residential communities, much of the land on CCSFS is undeveloped. Despite the mostly natural landscape, an increase in rocket launch activities has led to the construction of multiple launchpads by commercial spaceflight companies on CCSFS. These launchpads are permitted to use white light during hazardous operations, including the testing and launching of rockets. These launch activities result in increased artificial lighting visible from the beach. Offsite lighting is also visible on the nesting beach from Port Canaveral, a highly trafficked cruise ship and cargo terminal at the southern terminus of the beach.

On CCSFS, raccoons and coyotes (*Canis latrans)* are removed to protect sea turtle nests. Raccoons are also important predators of ghost crabs (Barton and Roth 2008), so this management effort may indirectly benefit crabs. In addition to the removal of crabs’ primary predators, the environmental conditions on CCSFS may be ideal for crabs to thrive. Except for the few biologists that work on the CCSFS beach, there is almost a complete lack of human presence. CCSFS is a natural sand beach, with no nourishment activities, making it a preferable site for both nesting sea turtles and ghost crabs. Due to high sea turtle nesting activity, eggs and hatchlings are abundant seasonal food sources for predators. With management initiatives targeted at controlling mammalian predators rather than invertebrates, ghost crabs are left largely unchecked. Beach illumination by artificial light sources further aids crabs in the pursuit of vulnerable sea turtle hatchlings on their path to the sea.

The goal of my thesis was to better understand how ghost crabs affect sea turtle eggs and hatchlings. Specifically, the main objectives for this study were to (1) quantify predation rates by ghost crabs on sea turtle eggs and hatchlings and explore causes of spatial and temporal variation in predation, (2) explore spatiotemporal drivers of ghost crab abundance on sea turtle nesting beaches and (3) test small- and large-scale methods of reducing ghost crab abundance and their subsequent impacts on predation of eggs and hatchlings.

This three-year study was conducted on the CCSFS beach on the east coast of Florida, USA. Biologists who have monitored this nesting beach since 1991 anecdotally observed an increase in ghost crabs and their burrows for several years leading up to this study. During nest emergences, they observed numerous hatchlings falling into crab burrows or being attacked by crabs on their way to the water. To protect sea turtle nests, CCSFS has removed mammalian predators for decades, and contracted the United States Department of Agriculture (USDA) to begin intensive removals in 2016. These efforts reduced mammal predation rates from 95% of nests prior to the initiation of the trapping program to an average of 10% in recent years (Space Launch Delta 45, 2022). Concern that the successful removal of raccoon predators may have driven the increase in the size and abundance of ghost crabs (Barton & Roth 2008) resulted in the initiation of this study.

In chapter two, we explored ghost crab predation of both hatchlings and eggs. We assessed eggs damaged by crabs and missing from nests (~100 nests per year) to better understand the total impact of crabs at the nest level. During nest emergences, we evaluated the number of hatchlings attacked by crabs on their way to the water and explored the effects of disorientation on these predation rates. In chapter three, we assess two different methods of measuring ghost crab abundance and activity, transect burrow counts and visual live crab counts. We examined how environmental variables and their interactions influenced both metrics of crab abundance. Further, we tested both small- and large-scale methods of crab removal, to reduce crab abundance and their predation of eggs and hatchlings. This thesis provides novel information on the effects of ghost crabs on sea turtle mortality and is the first study to implement invertebrate removal methods to reduce mortality.

1.1 References

Ali, A., & Ibrahim, K. (2002). Crab predation on green turtle (*Chelonia mydas)* eggs incubated on a natural beach and in turtle hatcheries. *Proceedings of the 3rd Workshop on SEASTAR 2000.* Kyoto, pp. 95-100.

Antiqueira, P. A. P., Petchey, O. L., & Romero, G. Q. (2018). Warming and top predator loss drive ecosystem multifunctionality. *Ecology Letters*, *21*(1), 72–82. https://doi.org/10.1111/ele.12873

Antworth, R. L., Pike, D. A., & Stiner, J. C. (2006). Nesting ecology, current status, and conservation of sea turtles on an uninhabited beach in Florida, USA. *Biological Conservation*, *130*(1), 10–15. https://doi.org/10.1016/j.biocon.2005.11.028

Avenant, C., Whiting, S., Fossette, S., Barnes, P., & Hyndes, G. A. (2023). Extreme predation of eggs and hatchlings for loggerhead turtles in eastern Indian Ocean. *Biodiversity and Conservation*, *33*(1), 135–159. https://doi.org/10.1007/s10531-023-02739-z

Barros, F. (2001). Ghost crabs as a tool for rapid assessment of human impacts on exposed sandy beaches. *Biological Conservation*, *97*(3), 399–404. https://doi.org/10.1016/S0006-3207(00)00116-6

Barton, B. T., & Roth, J. D. (2008). Implications of intraguild predation for sea turtle nest protection. *Biological Conservation*, *141*(8), 2139–2145. https://doi.org/10.1016/j.biocon.2008.06.013

Bolten, A. B. (2003). Active swimmers – passive drifters: The oceanic juvenile stage of loggerheads in the Atlantic system. In A. B. Bolten & B. E. Witherington (Eds.), *Loggerhead sea turtles*. (pp. 63–78). Smithsonian Institution Press. https://accstr.ufl.edu/wp-content/uploads/sites/98/Bolten_Chapter4Smithsonian-Press.pdf

Bouchard, S. S., & Bjorndal, K. A. (2000). Sea Turtles as Biological Transporters of Nutrients and Energy from Marine to Terrestrial Ecosystems. *Ecology*, *81*(8), 2305–2313. https://doi.org/10.1890/0012-9658(2000)081[2305:STABTO]2.0.CO;2

Branco, J. O., Hillesheim, J. C., Fracasso, H. A. A., Christoffersen, M. L., & Evangelista, C. L. (2010). Bioecology of the Ghost Crab *Ocypode quadrata* (Fabricius, 1787) (Crustacea: Brachyura) Compared with Other Intertidal Crabs in the Southwestern Atlantic. *Journal of Shellfish Research*, *29*(2), 503–512. https://doi.org/10.2983/035.029.0229

Brown, J. (2009). *Factors Affecting Predation Of Marine Turtle Eggs By Raccoons And Ghost Crabs On Canaveral National Seashore, Fl* (Master's thesis, University of Central Florida). https://stars.library.ucf.edu/cgi/viewcontent.cgi?article=5043&context=etd

Butler, Z. P., Wenger, S. J., Pfaller, J. B., Dodd, M. G., Ondich, B. L., Coleman, S., Gaskin, J. L., Hickey, N., Kitchens-Hayes, K., Vance, R. K., & Williams, K. L. (2020). Predation of loggerhead sea turtle eggs across Georgia's barrier islands. *Global Ecology and Conservation*, *23*, e01139. https://doi.org/10.1016/j.gecco.2020.e01139

Call, M. N., Pongnon, R. S., Wails, C. N., Karpanty, S. M., Lapenta, K. C., Wilke, A. L., Boettcher, R., Alvino, C. R., & Fraser, J. D. (2024). Biotic and abiotic factors affecting Atlantic ghost crab (*Ocypode quadrata*) spatiotemporal activity at an important shorebird nesting site in Virginia. *PLOS ONE*, *19*(8), e0307821. https://doi.org/10.1371/journal.pone.0307821

Casale, P., & Tucker, A. D. (2015). *Caretta caretta (Loggerhead Turtle)*. The IUCN Red List of Threatened Species. http://dx.doi.org/10.2305/IUCN.UK.2015-4.RLTS.T3897A83157651.en

Ceriani, S. A., Brost, B., Meylan, A. B., Meylan, P. A., & Casale, P. (2021). Bias in sea turtle productivity estimates: Error and factors involved. *Marine Biology*, *168*(4), 41. https://doi.org/10.1007/s00227-021-03843-w

Crouse, D. T., Crowder, L. B., & Caswell, H. (1987). A Stage-Based Population Model for Loggerhead Sea Turtles and Implications for Conservation. *Ecology*, *68*(5), 1412–1423. https://doi.org/10.2307/1939225

Donlan, C. J., Wingfield, D. K., Crowder, L. B., & Wilcox, C. (2010). Using expert opinion surveys to rank threats to endangered species: A case study with sea turtles. *Conservation*

Biology: The Journal of the Society for Conservation Biology, *24*(6), 1586–1595. https://doi.org/10.1111/j.1523-1739.2010.01541.x

Edwards, M. S., & Konar, B. (2020). Trophic downgrading reduces spatial variability on rocky reefs. *Scientific Reports*, *10*(1), 18079. https://doi.org/10.1038/s41598-020-75117-2

Engeman, R. M., Addison, D., & Griffin, J. C. (2014). Defending against disparate marine turtle nest predators: Nesting success benefits from eradicating invasive feral swine and caging nests from raccoons. *Oryx*, *50*(2), 289–295. https://doi.org/10.1017/S0030605314000805

Erb, V., & Wyneken, J. (2019). Nest-to-Surf Mortality of Loggerhead Sea Turtle (Caretta caretta) Hatchlings on Florida's East Coast. *Frontiers in Marine Science*, *6*(271). https://doi.org/10.3389/fmars.2019.00271

Estes, J. A., Terborgh, J., Brashares, J. S., Power, M. E., Berger, J., Bond, W. J., Carpenter, S. R., Essington, T. E., Holt, R. D., Jackson, J. B. C., Marquis, R. J., Oksanen, L., Oksanen, T., Paine, R. T., Pikitch, E. K., Ripple, W. J., Sandin, S. A., Scheffer, M., Schoener, T. W., … Wardle, D. A. (2011). Trophic downgrading of planet Earth. *Science (New York, N.Y.)*, *333*(6040), 301–306. https://doi.org/10.1126/science.1205106

Fortaleza, M. O., Maria Lemos Girão, M., Franklin Junior, W., Pinto De Lima, J., & De Almeida Rocha-Barreira, C. (2020). Which moon phase do we find more ghosts? Effects of the lunar cycle on the ghost crab *Ocypode quadrata* (Fabricius, 1787). *Arquivos de Ciências Do Mar*, *52*(2), 85–97. https://doi.org/10.32360/acmar.v52i2.42737

Gammon, M., Whiting, S., & Fossette, S. (2023). Vulnerability of sea turtle nesting sites to erosion and inundation: A decision support framework to maximize conservation. *Ecosphere*, *14*(6), e4529. https://doi.org/10.1002/ecs2.4529

Gül, M. R., & Griffen, B. D. (2018). A Reliable Bioindicator of Anthropogenic Impact on the Coast of South Carolina. *Southeastern Naturalist*, *17*(2), 357–364. https://doi.org/10.1656/058.017.0217

Gül, M. R., & Griffen, B. D. (2019). Burrowing behavior and burrowing energetics of a bioindicator under human disturbance. *Ecology and Evolution*, *9*(24), 14205–14216. https://doi.org/10.1002/ece3.5853

Hatase, H., Takai, N., Matsuzawa, Y., Sakamoto, W., Omuta, K., Goto, K., Arai, N., & Fujiwara, T. (2002). Size-related differences in feeding habitat use of adult female loggerhead turtles *Caretta caretta* around Japan determined by stable isotope analyses and satellite telemetry. *Marine Ecology Progress Series*, *233*, 273–281.

Hawkes, L. A., Broderick, A. C., Coyne, M. S., Godfrey, M. H., Lopez-Jurado, L.-F., Lopez-Suarez, P., Merino, S. E., Varo-Cruz, N., & Godley, B. J. (2006). Phenotypically linked dichotomy in sea turtle foraging requires multiple conservation approaches. *Current Biology*, *16*(10), 990–995. https://doi.org/10.1016/j.cub.2006.03.063

Hitchins, P. M., Bourquin, O., & Hitchins, S. (2004). Nesting success of hawksbill turtles (*Eretmochelys imbricata*) on Cousine Island, Seychelles. *Journal of Zoology*, *264*(4), 383–389. https://doi.org/10.1017/S0952836904005904

Jachowski, D. S., Butler, A., Eng, R. Y. Y., Gigliotti, L., Harris, S., & Williams, A. (2020). Identifying mesopredator release in multi-predator systems: A review of evidence from North America. *Mammal Review*, *50*(4), 367–381. https://doi.org/10.1111/mam.12207

Jonah, F. E., Agbo, N. W., Agbeti, W., Adjei-Boateng, D., & Shimba, M. J. (2015). The ecological effects of beach sand mining in Ghana using ghost crabs (*Ocypode species*) as biological indicators. *Ocean & Coastal Management*, *112*, 18–24. https://doi.org/10.1016/j.ocecoaman.2015.05.001

Laloë, J.-O., Cozens, J., Renom, B., Taxonera, A., & Hays, G. C. (2014). Effects of rising temperature on the viability of an important sea turtle rookery. *Nature Climate Change*, *4*(6), 513–518. https://doi.org/10.1038/nclimate2236

Leighton, G. R. M., Froneman, W., Serieys, L. E. K., & Bishop, J. M. (2023). Trophic downgrading of an adaptable carnivore in an urbanising landscape. *Scientific Reports*, *13*(1), 21582. https://doi.org/10.1038/s41598-023-48868-x

Lorne, J. K., & Salmon, M. (2007). Effects of exposure to artificial lighting on orientation of hatchling sea turtles on the beach and in the ocean. *Endangered Species Research*, *3*, 23–30. https://doi.org/10.3354/esr003023

Lucrezi, S. (2015). Ghost crab populations respond to changing morphodynamic and habitat properties on sandy beaches. *Acta Oecologica*, *62*, 18–31. https://doi.org/10.1016/j.actao.2014.11.004

Lucrezi, S., Schlacher, T. A., & Walker, S. (2009). Monitoring human impacts on sandy shore ecosystems: A test of ghost crabs (*Ocypode* spp.) as biological indicators on an urban beach. *Environmental Monitoring and Assessment*, *152*(1–4), 413–424. https://doi.org/10.1007/s10661-008-0326-2

Lucrezi, S., & Schlacher, T. A. (2014). The Ecology of Ghost Crabs. In R. N. Hughes, Hughes, D. J., & I. P. Smith (Eds.), *Oceanography and Marine Biology* (pp. 201–256). CRC Press. https://doi.org/10.1201/b17143

Marco, A., da Graça, J., García-Cerdá, R., Abella, E., & Freitas, R. (2015). Patterns and intensity of ghost crab predation on the nests of an important endangered loggerhead turtle population. *Journal of Experimental Marine Biology and Ecology*, *468*, 74–82. https://doi.org/10.1016/j.jembe.2015.03.010

Maros, A., Louveaux, A., Godfrey, M. H., & Girondot, M. (2003). *Scapteriscus didactylus* (Orthoptera, Gryllotalpidae), predator of leatherback turtle eggs in French Guiana. *Marine Ecology Progress Series*, *249*, 289–296. https://doi.org/10.3354/meps249289

Martins, S., Sierra, L., Rodrigues, E., Oñate-Casado, J., Galán, I. T., Clarke, L. J., & Marco, A. (2021). Ecological drivers of the high predation of sea turtle hatchlings during emergence. *Marine Ecology Progress Series*, *668*, 97–106. https://doi.org/10.3354/meps13751

McClellan, C. M., & Read, A. J. (2007). Complexity and variation in loggerhead sea turtle life history. *Biology Letters*, *3*(6), 592–594. https://doi.org/10.1098/rsbl.2007.0355

Mroziak, M., Salmon, M., & Rusenko, K. (2000). Do wire cages protect sea turtles from foot traffic and mammalian predators? *Chelonian Conservation and Biology*, *3*(4), 693–698.

National Marine Fisheries Service (NMFS) and U.S. Fish and Wildlife Service (USFWS). (2008). Recovery Plan for the Northwest Atlantic Population of the Loggerhead Sea Turtle (*Caretta caretta*), Second Revision. National Marine Fisheries Service, Silver Spring, MD.

O'Connor, J. M., Limpus, C. J., Hofmeister, K. M., Allen, B. L., & Burnett, S. E. (2017). Anti-predator meshing may provide greater protection for sea turtle nests than predator removal. *PLOS ONE*, *12*(2), e0171831. https://doi.org/10.1371/journal.pone.0171831

Peterson, C. H., Hickerson, D. H. M., & Johnson, G. G. (2000). Short-Term Consequences of Nourishment and Bulldozing on the Dominant Large Invertebrates of a Sandy Beach. *Journal of Coastal Research*, *16*(2), 368–378.

Peterson, C. H., Fegley, S. R., Voss, C. M., Marschhauser, S. R., & VanDusen, B. M. (2013). Conservation implications of density-dependent predation by ghost crabs on hatchling sea turtles running the gauntlet to the sea. *Marine Biology*, *160*(3), 629–640. https://doi.org/10.1007/s00227-012-2118-z

Pheasey, H., McCargar, M., Glinsky, A., & Humphreys, N. (2018). Effectiveness of Concealed Nest Protection Screens Against Domestic Predators for Green (*Chelonia mydas*) and Hawksbill (*Eretmochelys imbricata*) Sea Turtles. *Chelonian Conservation and Biology*, *17*(2), 263–270. https://doi.org/10.2744/CCB-1316.1

Pombo, M., & Turra, A. (2013). Issues to Be Considered in Counting Burrows as a Measure of Atlantic Ghost Crab Populations, an Important Bioindicator of Sandy Beaches. *PLOS ONE*, *8*(12), e83792. https://doi.org/10.1371/journal.pone.0083792

Pombo, M., de Oliveira, A. L., Xavier, L. Y., Siegle, E., & Turra, A. (2017). Natural drivers of distribution of ghost crabs *Ocypode quadrata* and the implications of estimates from burrows. *Marine Ecology Progress Series*, *565*, 131–147. https://doi.org/10.3354/meps11991

Provancha, J. A., & Ehrhart, L. M. (1987). Sea turtle nesting trends at Kennedy Space Center and Cape Canaveral Air Force Station, Florida, and relationships with factors influencing nest site selection. In W. N. Witzell (Ed.), *Ecology of East Florida sea turtles* (pp. 33–44). *NOAA Technical Report NMFS* (No. 53).

Ratnaswamy, M. J., Warren, R. J., Kramer, M. T., & Adam, M. D. (1997). Comparisons of Lethal and Nonlethal Techniques to Reduce Raccoon Depredation of Sea Turtle Nests. *The Journal of Wildlife Management*, *61*(2), 368–376. https://doi.org/10.2307/3802593

Reneker, J. L., & Kamel, S. J. (2016). Climate change increases the production of female hatchlings at a northern sea turtle rookery. *Ecology*, *97*(12), 3257–3264. https://doi.org/10.1002/ecy.1603

Ripple, W. J., Estes, J. A., Schmitz, O. J., Constant, V., Kaylor, M. J., Lenz, A., Motley, J. L., Self, K. E., Taylor, D. S., & Wolf, C. (2016). What is a Trophic Cascade? *Trends in Ecology & Evolution*, *31*(11), 842–849. https://doi.org/10.1016/j.tree.2016.08.010

Ritchie, E. G., & Johnson, C. N. (2009). Predator interactions, mesopredator release and biodiversity conservation. *Ecology Letters*, *12*(9), 982–998. https://doi.org/10.1111/j.1461-0248.2009.01347.x

Rosenberg, J., & Langer, H. (2001). Ultrastructural Changes of Rhabdoms of the Eyes of *Ocypode* Species in Relation to Different Regimes of Light and Dark Adaptation. *Journal of Crustacean Biology*, *21*(2), 345–353. https://doi.org/10.1163/20021975-99990134

Sakai, K., & Türkay, M. (2013). Revision of the genus Ocypode with the description of a new genus, *Hoplocypode* (Crustacea: Decapoda: Brachyura). *Memoirs of the Queensland Museum*, *56*(2), 665–793. http://dx.doi.org/10.17082/j.2204-1478.56.2.2013-22

Schlacher, T. A., Lucrezi, S., Connolly, R. M., Peterson, C. H., Gilby, B. L., Maslo, B., Olds, A. D., Walker, S. J., Leon, J. X., Huijbers, C. M., Weston, M. A., Turra, A., Hyndes, G. A., Holt, R. A., & Schoeman, D. S. (2016). Human threats to sandy beaches: A meta-analysis of ghost crabs illustrates global anthropogenic impacts. *Estuarine, Coastal and Shelf Science*, *169*, 56–73. https://doi.org/10.1016/j.ecss.2015.11.025

Schmidt, T. S., & Burney, C. M. (1997). *Effects of Ghost Crab (Ocypode quadrata) Invasion on Loggerhead Sea Turtle (Caretta caretta) Nests at Hillsboro Beach, Florida*. Proceedings 17th Annual Sea Turtle Symposium, Orlando, FL. https://nsuworks.nova.edu/cgi/viewcontent.cgi?article=1297&context=occ_facpresentations

Silva, E., Marco, A., da Graça, J., Pérez, H., Abella, E., Patino-Martinez, J., Martins, S., & Almeida, C. (2017). Light pollution affects nesting behavior of loggerhead turtles and predation risk of nests and hatchlings. *Journal of Photochemistry and Photobiology B: Biology*, *173*, 240–249. https://doi.org/10.1016/j.jphotobiol.2017.06.006

Soulé, M. E., Bolger, D. T., Alberts, A. C., Wrights, J., Sorice, M., & Hill, S. (1988). Reconstructed Dynamics of Rapid Extinctions of Chaparral-Requiring Birds in Urban Habitat Islands. *Conservation Biology*, *2*(1), 75–92. https://doi.org/10.1111/j.1523-1739.1988.tb00337.x

Space Launch Delta (SLD) 45. (2022). *Integrated Natural Resources Management Plan (INRMP)*. https://www.denix.osd.mil/inrmp/denix-files/sites/98/2024/02/SLD-45-INRMP-T-EMP-2022.pdf

Stancyk, S. E. (1982). Non-human predators of sea turtles and their control. In K. A. Bjorndal (Ed.), *Biology and Conservation of Sea Turtles* (pp. 139–152). Smithsonian Institution Press.

Stokes, H. J., Esteban, N., & Hays, G. C. (2023). Predation of sea turtle eggs by rats and crabs. *Marine Biology*, *171*(1), 17. https://doi.org/10.1007/s00227-023-04327-9

Tiralongo, F., Messina, G., Marino, S., Bellomo, S., Vanadia, A., Borzì, L., Tibullo, D., Di Stefano, A., & Lombardo, B. M. (2020). Abundance, distribution and ecology of the tufted ghost crab *Ocypode cursor* (Linnaeus, 1758) (Crustacea: Ocypodidae) from a recently colonized urban sandy beach, and new records from Sicily (central Mediterranean Sea). *Journal of Sea Research*, *156*, 101832. https://doi.org/10.1016/j.seares.2019.101832

Tomillo, P. S., Paladino, F. V., Suss, J. S., & Spotila, J. R. (2010). Predation of Leatherback Turtle Hatchlings During the Crawl to the Water. *Chelonian Conservation and Biology*, *9*(1), 18–25. https://doi.org/10.2744/CCB-0789.1

Turra, A., Gonçalves, M. A. O., & and Denadai, M. R. (2005). Spatial distribution of the ghost crab *Ocypode quadrata* in low-energy tide-dominated sandy beaches. *Journal of Natural History*, *39*(23), 2163–2177. https://doi.org/10.1080/00222930500060165

Vernberg, W. B., & Vernberg, F. J. (1968). Physiological Diversity in Metabolism in Marine and Terrestrial Crustacea. *American Zoologist*, *8*(3), 449–458.

Weinstein, R. B., & Full, R. J. (1994). Thermal Dependence of Locomotor Energetics and Endurance Capacity in the Ghost Crab, Ocypode quadrata. *Physiological Zoology*, *67*(4), 855–872.

Whitmore, C. P., & Dutton, P. H. (1985). Infertility, embryonic mortality and nest-site selection in leatherback and green sea turtles in Suriname. *Biological Conservation*, *34*(3), 251–272. https://doi.org/10.1016/0006-3207(85)90095-3

Witherington, B. E., & Bjorndal, K. A. (1991). Influences of artificial lighting on the seaward orientation of hatchling loggerhead turtles *Caretta caretta*. *Biological Conservation*, *55*(2), 139–149. https://doi.org/10.1016/0006-3207(91)90053-C

Witherington, B. E., Martin, R. E., & Trindell, R. N. (2014). *Understanding, Assessing and Resolving Light-Pollution Problems on Sea Turtle Nesting Beaches* (FWRI Technical Report TR-2, Version 2; p. 94). Florida Fish and Wildlife Research Institute. https://f50006a.eos-intl.net/ELIBSQL12_F50006A_Documents/TR-2Rev2.pdf

Chapter 2: Ghost crabs impact loggerhead turtle egg and hatchling survival

Abstract

As a species of conservation concern, loggerhead turtles (*Caretta caretta*) face numerous threats throughout their lives, including predation on nests and hatchlings by ghost crabs (*Ocypode spp*.). Whether ghost crabs kill viable eggs or scavenge eggs that would not have hatched is unclear, making the impacts of ghost crabs difficult to evaluate. Furthermore, the impact of ghost crabs on hatchlings as they crawl from nest to ocean could be significant when crab densities are high but has rarely been quantified. We evaluated the effects of ghost crab abundance on loggerhead egg predation and hatchling survival on the Atlantic coast of Florida from 2021-2023. We marked ~100 loggerhead nests per year and monitored them for signs of predation by ghost crabs. Each year ghost crabs depredated on average 5-10% of eggs and attacked 6-13% of hatchlings during emergence. We quantified ghost crab density using two metrics, live crab counts and burrow density, and found that live counts influenced hatchling predation, with disoriented hatchlings experiencing more than double the predation rates of non-disoriented hatchlings, but egg predation rates were unaffected by variation in crab density. However, burrow activity in nests increased late into incubation and was higher at nests with viable eggs than at nests with unviable eggs. We found evidence that crabs both depredated eggs within the nest and removed them from the nest to consume them elsewhere. In 2023, we conducted an experiment that removed 4,300 ghost crabs from removal zones on the beach. We observed no effect of crab removal on egg predation, but hatchling attacks were reduced in removal zones and hatchling mortality declined from 13% in control zones to 3% in removal zones, highlighting a potential benefit of reducing mesopredator abundances for hatchling sea turtles. These results also demonstrate that nest to surf mortality may be an overlooked metric for assessing

reproductive success when only egg mortality is quantified. These insights into the complex interactions between ghost crabs and loggerhead sea turtles can inform effective management and conservation efforts for this threatened species.

2.1 Introduction

Loggerhead sea turtles (*Caretta caretta*) are a vulnerable species that continue to face a wide variety of threats to their population stability (Casale and Tucker 2015, Ceriani et al. 2019). Their complex life cycle, large home ranges, and amphibious habitat use makes conservation challenging (Heppell et al. 2002, Bolten et al. 2011). Loggerheads spend most of their lives in the ocean, where vessel strikes, pollution, disease, predation, and fisheries bycatch threaten their survival (Donlan et al. 2010, Bolten et al. 2011). However, conservation efforts tend to focus on terrestrial life stages (Crouse et al. 1987, Donlan et al. 2010) where management activities and their effects on eggs and hatchlings can be more easily monitored.

Predation and light pollution are two of the most significant threats to sea turtles while they are on land (Lorne and Salmon 2007, Witherington et al 2014, Erb and Wyneken 2019). In the southeastern United States, native raccoons (*Procyon lotor*) are often trapped and removed from nesting beaches to reduce predation on loggerhead eggs and hatchlings (Stancyk 1982, Engeman et al. 2014, Butler et al. 2020). However, raccoons are intraguild predators on Atlantic ghost crabs (*Ocypode quadrata*), another major sea turtle nest predator, and previous work suggests that their removal may allow ghost crab populations to increase (Barton and Roth 2008). Indeed, anecdotal observations of increasing ghost crab abundance on beaches where raccoons are removed have been reported on some Florida, USA beaches (A.L. Chambers, United States Space Force, personal communication). Although ghost crabs are also known to consume sea turtle eggs and hatchlings, the impact of increasing ghost crab abundance on egg and hatchling mortality is unclear.

Evaluating the impact of ghost crabs on sea turtle eggs is difficult for several reasons. The standard procedure for quantifying ghost crab egg predation is to evaluate eggshell remains during post-hatch nest excavations. However, researchers disagree on how to identify eggs that were preyed upon by ghost crabs. Some researchers claim that ghost crabs leave a tell-tale snip mark (Whitmore and Dutton 1985, Ali and Ibrahim 2002, Maros et al. 2003, Stokes et al. 2023), while others have observed that crabs do not always produce snip marks (Brown 2009, Avenant et al. 2023a, Avenant 2025). It is also unclear whether ghost crabs function primarily as scavengers or predators (Wolcott 1978). If ghost crabs only scavenge unviable eggs and hatchlings, then increasing ghost crab density may not be a concern for sea turtle management. However, if ghost crabs consume viable eggs and hatchlings, increasing ghost crab populations may pose a problem. Size of individual crabs may also affect their impact on turtles, as larger ghost crabs feed at a higher trophic level and likely consume more eggs and hatchlings (Barton and Roth 2008). Finally, ghost crabs can remove eggs from the nest and consume them elsewhere (Marco et al. 2015, Avenant et al. 2023a). Removed eggs can only be quantified if researchers counted the number of eggs initially deposited in the nest, which does not occur in all studies (Ceriani et al. 2021). If removed eggs are ignored, the impact of ghost crabs may be underestimated.

Few studies have investigated the effects of ghost crabs on loggerhead hatchlings (but see Peterson et al. 2013, Erb and Wyneken 2019, Martins et al. 2021, Avenant et al. 2023a). Hatchlings typically emerge from the nest at night and crawl directly to the sea. The distance between the nest and the water determines the amount of exposure to ghost crabs and other land predators, and exposure is minimized by crawling directly to the water (i.e., perpendicular to the coast). However, anthropogenic lighting may disorient hatchlings and cause them to move towards the water at an indirect angle or move away from the water (Witherington and Bjorndal 1991, Lorne and Salmon 2007, Witherington et al. 2014). The extra distance and time on the beach may increase their exposure to ghost crabs (Witherington et al 2014), which are also attracted to well-lit areas (Silva et al. 2017). While disorientation and predation by ghost crabs can be significant sources of nest-to-surf mortality (Erb and Wyneken 2019), their combined effects have not been reported in the literature.

We conducted a three-year field study on the impacts of ghost crabs on loggerhead eggs and hatchlings. Our main objectives were to evaluate how ghost crab abundance affects loggerhead egg and hatchling predation rates. We capitalized on the natural variation in ghost crab density that existed across the study site, as well as experimental manipulations of ghost crab density using small- and large-scale removal methods. We predicted that egg predation rates would increase with ghost crab density and crab activity at nests (including the number and size of burrows into nests). We also predicted that the effect of ghost crab abundance on hatchling predation would increase when hatchlings were disoriented. In our experimental removals of ghost crabs, we predicted that the predation of both eggs and hatchlings would be lower in removal areas compared to control. We tested these predictions by monitoring loggerhead nests, ghost crab abundance, and predation events on plots established across the beach. These data provide novel insight into the role of ghost crabs as sea turtle predators.

2.2 Methods

2.2.1 Study area

The study was conducted on Cape Canaveral Space Force Station (CCSFS) in Brevard County, Florida, USA. CCSFS is on a 6,394-hectare barrier island managed by the Department of Defense. The eastern border of CCSFS is 21 km of gently sloping sandy beach that is sea turtle nesting habitat (SLD 45 2022; Figure 2.1). Each year, between 3,000 and 6,000 sea turtle nests are deposited on the CCSFS beach, including nests from loggerhead, green (*Chelonia mydas)* and leatherback (*Dermochelys coriacea)* turtles (SLD 45 2022). As part of the sea turtle management plan, CCSFS has removed mammalian predators (e.g., raccoons, feral swine, and coyotes) from the beach and adjacent area but has not previously managed invertebrate predators (SLD 45, 2022).

Anthropogenic light is common on CCSFS. To the south, residential and commercial activity contributes to a bright skyglow that is visible from the CCSFS beach. Activities on the station also generate anthropogenic light. Commercial spaceflight companies that test and launch rockets from CCSFS are permitted to use white light during hazardous operations (SLD 45 2022), and lights are often kept on continuously for several days before and after launches. During this study, launchpads that are 0.25 – 1.0 km from the nesting beach were sometimes illuminated. Launch activity increased during our study, from 31 launches in 2021 to 57 in 2022 and 72 in 2023, and launch operations are expected to continue to increase in coming years (SLD 45 2022).

2.2.2 Study design

This study was conducted from 2021-2023 during the sea turtle nesting seasons (approximately May – October, but in 2021 field work began 26 June). Markers on the CCSFS beach designate each of the 21 1-km zones (Figure 2.1). Each year, we established plots within a subset of these zones to monitor loggerhead nests and estimate ghost crab abundance. To establish a plot, we placed labeled wooden posts and reflective driveway stakes at the dune-beach transition for boundaries to be visible both day and night. The length of a plot (from north to south) differed among years, and the width of the plot (from west to east) was determined by distance between dune and the high tide mark, which changed daily.

In 2021, our study design consisted of paired plots that were randomly assigned as control or removal treatments. We established one pair in each of the six northern-most zones of the study site. Plots were 300-m long and 200-m apart (Figure 2.S1). We removed ghost crabs from removal plots between 26 June and 16 October 2021 using live capture methods. We initially used pitfall traps, which were created by burying up to 6 7.6-liter buckets flush in the sand in each removal zone (Figure 2.S2A). Once sea turtle hatchlings began emerging from nests (1 July), we switched from pitfall traps to commercially available crayfish traps (foldable mesh traps with 6 openings; Figure 2.S2B). Both types of traps were baited with fishing bait (previously frozen shrimp and fish) and we deployed 3-4 traps in each removal zone between the high tide line and the dune for 2-3 hours in the morning. Ghost crabs were also opportunistically captured by hand from removal sites. All crabs were dispatched humanely through quick freezing, by submerging them in an ice slurry inside a cooler (Taylor et al. 2019; University of Manitoba Animal Care Protocol #F21-009).

In 2021, a subset of captured crabs was marked and released in an attempt to estimate population size via mark-recapture methods. Due to low rates of recapture this effort was abandoned. However, we did observe a marked crab 2 km from where it was marked, highlighting that crab foraging distance may be much higher than previously reported (300 m –

Wolcott 1978; 160 m – Schlacher and Lucrezi 2010), and therefore we spaced plots farther apart in the following years. In 2022, we created 200-m plots in the center of 15 zones (Figure 2.S1), which allowed at least 1 km between adjacent plots. We did not conduct any ghost crab removals in 2022.

In 2023, we conducted a large-scale removal experiment aimed at significantly reducing ghost crab density in treatment plots. The experimental design consisted of three pairs of removal and control (no removal) zones. Each zone was 2 km in length and was separated from an adjacent zone by a 1-km buffer. Within each zone we established two 200-m plots (Figure 2.S1) to monitor ghost crab abundance and sea turtle nests.

We reduced ghost crab density in removal zones by crushing crabs with a sod roller (227 kg, 0.5 x 1.2 m) towed behind a utility task vehicle (UTV; Figure 2.S2C). Removal efforts began on 13 March 2023, when nightly temperatures had increased to above 15° C, the minimum temperature ghost crabs have been described to be active (Lucrezi and Schlacher, 2014). We conducted removals 2-3 nights a week every other week, during incoming tides after dusk. To ensure we did not disturb nesting sea turtles, removal activities stopped when sea turtle nesting activity began to increase (25 May 2023).

Removals were conducted in the intertidal zone, between the water and the previous high tide line, where ghost crabs actively forage on small invertebrates at night (Morrow et al. 2014). Upon approaching a removal zone, the sod roller was attached to the UTV and towed at 16 km/h across the entire 2 km removal zone. If <10 crabs were observed, we proceeded to the next removal zone. If more than 10 crabs were observed, we made additional passes with the sod roller until <25 crabs were crushed in a pass (2-6 passes). In subsequent passes, crabs entered the removal zone to consume the carcasses of crabs rolled over during initial passes. Since removals were conducted in the intertidal zone at low tide, the incoming tide swept the crab carcasses out to sea, so they did not remain on the beach.

2.2.3 Nest marking

We used all-terrain vehicles (ATVs) and UTVs to conduct daily surveys beginning at sunrise. During this time, we identified nests to mark and visually examined previously marked nest areas for signs of predation or hatchling emergence. We were permitted to mark up to 120 nests and aimed to mark an equal proportion of nests in all plots. The number of plots changed each year, so each year we divided the 120 nests by the number of plots to aim for a similar number of marked nests in each plot. Not every nest within a plot was marked, and we selected nests to mark based on spatial and temporal distribution to evenly disperse marked nests across the beach and season. In 2023, nests laid landward of the vegetation line were not marked due to nests within the vegetation in 2021 and 2022 being nearly completely damaged by roots. We pre-counted all nests used in our study to determine initial clutch sizes. To do so, eggs were exhumed, counted, and placed back in the nest prior to 09:00 AM. Each marked nest was covered with a metal self-releasing screen (1.2 x 1.2 m with 5 x 10 cm openings) to deter mammalian predators while still allowing hatchlings to emerge unaided (Lovemore et al.2020). A labeled wooden stake was placed 0.5 m landward of the reburied clutch to identify individual nests.

2.2.4 Quantifying egg predation

Each marked nest was checked daily for signs of disturbance or emergence. In 2022 and 2023, we recorded the date and diameter of each new ghost crab burrow found within 1 m of the nest (i.e., within the nest screen on top of the nest, Figure 2.2C). To distinguish between new and previously established burrows, we drew diagrams of the screen with the size and placement of burrows within the screen on field data sheets. We recorded any evidence of eggs or hatchlings found outside of these burrows (Figure 2.2C). During nest excavation, any additional burrows found in the side of the egg chamber that did not enter the nest from above were added to the total number of burrows observed into the nest.

Hatchling emergences from nests were identified by the presence of hatchling tracks and a depression in the sand where hatchlings emerged. Nests were excavated and inventoried three days after evidence of an emergence was observed. Nests typically emerged after 45-65 days of incubation and nests with no evidence of hatchling emergences were excavated 70 days after they were laid following Florida Fish and Wildlife Conservation Commission protocols (FFWCC 2016). During the post-incubation inventory, unhatched eggs and eggshells were carefully removed from the nest to assess the fate of each egg. Eggs were categorized as hatched (>50% of empty eggshell remnant), pipped eggs (live and dead) and unhatched eggs (whole or damaged) following FFWCC protocol. Few nests had entirely whole eggs, which were opened and showed no discernable embryonic development (2021 n = 3, 2022 n =1, 2023 n = 0). Damaged eggs were further categorized by the source of damage (e.g., ghost crabs, plant roots, other or unknown). There is no universally accepted method for determining whether an egg was preyed upon by a ghost crab, and the snip mark approach (Whitmore and Dutton 1985, Ali and Ibrahim 2002, Maros et al. 2003, Stokes et al. 2023) may be too conservative based on personal observations and experiments conducted in similar species (Avenant et al. 2023b, Avenant 2025). Specifically, we categorized an egg as crab damaged when it had a snip mark and/or if it was torn open with rotten contents and decayed hatchling matter inside and there were no other predators or roots observed (Figure 2.2B). Occasionally, nests had rotten contents due to the presence of fire ants and maggots within nest chambers, which would obscure evidence of crab damage and make damage sources indistinguishable. In these cases, the source was recorded as unknown, thus our estimates of ghost crab damage are conservative. We summed all pipped eggs, unhatched eggs and hatched eggshell remnants (>50% complete) to determine a post-emergence egg count (Miller 1999, FFWCC 2016). This value was subtracted from the pre-count to estimate the number of eggs missing. We calculated hatch success by dividing the number of hatched eggs by the number of eggs counted when the nest was initially marked. We considered nests to be viable if they produced hatchlings, and unviable nests had no hatched eggs or hatchling emergence.

2.2.5 Quantifying hatchling predation during emergence

Every day during morning surveys we searched for hatchling tracks that indicated hatchlings had emerged from a nest the previous night. In addition to marked nests (n = 174), we opportunistically included emergences from unmarked nests that were laid within a plot (n = 176). We assessed the directionality of the emergence as a measure of disorientation. Emergences where hatchling tracks were oriented directly towards the water (i.e., approximately perpendicular to the beach) were recorded as direct emergences. However, if the tracks were oriented parallel with the beach or towards the dune, we considered them indirect emergences. Hatchling orientation typically followed a bimodal distribution, with a majority (>75%) of hatchlings orienting in the same direction.

We estimated hatchling predation rates using a similar approach as Erb and Wyneken (2019). Ghost crabs drag hatchlings to their burrows or other areas to consume them, and in the process leave signature drag marks in the sand (Figure 2.2D). We surveyed the entire emergence area and followed all hatchling tracks for as long as possible to count the number of drag marks left in the sand. In 2021 and 2022, we attempted to record emergences using infrared cameras, but abandoned this effort due to low success rates, technical difficulties, and nests disorienting out of camera frames (Appendix 2.A). For marked nests, nest to surf mortality rates were calculated by dividing the number of drag marks observed by the total number of hatchlings that emerged. This total number of emerged hatchlings could be calculated in nests by subtracting the number of hatchlings remaining in the nest (live and dead) from the total number of hatched eggs.

2.2.6 Ghost crab abundance estimates

We used ghost crab burrow and live count surveys as two indices of ghost crab population size. In all three years, we conducted biweekly surveys to quantify ghost crab burrow density within plots. Surveys were conducted in the morning beginning at sunrise and continued throughout the sea turtle nesting season (approximately May-October each year). Burrow surveys were completed by driving a UTV the entire length of a plot (parallel to the ocean) at 4 km/h and using a handheld tally counter to count all active burrows within the width of the UTV tires (width = 1.3 m). To exclude inactive burrows, we conducted surveys below the most recent high tide line and only counted burrows with freshly dug sand outside the burrow opening. Burrow density was calculated by dividing the number of burrows counted by the area surveyed (plot length x 1.3 m).

In years two and three we also conducted visual surveys of live crabs at night. To standardize the timing of the visual and burrow count data, visual surveys were conducted the night preceding burrow surveys. Visual surveys began near low tide so all plots could be surveyed before the next high tide. We conducted visual surveys from a UTV with translucent red film covering the headlights to minimize light disturbance of any nesting turtles. We drove the length of the plot through the intertidal zone at 8 km/h and counted the number of crabs visible in the light from the UTV headlights within plot boundaries. The red headlights allowed us to see approximately 10 m in front of the UTV, but unlike the tire width used in the burrow counts, the headlights did not provide a clear sampling boundary and crabs could move in and out of the light. Therefore, live survey data were analyzed as counts and not converted to density.

2.2.7 Data analysis

To examine potential factors that could influence the number of eggs depredated and hatchlings attacked by crabs, we used generalized linear models (GLM) with a negative binomial family to correct for overdispersion. These analyses were completed using the “stats” packages in R statistical software (Version 4.2.2). All models used were examined using the “plotQQunif” function from the “DHARMa” package to examine residual distribution and confirm normality. We also confirmed that variables were not multicollinear. We used an Analysis of Variance (ANOVA) with Type-III Sums of Squares to summarize our results for each model and assess the significance of each predictor variable while accounting for the presence of other variables in the model.

To explore egg predation, we examined two different response variables: (1) the number of eggs damaged by crabs within a nest (Figure 2.3A,B) and (2) the total number of eggs affected by ghost crabs, including eggs damaged within the nest and eggs removed (missing at inventory or found outside burrows, Figure 2.3C) from the nest. We created different models using the different metrics of crab density: crab burrow density and live crab counts. Using nests from control plots only, we first created global models using the variables that were collected all years (number of burrows in the nest), and then analyzed each year individually with variables collected that year (e.g., the largest burrow in the nest) and plausible interactions. For all models, we included clutch size as an offset variable. Live crab counts and burrow density associated with each individual nest were calculated between the date the nest was laid and the date the nest was inventoried using the plot that contained the nest. Lastly, using our complete dataset with nests from control and removal plots, we analyzed whether our two experimental removal treatments influenced egg predation.

To explore hatchling predation, we examined whether the number of newly emerged hatchlings that were attacked by ghost crabs (drag marks) was influenced by emergence orientation (direct or indirect movement toward the ocean) or crab abundance (either burrow density or live counts), or if the effect of crab abundance depended on orientation (an interaction). For these models, we used data from nests in control plots only and included the number of hatchlings that emerged as an offset variable and year. Hatch date was excluded due to its relationship with crab density ($p < 0.001$, $R^2 = 0.19$). We also examined whether hatchling predation was influenced by our live capture and sod roller experimental treatments and included track orientation and the interaction between treatment and orientation.

2.3 Results

2.3.1 Crab abundance and removals

From 2021-2023, burrow density averaged 0.27-0.32 burrows / m^2 (Table 2.1), and live crab counts averaged 43.3 to 50.5 crabs per 200-m transect in 2022-2023 (Table 2.1). In 2021, we removed 896 ghost crabs in 63 days using live capture methods. The maximum number of crabs removed in a single day using multiple traps was 65 (mean 13.5, range 1-65), but this removal effort did not affect crab burrow density compared to control plots (Wilcoxon Rank-Sum test, $p = 0.61$). In 2023, we removed 4,301 ghost crabs in 13 nights using the sod roller. The total number of crabs removed ranged from 810 to 1748 per plot, and a maximum of 744 were removed in a single day. The 2023 removal experiment significantly reduced ghost crab burrow density and live crab abundance in removal plots (Wilcoxon Rank-Sum test, both $p < 0.001$, Figure 2.3A, B).

2.3.2 Egg predation

Ghost crab burrows were observed in 72% of turtle nests in control plots and were much more common in viable nests than unviable nests (75% vs 37%; Fisher's exact test, $p = 0.003$, $n = 191$, 16 unviable and 175 viable). The first day a burrow appeared at a nest was skewed toward later in incubation, when eggs and hatchlings would be more developed (Shapiro-Wilk normality test, $p <0.0001$, $W = 0.725$, Figure 2.4).

Clutch size in pre-counted nests in control zones averaged 110.5 eggs (±1.8 SE, n=175, Table 2.1). We found no difference in pre-count and post-emergence egg numbers for 53% of nests, indicating no missing eggs. In 29% of nests, we estimated 1-3 missing eggs, which could potentially be explained by fragmented egg pieces obscuring our counts during the post-emergence inventory, although loggerhead nest inventories have the lowest human error (Ceriani et al. 2021). However, in 18% of nests, we estimated 4-24 eggs were missing, suggesting some eggs likely had been removed from nests. Overall, crabs damaged fewer eggs in more nests compared to plant roots, but when present, roots had a more prolific impact on clutches, in fewer nests (Table 2.1).

We found no evidence that ghost crab density affected egg predation, whether it was modeled as burrow density or live counts, and whether we modeled eggs damaged within nests or total eggs predated by ghost crabs (Tables 2.2, 2.3). However, the number of burrows leading into nests significantly affected egg predation, for both response variables, damaged eggs and total egg predation, in the global models and in 2021 (Tables 2.2, 2.3). In 2022, when burrow density was included, both response variables were significantly affected by the interaction between the size of the largest burrow and the number of burrows into nests, as the effect of the number of burrows on eggs impacted depended on the size of the largest burrow observed. We found the number of damaged eggs increased with larger crab size when few burrows were observed (1-2), but not when more burrows were observed (3-8; Figure 2.5). Using live counts, largest burrow size was the only significant predictor of both response variables (Table 2.3). In 2023, no predictors were significant for either response variable (Table 2.2, 2.3). In 2021, the live capture removal efforts did not affect eggs damaged within the nest ($\chi^2 = 0.015$, $p = 0.900$, n = 74) or total eggs predated ($\chi^2 < 0.001$, $p = 0.999$, n = 74). Likewise, the sod roller removals did not affect eggs damaged in the nest ($\chi^2 = 0.118$, $p = 0.732$, n = 78) or total eggs predated ($\chi^2 = 0.038$, $p = 0.845$, n = 78, Figure 2.3C).

2.3.3 Hatchling predation

We detected drag marks at 91% of emergences (165 of 175 marked and unmarked nests from control plots). Using marked nests in control plots, for which the total number of hatchlings emerged from the nest was known, we estimated that in all three years 8.7 ± 12.0% (mean ± SD) hatchlings were attacked on their way to the water. Drag marks often led to burrows. To confirm that drag marks leading to burrows resulted in dead hatchlings, we examined five such burrows using an industrial endoscope with a pipe camera. All five burrows examined contained dead hatchlings. We occasionally saw evidence of hatchling predation by mammals, based on tracks in the sand, but only attacks by ghost crabs were quantified.

Disoriented nests often had many more drag marks than nests that oriented straight to the water (Table 2.4, Figure 2.6); 14.0 ± 16.0% of hatchlings from nests that disoriented were attacked, and 6.5 ± 1.3% of hatchlings were attacked for nests that oriented directly to the water. Hatchling predation was not affected by crab burrow density but increased with live crab counts (Table 2.4), and we found no interaction between disorientation and either estimate of crab density (Table 2.4). Hatchling predation was unaffected by either removal treatment or track orientation in 2021, when only 4 marked nests disoriented (Table 2.5). However, hatchling predation was lower in ghost crab removal plots following our sod roller removals in 2023 (Table 2.5), and in disoriented nests (Table 2.5; Figure 2.6), but we found no interaction between disorientation and removals (Table 2.5).

2.4 Discussion

Sea turtle biologists often debate whether ghost crabs are important sources of mortality. Successful embryonic development (i.e., hatch success) can vary considerably for sea turtles and not every egg laid will produce a hatchling. If ghost crabs are scavenging unviable eggs that would not have produced a hatchling, then their egg consumption does not cause mortality and may not affect conservation of this species. However, predation of viable embryos and hatchlings would represent additive mortality that reduces recruitment. By comparing ghost crab burrowing activity around viable and unviable marked nests, we found that ghost crabs preferentially burrowed into viable nests at twice the rate of unviable nests. Importantly, we found that ghost crabs started burrowing into nests near the end of embryonic development when hatchlings are beginning to move around the nest chamber prior to emergence (Godfrey and Mrosovsky, 1997). Ghost crabs have specialized sensory organs that detect substrate vibrations (Horch 1971), and it is possible these organs allow crabs to detect hatchlings moving beneath the beach surface.

However, we found no evidence that variation in ghost crab abundance affects egg predation. Using both burrow density and live counts as indices of ghost crab population size and three years of egg predation data, our analyses revealed no evidence that egg predation rates were related to burrow density or live counts. Similarly, neither type of removal of ghost crabs influenced egg predation rates.

Our analyses revealed mixed results regarding ghost crab abundance and hatchling predation. We found no relationship between burrow density and hatchling predation, but we found a positive effect of live crab counts on hatchling predation. It is unclear why these two metrics provided different results. Burrow surveys are common in published studies, but some question their utility as an index of population size. These surveys assume that burrow effort by ghost crabs is consistent over space and time, but that assumption has not been well explored. Ghost crab behavior (activity on the surface and burrow excavation) may vary due to environmental conditions (see Chapter 3). The relationship between live counts and burrow counts is unclear, in addition to the relationship between these metrics and actual crab population size and warrants further investigation.

Both metrics revealed that track orientation affects hatchling predation rates. Although it has been speculated previously (e.g., Witherington et al. 2014), our study provides the first quantitative evidence that disoriented hatchlings suffer higher rates of predation by ghost crabs. Specifically, we found that disoriented emergences had on average over two times more drag marks than those that headed directly to the water. Disorientations have been a concern in sea turtle conservation for a long time, but usually focus on hatchlings that move inland and were unlikely to find their way back to the ocean. Our results show that less severe disorientations where hatchlings take a longer, non-perpendicular path towards the water can increase mortality when predators are abundant. Although drag marks may overestimate predation events because some hatchlings may escape, even non-fatal attacks result in wasted energy and possible injuries that may reduce survival.

We found more drag marks for disoriented emergences in our large-scale removal plots (lower crab density) than in control plots that did not disorient. This result suggests that mitigating anthropogenic light that causes disorientation may be more impactful than reducing the abundance of these native predators. In our study site, 30% of nests took indirect paths to the water or disoriented away from the water. Although we did not identify the causes of specific nest disorientations, anecdotal evidence suggests that light from the port, nearby cities, and launchpads contributed to disorientations. Reducing these sources of light pollution would likely reduce disorientations and reduce hatchling predation rates.

We estimated how many hatchlings were protected from ghost crab predation in our removal plots by comparing the estimated number attacked in removal and control plots. For each plot, we multiplied the ghost crab attack rate (drag marks/emerged hatchlings, averaged for the marked nests in that plot) by the average number of emerged hatchlings, and then by the total number of nests in the plot. We estimated that 5,611 hatchlings would have been attacked in the three control (no removal) zones of our experiment and that 4,100 hatchlings would have been attacked in the three removal zones. This difference (1,511 hatchlings saved) compared to 4,301 crabs removed suggests that we saved one hatchling from being attacked for every three crabs removed. However, <0.1% of hatchlings that reach the ocean survive to adulthood (Frazer 1986, Bolten et al. 2011), and therefore our large-scale removal efforts may equate to the addition of a single loggerhead to the breeding population. Indirect effects of this removal technique are unknown. Ghost crabs are a native predator and prey, and reducing their density may have other effects on beach ecosystems, as well as in the near-shore ocean ecosystems where they reproduce. Conversely, ghost crab densities may be inflated by the reduction of predators that consume them, leading to an imbalance in their numbers (Barton and Roth 2008).

Findings from this study suggest that the current practice of measuring ghost crab egg predation only by the presence of snip marks in eggs underestimate the impact of ghost crabs on turtle eggs. First, snip marks may not always be evident on the remains of an egg that was consumed by a ghost crab. We often found eggs on the surface of the sand outside of ghost crab burrows that were either torn open with decaying hatchling matter, or highly fragmented shell remnants. This perspective has been shared by others (Brown 2009, Avenant et al. 2023b). Second, snip marks cannot account for eggs removed from the nest. While it is not feasible to pre-count all sea turtle nests to account for the possibility of missing eggs, collecting this information on a subset of nests is necessary to accurately estimate ghost crab predation rates.

In addition to quantifying hatchling attacks through drag marks, we also attempted to record emergences using infrared cameras (Appendix 2.A). Both of these methods reduce bias due to observer presence, but each has limitations. Using drag marks may over-estimate hatchling predation rates if hatchlings escape, or underestimate predation if drag mark visibility is affected by environmental factors such as weather and beach composition or does not capture every attack. In the video footage from pre-installed cameras, crabs occasionally carried hatchlings above the sand or below the high tide line without leaving visible drag marks, and we also observed crabs entering nest chambers before and after emergence to remove hatchlings from the nest. However, disoriented hatchlings often moved out of camera range, reducing our ability to assess hatchling predation with cameras.

Results differed at the nest level compared to the plot level. Marco et al. (2015) found a negative relationship between egg predation and crab size and suggested that larger crabs may defend the nests they prey on. We found the number of damaged eggs increased with larger crab size when few burrows were observed but in general, predation was higher with more burrows observed into the nest. However, some crabs can have multiple burrow entrances to the nest, and larger burrows corresponded to more eggs predated. Crab territoriality may limit crab interactions within the nest (Marco et al. 2015), but not the predation of dispersed emergent hatchlings. Egg predation has been extensively tracked and studied, but studies investigating nest to surf mortality are less common (but see Tomillo et al. 2010, Peterson et al. 2013, Erb and Wyneken 2019, Martins et al. 2021, Avenant et al. 2023a). Further investigation of hatchling predation for both loggerheads and other sea turtle species would be beneficial in assessing this data gap and identifying how hatchling predation varies and is influenced by disorientation across nesting beaches.

The results of this study provide valuable insight into the complex interactions between ghost crabs and loggerhead sea turtles. We found that ghost crabs preferentially target viable nests, with nearly 10% of eggs damaged or removed each year. We also identified a clear association between hatchling predation and disorientation and found that light on the beach can exacerbate ghost crab predation of hatchlings. Our large-scale crab removal experiment suggests that reducing artificial lighting may be a more effective strategy for reducing hatchling predation than controlling ghost crab populations. Although the crab removal experiment reduced hatchling predation, the benefit was marginal and the ecological consequences of altering native species numbers are unknown. This study also underscores some limitations of predator monitoring methods and discusses improved methods to quantify ghost crab predation of both eggs and hatchlings more accurately. Ultimately, these results can inform the management and conservation practices aimed to protect threatened loggerhead sea turtle populations.

2.5 References

Ali, A., & Ibrahim, K. (2002). Crab predation on green turtle (*Chelonia mydas)* eggs incubated on a natural beach and in turtle hatcheries. *Proceedings of the 3rd Workshop on SEASTAR 2000.* Kyoto, pp. 95-100.

Avenant, C., Whiting, S., Fossette, S., Barnes, P., & Hyndes, G. A. (2023a). Extreme predation of eggs and hatchlings for loggerhead turtles in eastern Indian Ocean. *Biodiversity and Conservation*, *33*(1), 135–159. https://doi.org/10.1007/s10531-023-02739-z

Avenant, C., Fossette, S., Whiting, S., Hopkins, A. J. M., & Hyndes, G. A. (2023b). Sea Turtle Eggs and Hatchlings are a Seasonally Important Food Source for the Generalist Feeding Golden Ghost Crab (*Ocypode convexa*). *Estuaries and Coasts*, *47*(3), 821–838. https://doi.org/10.1007/s12237-023-01309-4

Avenant, C. (2025). Insights into prey handling and feeding strategies by ghost crabs on sea turtle eggs and hatchlings. *Food Webs*, *43*, e00400. https://doi.org/10.1016/j.fooweb.2025.e00400

Barton, B. T., & Roth, J. D. (2008). Implications of intraguild predation for sea turtle nest protection. *Biological Conservation*, *141*(8), 2139–2145. https://doi.org/10.1016/j.biocon.2008.06.013

Bolten, A. B., Crowder, L. B., Dodd, M. G., MacPherson, S. L., Musick, J. A., Schroeder, B. A., Witherington, B. E., Long, K. J., & Snover, M. L. (2011). Quantifying multiple threats to endangered species: An example from loggerhead sea turtles. *Frontiers in Ecology and the Environment*, *9*(5), 295–301. https://doi.org/10.1890/090126

Brown, J. (2009). *Factors Affecting Predation Of Marine Turtle Eggs By Raccoons And Ghost*

Crabs On Canaveral National Seashore, Fl (Master's thesis, University of Central Florida). https://stars.library.ucf.edu/cgi/viewcontent.cgi?article=5043&context=etd

Butler, Z. P., Wenger, S. J., Pfaller, J. B., Dodd, M. G., Ondich, B. L., Coleman, S., Gaskin, J. L., Hickey, N., Kitchens-Hayes, K., Vance, R. K., & Williams, K. L. (2020). Predation of loggerhead sea turtle eggs across Georgia's barrier islands. *Global Ecology and Conservation*, *23*, e01139. https://doi.org/10.1016/j.gecco.2020.e01139

Casale, P., & Tucker, A. D. (2015). *Caretta caretta (Loggerhead Turtle)*. The IUCN Red List of Threatened Species. http://dx.doi.org/10.2305/IUCN.UK.2015-4.RLTS.T3897A83157651.en

Ceriani, S. A., Casale, P., Brost, M., Leone, E. H., & Witherington, B. E. (2019). Conservation implications of sea turtle nesting trends: Elusive recovery of a globally important loggerhead population. *Ecosphere*, *10*(11), e02936. https://doi.org/10.1002/ecs2.2936

Ceriani, S. A., Brost, B., Meylan, A. B., Meylan, P. A., & Casale, P. (2021). Bias in sea turtle productivity estimates: Error and factors involved. *Marine Biology*, *168*(4), 41. https://doi.org/10.1007/s00227-021-03843-w

Crouse, D. T., Crowder, L. B., & Caswell, H. (1987). A Stage-Based Population Model for Loggerhead Sea Turtles and Implications for Conservation. *Ecology*, *68*(5), 1412–1423. https://doi.org/10.2307/1939225

Donlan, C. J., Wingfield, D. K., Crowder, L. B., & Wilcox, C. (2010). Using expert opinion surveys to rank threats to endangered species: A case study with sea turtles. *Conservation Biology: The Journal of the Society for Conservation Biology*, *24*(6), 1586–1595. https://doi.org/10.1111/j.1523-1739.2010.01541.x

Engeman, R. M., Addison, D., & Griffin, J. C. (2014). Defending against disparate marine turtle nest predators: Nesting success benefits from eradicating invasive feral swine and caging nests from raccoons. *Oryx*, *50*(2), 289–295. https://doi.org/10.1017/S0030605314000805

Erb, V., & Wyneken, J. (2019). Nest-to-Surf Mortality of Loggerhead Sea Turtle (Caretta caretta) Hatchlings on Florida’s East Coast. *Frontiers in Marine Science*, *6*(271). https://doi.org/10.3389/fmars.2019.00271

Frazer, N. B. (1986). Survival from Egg to Adulthood in a Declining Population of Loggerhead Turtles, Caretta caretta. *Herpetologica*, *42*(1), 47–55.

Godfrey, M., & Mrosovsky, N. (1997). Estimating the time between hatching of sea turtles and their emergence from the nest. *Chelonian Conservation and Biology*. *2*(4): 581-585.

Heppell, S. S., Snover, M. L., & Crowder, L. B. (2002). Sea turtle population ecology. In P. L. Lutz, J. A. Musick, & J. Wyneken (Eds.), *The Biology of Sea Turtles: Vol. II* (pp. 275–306). CRC Press. https://doi.org/10.1201/9781420040807

Horch, K. (1971). An organ for hearing and vibration sense in the ghost crab Ocypode. *Zeitschrift Für Vergleichende Physiologie*, *73*(1), 1–21. https://doi.org/10.1007/BF00297698

Lorne, J. K., & Salmon, M. (2007). Effects of exposure to artificial lighting on orientation of hatchling sea turtles on the beach and in the ocean. *Endangered Species Research*, *3*, 23–30. https://doi.org/10.3354/esr003023

Lovemore, T. E. J., Montero, N., Ceriani, S. A., & Fuentes, M. M. P. B. (2020). Assessing the effectiveness of different sea turtle nest protection strategies against coyotes. *Journal of Experimental Marine Biology and Ecology*, *533*, 151470. https://doi.org/10.1016/j.jembe.2020.151470

Lucrezi, S., & Schlacher, T. A. (2014). The Ecology of Ghost Crabs. In R. N. Hughes, Hughes, D. J., & I. P. Smith (Eds.), *Oceanography and Marine Biology* (pp. 201–256). CRC Press. https://doi.org/10.1201/b17143

Marco, A., da Graça, J., García-Cerdá, R., Abella, E., & Freitas, R. (2015). Patterns and intensity of ghost crab predation on the nests of an important endangered loggerhead turtle population. *Journal of Experimental Marine Biology and Ecology*, *468*, 74–82. https://doi.org/10.1016/j.jembe.2015.03.010

Maros, A., Louveaux, A., Godfrey, M. H., & Girondot, M. (2003). *Scapteriscus didactylus* (Orthoptera, Gryllotalpidae), predator of leatherback turtle eggs in French Guiana. *Marine Ecology Progress Series*, *249*, 289–296. https://doi.org/10.3354/meps249289

Martins, S., Sierra, L., Rodrigues, E., Oñate-Casado, J., Galán, I. T., Clarke, L. J., & Marco, A. (2021). Ecological drivers of the high predation of sea turtle hatchlings during emergence. *Marine Ecology Progress Series*, *668*, 97–106. https://doi.org/10.3354/meps13751

Miller, J. D. (1999). Determining clutch size and hatching success. In K. L. Eckert, K. A. Bjorndal, F. A. Abreu-Grobois, & M. Donnelly (Eds.), *Research and Management Techniques for the Conservation of Sea Turtles.* IUCN/SSC Marine Turtle Specialist Group Publication No 4. (pp. 124–129).

Morrow, K., Bell, S. S., & Tewfik, A. (2014). Variation in ghost crab trophic links on sandy beaches. *Marine Ecology Progress Series*, *502*, 197–206. https://doi.org/10.3354/meps10728

Peterson, C. H., Fegley, S. R., Voss, C. M., Marschhauser, S. R., & VanDusen, B. M. (2013). Conservation implications of density-dependent predation by ghost crabs on hatchling sea turtles running the gauntlet to the sea. *Marine Biology*, *160*(3), 629–640. https://doi.org/10.1007/s00227-012-2118-z

Schlacher, T. A., & Lucrezi, S. (2010). Compression of home ranges in ghost crabs on sandy beaches impacted by vehicle traffic. *Marine Biology*, *157*(11), 2467–2474. https://doi.org/10.1007/s00227-010-1511-8

Silva, E., Marco, A., da Graça, J., Pérez, H., Abella, E., Patino-Martinez, J., Martins, S., & Almeida, C. (2017). Light pollution affects nesting behavior of loggerhead turtles and predation risk of nests and hatchlings. *Journal of Photochemistry and Photobiology B: Biology*, *173*, 240–249. https://doi.org/10.1016/j.jphotobiol.2017.06.006

Space Launch Delta (SLD) 45. (2022). Integrated Natural Resources Management Plan (INRMP). https://www.denix.osd.mil/inrmp/denix-files/sites/98/2024/02/SLD-45-INRMP-T-EMP-2022.pdf

Stancyk, S. E. (1982). Non-human predators of sea turtles and their control. In K. A. Bjorndal (Ed.), *Biology and Conservation of Sea Turtles* (pp. 139–152). Smithsonian Institution Press.

Stokes, H. J., Esteban, N., & Hays, G. C. (2023). Predation of sea turtle eggs by rats and crabs. *Marine Biology*, *171*(1), 17. https://doi.org/10.1007/s00227-023-04327-9

Taylor, J. R. A., deVries, M. S., & Elias, D. O. (2019). Growling from the gut: Co-option of the gastric mill for acoustic communication in ghost crabs. *Proceedings of the Royal Society B: Biological Sciences*, *286*(1910), 20191161. https://doi.org/10.1098/rspb.2019.1161

Tomillo, P. S., Paladino, F. V., Suss, J. S., & Spotila, J. R. (2010). Predation of Leatherback Turtle Hatchlings During the Crawl to the Water. *Chelonian Conservation and Biology*, *9*(1), 18–25. https://doi.org/10.2744/CCB-0789.1

Whitmore, C. P., & Dutton, P. H. (1985). Infertility, embryonic mortality and nest-site selection in leatherback and green sea turtles in Suriname. *Biological Conservation*, *34*(3), 251–272. https://doi.org/10.1016/0006-3207(85)90095-3

Witherington, B. E., & Bjorndal, K. A. (1991). Influences of artificial lighting on the seaward orientation of hatchling loggerhead turtles *Caretta caretta*. *Biological Conservation*, *55*(2), 139–149. https://doi.org/10.1016/0006-3207(91)90053-C

Witherington, B. E., Martin, R. E., & Trindell, R. N. (2014). *Understanding, Assessing and Resolving Light-Pollution Problems on Sea Turtle Nesting Beaches* (FWRI Technical Report TR-2, Version 2; p. 94). Florida Fish and Wildlife Research Institute. https://f50006a.eos-intl.net/ELIBSQL12_F50006A_Documents/TR-2Rev2.pdf

Wolcott, T. G. (1978). Ecological role of ghost crabs, *Ocypode quadrata* (Fabricius) on an ocean beach: Scavengers or predators? *Journal of Experimental Marine Biology and Ecology*, *31*(1), 67–82. https://doi.org/10.1016/0022-0981(78)90137-5

2.6 Figures

Figure 2.1: A map of Cape Canaveral Space Force Station in Brevard County, Florida, USA, showing the location of the 1-km zones throughout the beach. The southern boundary of CCSFS abuts Port Canaveral, and the northern boundary abuts Kennedy Space Center.

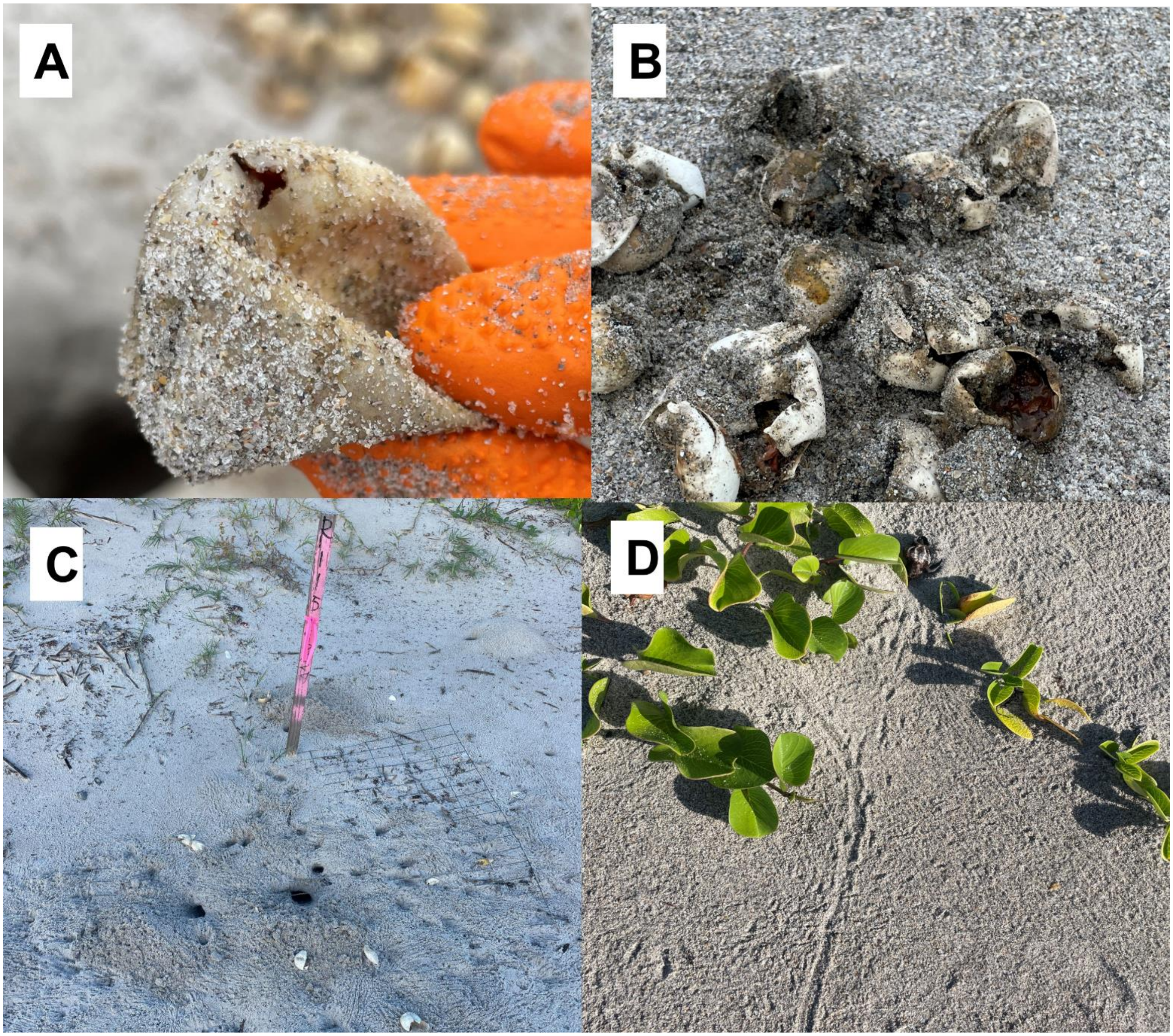


Figure 2.2: A ghost crab snip mark observed in a damaged egg (A), other eggs found in a nest with a large ghost crab burrow (5 cm), which were torn open and contained rotten hatchling contents, and were presumed to be damaged by crabs (B), ghost crab burrows into nest screen with eggs removed from an incubating nest (C), and a drag mark leading to a dead hatchling (D).

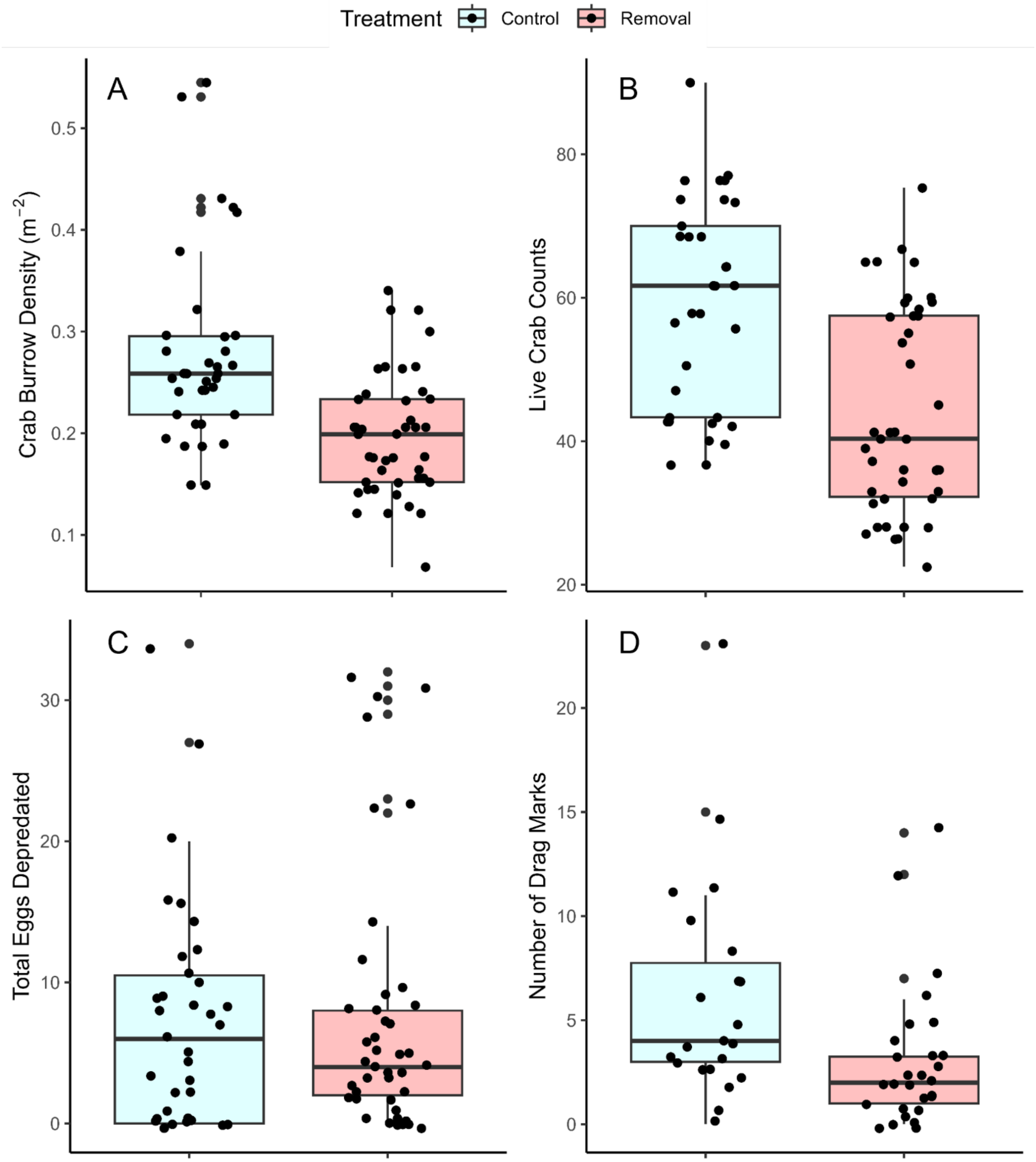


Figure 2.3: Ghost crab burrow density (A), live crab counts (B), turtle egg predation, including both eggs damaged within the nest and eggs missing from the nest (C), and hatchling attacks (D) in control and removal plots in 2023 on Cape Canaveral Space Force Station.

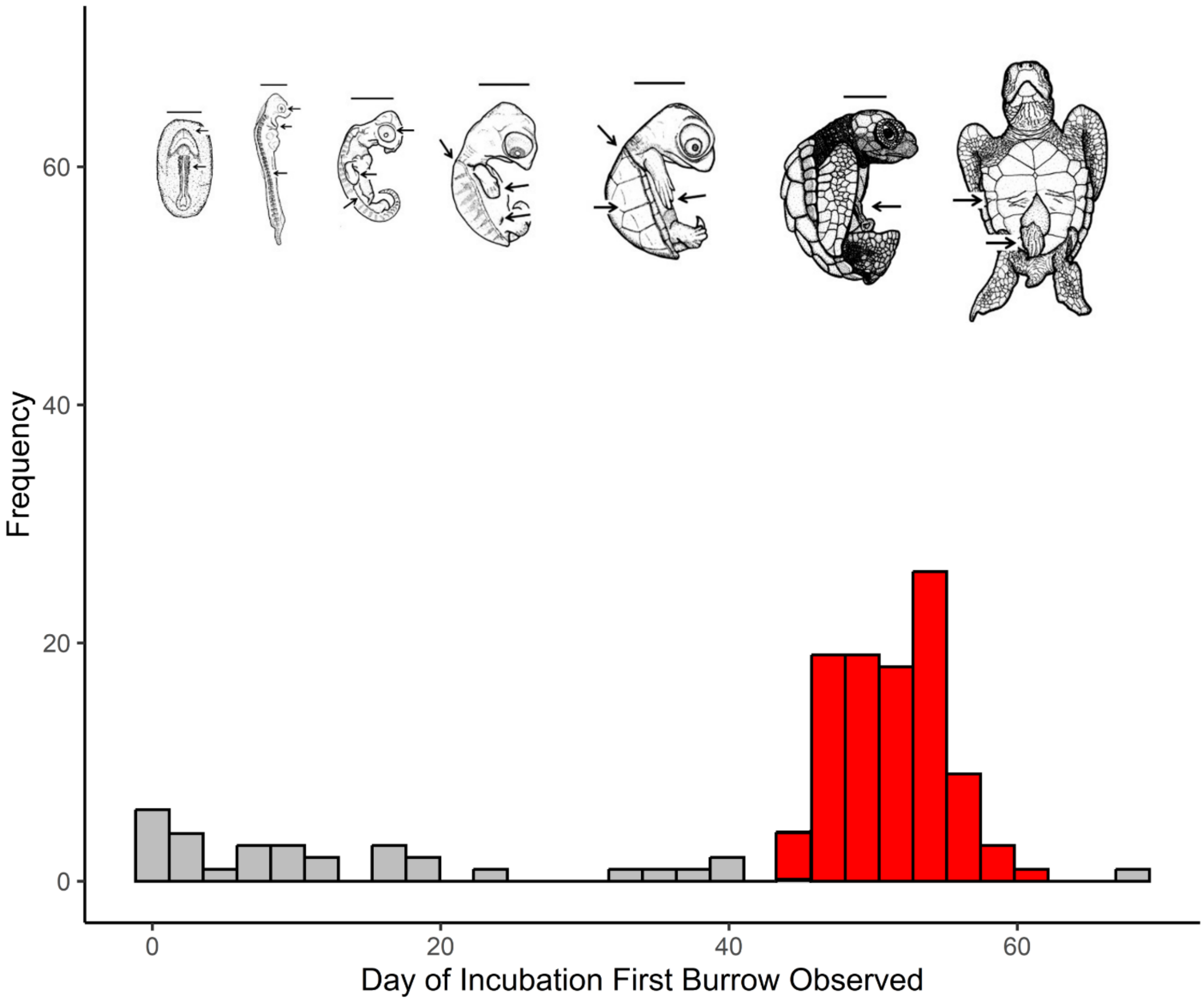


Figure 2.4: Histogram of the incubation day when burrows first appeared in nests in 2022 and 2023 on Cape Canaveral Space Force Station, with sea turtle development stages indicated (Miller et al. 2017; *n*=175 nests). Nest hatch and emergence for loggerhead turtles is between 45 and 65 days (shown with red).

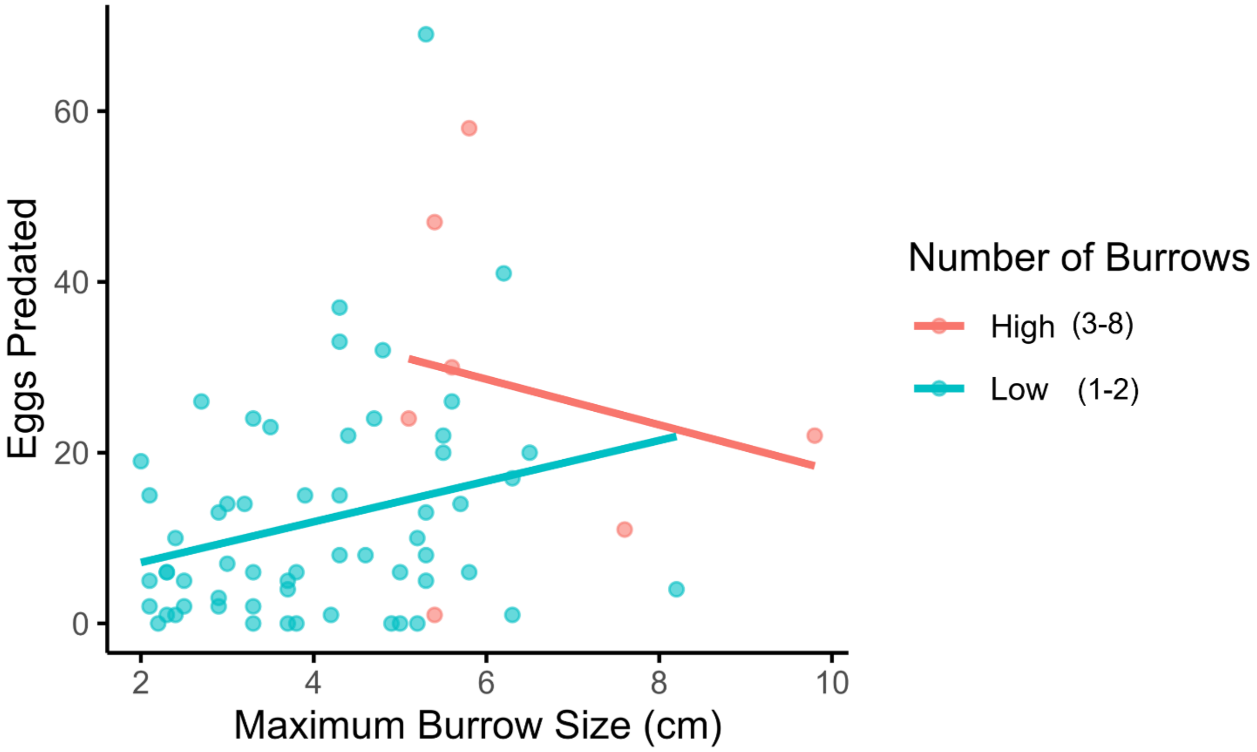


Figure 2.5: Effect of burrow size (the diameter of the largest ghost crab burrow entering into the nest chamber) and the total number of burrows observed into the nest chamber on eggs predated by crabs using 2022 nests with burrowing activity (n = 65).

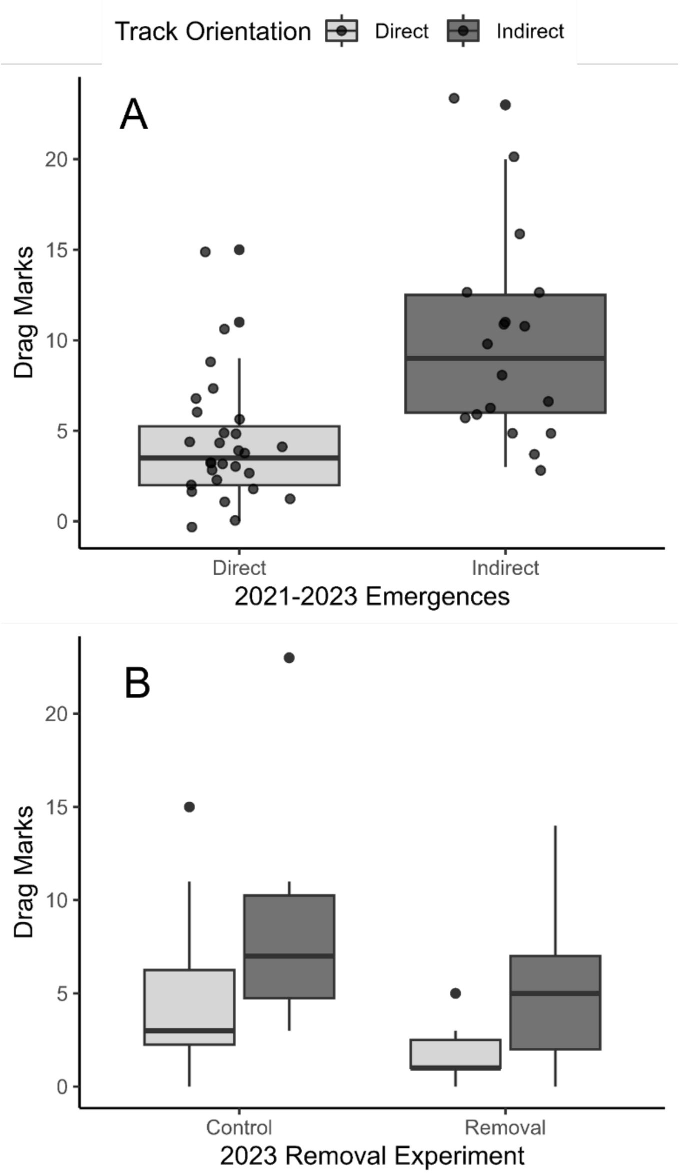


Figure 2.6: Number of ghost crab attacks, inferred from hatchling drag marks in the sand, observed on hatchling emergences at Cape Canaveral Space Force Station. A) number that oriented straight to the water (direct, left) and oriented away from the water or took a longer, indirect path to the water (indirect, right) using both marked and unmarked nests from control zones (*n* = 182) from 2021-2023. B) number of attacks in nests in control and removal plots in 2023 (*n* = 50) when tracks oriented straight to the water (direct) or oriented away from the water or took a longer, indirect path to the water (indirect).

2.7 Tables

Table 2.1: Summary statistics showing variability in loggerhead turtle nest marking, nest productivity, predation, and ghost crab density from 2021-2023 on Cape Canaveral Space Force Station. In disoriented nests, hatchling tracks led in an indirect path to the water or away from the water. Ranges in parentheses.

	2021	**2022**	**2023**
Nest marking and monitoring duration	June 26 – October 11	May 3 – September 3	April 28 – October 24
Total # of marked nests	84	120	97
Nests excluded from analyses due to other impacts*	10	13	19
Nests in removal zones (not included in following summary data)	41	NA	43
Nests in control zones (used in following summary data)	33	107	35
Clutch size (mean ± SD)	113.0 ± 21.0	113.4 ± 22.8	99.1 ± 27.3
Hatched nests (%)	88	90	81
Nest disorientation rate (# of nests disoriented / # marked nests; %)	0	25.2	22.2
Hatch success (% of eggs)	56.5 ± 32.6	59.2 ± 28.4	69.7 ± 30.9
Live crab counts on 200-m transects	NA	43.3 ± 11.9	50.5 ± 16.2
Burrow density (m^{-2})	0.35 ± 0.06	0.32 ± 0.13	0.27 ± 0.09
Diameter of burrows in nest (cm)	NA	4.3 ± 1.6	3.3 ± 0.8
# of nests impacted by crabs	16	70	23
Eggs damaged by crabs in impacted nests	14.5 (0-85)	8.6 (0-59)	4.5 (0-21)
Eggs missing from the nest	1.4 (0-9)	2.0 (0-24)	2.7 (0-13)
# of nests impacted by roots**	14	26	3
Eggs damaged by roots in impacted nests	60.5 (0-109)	51.4 (0-144)	75.0 (0-97)
Drag marks	3.1 (0-8)	4.8 (0-49)	6.1 (0-23)
Nest to surf mortality (# of drag marks / # hatchlings emerged; %)	6.2 (0-20)	8.1 (0-63)	13.4 (0-79)

*In 2021, some nests were excluded from analyses due to near complete root inundation (n=7) or lacking embryonic development (n=3). In 2022, nests were excluded due to complete predation by raccoons (n =2), complete washouts (n=3), near complete root inundation (n=7) or no sign of embryonic development due to extreme wash over and sand accretion (n =1). In 2023, nests were excluded due to complete washout (n =5), several feet of sand accretion (n=2), damage by another nesting turtle (n=1), near complete root damage (n=3), no sign of embryonic development (n=2), fungus (*Fusarium*) in the nest leading to nest failure (n=2), predation by armadillo (n =3), and predation by coyote (n=1).
**Includes some nests that were excluded from main crab predation analyses indicated above.

Table 2.2: Results for models using crab burrow density to examine influences on egg predation by ghost crabs on Cape Canaveral Space Force Station. Clutch size was included as an offset variable in each model, and each variable had one degree of freedom. These analyses used nests from control plots only. Analyses for 2022 and 2023 included only nests with burrow diameter recorded so the impact of crab size could be assessed.

	Damaged in nest		***Damaged in nest + missing***	
Independent Variable	χ^2	***P***	χ^2	***P***
Combined years, 2021-2023 (n = 175)				
Burrow density (m^{-2})	0.827	0.363	0.790	0.374
Number of burrows in nest	**18.880**	**<0.001**	**25.940**	**<0.001**
Year	**4.355**	**0.037**	2.732	0.098
2021 (n = 33)				
Burrow density (m^{-2})	0.081	0.776	0.595	0.440
Number of burrows in nest	**19.654**	**<0.001**	**25.986**	**<0.001**
2022 (n = 65)				
Burrow density (m^{-2})	0.634	0.426	1.403	0.236
Number of burrows in nest	3.800	0.051	**4.115**	**0.043**
Largest burrow diameter	**6.993**	**0.008**	**8.487**	**0.004**
Number of burrows * largest burrow	**3.831**	**0.050**	**4.001**	**0.045**
2023 (n = 26)				
Burrow density (m^{-2})	0.012	0.910	0.175	0.676
Number of burrows in nest	1.864	0.172	2.851	0.091
Largest burrow diameter	0.074	0.784	0.916	0.338
Number of burrows * largest burrow	1.510	0.219	2.384	0.123

Table 2.3: Results for models using live crab counts to examine influences on egg predation by ghost crabs on Cape Canaveral Space Force Station. Clutch size was included as an offset variable in each model, and each variable had one degree of freedom. These models used nests from control plots only. Live counts were not conducted in 2021.

	Damaged in nest		***Damaged in nest + missing***	
Independent Variable	χ^2	***P***	χ^2	***P***
Combined years, 2022-2023 (n = 138)				
Live crab counts	0.508	0.476	1.949	0.163
Number of burrows in nest	**8.885**	**0.002**	**13.657**	**<0.001**
Year	**5.602**	**0.024**	**4.444**	**0.031**
2022 (n = 64)				
Live crab counts	0.605	0.437	1.880	0.170
Number of burrows in nest	2.394	0.122	2.029	0.154
Largest burrow diameter	**5.121**	**0.023**	**5.738**	**0.017**
Number of burrows * largest burrow	2.422	0.119	1.987	0.159
2023 (n = 25)				
Live crab counts	3.399	0.065	2.128	0.145
Number of burrows in nest	1.476	0.224	2.208	0.137
Largest burrow diameter	0.063	0.801	0.618	0.432
Number of burrows * largest burrow	1.163	0.281	1.782	0.182

Table 2.4: Hatchling predation model results using the number of drag marks as the response variable to examine factors influencing the number of hatchling attacks by ghost crabs during emergence, excluding nests from removal plots on Cape Canaveral Space Force Station. The number of hatchlings emerged from the nest was included as an offset variable in the models.

Independent Variable	χ^2	***P***
Results for hatchling predation using burrow density (2021-2023, n = 122)		
Burrow density (m^2)	0.531	0.466
Track orientation	**6.842**	**0.009**
Year	1.537	0.215
Burrow density x track orientation	1.245	0.264
Results for hatchling predation using live crab counts (2022-2023, n =107)		
Live crab counts	**7.979**	**0.005**
Track orientation	**6.628**	**0.022**
Year	0.171	0.679
Live counts x track orientation	1.013	0.314

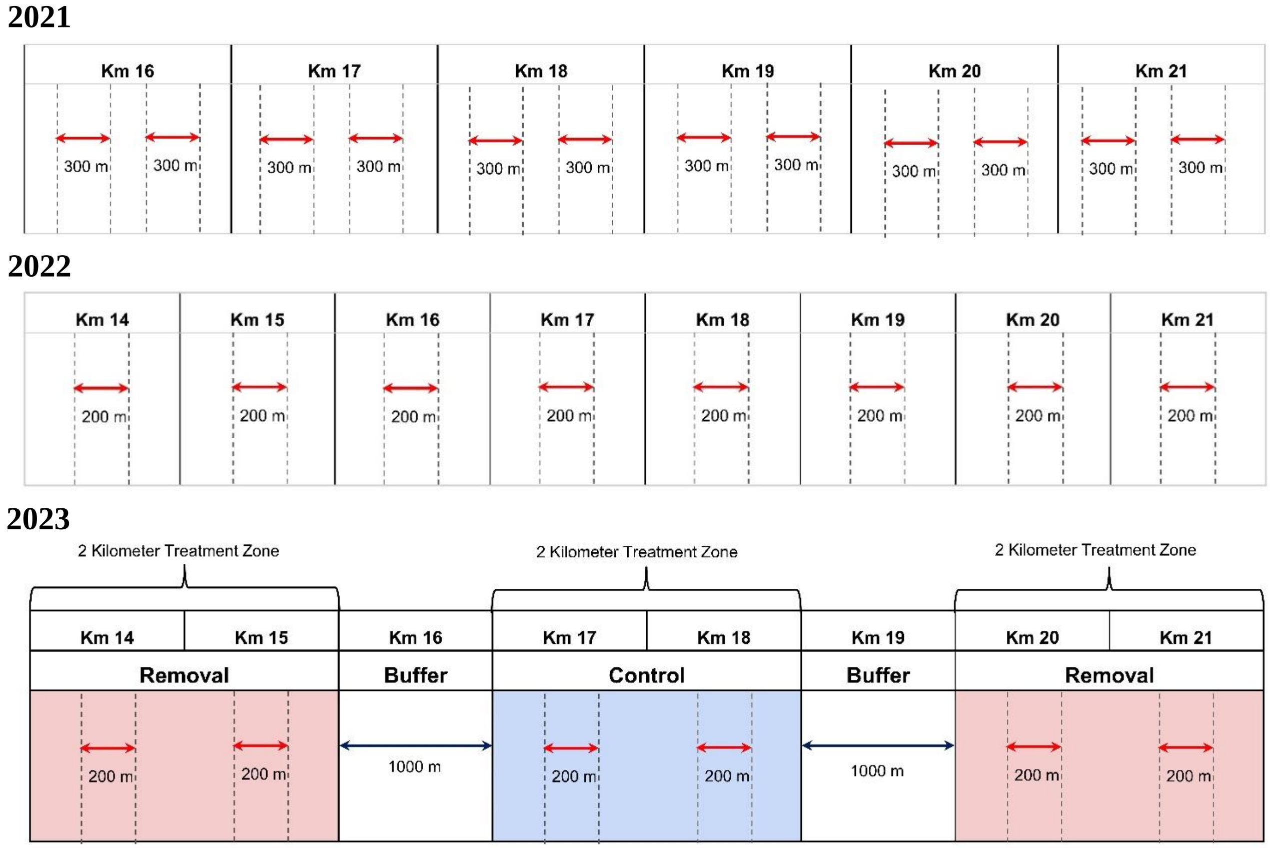
Table 2.5: Effects of removal treatment on hatchling predation by ghost crabs to assess the effects of the live capture treatment (2021) and sod roller treatment (2023) on the number of drag marks per nest, reflecting ghost crab predation on loggerhead turtle hatchlings at Cape Canaveral Space Force Station.

Independent Variable	χ^2	***P***
	2021, n = 30	
Treatment	1.215	0.270
Track orientation	0.730	0.392
	2023, n = 46	
Treatment	**13.380**	**<0.001**
Track orientation	**4.127**	**0.042**
Treatment x track orientation	0.188	0.664

2.8 Supplemental Information

Figure 2.S1: Study design for monitoring ghost crab predation and density on the 21 km of beach at the Cape Canaveral Space Force Station from 2021-2023, showing A) plot configuration per year and B) plot locations on the beach. In 2021, plots were 300 m long and spaced 200 m apart, with 2 plots per km on the northern 6 km of the beach. In 2022, plots were 200 m long and spaced 1 km apart, with one plot each on km 1-5, 9, 11, and 14-21, which remained accessible during high tides. In 2023, we had 2-km treatment zones, with a 200-m monitoring plot in the middle of each km and a 1-km buffer between treatments. The dashed lines represent the monitoring plot boundaries in each figure (from dune to surf).

A) Plot configuration each year



B) Plot locations across the beach

Kilometer	**2021**	**2022**	**2023**
1		Monitoring plot	Control plot
2		Monitoring plot	Control plot
3		Monitoring plot	
4		Monitoring plot	Removal plot
5		Monitoring plot	Removal plot
6			
7			Control plot
8			Control plot
9		Monitoring plot	
10			
11		Monitoring plot	
12			
13			
14		Monitoring plot	Removal plot
15		Monitoring plot	Removal plot
16	Paired plots	Monitoring plot	
17	Paired plots	Monitoring plot	Control plot
18	Paired plots	Monitoring plot	Control plot
19	Paired plots	Monitoring plot	
20	Paired plots	Monitoring plot	Removal plot
21	Paired plots	Monitoring plot	Removal plot

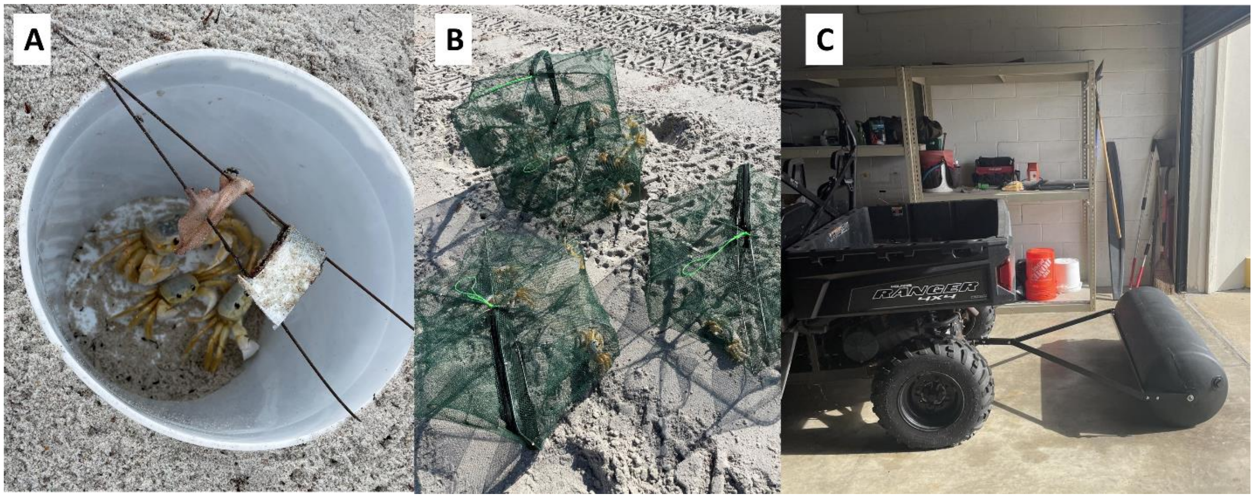


Figure 2.S2: Photos of the three types of removal methods used during this study, including A) pitfall traps (7.6-liter buckets) and B) commercially available crayfish traps (60-cm 6-sided foldable mesh traps with 6 openings) used in the live capture removals in 2021 and C) a sod roller (227 kg, 0.5 x 1.2 m) used in the large-scale removals in 2023.

Appendix 2.A: Using infrared cameras to investigate ghost crab attacks of hatchlings

Methods

Hatch dates and times are unpredictable and can vary based on environmental factors. We used historical data from CCSFS that showed the typical incubation period for loggerheads is between 45 and 65 days. After observing emergences on the first few marked nests, we were able to estimate incubation length and selected nests nearing their hatch windows to use to record emergences. Hatchlings typically emerge at night after temperature declines, but timing can be unpredictable (Witherington et al. 1990 & Moran et al. 1999). For this reason, we used the Wyze V3 home security camera due to its ability to record an entire night of footage without emitting any disruptive visible light. We mounted cameras on metal t-posts so that cameras were 2 m above the sand surface. One fence post was placed 5 m seaward of the nest, with one camera facing east towards the nest, and one facing west towards the water. The cameras were connected to portable battery packs stored in dry bags with the capacity to record an entire night of footage. This dual camera setup was repeated every 5 m to the high tide line to capture the entire path to the ocean, and each emergence was recorded using 2-6 cameras depending on distance to the high tide line (Figure 2.A1). To increase our odds of recording an emergence on camera, we deployed cameras on 2-5 nests each night.

Results

In 2021, we deployed cameras 105 times to attempt to record nest emergences over 26 different nights. Of those 105 attempts, 22 nests emerged (21% success rate). This low success rate was largely due to the unpredictability of emergence timing, and in some instances, nests selected based on emergence windows did not have any emergence. Of the 22 emergence recordings, footage from eight nests were lost due to hard drive failure, and four others were incomplete due to one of the multiple cameras used on each nest failing. Camera failures included the infrared light failing to turn on, cameras would shut off during the night, or footage was missing from the SD card. In 2022, cameras were deployed 95 times to attempt to record emergences from multiple nests per night over 24 nights. Of those 95 attempts, 25 selected nests emerged. Of those 25, eight had partial camera failures, and five nests disoriented away from the cameras. Since each nest had 2-6 cameras depending on distance to the water, the remaining footage was reviewed to examine attacks recorded on functioning cameras. In reviewing remaining footage from 35 emergences, we saw an average of 2.4 +/- 2.1 SD attacks in each emergence, with a maximum of 8 attacks observed from single a single nest. In 34 emergence recordings, we observed 82 instances of crabs attacking hatchlings. We observed five hatchlings escape the crab's grip and crawl away, and 26 were observed being consumed on camera until they became lifeless and were thus confirmed mortalities. There were 54 hatchlings with undeterminable fate, as they were dragged out of view from the cameras. For the 29 emergences that had both camera recordings and drag mark data recorded from tracks in the sand following emergences, we observed more attacks from drag marks in 15 emergences, 10 emergences had more attacks on camera, and four had the same result for both.

Discussion

Cameras were unreliable if nests disoriented, but occasionally helpful in determining hatchling fates. They also revealed useful information about crab predation that could not be determined by counting drag marks. With the cameras we were able to observe the duration of nest emergences (which ranged from 4-63 minutes), the timing of crab attacks, and crab behavior on nights of nest emergences. We observed six instances of crabs entering nest chambers and removing hatchlings from within the nest before and after nests emerged, supporting our hypothesis that they sense hatchling movement beneath the sand to target nests. In future studies, drag marks in the sand are a low cost, easy to implement method to better understand hatchling predation. In comparison, the use of infrared video cameras required much more effort to implement. Assessing drag marks is opportunistic and requires no equipment, and the success of this method does not depend on the ability to predict the timing of nest emergences. In addition, this method is better suited in areas where disorientation is common, as hatchlings can crawl out of view of the cameras.

References

Moran, K. L., Bjorndal, K. A., & Bolten, A. B. (1999). Effects of the thermal environment on the temporal pattern of emergence of hatchling loggerhead turtles Caretta caretta. *Marine Ecology Progress Series*, *189*, 251–261. https://doi.org/10.3354/meps189251

Witherington, B. E., Bjorndal, K. A., & McCabe, C. M. (1990). Temporal Pattern of Nocturnal Emergence of Loggerhead Turtle Hatchlings from Natural Nests. *Copeia*, *1990*(4), 1165–1168. https://doi.org/10.2307/1446507

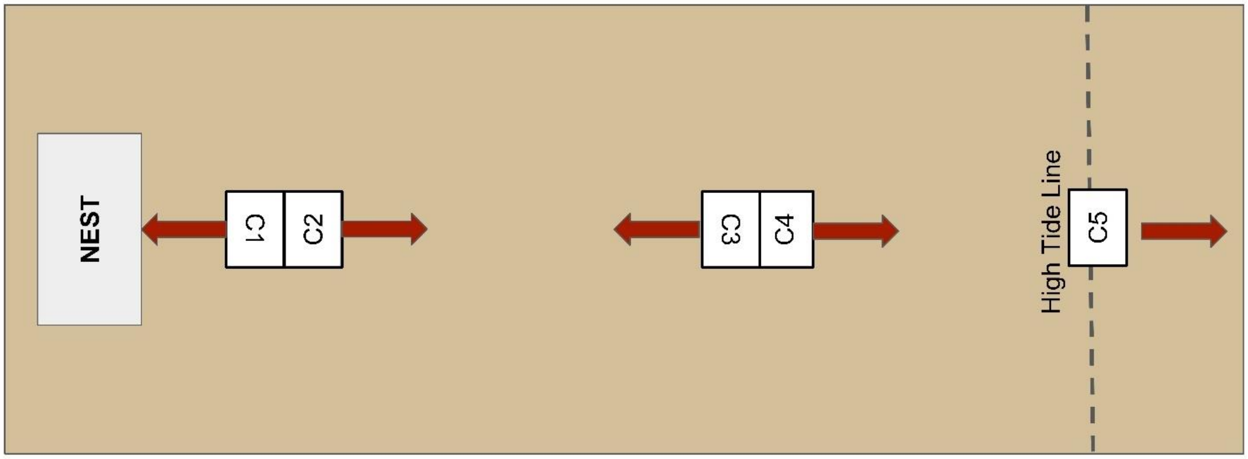


Figure 2.A1: Camera setup for recording nest emergences, showing directions cameras were pointed from the nest to the water during 2021 and 2022 on Cape Canaveral Space Force Station.

Chapter 3: Drivers and control of ghost crab abundance on sea turtle nesting beaches

Abstract

Predation is one of the greatest threats to sea turtles in their early life stages, but complex trophic interactions, including intraguild predation, may confound management efforts to reduce predator impacts. The Atlantic ghost crab (*Ocypode quadrata)* is a common predator on sandy beaches, and preys upon sea turtle eggs and hatchlings where these species overlap. However, ghost crab density varies spatially and temporally in response to many factors, including predation by mammals, human activity, sand composition, temperature, lunar phase, and ambient light. Ghost crabs are fossorial and generally remain belowground during the day. Many studies quantify burrow density as a proxy for crab density, but the reliability of this approach has been questioned. In this study, we estimated ghost crab density using both live crab counts at night and burrow counts to evaluate the effect of several environmental factors and management. The study was conducted between 2021 and 2023 on 21-km of beach on the east coast of Florida, USA. Our results revealed that temperature and ambient light had a negative relationship with both crab density metrics at higher temperatures but had a positive relationship at lower temperatures. Similarly, moon luminosity positively affected live crab density at low temperatures, but the inverse was true for burrow density. After accounting for environmental variables, we found no relationship between burrow density and live counts, suggesting the two metrics are not interchangeable. We evaluated two methods for managing ghost crab abundance. Live capture efforts removed 896 crabs over 63 trapping days but did not significantly reduce ghost crab burrow density. In contrast, a novel method using a sod roller to crush crabs resulted in the removal of 4,300 crabs in just 13 days, and significantly reduced both estimates of crab abundance and hatchling predation. Although the sod roller method could be explored as a tool

for ghost crab removal, we caution against its use until the broader ecosystem effects of such an intensive disturbance are evaluated.

3.1 Introduction

Conservation often requires navigating complex predator-prey interactions, where removing one predator may inadvertently affect another, altering their impact on prey (Crooks and Soulé 1999, Vance-Chalcraft et al. 2007). Loggerhead sea turtles (*Caretta caretta*) are a threatened species, and predation by a range of vertebrates and invertebrates is one of the biggest threats to survival in their early life stages (Stancyk 1982, Welicky et al. 2012, Engeman et al. 2014, Butler et al. 2020). On some beaches, predators such as raccoons (*Procyon lotor)* and coyotes (*Canis latrans)* are trapped and removed in an attempt to increase sea turtle egg and hatchling survival (Garmestani and Percival 2005, Barton and Roth 2007, Engeman et al. 2014). However, invertebrate predators of sea turtle eggs and hatchlings have largely been unmanaged. Ghost crabs (*Ocypode quadrata)* are common predators and scavengers on sea turtle nesting beaches, and often considered the second most common source of predation for sea turtle eggs (Bouchard and Bjorndal 2000, Antworth et al. 2006). However, ghost crabs are also preyed upon by mammalian predators (Barton and Roth 2007). Consequently, the removal of mammalian predators may reduce intraguild predation on ghost crabs, potentially leading to an increase in crab populations and reducing or negating the benefits of mammal trapping for the protection of sea turtle eggs and hatchlings (Barton and Roth, 2008). Given this complexity, resource managers can benefit by understanding the factors that drive ghost crab population dynamics.

Ghost crabs are fossorial and primarily nocturnal (Wolcott 1978, Leber 1982, Valero-Pacheco et al. 2007, Lucrezi and Schlacher 2014). They spend much of the daytime below the beach surface, where their intricate tunnels provide moisture and a stable thermal environment

(Christoffers 1986, Kristensen et al. 2012), as well as safety from predators. Since ghost crabs are hidden throughout the day, quantifying their population size is difficult. Consequently, burrow density has been used by many studies to estimate ghost crab density (Barton and Roth 2008, Schlacher et al. 2016a, Schlacher et al. 2016b). However, the reliability of burrow counts as population estimates has been questioned as there is large uncertainty and variation associated with their predictability (Schlacher et al. 2016b).

While some argue that burrow density may be a feasible and low-impact method of estimating population size (de Oliveira et al. 2016, Fortaleza et al. 2020), burrow density may not be a good estimator of population size for several reasons. First, burrows do not provide a one-to-one estimate of ghost crab population size (Schlacher et al. 2016b). Crabs can build multiple burrows or have multiple entrances to their tunnel systems (Silva and Calado 2013, Costa et al. 2021). Second, burrow occupancy can also vary considerably (Schlacher et al. 2016b), specifically for *O. quadrata,* which may have 0.19-0.71 individuals per burrow (Pombo and Turra 2013, Silva and Calado 2013, Robinson 2024). Third, burrows are not just a function of crab abundance but also crab behavior and activity. Crab activity and burrow construction behavior vary with environmental variables and among different age classes of crabs, challenging attempts to estimate crab abundance with burrow density (Fortaleza et al. 2020). Despite these potential weaknesses, studies still primarily rely on indirect proxies such as burrow density to reflect crab abundance and direct methods such as visual surveys are rare (Schlacher et al. 2016b).

Ghost crabs are nocturnal, and thus adapted to low-light conditions, and are sensitive to changes in natural (lunar) and anthropogenic light (Rosenberg and Langer 2001). Lunar cycles affect crab activity and burrow distribution due to changes in both lighting and tidal variation.

Specifically, burrow abundance and average burrow size increase near full moons (Fortaleza et al. 2020). This pattern is potentially explained by reproductive behaviors in adult crabs, as courtship displays and egg release are highest during new and full moons (Christoffers 1986, Lucrezi and Schlacher 2014).

Urban development has increased nighttime artificial lighting (Cinzano et al. 2001) and may affect ghost crabs and their roles as predators. Silva et al. (2017) compared different types of lighting to crab abundance and behavior and found that ghost crabs were more evenly distributed on the beach on darker nights but attracted to illuminated sections of the beach during experiments with artificial lighting. Ghost crabs also detected and consumed prey items more when the beach was exposed to artificial light than in darker control areas (Silva et al. 2017). (Silva et al. 2017). While most beaches have implemented sea-turtle friendly lighting with longer wavelengths (yellow, orange, red) that are thought to be less attractive to hatchlings, ghost crabs are still attracted to this lighting of lower wavelengths as well (Silva et al. 2017).

The abundance of crabs and their burrows is seasonal, and typically highest in summer in a related species (Tiralongo et al. 2020). Recruitment in *O. quadrata* occurs throughout the year, and peaks in summer (Leber 1982, Christoffers 1986, Lucrezi and Schlacher 2014). Increased metabolic activity associated with higher temperatures (Vernberg and Vernberg 1968, Weinstein and Full 1994) may encourage crab surface activity. The minimum temperature threshold for crab activity varies by region but is typically between 12-16°C in the southeastern United States (Lucrezi and Schlacher 2014). While winter behavior is less understood, crabs are thought to overwinter in burrows behind the dunes during colder months (Vernberg and Vernberg 1968, Wolcott and Wolcott 1999). Temperature can also influence predator-prey interactions, and higher sediment temperature correlates with increased crab predation of sea turtle eggs (Martins et al. 2022).

Ghost crab burrow density is affected by substrate characteristics. Previous work reported lower burrow abundance in poorly sorted sand (Turra et al., 2005) and in areas with more shell cover (Call et al., 2024). Several studies report a negative relationship between sand grain size and burrow density, with finer grains associated with higher burrow densities (Turra et al. 2005, Brown 2009*,* Lucrezi 2015, Jonah et al. 2015, Pombo et al. 2017). Beaches that perform nourishment or bulldozing activities to combat erosion suppress abundances of crabs and burrows through deposition of unfavorable coarse sand and direct mortality from burial or crushing (Peterson et al. 2000, Peterson et al. 2014, Schlacher et al. 2016a).

To advance our understanding of factors that influence ghost crab abundance, we conducted a three-year study in east central Florida, USA. We used two different indices of ghost crab density, live crab counts and burrow density, and predicted that they would be positively correlated. We examined the individual and interactive effects of temperature, moon luminosity, and ambient light levels on the two density metrics. Additionally, we conducted ghost crab removal experiments to evaluate how two different removal methods affected ghost crab abundance. These analyses provide novel insight to understanding the ecology and behavior of this widespread predator.

3.2 Methods

3.2.1 Study site and sampling design

This study was conducted from 2021-2023 at Cape Canaveral Space Force Station (CCSFS) on a barrier island on the Atlantic coast of Florida. The CCSFS beach has 21 km of gently sloping coastline that supports nesting by threatened and endangered sea turtles and shorebirds. CCSFS is one of few remaining natural sand beaches in Florida without any beach nourishment activities that may alter the beach face and sand characteristics. Although this beach is closed to the public, nearby tourist destinations and spaceflight activity generate significant sources of artificial lighting.

The CCSFS beach is divided into 21 1-km zones. Each year, we established monitoring plots of 200-300 m to capture spatial variation across the beach. Plots were demarcated using wooden stakes wrapped in reflective tape to be visible both day and night. In 2021, we established two 300-m plots of alternating treatments (control and removal), separated by 200 m, in each of the northern six 1-km zones (Chapter 2, Figure 2.S1A). During a pilot mark-recapture trial we recaptured crabs >2 km from where they were marked, which indicated they could travel >2 km from where they were marked. Thus, in subsequent years we increased the distance between plots to increase the independence of samples and better represent the entire study area. In 2022, we created 200-m plots in the center of each of 15 1-km zones (Chapter 2, Figure 2.S1A, Figure 2.S1B). This updated design resulted in at least 1 km between adjacent plots.

In 2023, the study design was altered to incorporate a large-scale removal experiment (see 3.2.3 Crab removals for details). The experimental design consisted of three pairs of ghost crab removal and control zones. Each zone was 2-km in length and was separated from an adjacent zone by a 1-km buffer. Within each zone we established two 200-m monitoring plots spaced 1-km apart (Chapter 2, Figure 2.S1A). The 12 plots were used to quantify ghost crab abundance.

3.2.2 Ghost crab density estimates

We completed biweekly burrow surveys within monitoring plots during the marine turtle nesting season to assess ghost crab activity. The timing of these counts varied by year, and were conducted from 27 July – 14 October in 2021, 2 May – 14 October in 2022 and 25 April – 20 September in 2023. Additionally, between 2022 and 2023, we continued our crab density measurements at least once monthly outside of the sea turtle nesting season (November 2022 to March 2023) to assess behavior of ghost crabs outside of turtle nesting season.

For each survey, we drove the length of the plot with a utility terrain vehicle (UTV) and counted the number of burrows within the width of the UTV tires (1.3 m; Figure 3.S1B). These counts were conducted below the most recent high tide line to record only burrows constructed within the last six hours (Figure S.31B). Burrow density was calculated by dividing the number of burrows by the area surveyed, using the plot length (200 or 300 m) multiplied by the width of the UTV track (1.3 m). In 2022 and 2023, we conducted monthly live crab surveys on the beach at night to quantify the number of crabs visible within plot boundaries (Figure S.31C). These surveys involved slowly driving the length of the plot (8 km/h) and counting the number of crabs visible within red-covered UTV headlights. During the nighttime surveys in 2022 and 2023, a handheld light meter (*Unihedron Sky Quality Meter; Model SQM-L, Unihedron,* Ontario, Canada) was used to record ambient light measurements in each plot by holding the meter overhead to record the zenith sky brightness. Every nighttime survey in 2022 included a light reading, and light readings were recorded during only a subset of surveys in 2023, due to more rigid schedule restraints from increased launch activity. We conducted burrow counts the following morning to compare burrow density to live crab activity in the same twelve-hour period. On the day of each survey, we also recorded the maximum tide height and moon luminosity (the percent of the moon illuminated based on moon phase, on the survey date for Cape Canaveral) regardless of cloud cover and sky position, and the daily high and low temperatures recorded by the CCSFS weather station.

3.2.3 Crab removals

In 2021, we attempted to manipulate ghost crab density in removal plots using traps and hand nets. We initially used pitfall traps but switched to commercially available crayfish traps (Chapter 2, Figure 2.S2B) once sea turtle hatchlings began emerging in mid-July. We created pitfall traps by burying 7.6-liter plastic buckets flush with the sand (Chapter 2, Figure 2.S2A). Traps were baited with shrimp and fish in the morning and left for several hours. Ghost crabs were also opportunistically hand-captured for removals. All crabs that were captured were euthanized using quick freezing (Taylor et al. 2019; Animal Care Protocol F21-009). The first 513 captured crabs were preserved in a freezer and later measured and sexed to determine sex and size distribution in the population.

In 2023, we created removal treatments by towing a 227-kg sod roller behind a UTV on the beach at night to crush crabs in the intertidal zone. Removals were conducted after dusk during incoming tides, typically one hour after sunset and low tide. Conducting removals during incoming tides limited the width of the beach available for crabs to disperse and made them more susceptible to being crushed by the roller. Crushing is an effective euthanasia method for small animals because they become immediately unconscious (Smith 1965) and is a recommended method for destroying other arthropods and their egg masses, such as the invasive apple snails (*Pomacea canaliculate;* Horgan 2017) and spotted lanternflies (*Lycorma delicatula;* Leach et al. 2024). Removal activities were conducted with two people, including a driver and a passenger who watched for emerging sea turtles and counted the number of crabs crushed. The full 2-km removal zone was driven repeatedly until <25 crabs were removed in a single pass (range: 2-6 passes). At the end of each pass, the UTV was parked for 3-5 minutes to allow foraging crabs to reenter the removal zone and be crushed in subsequent passes. White light was used for the UTV headlights during crab removals to stun ghost crabs in place after trials with red light proved less effective. The UTV was driven 16 km/h, which was quick enough to roll over stunned crabs but enabled the driver and spotter to observe emergent nesting turtles from a distance and cease removal activities. We conducted the first removals on 13 March 2023 and ceased all removal activities by 25 May 2023 when sea turtle nesting activity increased to prevent any interactions with emerging turtles.

3.2.4 Data analysis

We used mixed-effect models to determine which variables affected burrow density and live crab counts. Our global models contained year and all variables that were collected every year, excluding data from the removal plots in 2021 and 2023. We also ran separate models for each year to examine the effects of additional variables that were not collected every year, including the effects of removals. Kilometer zone was included as a random effect for each model. We excluded maximum tide height from the models due to multicollinearity with moon luminosity, and because we could not account for plot-level variation in tide height. We also excluded date because it was quadratically related to temperature. We did not observe a relationship between moon luminosity and ambient light readings ($p = 0.119$). Sand grain metrics are known to influence crab density, but due to spatial and interannual variation, we excluded these metrics from our models (Figure 3.A1). We conducted analyses using the lmer() package in R statistical software (Version 4.2.2) using a Type III Sum of Squares Analysis of Variance (ANOVA). We assessed residual distribution and normality using the “plotQQunif” function for each model. To explore the relationship between live counts and burrow density, we created competing models with various combinations of abiotic factors and used AIC to select the best model.

3.3 Results

3.3.1 Spatial and temporal variation

Ghost crab burrow density and live counts varied over both space (Figure 3.1) and time (Figure 3.2). Overall, we observed nearly twice as much variation in burrow density (CV = 61.37) than live counts (CV = 39.76). Light readings were highest near the southern end of the beach near Port Canaveral and the north end near active launchpads (Figure 3.1A). Burrow density and live crab counts substantially decreased in winter (Figure 3.3), but crabs and burrows were still present on the beach during each survey.

3.3.2 Variables influencing crab density

We consistently observed a significant interaction between moon luminosity and temperature in models explaining both burrow density (Table 3.1) and live crab counts (Table 3.2). The interaction between moon luminosity was significant for burrow density in the global model and 2021 and 2022, but not 2023 when we conducted the sod roller removals. In the global model, ambient temperature had little effect on burrow density closer to a new moon phase (moon luminosity = 0), but positively affected burrow density near full moons (moon luminosity = 1; Figure 3.4A). Likewise, the interaction between moon luminosity and temperature was significant in the models explaining live counts, in both the global model and individual years (Table 3.2). However, the effects of moon luminosity and temperature on live counts differed from burrow density. At higher temperatures (yellow line), live counts decreased with luminosity, but burrow density increased (Figure 3.4). At lower temperatures (purple line), live counts increased with luminosity, but burrow density decreased (Figure 3.4).

In 2022, the interaction between ambient light and temperature was significant for both burrow density ($p = 0.004$, Table 3.1) and live counts ($p = 0.012$, Table 3.2) and the effects on both metrics were similar. At higher temperatures, crab burrow density and live counts decreased with increased lighting, but at lower temperatures, both metrics increased with increased lighting (Figure 3.5).

Live counts and burrow density were positively related, but with low fit (p = <0.001, R^2 = 0.09, Figure 3.6). The best model to explain the relationship between live counts and burrow counts included year and the interaction between moon luminosity and temperature (Table 3.3). When accounting for these environmental variables, burrow density was no longer a significant predictor of live counts (Table 3.4, P = 0.087).

3.3.3 Removals

In 2021, we removed 896 crabs from treatment zones over 63 days of live captures. However, we found no effect of removal on burrow density in 2021 (Wilcoxon Rank-Sum test, p =0.61, Figure 3.7), nor was removal treatment among the significant predictors of burrow density in the 2021 model (p = 0.310, Table 3.1). Analyzing these crabs revealed the sex ratio of removed crabs (n=513) was male based (12.5% female; binomial test, p<0.0001). The average carapace width was significantly larger for male crabs (4.8 ± 0.9 cm) than females (4.0 ± 0.8 cm; Wilcoxon Rank-Sum test, p < 0.0001; Figure 3.S2). The largest crab captured was a male with a carapace width of 6.3 cm.

In 2023, we used the sod-roller method to remove 4,306 crabs from treatment zones in 13 days. During removals, the number of crabs removed decreased by approximately 50% with each pass (Figure 3.8). This large-scale treatment significantly reduced both burrow density (p = 0.008, Table 3.1, Figure 3.7) and live counts (p = 0.047, Table 3.2). Temperature and moon luminosity still affected live crab counts (Table 3.2), but not burrow density this year (Table 3.1).

3.4 Discussion

Our results revealed that both burrow density and live counts demonstrated spatial and temporal variability and were shaped by environmental covariates and their interactions. While these two indices were positively related, their relationship was influenced by other covariates, such as lighting, moon luminosity, temperature, and interactions between these variables. The influence of temperature on ghost crab abundance aligns with ectothermic physiology. However, the effects of temperature were modulated by artificial and natural (lunar) lighting. We consistently observed a significant interaction between moon luminosity and temperature, and ambient light and temperature, for both indices of crab abundance, but each one responded differently. Based on the observed complexity of the two indices, we further evaluated the variables that influenced them both spatially and temporally.

Estimating ghost crab population size directly is difficult and therefore biologists rely on indices of abundance to examine influences on ghost crab abundance. We initially planned to use mark-recapture techniques to estimate population size. Despite our efforts in 2021, we had low recapture rates and abandoned that objective. However, the mark-recapture activity did demonstrate that ghost crabs can travel farther than previously expected. One marked crab was recaptured 2 km from its initial capture location, suggesting that previous studies have underestimated the distance they can travel in a night (300 m; Wolcott 1978). For the remainder of the study, we focused on ghost crab burrow density and live counts as indices of population size. As expected, ghost crab burrow density and ghost crab live counts were positively related, but this relationship had low explanatory power ($R^2 = 0.09$). Using model selection, we found that burrow density was not a significant predictor of live crab counts when other environmental variables were included. These results highlight that burrow counts and live counts are not interchangeable.

We found that burrow density and live counts varied within years. Seasonal variation was most evident when we sampled at least once monthly between June 2022 and October 2023. Although indices were lower in the winter, we observed fresh burrows and live crabs on the beach in all months. Ghost crabs have previously been reported to move to inland burrows during the winter (Vernberg & Vernberg 1968; Wolcott & Wolcott 1999) and their abundance and behavior in the winter is largely unstudied. However, our results demonstrate that ghost crab are present and active in the winter, albeit at lower densities. Although dates surveyed differed in years, both indices increased early in the year, peaked mid-summer, and decreased later in the year. This pattern differs from Brown (2009), which found decreasing crab burrow density mid-summer, possibly due to increasing raccoon density during these months. We did not collect density measurements of ghost crab predators (such as raccoons) that may have influenced crab density. It is noteworthy that raccoons are still abundant on CCSFS and are controlled but not eradicated by mammalian removal efforts.

Intra-annual variation in ghost crab indices may be due to change in behavior and activity and is likely not a result of population-level changes**.** Due to detectability, both indices of crab abundance may be biased towards larger adult crabs. The larval stage of ghost crabs can last up to 42 days, and they take nearly a year to reach sexual maturity (19-26 mm carapace width) and have an estimated life span of approximately 3 years (Haley, 1972). Ghost crabs in warmer regions, including the southern US, reproduce year-round, with peaks during summer (Lucrezi and Schlacher 2014). Immigration or emigration may cause changes in abundance, but this movement would only be possible on the north end of the beach where it extends into Merritt Island National Wildlife Refuge, while the southern end terminates at a rock jetty and Port

Canaveral. Thus, changes in these indices are more likely to be driven by changes in activity. Ghost crabs are ectotherms, and the changes in abundance and activity follow intra-annual variation in temperature. However, ghost crab activity also follows the peak in sea turtle and shorebird nesting and hatching patterns observed by biologists that work on these and other Florida beaches. Increased availability of prey during this time may correspond to increased crab burrowing and live counts. This pattern likely reflects short-term environmental responses rather than life cycle events.

Spatial patterns in ghost crab abundance on the beach suggest potential edge effects related to habitat characteristics. In general, live counts were less variable across the beach than burrow density**.** Both indices were higher on the north and south ends of the beach, and lower in the middle. When collecting sand samples across the entire beach and multiple beach zones in 2022, from the southernmost part of the beach (kilometer 1) through kilometer 15, the sand was categorized as gravelly coarse sand, while the northern five kilometers of the beach (17-21) were comprised of finer sand (Appendix 3.A). While we did not include sand grain metrics in our models due to temporal variability (Appendix 3.A), ghost crabs prefer finer sand (Turra et al. 2005, Brown 2009*,* Lucrezi 2015, Jonah et al. 2015, Pombo et al. 2017), which may contribute to the higher observed density in the northern part of the beach. Although access to CCSFS is restricted to the public, the north and south ends are influenced by anthropogenic activities. Specifically, the south end is adjacent to Port Canaveral, which is a tourist destination and active shipping port, and the north end is subjected to activities related to rocket launching and testing. Unsurprisingly, we observed the highest light readings in the south and north areas.

We expected that increased temperature and luminosity (both natural and artificial) would increase crab activity. In 2022, we measured ambient light on the beach and found interactive effects of temperature and light. Although we sampled on seven nights, serendipitously these nights experienced only three low temperatures (22.2, 22.8, and 23.9 C). Despite the small variation in temperature (range = 1.7 C), we found that burrow counts and live counts responded similarly to changes in temperature and ambient lighting. When temperatures were lower, ambient light had a positive effect on ghost crab population indices (burrow density and live counts). In contrast, when temperatures were higher, ambient light had a negative effect on ghost crab population indices. Schlacher et al. (2016b) reported a data deficiency regarding ghost crab responses to artificial light and hypothesized that artificial light can influence crab predation risk and behavior. One hypothesis explaining why temperature modulates the effects of light may be related to interspecific competition or intraspecific predation risk. We are aware of just one experimental study that examined ghost crab responses to artificial lighting. Silva et al. (2017) found that crabs were more evenly distributed on the beach in darker nights, but attracted to areas that were illuminated with artificial light, and pursuit of prey increased in treatment areas with lighting. Silva et al. (2017) also observed territorial behavior by large crabs, which entered illuminated areas to attack smaller crabs. Thus, the observed decrease of crab abundance on higher temperature, brighter nights could be a result of social or competitive interactions.

Beach mice, like ghost crabs, are a nocturnal and fossorial species on coastal beaches. Studies of beach mice have found that foraging activities decrease with increasing nocturnal luminosity, suggesting that luminosity increases predation risk on full moon nights (Bird et al. 2004, Wilkinson et al. 2013). However, Falcy and Danielson (2013) observed that lower temperatures reduced mouse foraging, and higher temperatures increased foraging, possibly because the types of active predators shift with temperature. We observed the opposite effect on crab metrics, and higher temperatures decreased both metrics on brighter nights. Unlike beach mice, which are herbivorous and prey for many nocturnal predators, and thus highly sensitive to predation risk, crabs fill the role of both predator and prey. Additionally, crabs are ectothermic and thus have different sensitivities to temperature. In lower temperatures and higher light, they may be more likely to risk venturing out of burrows because the light increases their ability to detect prey.

We also found an interactive effect of temperature and moon luminosity on both indices. Similar to the ambient light results, we found that that ghost crab live counts were positively related to moon luminosity at lower temperatures and negatively related to moon luminosity at higher temperatures. However, the opposite was true for burrow density. At lower temperatures burrow density decreased with moon luminosity, and at higher temperatures burrow density increased with moon luminosity. Our burrow density results are consistent with other studies that observed ghost crabs intensifying burrowing activity in higher temperatures (Haley, 1972, Lucrezi and Schlacher 2014). Fortaleza et al. (2020) hypothesized that nocturnal luminosity associated with full moons explained the increase in burrow size and abundance near full moons, possibly due to increased visual acuity and foraging areas due to larger intertidal zones during full moons. It is unclear why the two indices would respond to temperature and luminosity differently, but behavioral changes may play a role. We did not find other studies that used observations of live crabs to estimate density or activity, so it is challenging to put our results into a broader context. Our results highlight that predator-prey interactions are not static but context dependent and influenced by environmental factors that shift risks and rewards.

Although ambient light and moon luminosity seem like they should affect crabs similarly, they had different effects on burrow counts. Moon luminosity is correlated with moon phase, which affects ghost crab reproductive behavior, tidal range and subsequent foraging area.

Courtship displays and egg release increase during new and full moons (Christoffers 1986, Lucrezi and Schlacher 2014), which may explain the increase in burrow density near new moons and live counts near full moons despite lower temperatures. We also did not find a relationship between moon luminosity and ambient light, likely because of both cloud cover and artificial light. Studies of night sky brightness using the same light meter have observed that artificial lighting masks lunar cycles, and cloud cover brightens the environment rather than darkening it (Kyba et al. 2015) so overcast nights with light pollution provide brighter readings than clear full moon nights (Puschnig et al. 2014). Also, moon luminosity was calculated based on moon phase, such that full moons were the brightest and new moons were darkest. However, in practice, the position of the moon (e.g., altitude), cloud cover, and other factors may reduce the amount of light that reaches the beach and explain why moon luminosity (moon phase) does not correlate with ambient light.

While anecdotal observations suggest that CCSFS hosts high ghost crab densities relative to surrounding beaches, our novel method of quantifying burrow density parallel to the water below the high tide limits comparisons with other sites and studies, which often use raked transects perpendicular to the shore above the high tide line (Barton and Roth 2008). Higher burrow densities are observed on isolated beaches with low human activity compared to urban beaches (Barros, 2001, Ocaña et al. 2016), and human disturbance is a well-documented factor in influencing crab abundance (Steiner and Leatherman 1981, Lucrezi et al. 2009, Schlacher et al. 2016a, Gül and Griffen 2018). However, there is no public access to the CCSFS beach. Ghost crabs have the highest burrow fidelity and longevity at sites with low levels of human impact (Gül and Griffen 2019), suggesting that burrow counts may be a more reliable reflection of abundance on highly disturbed sites. In undisturbed areas, crabs may be more active and construct more burrows or modify existing burrows frequently, whereas human activity may disrupt crab activity and force them to limit burrowing activity and rely on fewer, more stable burrows. CCSFS is relatively pristine compared to other beaches, so crabs on this beach may be more sensitive to other environmental influences.

Our study underscores that burrow density alone may not reliably predict ghost crab abundance. Burrow occupancy and the number of burrows per crab can vary, and visual surveys for live crabs may provide more precise data on true crab densities. A more accurate estimation of ghost crab populations may require integrated models that consider luminosity, temperature, and additional environmental variables. Development of such models could significantly enhance understanding and management of ghost crab abundance on dynamic coastal ecosystems.

Because crabs are predators of threatened and endangered species, there is growing interest in controlling their numbers. However, we identified just one other study that experimentally removed ghost crabs to protect nesting shorebirds (Pruner and Addison 2022). The removal methods were similar to our live capture trapping methods used in 2021. Trapping crabs with pitfalls or other traps is labor intensive and produced relatively few captures. Despite trapping on 63 days and removing 896 crabs, we observed no effect of trapping on burrow density. In contrast, the large-scale sod-roller method to crush crabs was very efficient, removing over four times the number of crabs (4,306) in a fraction of time (13 days). In our burrow density model results, the large-scale treatment in 2023 may have overshadowed the effects of other main and interactive predictors, as this year was the only one in which no environmental variables were significant.

The sod-roller method effectively reduced ghost crab numbers and might be a useful management tool, but the broader impacts are unknown. Both types of crab removals were costly in terms of time, equipment, and effort, and overall may only marginally increase loggerhead recruitment. In the execution of these removals, we used mitigation measures to prevent any potential impacts to other protected species on the beach, which would be imperative if adopted as a management tool. Further studies should consider the broader ecosystem impacts of removing a native species from its ecosystem. Ghost crabs are predators of many species, and removing their function as predators could have effects on their prey (e.g., coquina clams and mole crabs). Ghost crabs are also scavengers that provide an ecosystem service by consuming and removing carrion. As consumers, ghost crabs may also play a role in the allochthonous flow of marine derived nutrients to dunes and the areas behind dunes. In addition to being prey for terrestrial predators, ghost crab eggs and larva are likely prey for fish and other marine species. Consideration should also be given to the disruptive nature of driving UTVs back and forth on the beach, as well as sand compaction and other physical effects of the sod roller. Long-term mammalian predator removal may facilitate mesopredator release, as shown in prior studies (Barton and Roth 2008), and examining these cascading effects would be worthwhile, to consider the net benefit of predator control for protected species prior to adopting crab removals as a management tool.

3.5 References

Antworth, R. L., Pike, D. A., & Stiner, J. C. (2006). Nesting ecology, current status, and conservation of sea turtles on an uninhabited beach in Florida, USA. *Biological Conservation*, *130*(1), 10–15. https://doi.org/10.1016/j.biocon.2005.11.028

Barros, F. (2001). Ghost crabs as a tool for rapid assessment of human impacts on exposed sandy beaches. *Biological Conservation*, *97*(3), 399–404. https://doi.org/10.1016/S0006-3207(00)00116-6

Barton, B. T., & Roth, J. D. (2007). Raccoon Removal on Sea Turtle Nesting Beaches. *The Journal of Wildlife Management*, *71*(4), 1234–1237. https://doi.org/10.2193/2006-014

Barton, B. T., & Roth, J. D. (2008). Implications of intraguild predation for sea turtle nest protection. *Biological Conservation*, *141*(8), 2139–2145. https://doi.org/10.1016/j.biocon.2008.06.013

Bird, B. L., Branch, L. C., & Miller, D. L. (2004). Effects of coastal lighting on foraging behavior of beach mice. *Conservation Biology*, *18*(5), 1435–1439. Scopus. https://doi.org/10.1111/j.1523-1739.2004.00349.x

Bouchard, S. S., & Bjorndal, K. A. (2000). Sea Turtles as Biological Transporters of Nutrients and Energy from Marine to Terrestrial Ecosystems. *Ecology*, *81*(8), 2305–2313. https://doi.org/10.1890/0012-9658(2000)081[2305:STABTO]2.0.CO;2

Brown, J. (2009). *Factors Affecting Predation Of Marine Turtle Eggs By Raccoons And Ghost Crabs On Canaveral National Seashore, Fl* [University of Central Florida]. https://stars.library.ucf.edu/cgi/viewcontent.cgi?article=5043&context=etd

Butler, Z. P., Wenger, S. J., Pfaller, J. B., Dodd, M. G., Ondich, B. L., Coleman, S., Gaskin, J. L., Hickey, N., Kitchens-Hayes, K., Vance, R. K., & Williams, K. L. (2020). Predation of loggerhead sea turtle eggs across Georgia’s barrier islands. *Global Ecology and Conservation*, *23*, e01139. https://doi.org/10.1016/j.gecco.2020.e01139

Call, M. N., Pongnon, R. S., Wails, C. N., Karpanty, S. M., Lapenta, K. C., Wilke, A. L., Boettcher, R., Alvino, C. R., & Fraser, J. D. (2024). Biotic and abiotic factors affecting

Atlantic ghost crab (Ocypode quadrata) spatiotemporal activity at an important shorebird nesting site in Virginia. *PLOS ONE*, *19*(8), e0307821. https://doi.org/10.1371/journal.pone.0307821

Christoffers, Edward William. (1986). *Ecology of the ghost crab Ocypode quadrata (Fabricius) on Assateague Island, Maryland and the impacts of various human uses of the beach on their distribution and abundance* [Michigan State University]. https://doi.org/10.25335/ZNQ5-6Z57

Cinzano, P., Falchi, F., & Elvidge, C. D. (2001). The first World Atlas of the artificial night sky brightness. *Monthly Notices of the Royal Astronomical Society*, *328*(3), 689–707. https://doi.org/10.1046/j.1365-8711.2001.04882.x

Costa, L. L., Soares-Gomes, A., & Zalmon, I. R. (2021). Burrow occupation rates and spatial distribution within habitat of the ghost crab *Ocypode quadrata* (Fabricius, 1787): Implications for impact assessments. *Regional Studies in Marine Science*, *44*, 101699. https://doi.org/10.1016/j.rsma.2021.101699

Crooks, K. R., & Soulé, M. E. (1999). Mesopredator release and avifaunal extinctions in a fragmented system. *Nature*, *400*(6744), 563–566. https://doi.org/10.1038/23028

de Oliveira, C. A. G., Souza, G. N., & Soares-Gomes, A. (2016). Measuring burrows as a feasible non-destructive method for studying the population dynamics of ghost crabs. *Marine Biodiversity*, *46*(4), 809–817. https://doi.org/10.1007/s12526-015-0436-3

Engeman, R. M., Addison, D., & Griffin, J. C. (2014). Defending against disparate marine turtle nest predators: Nesting success benefits from eradicating invasive feral swine and caging nests from raccoons. *Oryx*, *50*(2), 289–295. https://doi.org/10.1017/S0030605314000805

Falcy, M. R., & Danielson, B. J. (2013). A complex relationship between moonlight and temperature on the foraging behavior of the Alabama beach mouse. *Ecology*, *94*(11), 2632–2637. https://doi.org/10.1890/13-0426.1

Fortaleza, M. O., Girão, M. M. L., Franklin Junior, W., Pinto De Lima, J., & De Almeida Rocha-Barreira, C. (2020). Which moon phase do we find more ghosts? Effects of the lunar cycle on the ghost crab *Ocypode quadrata* (Fabricius, 1787). *Arquivos de Ciências Do Mar*, *52*(2), 85–97. https://doi.org/10.32360/acmar.v52i2.42737

Garmestani, A. S., & Percival, H. F. (2005). Raccoon Removal Reduces Sea Turtle Nest Depredation in the Ten Thousand Islands of Florida. *Southeastern Naturalist*, *4*(3), 469-472.

Gül, M. R., & Griffen, B. D. (2018). A Reliable Bioindicator of Anthropogenic Impact on the Coast of South Carolina. *Southeastern Naturalist*, *17*(2), 357–364. https://doi.org/10.1656/058.017.0217

Gül, M. R., & Griffen, B. D. (2019). Burrowing behavior and burrowing energetics of a bioindicator under human disturbance. *Ecology and Evolution*, *9*(24), 14205–14216. https://doi.org/10.1002/ece3.5853

Haley, S. R. (1972). Reproductive Cycling in the Ghost Crab, *Ocypode quadrata* (Fabr.) (Brachyura, Ocypodidae). *Crustaceana*, *23*(1), 1–11.

Horgan, F. G. (2017). Ecology and Management of Apple Snails in Rice. In B. S. Chauhan, K. Jabran, & G. Mahajan (Eds.), *Rice Production Worldwide* (pp. 393–417). Springer International Publishing. https://doi.org/10.1007/978-3-319-47516-5_15

Jonah, F. E., Agbo, N. W., Agbeti, W., Adjei-Boateng, D., & Shimba, M. J. (2015). The ecological effects of beach sand mining in Ghana using ghost crabs (Ocypode species) as biological indicators. *Ocean & Coastal Management*, *112*, 18–24. https://doi.org/10.1016/j.ocecoaman.2015.05.001

Kristensen, E., Penha-Lopes, G., Delefosse, M., Valdemarsen, T. B., Quintana, C. O., & Banta, G. T. (2012). What is bioturbation? The need for a precise definition for fauna in aquatic sciences. *Marine Ecology Progress Series*, *446*, 285–302. https://doi.org/10.3354/meps09506

Kyba, C. C. M., Tong, K. P., Bennie, J., Birriel, I., Birriel, J. J., Cool, A., Danielsen, A., Davies, T. W., den Outer, P. N., Edwards, W., Ehlert, R., Falchi, F., Fischer, J., Giacomelli, A., Giubbilini, F., Haaima, M., Hesse, C., Heygster, G., Hölker, F., … Gaston, K. J. (2015). Worldwide variations in artificial skyglow. *Scientific Reports*, *5*(1), 8409. https://doi.org/10.1038/srep08409

Leach, H., Swackhamer, E., Korman, A., & Walsh, B. (2024). *Spotted Lanternfly Management Guide*. PennState Extension. https://extension.psu.edu/spotted-lanternfly-management-guide

Leber, K. M. (1982). Seasonality of Macroinvertebrates on a Temperate, High Wave Energy Sandy Beach. *Bulletin of Marine Science*, *32*(1), 86–98.

Lucrezi, S. (2015). Ghost crab populations respond to changing morphodynamic and habitat properties on sandy beaches. *Acta Oecologica*, *62*, 18–31. https://doi.org/10.1016/j.actao.2014.11.004

Lucrezi, S., & Schlacher, T. A. (2014). The Ecology of Ghost Crabs. In R. N. Hughes, Hughes, D. J., & I. P. Smith (Eds.), *Oceanography and Marine Biology* (pp. 201–256). CRC Press. https://doi.org/10.1201/b17143

Lucrezi, S., Schlacher, T. A., & Walker, S. (2009). Monitoring human impacts on sandy shore ecosystems: A test of ghost crabs (Ocypode spp.) as biological indicators on an urban beach. *Environmental Monitoring and Assessment*, *152*(1–4), 413–424. https://doi.org/10.1007/s10661-008-0326-2

Martins, R., Marco, A., Patino-Martinez, J., Yeoman, K., Vinagre, C., & Patrício, A. R. (2022). *Ghost crab predation of loggerhead turtle eggs across thermal habitats*. http://hdl.handle.net/10400.12/8675

Ocaña, F. A., Navarrete, A. D. J., Carrillo, R. M. D. J., & Rivera, J. J. O. (2016). Effects of human disturbance on the population dynamics of *Ocypode quadrata* (Decapoda: Ocypodidae) in beaches of the Mexican Caribbean. *Revista de Biología Tropical*, *64*(4), Article 4. https://doi.org/10.15517/rbt.v64i4.19909

Peterson, C. H., Bishop, M. J., D’Anna, L. M., & Johnson, G. A. (2014). Multi-year persistence of beach habitat degradation from nourishment using coarse shelly sediments. *Science of The Total Environment*, *487*, 481–492. https://doi.org/10.1016/j.scitotenv.2014.04.046

Peterson, C. H., Hickerson, D. H. M., & Johnson, G. G. (2000). Short-Term Consequences of Nourishment and Bulldozing on the Dominant Large Invertebrates of a Sandy Beach. *Journal of Coastal Research*, *16*(2), 368–378.

Pombo, M., & Turra, A. (2013). Issues to Be Considered in Counting Burrows as a Measure of Atlantic Ghost Crab Populations, an Important Bioindicator of Sandy Beaches. *PLOS ONE*, *8*(12), e83792. https://doi.org/10.1371/journal.pone.0083792

Pombo, M., de Oliveira, A. L., Xavier, L. Y., Siegle, E., & Turra, A. (2017). Natural drivers of distribution of ghost crabs *Ocypode quadrata* and the implications of estimates from burrows. *Marine Ecology Progress Series*, *565*, 131–147. https://doi.org/10.3354/meps11991

Pruner, R., & Addison, L. (2022). *Ghost Crab Management*. 2022 Meeting of the American Oystercatcher Working Group, St. Simons Island, GA. https://amoywg.org/wp-content/uploads/2022/12/Pruner-Addison-ghost-crab-2022.pdf

Puschnig, J., Schwope, A., Posch, T., & Schwarz, R. (2014). The night sky brightness at Potsdam-Babelsberg including overcast and moonlit conditions. *Journal of Quantitative Spectroscopy and Radiative Transfer*, *139*, 76–81. https://doi.org/10.1016/j.jqsrt.2013.12.011

Robinson, T. (2024). Inspection of ghost crab (Ocypode quadrata) burrows with an articulating borescope: A tool to detect occupancy. *Estuarine, Coastal and Shelf Science*, *310*, 109004. https://doi.org/10.1016/j.ecss.2024.109004

Rosenberg, J., & Langer, H. (2001). Ultrastructural Changes of Rhabdoms of the Eyes of Ocypode Species in Relation to Different Regimes of Light and Dark Adaptation. *Journal of Crustacean Biology*, *21*(2), 345–353. https://doi.org/10.1163/20021975-99990134

Schlacher, T. A., Lucrezi, S., Connolly, R. M., Peterson, C. H., Gilby, B. L., Maslo, B., Olds, A. D., Walker, S. J., Leon, J. X., Huijbers, C. M., Weston, M. A., Turra, A., Hyndes, G. A., Holt, R. A., & Schoeman, D. S. (2016a). Human threats to sandy beaches: A meta-analysis of ghost crabs illustrates global anthropogenic impacts. *Estuarine, Coastal and Shelf Science*, *169*, 56–73. https://doi.org/10.1016/j.ecss.2015.11.025

Schlacher, T. A., Lucrezi, S., Peterson, C. H., Connolly, R. M., Olds, A. D., Althaus, F., Hyndes, G. A., Maslo, B., Gilby, B. L., Leon, J. X., Weston, M. A., Lastra, M., Williams, A., & Schoeman, D. S. (2016b). Estimating animal populations and body sizes from burrows: Marine ecologists have their heads buried in the sand. *Journal of Sea Research*, *112*, 55–64. https://doi.org/10.1016/j.seares.2016.04.001

Silva, E., Marco, A., da Graça, J., Pérez, H., Abella, E., Patino-Martinez, J., Martins, S., & Almeida, C. (2017). Light pollution affects nesting behavior of loggerhead turtles and predation risk of nests and hatchlings. *Journal of Photochemistry and Photobiology B: Biology*, *173*, 240–249. https://doi.org/10.1016/j.jphotobiol.2017.06.006

Silva, W., & Calado, T. (2013). Number of ghost crab burrows does not correspond to population size. *Open Life Sciences*, *8*(9), 843–847. https://doi.org/10.2478/s11535-013-0208-7

Smith, D. C. (1965). Methods of Euthanasia and Disposal of Laboratory Animals. In W. I. Gay (Ed.), *Methods of Animal Experimentation* (pp. 167–195). Academic Press. https://doi.org/10.1016/B978-1-4832-3220-1.50012-7

Stancyk, S. E. (1982). Non-human predators of sea turtles and their control. In K. A. Bjorndal (Ed.), *Biology and Conservation of Sea Turtles* (pp. 139–152). Smithsonian Institution Press.

Steiner, A. J., & Leatherman, S. P. (1981). Recreational impacts on the distribution of ghost crabs *Ocypode quadrata* fab. *Biological Conservation*, *20*(2), 111–122. https://doi.org/10.1016/0006-3207(81)90022-7

Taylor, J. R. A., deVries, M. S., & Elias, D. O. (2019). Growling from the gut: Co-option of the gastric mill for acoustic communication in ghost crabs. *Proceedings of the Royal Society B: Biological Sciences*, *286*(1910), 20191161. https://doi.org/10.1098/rspb.2019.1161

Tiralongo, F., Messina, G., Marino, S., Bellomo, S., Vanadia, A., Borzì, L., Tibullo, D., Di Stefano, A., & Lombardo, B. M. (2020). Abundance, distribution and ecology of the tufted ghost crab *Ocypode cursor* (Linnaeus, 1758) (Crustacea: Ocypodidae) from a recently colonized urban sandy beach, and new records from Sicily (central Mediterranean Sea). *Journal of Sea Research*, *156*, 101832. https://doi.org/10.1016/j.seares.2019.101832

Turra, A., Gonçalves, M. A. O., & and Denadai, M. R. (2005). Spatial distribution of the ghost crab *Ocypode quadrata* in low-energy tide-dominated sandy beaches. *Journal of Natural History*, *39*(23), 2163–2177. https://doi.org/10.1080/00222930500060165

Valero-Pacheco, E., Alvarez, F., Abarca-Arenas, L., & Escobar, M. (2007). Population density and activity pattern of the ghost crab, *Ocypode quadrata*, in Veracruz, Mexico. *Crustaceana*, *80*(3), 313–325. https://doi.org/10.1163/156854007780162479

Vance-Chalcraft, H. D., Rosenheim, J. A., Vonesh, J. R., Osenberg, C. W., & Sih, A. (2007). The influence of intraguild predation on prey suppression and prey release: A meta-analysis. *Ecology*, *88*(11), 2689–2696. https://doi.org/10.1890/06-1869.1

Vernberg, W. B., & Vernberg, F. J. (1968). Physiological Diversity in Metabolism in Marine and Terrestrial Crustacea. *American Zoologist*, *8*(3), 449–458.

Weinstein, R. B., & Full, R. J. (1994). Thermal Dependence of Locomotor Energetics and Endurance Capacity in the Ghost Crab, Ocypode quadrata. *Physiological Zoology*, *67*(4), 855–872.

Welicky, R. L., Wyneken, J., & Noonburg, E. G. (2012). A retrospective analysis of sea turtle nest depredation patterns. *The Journal of Wildlife Management*, *76*(2), 278–284. https://doi.org/10.1002/jwmg.255

Wilkinson, E. B., Branch, L. C., & Miller, D. L. (2013). Functional habitat connectivity for beach mice depends on perceived predation risk. *Landscape Ecology*, *28*(3), 547–558. https://doi.org/10.1007/s10980-013-9858-0

Wolcott, T. G. (1978). Ecological role of ghost crabs, *Ocypode quadrata* (Fabricius) on an ocean beach: Scavengers or predators? *Journal of Experimental Marine Biology and Ecology*, *31*(1), 67–82. https://doi.org/10.1016/0022-0981(78)90137-5

Wolcott, D. L., & Wolcott, T. G. (1999). High Mortality of Piping Plovers on Beaches with Abundant Ghost Crabs: Correlation, Not Causation. *The Wilson Bulletin*, *111*(3), 321–329.

3.6 Figures

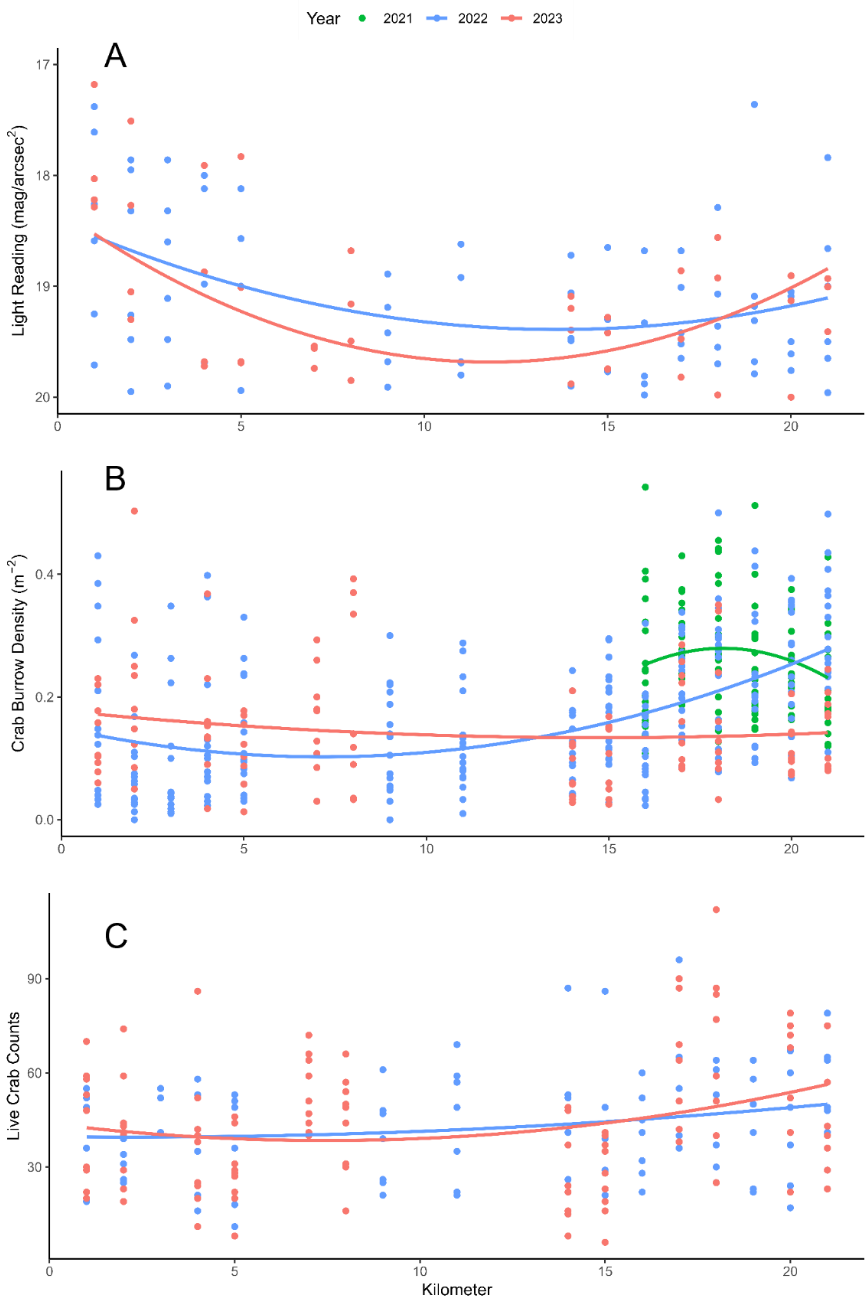


Figure 3.1: Spatial variation across the beach by kilometer zone in light readings (recorded in mag/arcsec² (A), crab burrow density (B) and live crab counts (C) on Cape Canaveral Space Force Station. Light readings were recorded for every survey in 2022 but only a subset of surveys of 2023. No live counts were conducted in 2021.

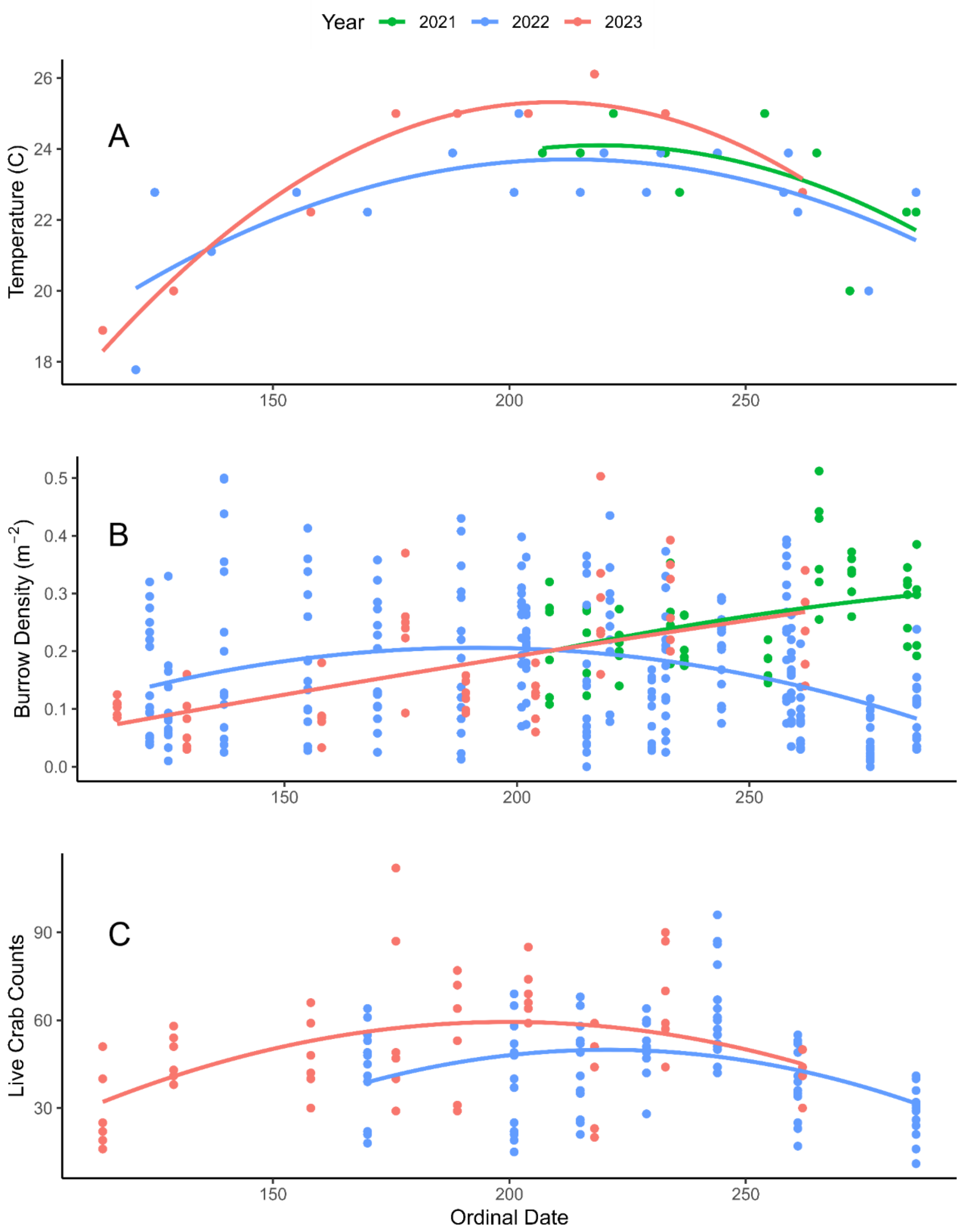


Figure 3.2: Changes in temperature (A), burrow density (B) and live crab counts (C) by ordinal date on Cape Canaveral Space Force Station. Sea turtle nesting begins in early May (ordinal date 122) and nesting and hatching peak in mid- to late-July (ordinal date 200). No live counts were conducted in 2021.

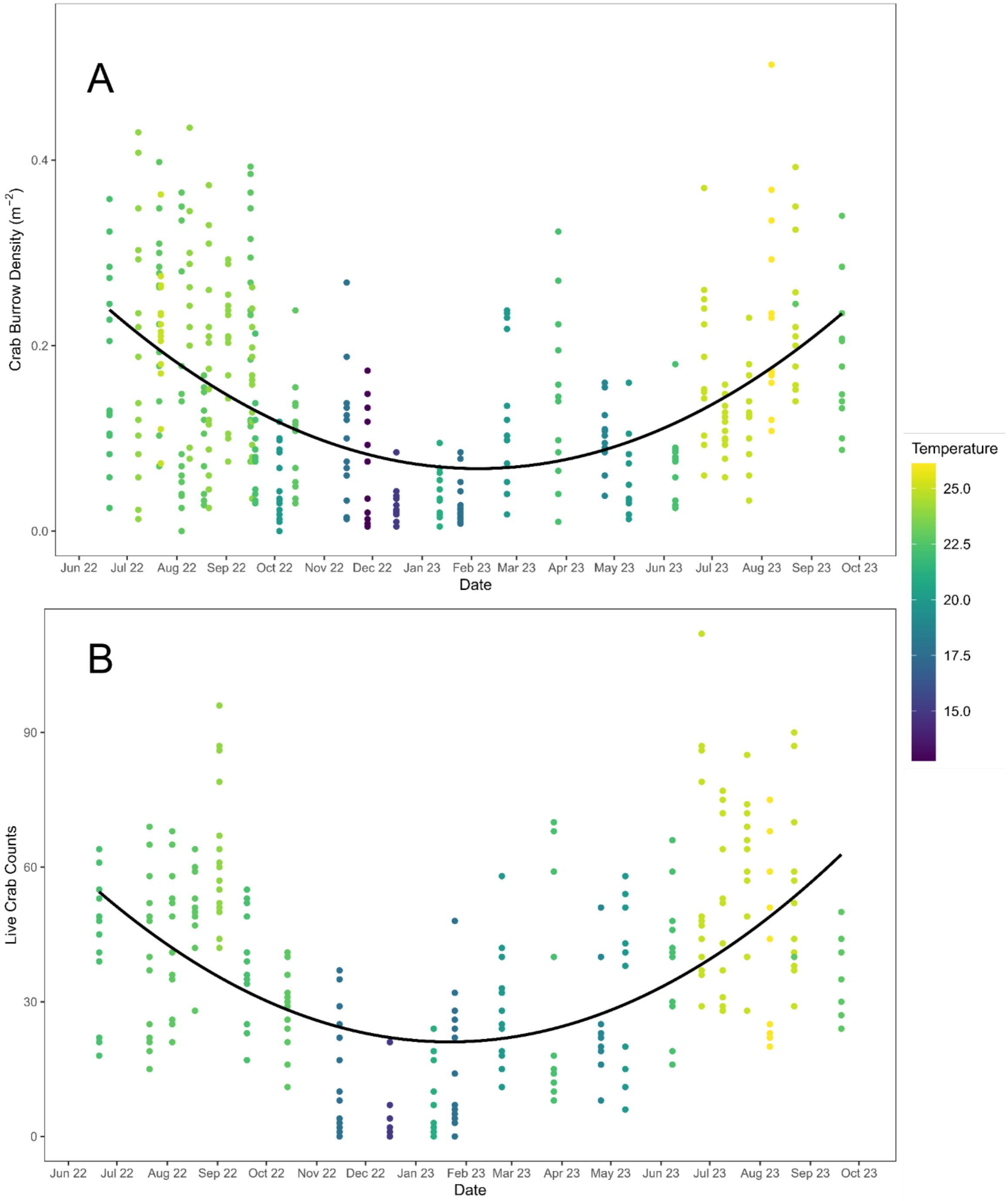


Figure 3.3: Crab burrow density (A) and live crab counts (B) on 12-15 200-m plots over the 2022-2023 winter on Cape Canaveral Space Force Station. The experimental design and plot locations changed on February 23, 2023, to initiate large-scale removals (Figure 2.S1), and only counts from 2023 control zones are included in this figure.

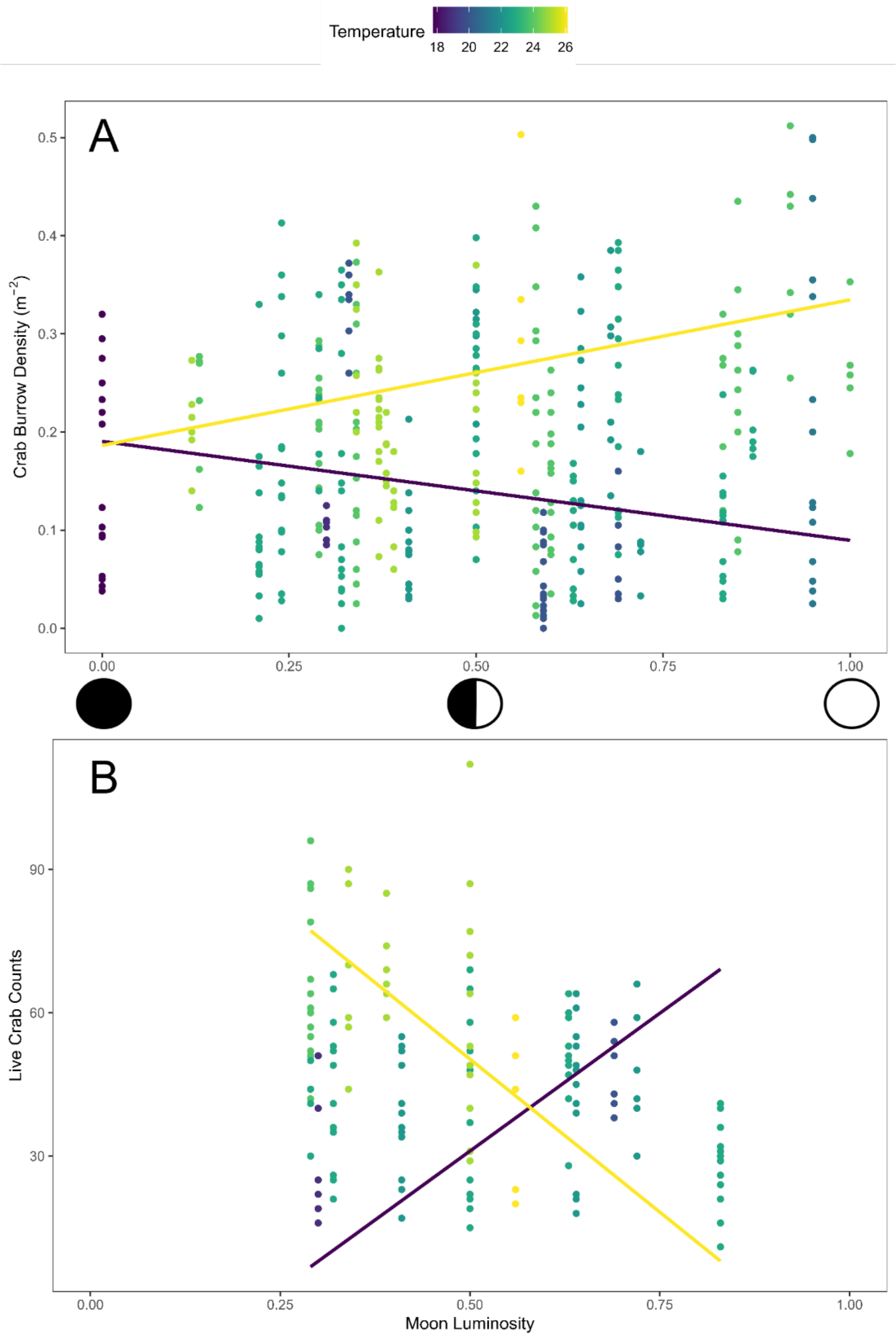


Figure 3.4 Interaction between moon luminosity and temperature in our global models on both burrow density from 2021-2023 (A) and live crab counts from 2022-2023 (B) on Cape Canaveral Space Force Station. Moon luminosity varies between new moon (0.0) and full moon (1.0). The yellow line represents the warmest temperature recorded during these surveys (26° C) and the purple line represents the lowest temperature recorded (18° C).

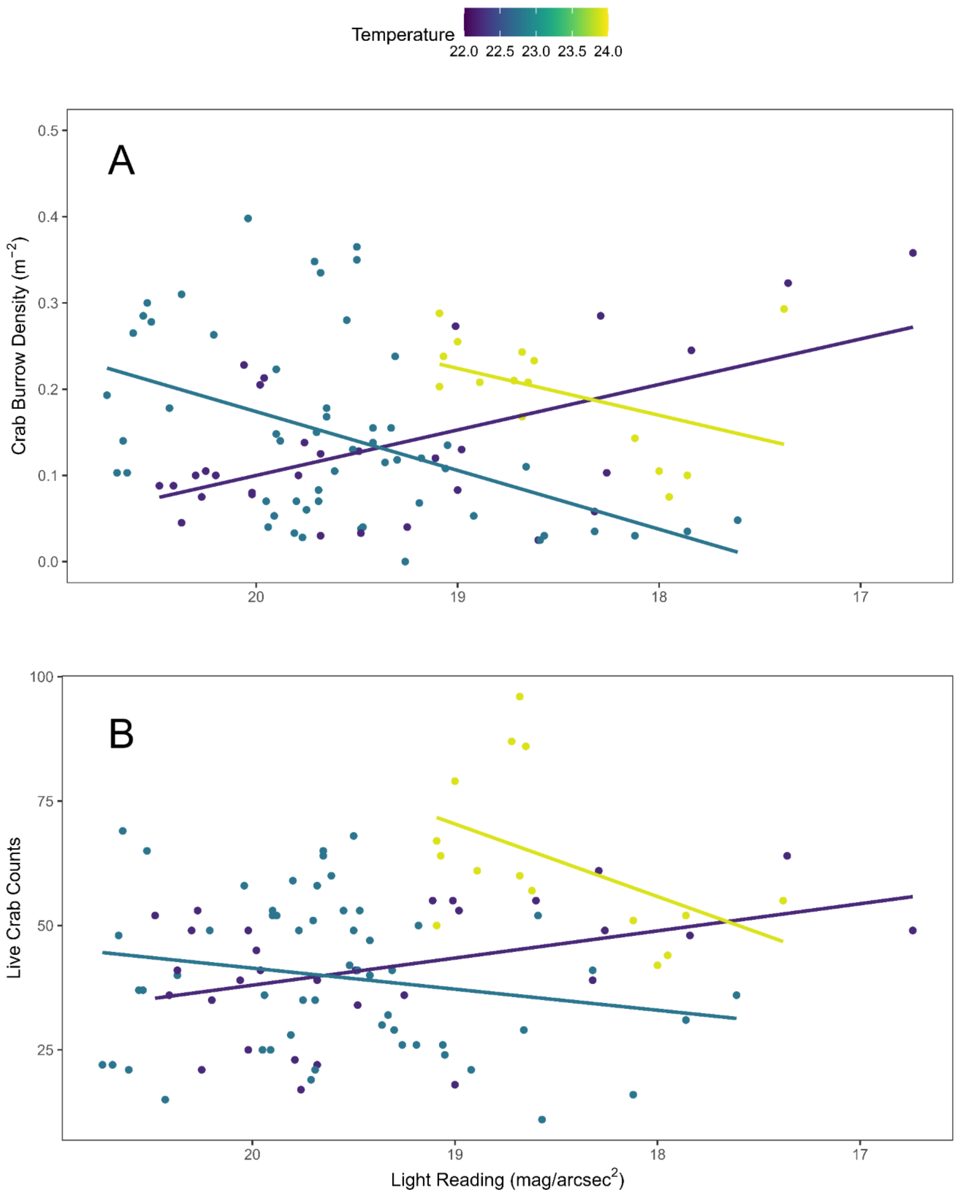


Figure 3.5: Interactive effects of ambient light and the overnight low temperature on both burrow density (A) and live crab counts (B) in 2022 on Cape Canaveral Space Force Station. The x-axis has been reversed as lower readings (17 mag/arcsec²) reflect more visible light, and higher readings reflect darker observations and less visible light (22 mag/arcsec²). The three different lines for temperature were used to display the limited variability in temperature recorded during live crab counts in 2022, including the yellow line (23.9 °C), the blue line (22.8° C) and the purple line (22.2° C).

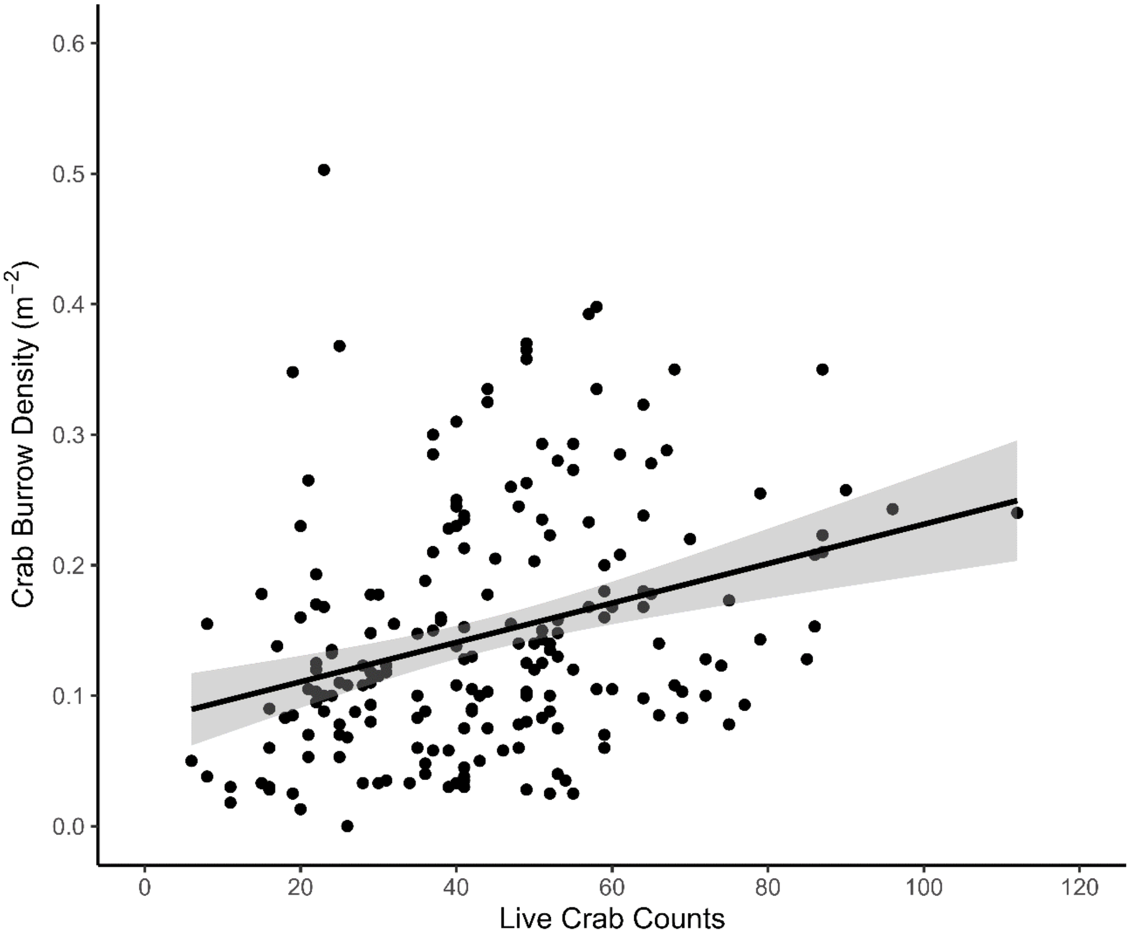


Figure 3.6: Relationship between ghost crab burrow density and live crab counts at Cape Canaveral Space Force Station from summers 2022 and 2023 ($R^2 = 0.09$).

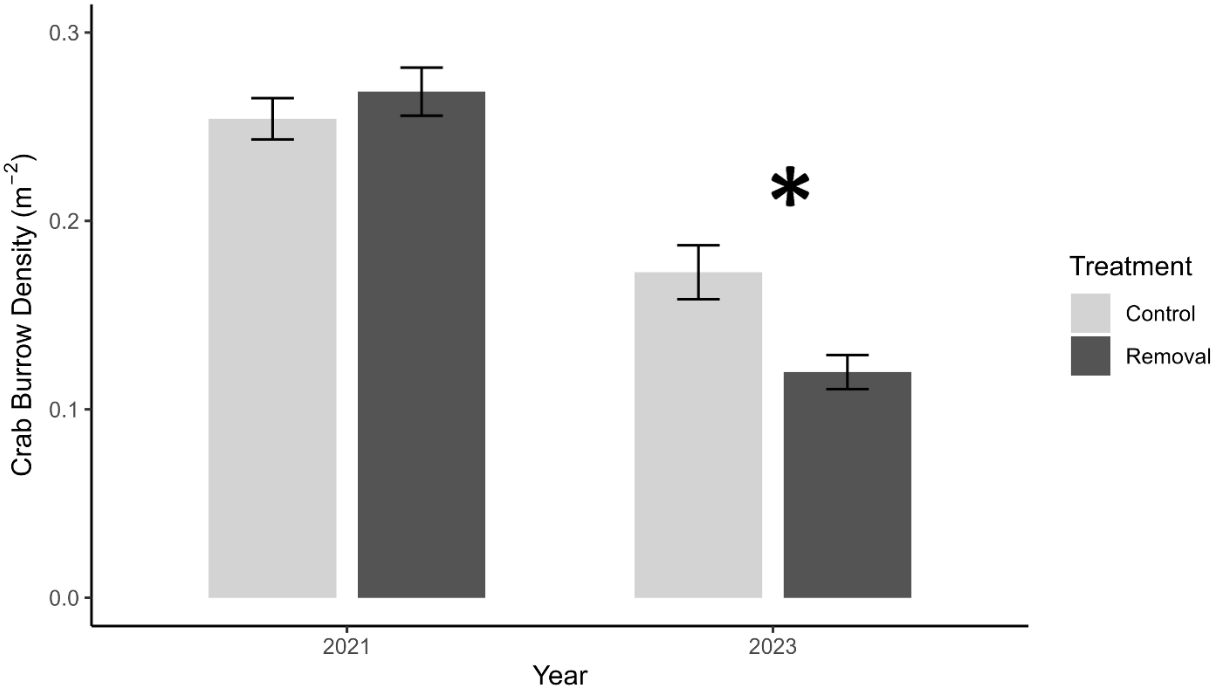


Figure 3.7 Effects of crab removals in 2021 (live captures) and 2023 (sod roller) on ghost crab burrow density (*$p = 0.009$) on Cape Canaveral Space Force Station.

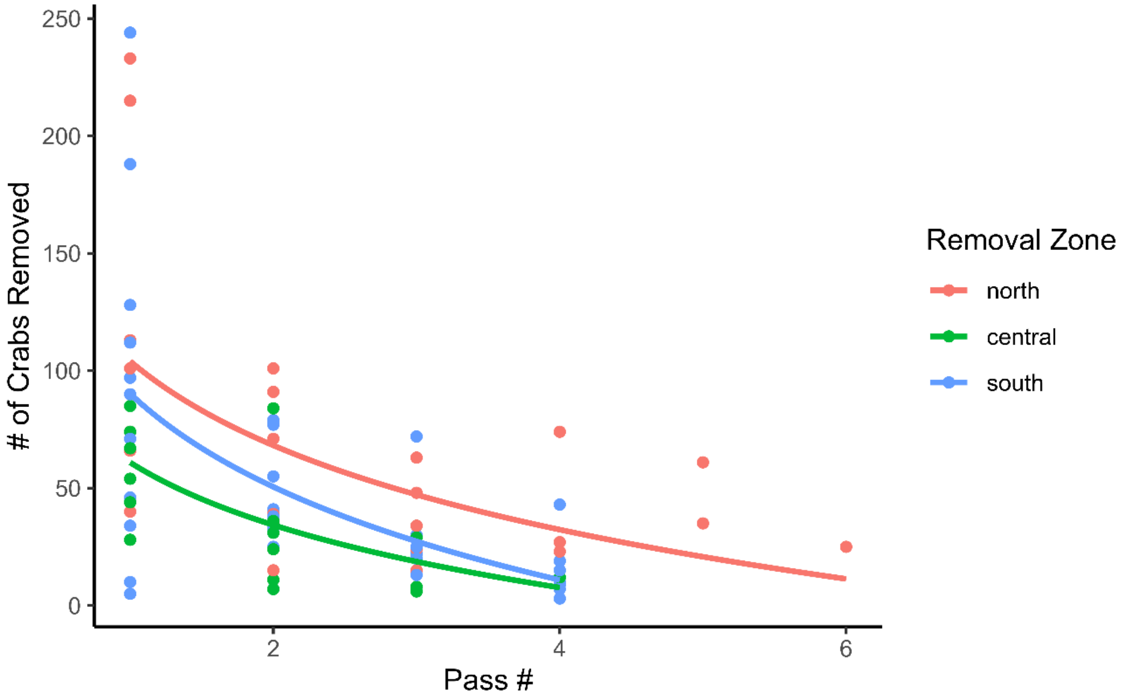


Figure 3.8: During the sod roller removal experiment on Cape Canaveral Space Force Station in 2023, we completed multiple passes in each removal zone. The number of crabs removed by pass varied by zone, but continuously declined after the first pass.

3.7 Tables

Table 3.1: Ghost crab burrow density mixed-effect model results on Cape Canaveral Space Force Station. Kilometer was included as a random effect in each model, and the global model uses data from non-removal plots only. In 2021, the model includes the live-trapping treatment and in 2023, the model includes the sod roller treatment. The 2022 model includes light but no experimental removal treatment.

Independent Variable	**Sum of Squares**	**DF**	**F-Ratio**	***P***
Global model (2021-2023)				
Moon luminosity	**0.095**	**1, 352.7**	**10.379**	**0.001***
Low temperature	0.000	1, 352.6	0.016	0.901
Moon luminosity * low temperature	**0.099**	**1, 352.8**	**10.804**	**0.001***
Year	**0.069**	**2, 335.8**	**3.785**	**0.024***
2021 Model				
Moon luminosity	**0.041**	**1, 110.0**	**6.811**	**0.010***
Low temperature	**0.133**	**1, 110.0**	**22.277**	**<0.001***
Moon luminosity * low temperature	**0.044**	**1, 110.0**	**7.309**	**0.008***
Treatment	0.006	1, 110.0	1.042	0.310
2022 Model				
Moon luminosity	**0.070**	**1, 86.3**	**11.433**	**0.001***
Low temperature	**0.034**	**1, 86.4**	**5.490**	**0.021***
Moon luminosity * low temperature	**0.072**	**1, 86.2**	**11.612**	**0.001***
Light	**0.052**	**1, 86.6**	**8.575**	**0.004***
Light * low temperature	**0.054**	**1, 86.7**	**8.888**	**0.004***
2023 Model				
Moon luminosity	0.005	1, 93.1	1.144	0.288
Low temperature	0.004	1, 93.4	0.791	0.376
Moon luminosity * low temperature	0.003	1, 93.1	0.516	0.474
Treatment	**0.058**	**1, 10.0**	**11.111**	**0.008***

Table 3.2: Live ghost crab count mixed-effect model results on Cape Canaveral Space Force Station. Kilometer was included as a random effect in each model, and the global model uses data from non-removal plots only. The 2022 model includes light but no experimental removal treatment. The 2023 model includes the sod roller treatment.

Independent Variable	**Sum of Squares**	**DF**	**F-Ratio**	***P***
Global model (2022-2023)				
Moon luminosity	**5191.1**	**1, 134.6**	**24.869**	**<0.001***
Low temperature	**8467.6**	**1, 134.6**	**40.565**	**<0.001***
Moon luminosity * low temperature	**5627.5**	**1, 134.6**	**26.960**	**<0.001***
Year	**982.9**	**1, 93.5**	**4.709**	**0.033***
2022 Model				
Moon luminosity	**1205.3**	**1, 89.8**	**6.237**	**0.014***
Low temperature	661.5	1, 92.6	3.423	0.067
Moon luminosity * low temperature	**1257.5**	**1, 89.7**	**6.507**	**0.012***
Light	**1095.5**	**1, 92.8**	**5.669**	**0.019***
Light * low temperature	**1086.0**	**1, 92.8**	**5.620**	**0.012***
2023 Model				
Moon luminosity	**1986.1**	**1, 87.2**	**9.596**	**0.003***
Low temperature	**4749.6**	**1, 87.1**	**22.947**	**<0.001***
Moon luminosity * low temperature	**2048.1**	**1, 87.2**	**9.895**	**0.002***
Treatment	**1070.2**	**1, 9.7**	**5.171**	**0.047***

Table 3.3: Comparison of models exploring relationship between live crab counts and crab burrow density, including environmental variables, to see which variables best predicted live crab counts on Cape Canaveral Space Force Station. All models contained kilometer as a random effect.

Model	**DF**	**AIC**	**ΔAIC**	**Weight**
Year + burrow density	5	1291.7	52.3	0
Year + burrow density + moon luminosity	6	1278.8	39.4	0
Year + burrow density + low temperature	6	1280.1	40.7	0
Year + burrow density + moon luminosity + low temperature	7	1267.7	28.2	0
Year + burrow density + moon luminosity * low temperature	**8**	**1239.5**	**0**	**1**

Table 3.4: Results of the best model to predict live crab counts based on model selection (Table 3.3), which included burrow density + year + moon luminosity * temperature.

Independent variable	**Sum of squares**	**DF**	**F-value**	***P***
Burrow density	614.8	1, 145.9	2.962	0.087
Year	**976.8**	**1, 89.3**	**4.705**	**0.033**
Moon luminosity	**5302.9**	**1, 133.9**	**25.546**	**<0.001**
Low temperature	**7964.0**	**1, 134.1**	**38.365**	**<0.001**
Moon luminosity * low temperature	**5709.0**	**1, 133.9**	**27.502**	**<0.001**

3.8 Supplemental Information

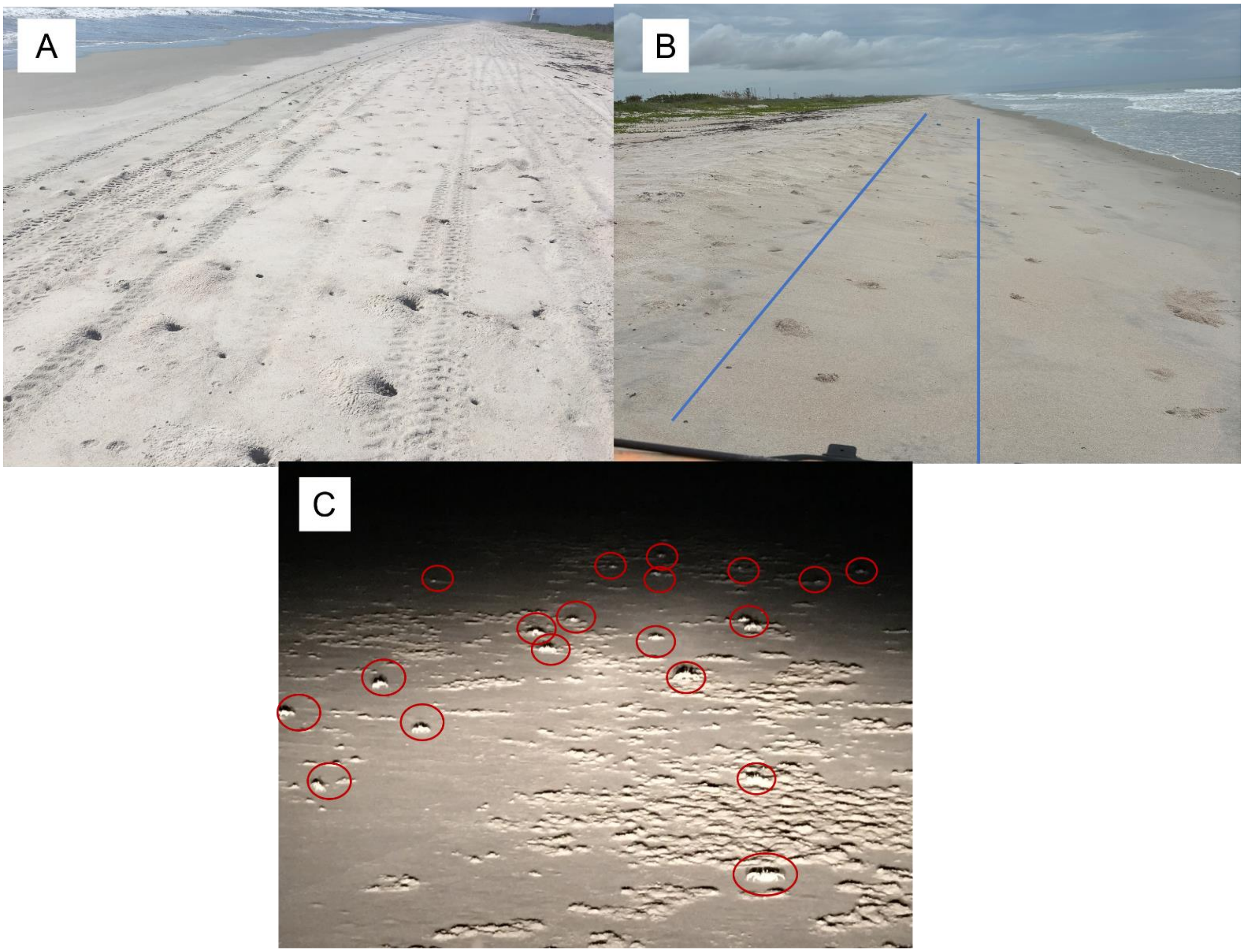


Figure 3.S1: The high abundance of large ghost crab burrows above the high tide line (A), the area of the beach below the high tide line where burrows were counted (B), and live crabs among sargassum on the beach during nighttime live counts (C) on the CCSFS beach.

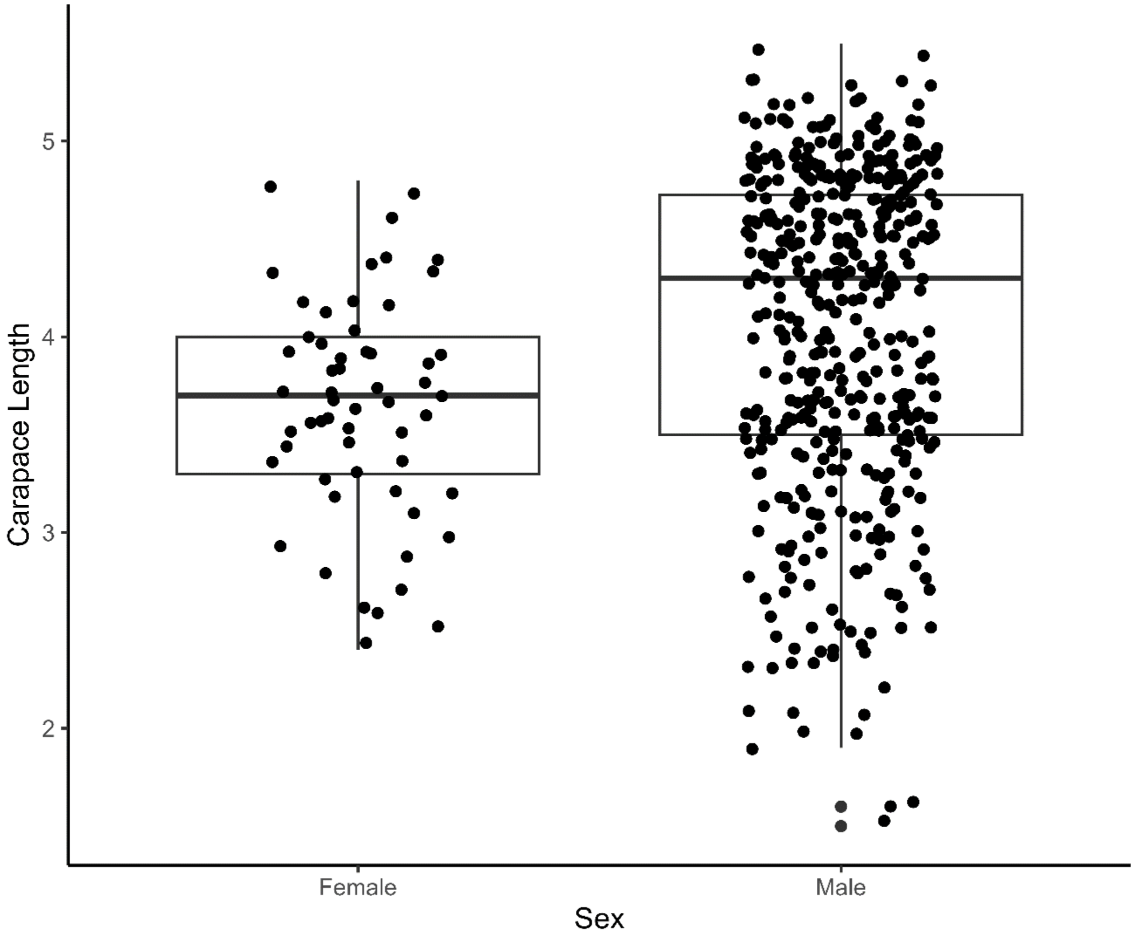


Figure 3.S2. Ghost crab size distribution by sex for crabs captured during the 2021 live capture removal efforts on the Cape Canaveral Space Force Station beach (n=64 females and 449 males).

Appendix 3.A: Sand grain analysis

Methods

We collected sand from monitoring plots on the beach to determine whether sand characteristics affected our crab density metrics in 2021 and 2022. We used a 35-cm PVC pipe to collect sediment cores from each plot. In 2021, plots were only established on the north end of the beach, from kilometers 16-21, and we collected samples only above the high-tide line in dry sand. In 2022, plots were established across the entire beach from kilometers 1-21, and samples were collected above, at, and below the high tide line. Samples above the high-tide line represented the area where sea turtle nests were present, samples on the high-tide line represented the area where burrow counts occurred, and samples below the high-tide line represented where live crabs were counted. Samples were shipped to Kasey Wade at FFWCC's Fish and Wildlife Research Institute for processing and dried in a drying oven for 24 hours at 60°C to remove moisture. When samples were received after drying, we individually sifted them through fine mesh sieves of descending size using a mechanical sieve kit (*Keck Sandshaker, Model SS-94, Geotech,* Colorado, United States). Samples were divided into size classes >2 mm, >1 mm, >0.5 mm, >0.25 mm and <0.25 mm, and raw weights for each size class were entered in the GRADISTAT software (Blott and Pye 2001) to calculate mean grain size and sorting coefficients using the Folk & Ward method (Folk 1966, Brown 2009). Each sample was also sorted into textural groups, categorized from coarse to fine.

Results

In 2021, when samples were collected only above the high tide line on the north end of the beach, samples were categorized as gravelly to medium grain sand (average size range 443-619 μm) but well sorted (sorting coefficient < 2). In 2022 when sampling across different zones, samples above the high tide line had the largest average grain size (502 ± 112 SD µm). Samples were comparable in average grain size at the high tide line (415 ± 178 µm) and below the high tide line (413 ± 122 µm) In 2022, our study design expanded to include plots across the entire beach. The south end of the beach (kms 1-15) was comprised of coarser, gravelly, poorly sorted sand (average size range 389-656 µm, sorting coefficient > 2). The northern end of the beach, (kms 16-21) was comprised of finer well-sorted sand (average size range 304-346 µm, sorting coefficient < 2). These results varied annually, and the mean grain size on the north end of the beach was larger in 2021 compared to 2022 (Fig. C1).

Discussion

The annual variation observed could be a result of sampling in different beach zones. Based on the annual variation observed, even from the same beach zone (above the high tide line), sand grain size likely would have to be collected more frequently to include in crab density models and perform an appropriate analysis. The beach is a dynamic system, which changes frequently due to tidal action that can result in erosion or accretion. We completed burrow counts biweekly and live counts monthly, and sand grain samples likely would have had to be taken more frequently during these sampling events to compare to the indices.

References

Blott, S. J., & Pye, K. (2001). GRADISTAT: A grain size distribution and statistics package for the analysis of unconsolidated sediments. *Earth Surface Processes and Landforms*, *26*(11), 1237–1248. https://doi.org/10.1002/esp.261

Brown, J. (2009). *Factors Affecting Predation Of Marine Turtle Eggs By Raccoons And Ghost Crabs On Canaveral National Seashore, Fl* (Master’s thesis, University of Central Florida). https://stars.library.ucf.edu/cgi/viewcontent.cgi?article=5043&context=etd

Folk, R. L. (1966). A Review of Grain-Size Parameters. *Sedimentology*, *6*(2), 73–93. https://doi.org/10.1111/j.1365-3091.1966.tb01572.x

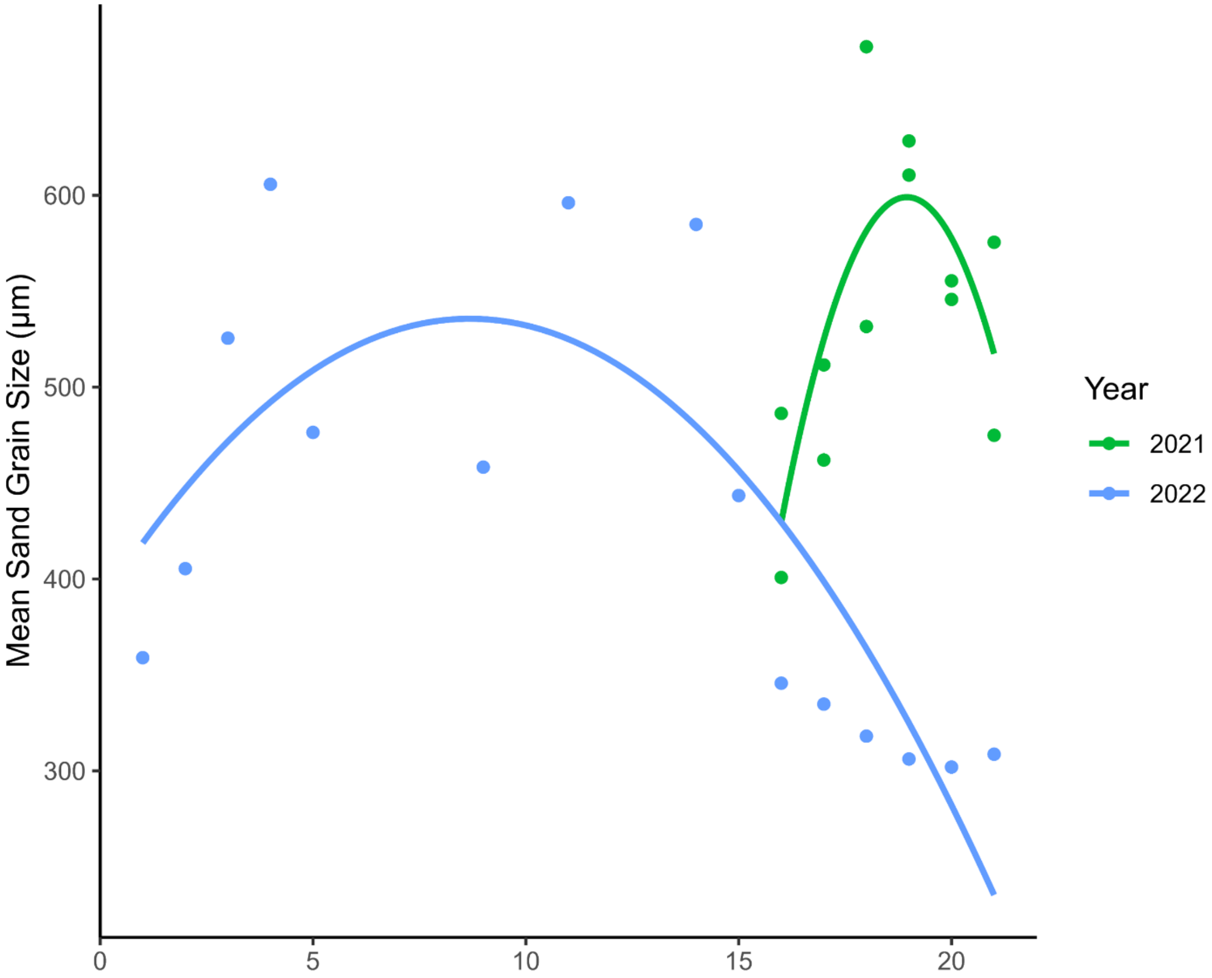


Figure 3.A1: Average sand grain size (µm) observed by kilometer zone in 2021 and 2022 on the Cape Canaveral Space Force Station beach.

Chapter 4: Conclusion

Florida beaches are an important rookery for nesting turtles, representing 89% of Northwest Atlantic loggerhead nests (Ceriani and Meylan, 2017). Although loggerheads are often touted as a conservation success story, that success may be overstated. A recent analysis of 30 years of loggerhead sea turtle nest counts in Florida revealed short term fluctuations in nesting numbers and presumed abundance of breeding females but found no evidence of increasing population trends and subsequent population recovery (Ceriani et al. 2019). Thus, continued vigilance and conservation efforts remain essential.

Within the Recovery Plan for this population segment of loggerhead turtles, it is recommended that ecologically sound predator control programs ensure that mammalian predation on nests is ≤10% within each recovery unit (NMFS and USFWS 2008). Additionally, the Florida FWC Marine Turtle Conservation Handbook also suggests implementing measures to protect nests when depredation becomes “a serious problem (as an approximate guide, when greater than 10% of nests are affected)” (FFWCC 2016). These thresholds of concern are general recommendations by sea turtle managers, but thresholds of predation and its impact on loggerhead population trajectory are debated. While many sea turtle advocates would argue any predation is too much, several papers using quantitative models argue that mortality during egg and hatchling stages is inconsequential to loggerhead population recovery (Crouse et al. 1987, Crowder et al. 1994). These studies advocate for focusing conservation efforts on juvenile and subadult life stages, though these stages are not well understood, and in-water threats are more challenging to manage.

Regardless of these models, Federal and State guidelines recommend management of nest predators for imperiled species when predation levels exceed 10% (NMFWS and USFWS 2008, FFWCC 2016). Some of the recommended measures of protecting nests from mammalian predators, such as screening or caging nests, are ineffective against ghost crabs. Management guidelines and efforts to reduce predation are often targeted at mammalian predators, and invertebrate predators are often overlooked. We identified just one other study in the grey literature that experimentally removed ghost crabs to protect nesting shorebirds (Pruner and Addison 2022).

Barton and Roth (2008) suggested maintaining moderate raccoon densities for controlling ghost crabs, and resource managers at Cape Canaveral Space Force Station (CCSFS) have discussed the possibility of reducing raccoon removal to regulate crab abundance. However, ceasing or reducing raccoon removal may not sufficiently reduce crab numbers or predation pressure on sea turtles. Engeman et al. (2006) found that ceasing mammal predator removal mid-season nearly tripled sea turtle predation rates. Prior to the initiation of the CCSFS sea turtle protection program in 1986, raccoon predation on the CCSFS beach reached 95% of nests but has been reduced in recent years through trapping by USDA to an average of 10% (SLD 45, 2022). Despite the removal of approximately 60 raccoons per year from CCSFS, raccoons remain the primary predators of nests (SLD 45, 2022). Sea turtle nests and hatchlings are seasonally abundant on the CCSFS beach (SLD 45, 2022), and are relatively defenseless and thus a more effortless prey source for raccoons compared to ghost crabs (*pers. obs.)*. Crabs are well-adapted to avoiding predation, they have acute senses, run swiftly, can retreat into burrows, and have large claws for defense. Given these factors, raccoons may be more likely to prefer sea turtle eggs and hatchlings as a food source.

Predation by mammalian predators on CCSFS and other beaches has been well documented for decades, but crab predation can be more cryptic and difficult to quantify. Based on observations of this study, relying solely on snip marks to attribute damaged eggs to crabs is likely underestimating predation estimates. We repeatedly found eggs in nests with large ghost crab burrows that were torn open without snip marks and found shredded eggs outside of burrows into nests. In a controlled feeding experiment with a similar species of crab (*O. convexa)*, crabs were observed tearing open eggs to consume their contents (Avenant et al. 2023a, Avenant 2025). The crabs used in this experiment were of comparable size to crabs captured on the CCSFS beach (Chapter 3, Figure 3.S2) at > 35 mm carapace width (Avenant et al. 2023a). Missing eggs presumed to be depredated by crabs can be substantial (Avenant et al. 2023b) and not accounting for missing eggs can bias productivity estimates (Ceriani et al. 2021) and further underestimate the impact of ghost crabs. While it may not be feasible to pre-count every nest to quantify missing eggs, pre-counts for a subset of nests may be useful to better understand crab impacts on individual beaches. For decades, FFWCC has recorded nest productivity data from nests across the entire state but refining the methods for attributing damaged eggs to ghost crabs would be worthwhile to better understand the impacts of crabs to sea turtle nests.

Disorientation is widely believed to increase hatchling predation risk, but the increased risk had not been quantified prior to this study. We found an average of 14% of hatchlings from disoriented nests were attacked on their way to the ocean, compared to 6.5% of hatchlings that took direct paths to the water. Disoriented hatchlings expend limited energy absorbed through their yolk sac crawling away from or parallel to the ocean rather than sustaining them in their swim to oceanic currents (Kraemer and Bennett 1981). Disorientation has a metabolic cost, consequently affecting their crawl speed, and increasing their periods of rest (Pankaew and Milton 2018). This extra time on the beach increases their exposure to predators (Witherington

1997, Witherington et al. 2014). Our results revealed that disoriented nests in large-scale removal zones had more drag marks than non-disoriented nests in control zones, highlighting that minimizing lighting and disorientation would benefit emergent hatchlings as much as the removal of crabs.

Biologists at CCSFS work with launch providers to minimize artificial lighting using Light Management Plans (Space Launch Delta 45, 2022). When practicable, shielded, lower wavelength lighting is used around CCSFS to prevent lighting visibility on the nesting beach. However, these precautions are not always feasible. Certain operational requirements exist for health and human safety, and launch providers are required to use white lighting during rocket launches and testing, including “up-lighting”, with skyward facing lights to illuminate the entire rocket. This type of lighting can be seen from farther distances and reflects off clouds to create a larger skyglow (Witherington et al. 2014). Our findings indicate that ambient lighting influenced crab abundance and activity, potentially due to their sensitivity and attraction to lighting (Rosenberg and Langer 2001, Silva et al. 2017), but the effects of lighting were modulated by temperature. The effects of artificial lighting on crab behavior are not well documented (Schlacher et al. 2016b). Moon luminosity also affected crab abundance in complex ways, which could possibly be tied to reproductive behavioral patterns (Christoffers 1986, Wellins et al. 1989, Lucrezi and Schlacher 2014, Fortaleza et al. 2020)

Crab abundance also varied spatially and was highest near the north and south edges of the beach, which may be due to higher observed artificial light or changes in sand composition. We also observed temporal variation in ghost crab abundance, which appeared to increase with sea turtle activity. Our findings challenge the reliability of burrow density as a proxy for crab abundance, and this metric may also reflect crab behavior and activity in addition to abundance.

Burrow abundance is the most commonly used metric of crab abundance (Schlacher et al. 2016a, Schlacher et al. 2016b) but this metric is highly variable based on behavior and environmental variables. To our knowledge, no other studies have used live crab surveys as indices of abundance, which limits comparisons with other sites. Live crab counts provide direct estimates but are more challenging to implement due to ghost crab behavior. We found that targeting surveys when crabs were observed to be most active on the surface (after dusk, below the high tide line during incoming tides) made these surveys successful. Additionally, driving the plots while counting allowed us to observe and count crabs before they retreated to their burrows or the water. Schlacher et al. (2016b) compared metrics used to estimate crab abundance, including burrow proxies, visual census, and physical collections, and advocated for improved methods in future studies.

While raccoon removal may increase crab size and abundance (Barton and Roth 2008), this management tool is unlikely the primary driver of crab abundance on the CCSFS beach, where access is highly restricted and thus human disturbance is minimal. Responses of ghost crabs to human disturbance are well documented, and multiple studies use ghost crabs as bioindicators (Schlacher et al. 2016a, Costa and Zalmon 2019, Pombo and Turra 2019, Barboza et al. 2021, Costa et al. 2022). Burrowing activity, burrow fidelity and longevity are highest at sites with low human impact, and weaker at pristine sites (Gül and Griffen 2019), suggesting that burrow counts may more accurately affect abundance in disturbed areas. Since the CCSFS beach is relatively pristine, crabs on this beach may be more sensitive to environmental variability, enabling them to capitalize on favorable conditions and pose a greater threat to turtles. In contrast, on beaches with higher human impact, crab populations may be suppressed and less likely to thrive under such conditions.

Ghost crab control efforts require careful ecological consideration, as the greater ecosystem impacts of removing this native species are unknown. Many sea turtle nesting beaches are in areas of high human activity, which may naturally suppress crab populations (Barros, 2001, Ocaña et al. 2016) and may not warrant management intervention. However, on low-disturbance beaches like CCSFS, crabs have been documented having a more significant impact. High predation rates have been recorded on other pristine beaches, including 50% hatchling predation by *O. cursor* in Cabo Verde (Martins et al. 2021) and 43% predation by *O. convexa* on the western coast of Australia (Avenant et al. 2023a). Further, ghost crab burrow diameter, and thus body size, is smaller on more disturbed beaches, possibly because survival is lower and fewer crabs make it to adult stages (Costa et al. 2022). Ghost crab size in addition to abundance can influence predation rates, as larger ghost crabs feed at higher trophic levels and likely consume more eggs and hatchlings (Barton and Roth 2008).

The large-scale crab removals significantly reduced crab abundance and hatchling predation, and we estimated that one hatchling was saved for every three crabs removed. Driving large machinery on the beach at night raises concerns for protected species, thus, we implemented mitigation measures to minimize any potential impacts. These included having a trained "spotter" in the UTV, driving at low speeds, restricting headlight use, and ceasing all removals when nests neared hatching. Year-round surveys showed that crabs remained active in winter, but at reduced levels, which would make conducting removals outside of protected species nesting periods less effective. Future management should carefully assess the need for intervention while minimizing the impacts to nesting shorebirds, sea turtles and other coastal wildlife.

Locally, threats on the beach at CCSFS are evolving. The impacts of increased launch operations are largely unknown, especially as larger and more powerful rockets begin to launch. Most launch sites are adjacent to the nesting beach, with some as close as 275 m. The lighting required during testing and launching of the newly activated launch programs could deter nesting females from using this important rookery (Witherington, 1992) and disorient both nesting females and hatchlings.

While conservation attention tends to focus on egg and hatchling stages, which occur on land (Donlan et al., 2010), life history models have demonstrated that oceanic sub-adults are the most important age class for increasing population growth rates (Crouse et al., 1987, Crowder et al. 1994). However, conservation concerns have evolved since these studies were published over 30 years ago. For example, these studies do not mention or account for escalating impacts of climate change. Rising temperatures are increasingly skewing hatchling sex ratios toward females (Laloë et al. 2014, Reneker & Kamel 2016, and Tomillo and Spotila 2020), raising serious concerns about future breeding populations. Additionally, climate-change induced sea level rise has already reduced the availability of suitable sea turtle nesting grounds (Donlan et al. 2010, Bolten et al. 2011, Fuentes et al. 2020), which can further reduce successful hatchling production. Given that < 0.1% of hatchlings that reach the water survive to adulthood (Frazer 1986, Bolten et al. 2011), addressing early-stage mortality should remain a priority. While the removal of ghost crabs may marginally increase the number of hatchlings that reach the water, their extreme mortality prior to reproductive age remains. Conservation strategies should evolve to include a holistic approach to increasing sea turtle recruitment and subsequent recovery by continually address threats to mortality at various life stages.

This study spanned three years, which enabled us to account for annual variation in crab predation and abundance trends. Over the course of this study, we classified 31,308 egg fates from 301 marked nests, with 18,222 hatchlings emerged, and assessed thousands of additional hatchling tracks from unmarked nests for predation. We also counted 45,166 crab burrows and 10,102 live crabs to compare to predation rates and environmental variables. Our results provide insight into ghost crab-sea turtle interactions and informs predator management on nesting beaches; however, key questions remain. Live crab counts and burrow density should be further evaluated to determine the most useful metric of ghost crab abundance. Integrated models that incorporate environmental variables could improve these estimates. Expanding research on the interactive effects of disorientation and predation across additional sea turtle species could reveal interspecies differences in vulnerability to ghost crab predation. Additionally, assessing the long-term impacts of crab removals, including impacts to other coastal species and post-removal population dynamics, could help assess whether removals result in lasting reductions in crab abundance and predation pressure. By integrating these findings with ongoing conservation efforts, managers can develop more effective strategies to increase sea turtle recruitment.

4.1 References

Avenant, C., Whiting, S., Fossette, S., Barnes, P., & Hyndes, G. A. (2023a). Extreme predation of eggs and hatchlings for loggerhead turtles in eastern Indian Ocean. *Biodiversity and Conservation*, *33*(1), 135–159. https://doi.org/10.1007/s10531-023-02739-z

Avenant, C., Fossette, S., Whiting, S., Hopkins, A. J. M., & Hyndes, G. A. (2023b). Sea turtle eggs and hatchlings are a seasonally important food source for the generalist feeding golden ghost crab (*Ocypode convexa*). *Estuaries and Coasts*, *47*(3), 821–838. https://doi.org/10.1007/s12237-023-01309-4

Avenant, C. (2025). Insights into prey handling and feeding strategies by ghost crabs on sea turtle eggs and hatchlings. *Food Webs*, *43*, e00400. https://doi.org/10.1016/j.fooweb.2025.e00400

Barboza, C. A. M., Mattos, G., Soares-Gomes, A., Zalmon, I. R., & Costa, L. L. (2021). Low densities of the ghost crab *Ocypode quadrata* related to large scale human modification of sandy shores. *Frontiers in Marine Science*, *8*. https://doi.org/10.3389/fmars.2021.589542

Barros, F. (2001). Ghost crabs as a tool for rapid assessment of human impacts on exposed sandy beaches. *Biological Conservation*, *97*(3), 399–404. https://doi.org/10.1016/S0006-3207(00)00116-6

Barton, B. T., & Roth, J. D. (2007). Raccoon Removal on Sea Turtle Nesting Beaches. *The Journal of Wildlife Management*, *71*(4), 1234–1237. https://doi.org/10.2193/2006-014

Barton, B. T., & Roth, J. D. (2008). Implications of intraguild predation for sea turtle nest protection. *Biological Conservation*, *141*(8), 2139–2145. https://doi.org/10.1016/j.biocon.2008.06.013

Bolten, A. B., Crowder, L. B., Dodd, M. G., MacPherson, S. L., Musick, J. A., Schroeder, B. A., Witherington, B. E., Long, K. J., & Snover, M. L. (2011). Quantifying multiple threats to endangered species: An example from loggerhead sea turtles. *Frontiers in Ecology and the Environment*, *9*(5), 295–301. https://doi.org/10.1890/090126

Ceriani, S. A., & Meylan, A. B. (2017). *Caretta caretta* (North West Atlantic subpopulation). IUCN Red List of Threatened Species. https://doi.org/10.2305/iucn.uk.2015-4.rlts.t84131194a84131608.en

Ceriani, S. A., Casale, P., Brost, M., Leone, E. H., & Witherington, B. E. (2019). Conservation implications of sea turtle nesting trends: Elusive recovery of a globally important loggerhead population. *Ecosphere*, *10*(11), e02936. https://doi.org/10.1002/ecs2.2936

Ceriani, S. A., Brost, B., Meylan, A. B., Meylan, P. A., & Casale, P. (2021). Bias in sea turtle productivity estimates: Error and factors involved. *Marine Biology*, *168*(4), 41. https://doi.org/10.1007/s00227-021-03843-w

Christoffers, Edward William. (1986). *Ecology of the ghost crab Ocypode quadrata (Fabricius) on Assateague Island, Maryland and the impacts of various human uses of the beach on their distribution and abundance* [Michigan State University]. https://doi.org/10.25335/ZNQ5-6Z57

Costa, L. L., Arueira, V. F., Ocaña, F. A., Soares-Gomes, A., & Zalmon, I. R. (2022). Are ghost crabs (Ocypode spp.) smaller on human-disturbed sandy beaches? A global analysis. *Hydrobiologia*, *849*(15), 3287–3298. https://doi.org/10.1007/s10750-022-04900-1

Costa, L. L., & Zalmon, I. R. (2019). Multiple metrics of the ghost crab *Ocypode quadrata* (Fabricius, 1787) for impact assessments on sandy beaches. *Estuarine, Coastal and Shelf Science*, *218*, 237–245. https://doi.org/10.1016/j.ecss.2018.12.013

Crouse, D. T., Crowder, L. B., & Caswell, H. (1987). A Stage-Based Population Model for Loggerhead Sea Turtles and Implications for Conservation. *Ecology*, *68*(5), 1412–1423. https://doi.org/10.2307/1939225

Crowder, L. B., Crouse, D. T., Heppell, S. S., & Martin, T. H. (1994). Predicting the Impact of Turtle Excluder Devices on Loggerhead Sea Turtle Populations. *Ecological Applications*, *4*(3), 437–445. https://doi.org/10.2307/1941948

Donlan, C. J., Wingfield, D. K., Crowder, L. B., & Wilcox, C. (2010). Using expert opinion surveys to rank threats to endangered species: A case study with sea turtles. *Conservation Biology: The Journal of the Society for Conservation Biology*, *24*(6), 1586–1595. https://doi.org/10.1111/j.1523-1739.2010.01541.x

Engeman, R. M., Martin, R. E., Smith, H. T., Woolard, J., Crady, C. K., Constantin, B., Stahl, M., & Groninger, N. P. (2006). Impact on predation of sea turtle nests when predator control was removed midway through the nesting season. *Wildlife Research*, *33*(3), 187–192.

Florida Fish and Wildlife Conservation Commission (FFWCC). (2016). *FWC Marine Turtle Conservation Handbook*.

Fortaleza, M. O., Girão, M. M. L., Franklin Junior, W., Pinto De Lima, J., & De Almeida Rocha-Barreira, C. (2020). Which moon phase do we find more ghosts? Effects of the lunar cycle on the ghost crab *Ocypode quadrata* (Fabricius, 1787). *Arquivos de Ciências Do Mar*, *52*(2), 85–97. https://doi.org/10.32360/acmar.v52i2.42737

Frazer, N. B. (1986). Survival from Egg to Adulthood in a Declining Population of Loggerhead Turtles, *Caretta caretta*. *Herpetologica*, *42*(1), 47–55.

Fuentes, M. M. P. B., Allstadt, A. J., Ceriani, S. A., Godfrey, M. H., Gredzens, C., Helmers, D., Ingram, D., Pate, M., Radeloff, V. C., Shaver, D. J., Wildermann, N., Taylor, L., & Bateman, B. L. (2020). Potential adaptability of marine turtles to climate change may be hindered by coastal development in the USA. *Regional Environmental Change*, *20*(3), 104. https://doi.org/10.1007/s10113-020-01689-4

Gül, M. R., & Griffen, B. D. (2019). Burrowing behavior and burrowing energetics of a bioindicator under human disturbance. *Ecology and Evolution*, *9*(24), 14205–14216. https://doi.org/10.1002/ece3.5853

Kraemer, J. E., & Bennett, S. H. (1981). Utilization of Posthatching Yolk in Loggerhead Sea Turtles, *Caretta caretta. Copeia*, *1981*(2), 406–411. https://doi.org/10.2307/1444230

Laloë, J.-O., Cozens, J., Renom, B., Taxonera, A., & Hays, G. C. (2014). Effects of rising temperature on the viability of an important sea turtle rookery. *Nature Climate Change*, *4*(6), 513–518. https://doi.org/10.1038/nclimate2236

Lucrezi, S., & Schlacher, T. A. (2014). The Ecology of Ghost Crabs. In R. N. Hughes, Hughes, D. J., & I. P. Smith (Eds.), *Oceanography and Marine Biology* (pp. 201–256). CRC Press. https://doi.org/10.1201/b17143

Martins, S., Sierra, L., Rodrigues, E., Oñate-Casado, J., Galán, I. T., Clarke, L. J., & Marco, A. (2021). Ecological drivers of the high predation of sea turtle hatchlings during emergence. *Marine Ecology Progress Series*, *668*, 97–106. https://doi.org/10.3354/meps13751

National Marine Fisheries Service, & U.S. Fish and Wildlife Service. (2008). *Recovery Plan for the Northwest Atlantic Population of the Loggerhead Sea Turtle (Caretta caretta)*. Retrieved March 25, 2025, from https://www.fisheries.noaa.gov/resource/document/recovery-plan-northwest-atlantic-population-loggerhead-sea-turtle-caretta-caretta

Ocaña, F. A., Navarrete, A. D. J., Carrillo, R. M. D. J., & Rivera, J. J. O. (2016). Effects of human disturbance on the population dynamics of *Ocypode quadrata* (Decapoda: Ocypodidae) in beaches of the Mexican Caribbean. *Revista de Biología Tropical*, *64*(4), Article 4. https://doi.org/10.15517/rbt.v64i4.19909

Pankaew, K., & Milton, S. L. (2018). The effects of extended crawling on the physiology and swim performance of loggerhead and green sea turtle hatchlings. *The Journal of Experimental Biology*, *221*(Pt 1), jeb165225. https://doi.org/10.1242/jeb.165225

Pombo, M., & Turra, A. (2019). The burrow resetting method, an easy and effective approach to improve indirect ghost-crab population assessments. *Ecological Indicators*, *104*, 422–428. https://doi.org/10.1016/j.ecolind.2019.05.010

Pruner, R., & Addison, L. (2022). *Ghost Crab Management*. 2022 Meeting of the American Oystercatcher Working Group, St. Simons Island, GA. https://amoywg.org/wp-content/uploads/2022/12/Pruner-Addison-ghost-crab-2022.pdf

Reneker, J. L., & Kamel, S. J. (2016). Climate change increases the production of female hatchlings at a northern sea turtle rookery. *Ecology*, *97*(12), 3257–3264. https://doi.org/10.1002/ecy.1603

Rosenberg, J., & Langer, H. (2001). Ultrastructural Changes of Rhabdoms of the Eyes of Ocypode Species in Relation to Different Regimes of Light and Dark Adaptation. *Journal of Crustacean Biology*, *21*(2), 345–353. https://doi.org/10.1163/20021975-99990134

Schlacher, T. A., Lucrezi, S., Connolly, R. M., Peterson, C. H., Gilby, B. L., Maslo, B., Olds, A. D., Walker, S. J., Leon, J. X., Huijbers, C. M., Weston, M. A., Turra, A., Hyndes, G. A., Holt, R. A., & Schoeman, D. S. (2016a). Human threats to sandy beaches: A meta-analysis of ghost crabs illustrates global anthropogenic impacts. *Estuarine, Coastal and Shelf Science*, *169*, 56–73. https://doi.org/10.1016/j.ecss.2015.11.025

Schlacher, T. A., Lucrezi, S., Peterson, C. H., Connolly, R. M., Olds, A. D., Althaus, F., Hyndes, G. A., Maslo, B., Gilby, B. L., Leon, J. X., Weston, M. A., Lastra, M., Williams, A., & Schoeman, D. S. (2016b). Estimating animal populations and body sizes from burrows: Marine ecologists have their heads buried in the sand. *Journal of Sea Research*, *112*, 55–64. https://doi.org/10.1016/j.seares.2016.04.001

Silva, E., Marco, A., da Graça, J., Pérez, H., Abella, E., Patino-Martinez, J., Martins, S., & Almeida, C. (2017). Light pollution affects nesting behavior of loggerhead turtles and predation risk of nests and hatchlings. *Journal of Photochemistry and Photobiology B: Biology*, *173*, 240–249. https://doi.org/10.1016/j.jphotobiol.2017.06.006

Space Launch Delta (SLD) 45. (2022). *Integrated Natural Resources Management Plan (INRMP)*. https://www.denix.osd.mil/inrmp/denix-files/sites/98/2024/02/SLD-45-INRMP-T-EMP-2022.pdf

Tomillo, P. S., & Spotila, J. R. (2020). Temperature-Dependent Sex Determination in Sea Turtles in the Context of Climate Change: Uncovering the Adaptive Significance. *BioEssays*, *42*(11), 2000146. https://doi.org/10.1002/bies.202000146

Wellins, C. A., Rittschof, D., & Wachowiak, M. (1989). Location of volatile odor sources by ghost crab *Ocypode quadrata* (Fabricius). *Journal of Chemical Ecology*, *15*(4), 1161–1169. https://doi.org/10.1007/BF01014819

Witherington, B. E. (1992). Behavioral Responses of Nesting Sea Turtles to Artificial Lighting. *Herpetologica*, *48*(1), 31–39.

Witherington, B. E. (1997). The problem of photopollution for sea turtles and other nocturnal animals. In J. R. Clemmons & R. Buchholz (Eds.), *Behavioral approaches to conservation* (pp. 303–328). Cambridge University Press.

Witherington, B. E., Martin, R. E., & Trindell, R. N. (2014). *Understanding, Assessing and Resolving Light-Pollution Problems on Sea Turtle Nesting Beaches* (FWRI Technical Report TR-2, Version 2; p. 94). Florida Fish and Wildlife Research Institute. https://f50006a.eos-intl.net/ELIBSQL12_F50006A_Documents/TR-2Rev2.pdf