Received: 30 April 2022 | Revised: 6 July 2022 | Accepted: 28 July 2022

DOI: 10.1002/ecy.3861

THE SCIENTIFIC NATURALIST

ECOLOGY
ECOLOGICAL SOCIETY OF AMERICA

Interspecific interactions among three species of sea turtle using a common resting area

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Handling Editor: John Pastor

KEYWORDS: animal-borne video, competition, Gulf of Mexico, loggerhead, niche, sea turtle

The competitive exclusion principle states that ecologically similar species sharing a niche cannot occupy the same space at the same time (Gause, 1932). Their coexistence depends on niche differentiation in at least one resource dimension, and assemblages of similar species typically partition resources to avoid competition (Amarasekare, 2003). Environmental heterogeneity can enable species co-occurrence and allow for increased species richness (Stein et al., 2014). Multispecies communities of sea turtles are not uncommon at foraging habitats. To coexist in these habitats, sea turtles partition diet items (Wildermann et al., 2019); however, food is not the only resource necessary for survival. At foraging sites, turtles also require resting spots and protection from predators (Petit et al., 2020).

As part of a larger study on turtle behavior, we have been deploying animal-borne cameras on three sea turtle species in St. Joseph Bay since 2018. St. Joseph Bay, located along the Northwest Florida coast in the northern Gulf of Mexico, covers about 26,000 ha. Loggerhead (*Caretta caretta*), green (*Chelonia mydas*), and Kemp's ridley (*Lepidochelys kempii*) sea turtles share foraging habitats in the bay (Lamont & Iverson, 2018) and appear to partition diet items to avoid foraging competition. On 1 July 2019, we deployed a GoPro Hero4 camera on an adult female loggerhead (86.7 cm straight carapace length; hereafter subject loggerhead). We programmed a delayed start of 21 h on the video recording to allow the turtle to normalize post capture. On 2 July 2019, the camera recorded 1 h, 23 min, 19 s of footage (Lamont et al., 2020). On 4 July 2019, we retrieved the camera package after it popped off the turtle via two galvanic links.

Three times during the video the subject loggerhead encountered a structure lying on the seafloor that appeared to be a piece of metal wire fencing measuring approximately 2 × 3 m. During each encounter with the structure, sea turtles could be seen apparently resting under the fencing, including another adult loggerhead (hereafter larger loggerhead) that appeared larger than our subject loggerhead. This larger loggerhead was present at the structure during all three visits by the subject loggerhead to the structure.

During the subject loggerhead's first encounter with the structure (Figure 1a, Video S1), the larger loggerhead was resting underneath the fencing. As the subject loggerhead approached the structure, the larger loggerhead moved forward toward the approaching subject loggerhead. The subject loggerhead continued swimming around the fencing and disturbed a juvenile green turtle from underneath the structure, which rapidly swam away. The subject loggerhead then swam away from the structure.

Approximately 3.5 min later, the subject loggerhead approached the structure again, and five turtles were

FIGURE 1 (a) The subject loggerhead first approached the structure where a larger loggerhead was resting. (b) Approximately 3 min later the subject loggerhead approached the structure again, and multiple turtles of three species were resting. (c) She approached and appeared to nip at the rear flippers of a Kemp's ridley and (d) a juvenile green turtle. (e and f) Those smaller turtles moved away from the fencing. (g) She then came face to face with the same larger loggerhead. The subject loggerhead then left the structure. (h) Less than 1 min later she swam past the fencing again, where the larger loggerhead was still resting, and no other turtles were present.

observed lying under the fencing, including the larger loggerhead (identified by scale patterns on its head), three juvenile green turtles, and one juvenile Kemp's ridley (Figure 1b, Video S2). As the subject loggerhead approached the fencing, all four juvenile turtles began to shift positions. As the subject loggerhead swam over the structure, she appeared to interact with each juvenile turtle individually, primarily by biting at its rear flippers (Figure 1c,d), and each turtle responded by moving away from the subject loggerhead (Figure 1e,f). Finally, as the subject loggerhead swam along the edge of the fencing, she came face to face with the larger loggerhead (Figure 1g), rapidly turned around, and swam away from the structure. Less than 1 min later, the subject loggerhead approached the structure for a third time, and the only turtle remaining at the structure was the larger loggerhead (Figure 1h). The subject loggerhead swam along the far end of the structure (opposite to where the larger loggerhead was resting) and did not return again during the video.

Although only a single observation, the behavior we observed introduces a new hypothesis regarding niche partitioning in multispecies aggregations of sea turtles. Ecological differences among species that result in partitioning can occur through species specialization of a resource or variations in spatial use or temporal use of a resource (Amarasekare, 2003). Loggerheads, Kemp's ridleys, and green turtles can coexist temporally and spatially while foraging because each species has specialized to a different diet group. For example, loggerheads are carnivorous and frequently forage on large benthic invertebrates, whereas the green turtle is herbivorous. Although also carnivorous, Kemp's ridleys forage primarily on crabs, thereby presumably reducing foraging competition with loggerheads (Schmid & Tucker, 2018).

This video provides evidence that multiple species of sea turtles share resting resources in this bay, and we suggest that, due to a lack of specialization in each species (e.g., morphological or behavioral), competition for this resource occurred among those individuals. The subject loggerhead appeared to dominate the smaller green and Kemp's ridley turtles (e.g., biting at rear flippers), whereas the larger loggerhead dominated the subject loggerhead (Schofield et al., 2007). For example, the juvenile green turtles and Kemp's ridley observed in the video moved away from the structure when approached by the subject loggerhead, which may suggest competition for space. Although larger than the green and Kemp's ridley turtles, the aggressive behaviors exhibited by the subject loggerhead may be driven less by body size than by species or individual level of aggression (Schofield et al., 2022). The aggressive movements by the subject loggerhead (e.g., biting at rear flippers; Gaos et al., 2021; Schofield et al., 2007) toward the green and Kemp's ridley turtles seem to have triggered their departure from the structure. The larger loggerhead's aggressive behavior toward the subject loggerhead, but apparently not toward the green turtles and Kemp's ridley turtles, might reflect an intraspecific response (Dujon et al., 2018; Schofield et al., 2022). Sea turtles exhibit fidelity to structures (Petit et al., 2020), and the continued presence of the larger loggerhead at this fencing suggests it may have been defending her territory from another loggerhead (Schofield et al., 2007).

Intraspecific interactions, including aggressive encounters, among sea turtles have been reported (Schofield et al., 2007; Thomson et al., 2015), but we were unable to find any accounts of interspecific interactions. Aggression among sea turtles has occurred more frequently in structured habitat than in unstructured habitat (Thomson et al., 2015) and while resting than while swimming (Schofield et al., 2007). Structure may be a particularly valuable resource for sea turtles because it allows turtles to rest on the seafloor without expending energy (Hays et al., 2000) and provides protection from predators (Thomson et al., 2015).

Frequent disturbance of turtles from resting locations could lower fitness and negatively affect life-history characteristics of the displaced individuals, including reducing growth rates (Eccard & Ylönen, 2003). Additionally, more aggressive individuals typically win fights over foraging resources, which might also have life-history consequences for the less aggressive individuals (Schofield et al., 2022). These consequences could be serious for all three species but particularly for Kemp's ridleys, whose population is recovering from a severe population bottleneck that occurred in the mid-1980s (Lamont et al., 2021). Genetic diversity of the Kemp's ridley population has not yet recovered from the bottleneck (Lamont et al., 2021). Low genetic diversity reduces the fitness of a population and the potential of a population to respond to a changing environment (Hoelzel, 1990). Most Kemp's ridleys at our study site are juveniles (Lamont & Johnson, 2021), and a decrease in juvenile growth rates can produce lower survival of those individuals, which could result in reduced recruitment. Although juvenile Kemp's ridleys experience many threats, including extreme cold and capture in commercial fishing gear, reduced fitness as a result of competition for resting locations could further limit population recovery.

The unique opportunity provided by the turtle-borne camera generated the proposed hypothesis discussed here; however, we acknowledge that this was one observation and, as such, requires further research. Interspecific behavior among individual sea turtles may

vary by body size, habitat type, fitness level, and season (Gaos et al., 2021; Schofield et al., 2007; Thomson et al., 2015). The competitive interactions we documented may not occur or may not be as intense during the nonbreeding season (i.e., winter; Schofield et al., 2007), although aggressive behaviors among sea turtles also take place outside of the breeding season, primarily associated with turtle density or food resources (Dujon et al., 2018; Gaos et al., 2021). Fluctuations in the frequency and intensity of aggressive interactions may reduce the severity of impacts on the life-history characteristics of displaced individuals. Although opportunistic, our animal-borne camera video provided a rare opportunity to generate and assess new hypotheses regarding multispecies interactions among adult and juvenile sea turtles, including how these behaviors may impact population recovery of endangered species.

ACKNOWLEDGMENTS

We thank D. Catizone, S. Wyandt, and M. Palandri for field assistance. All work was conducted under Florida Fish and Wildlife Conservation Commission Permit MTP-118 and National Marine Fisheries Service Permit 21366. All turtle handling and sampling were performed according to the Institutional Animal Care Protocols USGS-SESC-IACUC-2011-05 and USGSWARC-IACUC-2019-15. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the US government.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Metadata (Lamont et al., 2020) for the video recordings can be found in the U.S. Geological Survey (USGS) ScienceBase-Catalog at https://doi.org/10.5066/P9N8UQ43. Capture location data are sensitive and cannot be provided publicly. Additional data inquiries can be made to the Director of the USGS Wetland and Aquatic Research Center.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Lamont, Margaret M., Joseph Alday, and Carson Alday. 2023. "Interspecific Interactions among Three Species of Sea Turtle Using a Common Resting Area." *Ecology* 104(1): e3861. https://doi.org/10.1002/ecy.3861