Tiger sharks eat songbirds: scavenging a windfall of nutrients from the sky

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Tiger sharks (Galeocerdo cuvier) are notorious for their dietary breadth. As predators, tiger sharks actively hunt prey including crustaceans, fishes, sea snakes, sea turtles, sea birds, and marine mammals (Castro 2010), but as facultative scavengers, they also supplement their diet by opportunistically scavenging items such as whale carcasses (Clua et al. 2013). Surprisingly, tiger sharks consume terrestrial birds as well. While isolated and anecdotal accounts date back to the 1960s, we know little about the pervasiveness of, and mechanism behind, this unique trophic interaction.

In 2010, while conducting a long-term shark population monitoring survey along the Mississippi/Alabama coast, we captured a small tiger shark that regurgitated feathers prior to being tagged and released. We collected the feathers for further inspection; subsequent visual identification and DNA barcoding revealed that the feathers belonged to a brown thrasher Toxostoma rufum. During monthly surveys from 2010 to 2018, we opportunistically examined stomach contents from 105 tiger sharks for the presence of whole birds and bird remains (feathers, beaks, feet) using gut content analysis from dead sharks and gastric lavage from live sharks (Figure 1).

Tiger shark/bird interactions were pervasive and occurred each year from 2010 to 2018 with the exception of 2014; none of the tiger sharks caught that year were examined for bird remains. Most of the interactions took place in the fall (September, October, and November), although some interactions took place during the spring (April and May). Of the 105 sharks examined, 41 (39%) contained bird remains. We archived all bird remains for visual identification and DNA barcoding. These techniques facilitated conclusive identification of 11 bird species in 13 interactions: 8 passerine songbirds (barn swallow Hirundo rustica, eastern kingbird Tyrannus tyrannus, house wren Troglodytes aedon, common yellowthroat Geothlypis trichas, marsh wren Cistothorus palustris, eastern meadowlark Strunella magna, swamp sparrow Melospiza georgiana, and brown thrasher); 2 near passerine land birds (white-winged dove Zenaida asiatica and yellow-bellied sapsucker Sphyrapicus varius); and 1 waterbird (American coot Fulica Americana). Counter to our expectations, no marine birds were found in tiger shark stomachs.

To explore a potential mechanism underpinning the pervasiveness of tiger shark encounters with terrestrial birds, we used data from eBird (https://ebird.org), the world's largest biodiversity-related citizen science project. We queried bird sightings data from the Mississippi/Alabama coast for our 11 species of terrestrial birds during spring and fall migration (Able 1972), the periods corresponding to the trophic interactions. Peaks in coastal bird sightings for the 11 species we identified showed remarkable alignment with individual tiger shark/bird interactions (Figure 2A), suggesting that tiger shark consumption of these terrestrial birds is tied to predictable annual migrations rather than episodic events. In the spring, areas along coastal Mississippi and Alabama are the first stopover location for migratory birds flying north; in the fall, these same areas are the final stopover for southward-migrating birds prior to crossing the Gulf of Mexico. We predicted that tiger shark/bird interactions would occur primarily during the spring, when fatigued northward-migrating birds struggle to reach the Mississippi/Alabama coast following their long journey across the Gulf of Mexico. Surprisingly, 11 of the 13 interactions we documented took place in the fall, during the initial portion of the birds' southward migration. In coastal Alabama, departure decisions for southward-migrating birds are influenced by a combination of factors including energetic condition, weather, and date. Specifically, once migratory birds accumulate ample fat reserves, they strategically time their fall departure to coincide with favorable (i.e. southward) winds following cold fronts, which are more prevalent in late fall (after September 24th) (Deppe et al. 2015). However, following departure, unforeseen weather events can result in mass mortality (thousands of birds per event; Newton 2007). These inclement weather events force migratory birds to the surface of the water, where (unlike waterbirds) they are unable to rest and resume flight. We suggest that these weather events, while lethal for the birds, provide unique scavenging opportunities for tiger sharks.

Tiger sharks are capable of aligning their movements and/or altering their foraging strategy to coincide with seasonal peaks in resource availability. For example, individual tiger sharks travel thousands of kilometers to remote Hawaiian atolls specifically to prey on seasonally abundant fledgling albatross (*Phoebastria* spp.) during summer months (Meyer et al. 2010). Additionally, off the coast of Australia, tiger sharks rely on scavenging abundant green turtle (*Chelonia mydas*) carcasses as their principle feeding strategy during the nesting season (Hammerschlag et al. 2016). The events we observed differ from those in Hawaii and Australia in two primary ways. While the above-mentioned seasonal peaks in albatross and green turtle are spatially concentrated, weather-impacted migratory birds are a spatially diffuse resource. Despite this, the frequency of tiger shark/bird interactions reflects the sheer magnitude of seasonal bird migrations across the Gulf of Mexico (in excess of 2 billion birds per season; Horton et al. 2019). In addition, this seasonal pulse of nutrients benefits a particular portion of the tiger shark population. Our findings demonstrate that the timing of the fall migration for many North American birds coincides with annual peaks in the relative abundance of neonate (i.e. newborn) tiger sharks in the north-central Gulf of Mexico (Figure 2B). Of the 41 accounts of birds in tiger shark stomachs, nearly half (46%) involved consumption by neonates. At birth, neonate tiger sharks are a fraction (< 20%) of their mature size (Branstetter 1990), and they likely have very low predatory efficiency (Driggers et al. 2008). For these neonates, scavenging on easily accessible and seasonally predictable pulses of terrestrial birds may be a way to optimize foraging success before adult hunting strategies are learned. Spanish imperial eagles Aquila adalberti also use scavenging as an efficient means of acquiring food during the first year of life (Margalida et al. 2017).

Marine and terrestrial food webs are complex and coupled systems (Polis and Strong 1996), often subsidized by internal (autochthonous origin) or external (allochthonous origin) resources (Nowlin et al 2008). For example, seabirds indirectly (through guano) and directly (through carrion) transfer energy between marine and terrestrial systems, inciting numerical responses across a range of species from arthropods (Polis and Hurd 1996) to carnivorous mammals (Rose and Polis 1998). Similarly, our findings suggest a predictable transfer of avian-derived nutrients, yet the direction of energy exchange is reversed (i.e. terrestrial to marine). Because these birds are disproportionately consumed by neonates, the nutrients they contain may influence the dynamics of tiger shark populations. Unlike many shark species, tiger sharks do not use discrete areas as nurseries; rather, female tiger sharks may select areas of high localized primary productivity for parturition of their young (Driggers et al. 2008). For these facultative scavengers, a windfall of nutrients from the sky may explain the elevated occurrence of neonate tiger sharks in the northern Gulf of Mexico.

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Figure Legends:

Figure 1: Acquiring stomach contents from a live tiger shark (gastric lavage), and examples of avian remains recovered during this study. (Tiger shark gastric lavage photo by David Hay Jones).

Figure 2: A) Species-specific relative abundance (number of eBird sightings) from the coasts of Mississippi and Alabama for the 11 species of birds conclusively identified in tiger shark stomachs. Distributions in orange are during the spring migration (March, April and May) and distributions in purple are from the fall migration (August, September, October, November). Vertical lines in each plot mark the date the tiger sharks from the tiger shark/bird interaction were captured. Note that house wrens were consumed by tiger sharks in two separate years and thus shown with respect to two different bird distributions. Similarly, two yellow-bellied sapsuckers were consumed, but during the same year. **B)** Monthly relative abundance for tiger sharks (tiger sharks/100 hooks/hour) from a shark population monitoring survey (2010-2018) along the Mississippi/Alabama coast. Error bars represent standard error of the mean.

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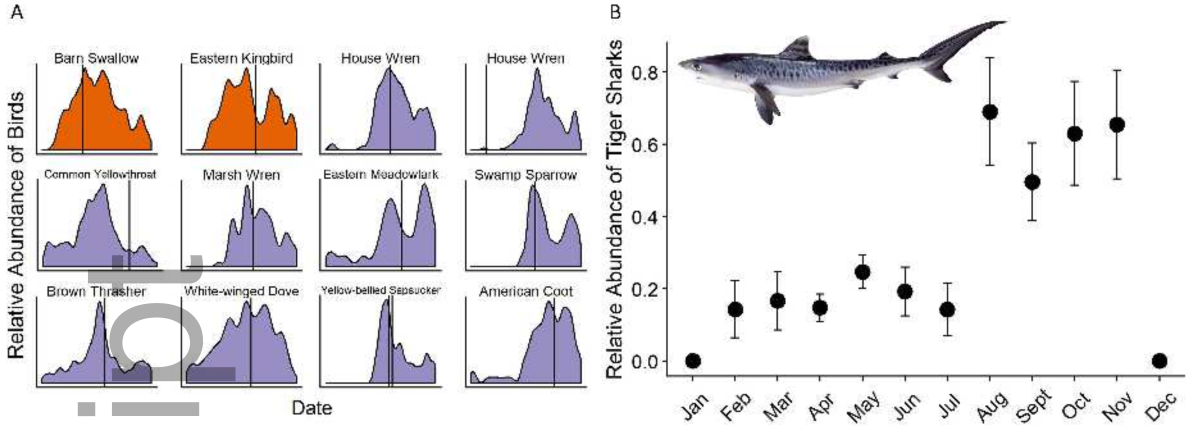

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