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Interactions Among Hawaiian Hawksbills Suggest Prevalence of Social Behaviors in Marine Turtles

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Abstract. – Social behaviors represent a central tenet of ecology and evolutionary biology, but remain widely undocumented in reptiles. Although marine turtles have been studied for decades, the prevalence, importance, and potential role of social behaviors have been largely overlooked. Consequently, marine turtles have predominantly been characterized as nonsocial animals in the literature. Here we report on visual observations of hawksbill turtles (*Eretmochelys imbricata*) inhabiting a nearshore coral reef in Hawai'i that reveal a complex array of social behaviors. Combined with recent evidence for social behaviors in other marine turtle species, our results confirm that traditional views of nonsocial life histories are incomplete and that social behaviors are likely prevalent in many marine turtle species. Our findings have important implications for marine turtle management and suggest increased research into social behaviors is warranted across the taxon.

Key Words. – animal behavior; reptiles; Cheloniidae; central north Pacific; communication; cooperation

The social behaviors of terrestrial and marine vertebrates have been studied for decades and can include tactile (e.g., caressing, hitting, biting, playing), visual (e.g., aggressive/submissive postures, courtship displays), auditory (e.g., warning cries, song communications), and chemosensory (e.g., territorial, attractant, and alarm pheromones) exchanges (Doody et al. 2013; Rubenstein and Rubenstein 2013). These behaviors support an amalgam of diverse functions, including communication, sexual selection, resource acquisition, risk avoidance, and habitat competition (Sachs et al. 2004; West et al. 2006; Noren 2008; Riesch and Deecke 2011; Breed and Moore 2012; Pitman et al. 2016; Campagna 2018). Information on social behaviors can also inform wildlife management decision making (Anthony and Blumstein 2000; Berger-Tal et al. 2016), which is particularly relevant for rare or threatened species. For instance, social animals often assemble in groups, thereby increasing their vulnerability to acute threats (Sadovy and Domeier 2005; Breed and Moore 2012).

Marine turtles represent a taxon of global conservation concern (Wallace et al. 2011; Mazaris et al. 2017). Despite the potential of social behavioral research to support marine turtle management and conservation, detailed records of social interactions in marine turtles remain extremely limited and primarily consist of behaviors associated with courtship and mating (Carr and Ogren 1960; Booth and Peters 1972; Comuzzie and Owens 1990; Miller 1997; Bevan et al. 2016; Merino-Zavala et al. 2018; Ye et al. 2020). Nonetheless, a handful of recent studies have described nonreproductive social behaviors in green turtles (*Chelonia mydas*) (Thomson et al. 2015) and loggerhead turtles (*Caretta caretta*) (Schofield et al. 2006, 2007; Smolowitz et al. 2015). Despite these studies, literature on marine turtle life history has largely overlooked the potential prevalence and significance of social behaviors in the taxon (Lutz and Musick 1996; Lutz et al. 2003; Wyneken et al. 2013). Correspondingly, the lack of documentation of social behaviors has led to general descriptions of marine turtles (and other reptiles) as primarily being "nonsocial" animals (Constantino and Salmon 2001; Wilkinson and Huber 2012; Doody et al. 2013).

Hawksbill turtles (*Eretmochelys imbricata*) are an endangered marine turtle species that is particularly rare in Hawai'i (Van Houtan et al. 2016; Gaos et al. 2020). Although a number of studies have described hawksbill movement, foraging, and nesting behaviors (e.g., Meylan 1988; George 1997; Miller 1997; Gaos et al. 2012a), research to evaluate nonreproductive social behaviors has never been undertaken. Here we document and describe

Table 1. Social behavior categories used to classify hawskbill turtle interactions in Maui, Hawai'i. With the exception of some phases of the Pursuit category, all social interactions consisted of turtles in close proximity (< 1 m).

Behavior	Description
Head Touch[a]	Touching, rubbing, or striking heads together; includes gyrating beak swipes and gular pumping
Contact	Any physical contact between 2 or more turtles aside from Head Touch or Bite
Bite[a]	A turtle biting any part of another turtle
Pursuit	Purposeful pursuit by one turtle of another turtle
Contest[b]	Aggressive interaction, could involve Head Touch, Bite, or Pursuit
Inspect[a]	Nonaggressive interaction without physical contact

[a] Adapted from Thomson et al. 2015.
[b] Adapted from Schofield et al. 2006.

several nonreproductive social behaviors in juvenile and adult female hawksbill turtles inhabiting a nearshore coral reef in Hawai'i. To our knowledge, this is the first study to provide evidence of nonreproductive social behaviors in hawksbill turtles.

METHODS

Hawksbill Observations and Filming. — Between September 2016 and April 2020, hawksbill turtles were opportunistically observed and filmed by a local naturalist while snorkeling at a nearshore reef of approximately 30,000 m^2 in western Maui, Hawai'i. Hawksbills were captured, tagged, and measured prior to the start of the study. We determined the life stage and sex (when possible) of turtles using a combination of carapace and tail lengths (Kobayashi et al. 2010), or via previous documentation of female turtles nesting on nearby beaches. When 2 or more turtles were observed interacting, a camera (Sony Action Cam 4K, Olympus OMD-5, or Olympus OMD-5 MKII) with underwater housing was held by the observer or placed on the ocean floor facing the turtles. The observer maintained a physical distance of > 3 m or quickly placed the camera on the substrate before moving away in order to minimize any disturbances or potential effects on behaviors.

Video Processing and Analysis. — Videos were visually inspected and social behavior (i.e., any physical interaction between individuals) data were logged (Table 1; Fig. 1; Supplemental Videos S1–S6), as well as the frequency of each social behavior (i.e., the number of times turtles engaged in a particular behavior). In cases where turtles mutually engaged in a behavior or where multiple behaviors were exhibited simultaneously (e.g., a turtle would exhibit the Head Touch behavior with another turtle, then one turtle would Bite), these behaviors were recorded independently. All data were tabulated, analyzed, and graphed using a combination of Microsoft Excel (v.14.16.2) and the package ggplot2 (Wickham 2016) in the R programming language (R Core Team 2018).

RESULTS

We analyzed 10 videos involving 2 or more turtles, totaling 54.5 min of footage, of which 34.4 min represented time during which turtles engaged in social behaviors. We recorded a total of 149 instances of social behaviors across 4 turtles, which consisted of 3 adult females and 1 juvenile of unknown sex (Females 1–3 and Juvenile, respectively). All 4 turtles were observed repeatedly over the 3.5-yr study period and Females 1–3 were previously (2015) equipped with satellite tags that transmitted for 3–11 mo, during which they remained in the vicinity of the reef (Pacific Islands Fisheries Science Center, unpubl. data, 2021), indicating all are resident turtles.

Head Touch (n = 66, 44.3% of observations) was the most common behavior observed, while Bite (n = 6, 4.0% of observations) was the least common (Fig. 2). The average duration of each instance of Head Touch was 5.7 ± 7.5 sec (range, 1–33 sec), Contact was 5.4 ± 6.1 sec (range, 1–21 sec), Bite was 1.0 ± 0.0 sec, Pursuit was 40.9 ± 21.3 sec (range, 13–73 sec), Contest was 22.8 ± 35.7 sec (range, 9–115 sec), and Inspect was 25.4 ± 45.4 sec (range, 9–159 sec).

Two of the turtles (Juvenile and Female 1) exhibited all 6 behaviors, 1 (Female 2) exhibited 5 behaviors, and 1 (Female 3) exhibited 4 behaviors (Fig. 2). Interactions occurred while turtles were resting, foraging, or in transit, and were most frequently initiated by the Juvenile (n = 65), followed by Female 1 (n = 40), Female 3 (n = 32), and Female 2 (n = 12). A total of 141 interactions involved 2 turtles and 8 interactions involved 3 turtles (Supplemental Video S7). We recorded no interactions involving more than 3 turtles. The shortest social encounter lasted 1 sec and consisted of a single behavior (e.g., Bite, Head Touch), while the longest encounter lasted a total of 2.7 min and consisted of multiple behaviors.

DISCUSSION

Although marine turtles have been studied for decades, the prevalence, importance, and potential role of social behaviors have been largely overlooked within the taxon. Our research demonstrates that Hawaiian hawksbills engage in a complex array of social behaviors, with all 4 turtles engaging in multiple interactions (Fig. 2). Turtles consisted of 3 adult females and 1 juvenile residing at a foraging ground, revealing that social behaviors extend beyond courtship and mating. Our findings coincide with recent research on green and loggerhead turtles in other ocean regions (Schofield et al. 2006, 2007; Smolowitz et al. 2015; Thomson et al. 2015), suggesting that nonreproductive social behaviors may be prevalent across multiple marine turtle species and populations. The findings also indicate that traditional views of marine turtles as nonsocial animals are incomplete.

The limited number of studies on social behaviors in marine turtles is primarily due to the inherent difficulties of conducting such research, as most marine turtles are

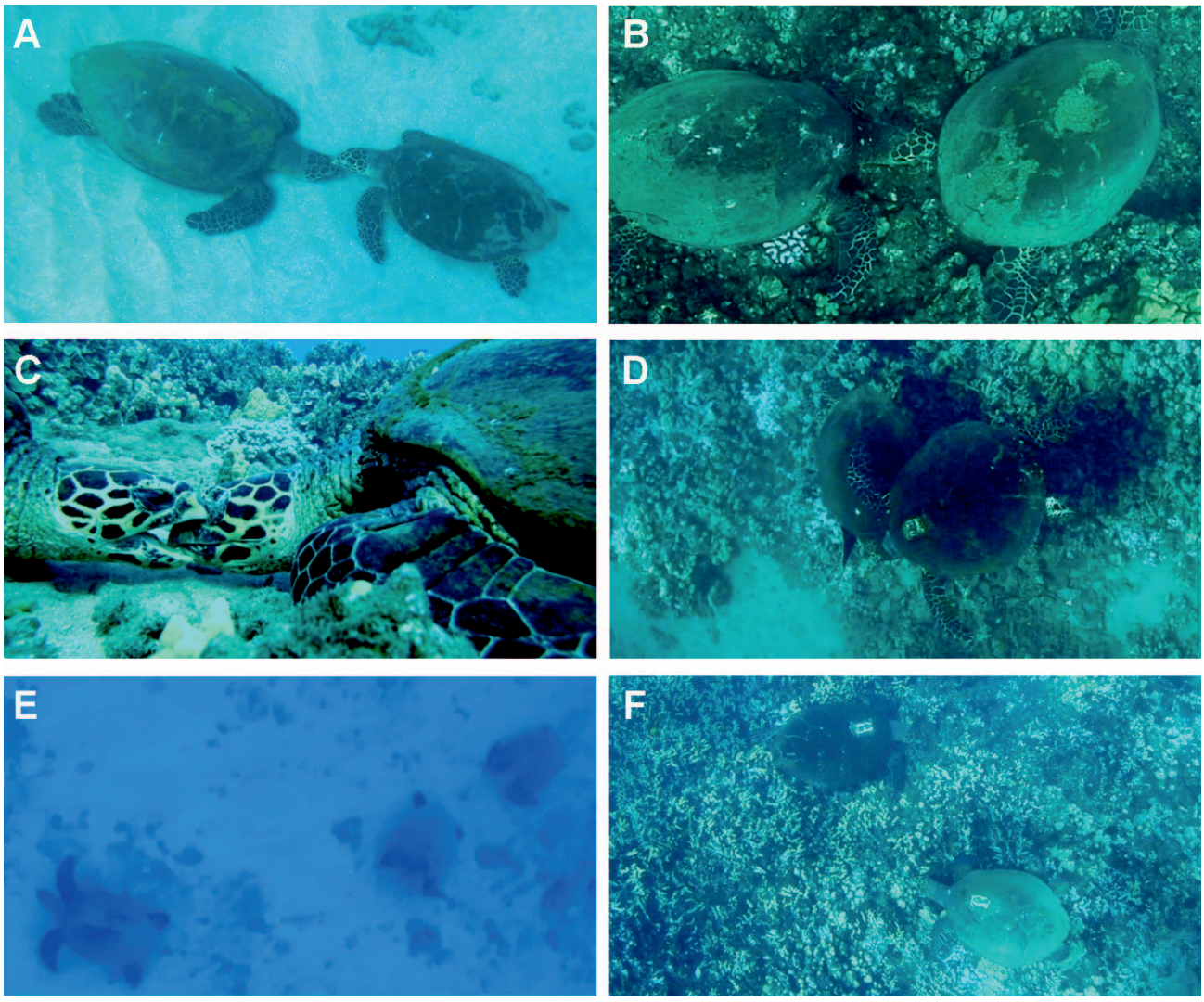

Figure 1. Images of social behaviors exhibited by hawksbills, including (A) Head Touch (Supplemental Video S1), (B) Contact (Supplemental Video S2), (C) Bite (Supplemental Video S3), (D) Contest (Supplemental Video S4), (E) Pursuit (Supplemental Video S5), (F) Inspect (Supplemental Video S6). Photos by Don McLeish.

elusive and avoid humans (Ye et al. 2020). Marine turtles in Hawai'i are generally habituated to human presence (Kelly and Homcy 2017), which provides valuable opportunities for firsthand observations and filming. The videos evaluated in this study, without which the behavioral observations we report would have likely remained undetected, were filmed by a local naturalist. Given the limited resources available to many researchers (McNeely et al. 1990), our findings demonstrate the utility of community-based science (i.e., citizen science) approaches, which can increase the likelihood of detecting ecological patterns that could otherwise be overlooked (Tulloch et al. 2013). Although animal-borne cameras, remotely operated (underwater) vehicles, and uncrewed aerial systems can be used to film marine turtle behaviors (Heithaus et al. 2002; Thomson et al. 2015; Bevan et al. 2016), these techniques require some level of expertise to operate and are often prohibitively expensive.

Both green and hawksbill turtles primarily settle in neritic habitats and typically exhibit high foraging site fidelity (e.g., Seminoff et al. 2002; Makowski et al. 2006; Senko et al. 2010; Gaos et al. 2012b; Wood et al. 2017), as do some loggerhead turtle populations (Peckham et al. 2011), and thus represent relatively accessible subjects for behavioral research. Studying social behaviors of marine turtle species and populations that exhibit more vagile life histories or that primarily forage in open-ocean habitats, such as leatherback turtles (*Dermochelys coriacea*) (Shillinger et al. 2008; Benson et al. 2011), would be considerably more challenging.

Although the overall frequency of social behaviors remains unclear, such interactions could have important management implications. If social behaviors concentrate turtles in time and space, it could increase their vulnerability to anthropogenic threats, such as directed take, fisheries bycatch, or vessel strikes (Donlan et al. 2010). Various reports of turtles observed congregating in groups of multiple individuals support this assertion (Roos et al. 2005; Bresette et al. 2010) and could present

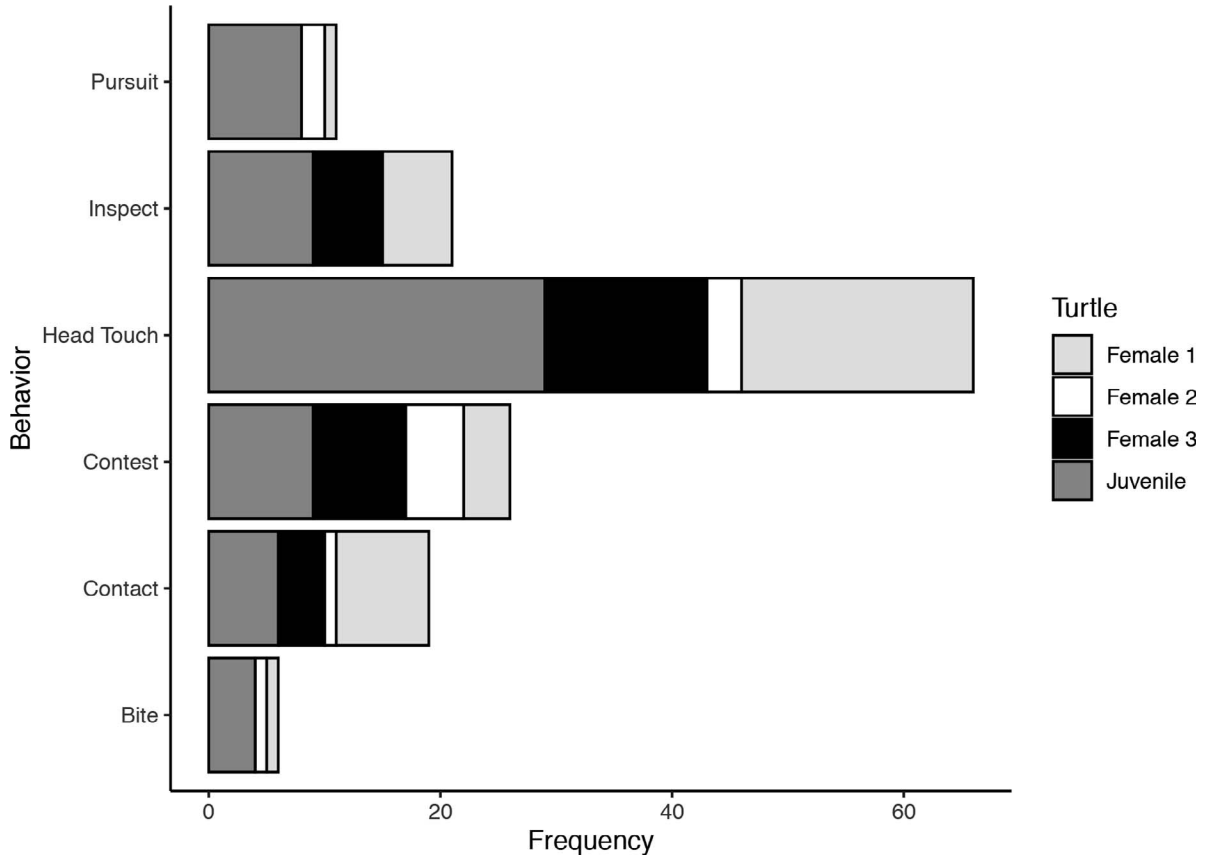

Figure 2. The frequency each of the 4 hawksbill turtles exhibited the social behaviors recorded during this study.

particular threats to hawksbills, which face the added threat of being hunted for their unique shells (i.e., tortoiseshell) (Mortimer and Donnelly 2008; Miller et al. 2019; Nahill et al. 2020).

Aggressive social behaviors are often related to resource competition (Breed and Moore 2012) and the hawksbills observed in this study often engaged in Contest behavior (Table 1) near resting holes, suggesting these activities could be related to habitat competition or territoriality. Nonetheless, although some interactions appeared aggressive, others seemed innocuous. The Head Touch category (Fig. 2B; Video S1) included instances where turtles would rub the sides of their faces together or exhibit gyrating beak swipes. On multiple occasions, these interactions involved gular pumping, where turtles would use their throats to pump water in and out of their mouths and noses (Walker 1959; Owerkowicz et al. 1999). Gular pumping generates a steady flow of water past the chemosensory organs and could essentially allow turtles to smell the water (Houghton et al. 2008) or in this case, each other.

Clearly, the intention, purpose, and significance of nonreproductive social behaviors in marine turtles remain unclear, but represent a relatively unexplored and fascinating line of research that would improve our understanding of marine turtle ecology. In turn, such research could support improved management decision making. Although this and previous studies (i.e., Schofield et al. 2006, 2007; Smolowitz et al. 2015; Thomson et al. 2015) on social behaviors have not evaluated the proportion of time turtles engage in social vs. nonsocial behaviors, doing so in the future is necessary to better understand the overall pervasiveness of these behaviors.

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Supplemental Material

All supplemental videos associated with this article can be found online as follows. Video S1: Video of the Head Touch behavior, which includes touching, rubbing

or striking heads together, as well as gyrating beak swipes and gular pumping; https://doi.org/10.2744/CCB-1481.1.s1. Video S2: Contact behavior, which includes any physical contact between two or more turtles that did not involve Head Touch or Bite; https://doi.org/10.2744/CCB-1481.1.s2. Video S3: Bite behavior, which includes a turtle biting any part of another turtle; https://doi.org/10.2744/CCB-1481.1.s3. Video S4: Pursuit behavior, which includes the purposeful following by one turtle of another turtle; https://doi.org/10.2744/CCB-1481.1.s4. Video S5: Contest behavior, which includes an aggressive interaction, not including Head Touch, Bite, or Pursuit; https://doi.org/10.2744/CCB-1481.1.s5. Video S6: Inspect behavior, which includes a nonaggressive interaction without physical contact; https://doi.org/10.2744/CCB-1481.1.s6. Video S7: Three hawksbill engaging in social behaviors; https://doi.org/10.2744/CCB-1481.1.s7. All videos courtesy of Don McLeish.

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