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ORIGINAL ARTICLE

Behavioral evidence suggests facultative scavenging by a marine apex predator during a food pulse

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Abstract

The ability of predators to switch between hunting and scavenging (facultative scavenging) carries both short-term survival and long-term fitness advantages. However, the mechanistic basis for facultative scavenging remains poorly understood. The co-occurrence of tiger sharks (*Galeocerdo cuvier*) and green turtles (*Chelonia mydas*) at Raine Island (Australia), provides an opportunity to examine a top marine predator's feeding mode in response to seasonal pulses in nesting turtles that offer both hunting and scavenging opportunities. Using satellite telemetry, we evaluated home range overlap between sharks and turtles and quantified their surfacing behavior around Raine Island during the turtle nesting season. We found core home range overlap to be highest during the nesting season. Both sharks and turtles spent significantly more time at the surface in areas of greatest range overlap closest to shore, where turtle density was highest. Both sharks and turtles showed decreased surfacing with increasing distance from Raine Island. Combined with published data on turtle demography at Raine Island, we propose the following: (1) sharks patrol the surface to increase scavenging opportunities on turtle carcasses and intercept weakened individuals after nesting; (2) healthy turtles may not perceive sharks as a major threat and/or other biological factors override anti-predatory responses; and (3) sharks during the nesting season may primarily scavenge on dead turtles individuals rather than actively hunt. Our study results and approach may be applicable to other situations in which direct observations of predator-prey interactions are limited.

Significance Statement

Every animal encounters dead or dying resources, yet the role of facultative scavenging has been difficult to study, and thus largely overlooked in marine behavioral ecological research. Movement analyses of tiger shark and green turtle movement and surfacing behavior at Raine Island (Australia) suggest that facultative scavenging may be a prevalent, yet underappreciated, feeding strategy in tiger sharks. Our integration of behavioral ecology theory with multi-species electronic tagging provided a valuable approach for investigating predator-prey interactions in situations where direct observations are limited or not possible.

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Introduction

Ephemeral increases in the abundance of prey due to migrations, aggregations, and mass mortality events occur in virtually all ecosystems and can have important regulating effects on food-web dynamics by driving functional responses of predators (Ostfeld and Keesing 2000). Many mobile carnivores will synchronize their movements to coincide with ephemeral pulses of food that are spatially and/or temporally predictable (Madsen and Shine 1996; Sims et al. 2006; Newton 2008). The dynamics of these pulses may also cause predators to switch foraging from active hunting to opportunistic scavenging (also known as facultative scavenging) (McShea 2000; DeVault et al. 2003). For example, in African savannah ecosystems, mammalian carnivores such as lions (*Panthera leo*) and hyenas (*Crocuta crocuta*) switch between hunting and scavenging based on seasonality in carrion supply and prey vulnerability to predation (Pereira et al. 2014). When scavenging opportunities are rare, these carnivores may target ungulate newborns, gravid females, or switch to kleptoparasitism or exploit non-animal food sources (Pereira et al. 2014).

Facultative scavenging is an important strategy for many carnivores (Paquet 1992) and this foraging mode can contribute to the behavioral plasticity of individuals and the adaptive capacity of species. While scavenging interactions can have strong impacts on food webs (McShea 2000; DeVault et al. 2003), the importance of this ubiquitous aspect of predator ecology is relatively underestimated and much more widespread than traditional theory implies (Wilson and Wolkovich 2011; Pereira et al. 2014). Further, the basis for switching between foraging modes in free-ranging animals remains considerably less understood. This is especially the case in marine systems, where even less is known about the role of facultative scavenging in shaping the behavioral ecology of apex predators. This is likely due to the inherent logistic and technological constraints of working in the ocean with mobile carnivores, coupled with the seemingly stochastic nature of scavenging events.

Some instances of behavioral switching have been documented in temperate marine systems. For example, in False Bay South Africa, white sharks (*Carcharodon carcharias*) aggregate seasonally at seal rookeries to actively hunt juvenile seals (Martin et al. 2005; Hammerschlag et al. 2006) but also act as facultative scavengers by switching to feed on whale carcasses when opportunities arise (Fallows et al. 2013). The analysis of field observations suggests that scavenging on whales may represent an underestimated and significant component of the foraging ecology of white sharks in the region

(Fallows et al. 2013). In temperate and tropical waters, tiger sharks (*Galeocerdo cuvier*) are wide-ranging apex predators that undertake seasonal movements to actively hunt pulses of vulnerable terrestrial and marine prey (e.g., fledgling albatross, *Phoebastria* spp., Meyer et al. 2010). They have also been documented scavenging on whale carcasses e.g., (Dudley et al. 2000; Clua et al. 2013) and seabirds (e.g., Gallagher et al. 2011).

Tiger sharks are recognized as habitat and dietary generalists but commonly feed on sea turtles (Heithaus 2001; Simpfendorfer et al. 2001). They also possess behavioral (subsurface stalking) and anatomical specializations (e.g., morphology of teeth, eyes, and head) that allow them to predate on sea turtles (Witzell 1987; Bonazzo and Collin 2000; Hart et al. 2006; Gallagher et al. 2015; Fu et al. 2016). When engaged in active hunting of sea turtles in open water, tiger sharks rely on stalking and ambush to successfully attack these prey because once detected, turtles are capable of using tight turning angles and positioning their carapace to outmaneuver sharks and deflect attacks (Heithaus et al. 2002). When at the surface, turtles are most vulnerable to tiger shark attack since their ability to detect the dark dorsum of a countershaded tiger shark hunting from below through deep water is limited. Moreover, at the water surface, turtles are silhouetted against the sky, have limited options of escape and little time to respond from a shark attacking from below (Heithaus and Frid 2003). Hays et al. (2001) suggested that migrating turtles may undertake deep dives to prevent being silhouetted at the surface to reduce predation risk from sharks. Consequently, when home ranges of tiger sharks and turtles overlap, sharks can increase stealth and ambush by increasing subsurface movements, whereas, turtles can reduce their vulnerability to shark attack by limiting exposure at the surface (Heithaus and Frid 2003; Hammerschlag et al. 2015) and selection of microhabitats (Heithaus et al. 2007). Adult female turtles may be particularly vulnerable to tiger sharks during periods of nesting where turtle movements are spatially and temporally predictable (e.g., Hammerschlag et al. 2015). Female sea turtles typically arrive at common locations to seasonally breed, such as nesting beaches, where they exit the water to dig nests and deposit eggs in sand above the high tide mark. The pairing of migration and nesting out of water is energetically costly to turtles. In some localities the process can take up to several hours and after long periods ashore, some turtles die or enter the water in a compromised state due to heat and energy exhaustion where they may become vulnerable to predation.

Raine Island, a coral cay in the northern Great Barrier Reef, supports the largest nesting concentration of green turtles (*Chelonia mydas*) in the world (Limpus et al. 2003). The Island is small (~1.8 km circumference, 32 ha) and has some steep drop-offs (Bell et al. 2009). The co-occurrence of tiger sharks and green turtles here provides an opportunity to examine the behavior of tiger sharks in response to seasonal

pulses in their prey that offer sharks both hunting and scavenging opportunities. An earlier satellite tracking study investigated the spatial movement of tiger sharks and green turtles relative to one another at Raine Island. Results revealed that the sharks do not follow turtles to and from seasonal foraging and nesting sites in the region, but instead generally concentrated their activity in the waters near Raine Island year-round, with periods of residency varying in duration among individuals (Fitzpatrick et al. 2012). Limpus et al. (2003) noted tiger sharks scavenging on the carcasses of green turtles that die onshore and then get washed into the water during high tide. These carcasses float at the surface and scavenging can last for up to an hour dependent on the number and size of scavenging sharks (direct observation). In contrast, there are few observations of tiger sharks attacking live adult green turtles a result which may be due to observer bias given the difficulty in detecting predation events in the marine environment (Limpus et al. 2003). Thus, it remains unknown whether sharks at Raine Island primarily scavenge or predate on turtles during the nesting season.

Predation risk of green turtles to tiger sharks is likely influenced by the distribution and diving decisions of both species (Heithaus et al. 2008). Consequently, here we used satellite tagging data from tiger sharks and green turtles at Raine Island during the turtle nesting season to evaluate spatial patterns in their surfacing behaviors. Using these data, we evaluated the following possible hypotheses generated from ecological theory and established predator-prey interactions between these species: (i) if tiger sharks are primarily hunting healthy green turtles at Raine Island during the nesting season, sharks should spend less time at the surface in areas of high overlap with turtles to enable ambush attacks; whereas, turtles should minimize time at the surface to lower their exposure and predation risk. However, (ii) if sharks are primarily scavenging on dead or weakened turtles during the nesting season, they should spend more time at the surface in areas of high overlap close to the Island to increase encounter rates with turtle carcasses and/or identify and consume weak turtles before they are dispersed by waves and currents. Moreover, (iii) if the threat of subsurface shark attack is perceived to be negligible by turtles and/or turtles are not responsive to predation risk, they may increase time at the surface near the Island for possible thermoregulation, resting, regular breathing, or visual selection of optimal nesting sites on the beach (Limpus et al. 2003).

Understanding the predator-prey relationship between tiger sharks and green turtles is particularly important given such dynamics between these species can indirectly impact ecosystems through trophic cascades (Heithaus et al. 2008; Burkholder et al. 2013), and both tiger sharks and green turtles are also vulnerable to human threats such as overfishing, climate change, and habitat degradation (Jackson et al. 2001; Lotze and Worm 2009). We also discuss our results as they relate to the behavioral ecology of a generalist top predator and the applicability of our research to other systems where predator-prey interactions are difficult to directly observe.

Methods

Study site

Raine Island (11° 35′ S, 144° 02′ E) is situated about ~80 km off northern Australia within the Great Barrier Reef Marine Park. The nesting season for green turtles occurs during the austral summer, peaking from November through April, when as many as 12,000 turtles may nest on just 32 ha of beach (Limpus et al. 2003; Fig. 1). The reef edge adjacent to the Island is abrupt, dropping to over 300 m depths only ~200 m from shore (Bell et al. 2009). Turtles may be most vulnerable to tiger shark attack when entering and exiting the water from nesting. After long periods of nesting, green turtles can become weakened or may die ashore, while others enter the waters in a compromised state due to heat stress and energy exhaustion (Limpus et al. 2003). Mortality also occurs on the Island when turtles accidentally invert after falling off uneven ground or off other turtles (Limpus et al. 2003). There is a positive relationship between turtle mortality and nesting turtle density, with as many as 80 individual mortality events per night at high levels (>10,000 turtles) of nesting density (Limpus et al. 2003). In some years, the cumulative mortality of nesting adult female turtles can be greater than 2000 individuals. These dead and weakened turtles are often washed into the sea by high tides and wave action; where carcasses float until consumed by sharks (direct observation).

Satellite tagging

Tiger sharks and green turtle data used in this study, except for an additional three individuals here (Table 1), were published in Fitzpatrick et al. (2012). While the former study evaluated movement patterns between these two species, data were analyzed differently here to evaluate core home range overlap and surfacing behavior of sharks and turtles. It was not possible to record data blind because our study involved focal animals in the field. Details on animal handling and tagging methodology can be found in Fitzpatrick et al. (2012). Briefly, tiger sharks were attracted to the research vessel using tuna fish bait on a line. Once the shark contacted the bait, the boat was positioned near the shark at which point a custom-designed tail clamp was attached to the caudal peduncle of the shark using a 4-m pole. The clamp was attached to a 5-m rope and large surface buoy

Fig. 1 **a** Aerial photograph of Raine Island and surrounding water showing thousands of turtles at the water surface. **b** Turtles in the water column on the reef edge at Raine Island. **c** Turtles hauled out on Raine Island. **d** A tiger shark (*foreground*) patrols the surface waters around the perimeter of Raine Island during green turtle nesting season (*background*, a large number of tracks of green turtles ascending and descending the beach can be seen on the sand). **e** and **f** Tiger sharks scavenging on a green turtle carcass at Raine Island. All images by Richard Fitzpatrick except (**a**) by Gary Bell/OceanwideImages.com
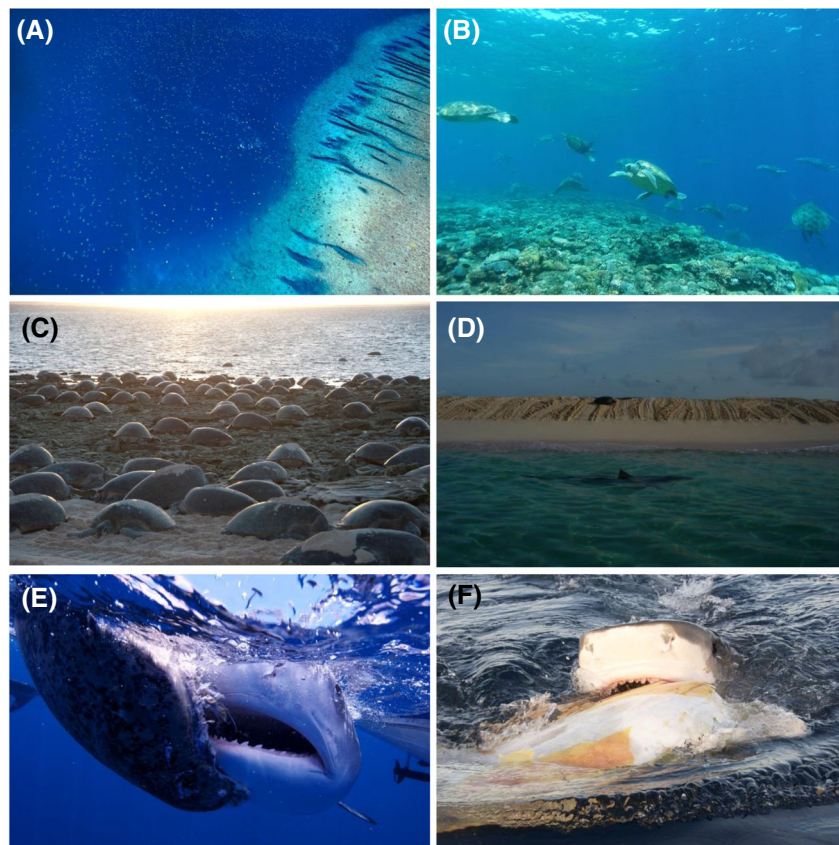
such that the movement of the shark was restricted due to the drag of the buoy. The shark was subsequently restrained using a harness at the stern of a larger vessel. Satellite tags were attached to the leading top edge of the shark's dorsal fin using two 5-mm diameter nylon rods through drilled holes secured with washers and nuts or plastic plates and nuts (Fitzpatrick et al. 2012). For green turtles, satellite tags were attached to the animals after they had successfully nested, either just following oviposition or as the turtle was returning to the sea. The tags were attached to each turtle carapace using a fast drying epoxy resin (International Epiglass HT9000 Fast laminating resin) (Fitzpatrick et al. 2012).

Satellite tags (SPOT5 and SPLASH tags, Wildlife Computers) were deployed on 11 tiger sharks at Raine Island during the turtle nesting season of 2002 to 2007, of which nine sharks generated more than 12 days of position data and were used in this study (Table 1). While all of these tags provided position estimates, SPLASH tags provided data on both position and swimming depth (see review Hammerschlag et al. 2011). Fin mounted SPLASH and SPOT tags were of similar size, mass and shape. Tagged sharks ranged in size from 288 to 368 cm total length (mean ± SD = 318.4 ± 30.7 cm). Ten green turtles ranging from 100 to 117 cm curved carapace length (mean ± SD = 108 ± 5.4 cm; 2007/8) were tagged at Raine Island during the nesting season with SPOT5 satellite tags that were used in this study (Table 1).

Movement data

Shark and turtle positions were determined from Doppler-shift calculations made by the Argos Data Collection and Location Service (Argos CLS, www.argos-system.org). Spatial accuracy for the positions used in this study ranged from 250 m to 3 km radius of error (Bernard and Belbeoch 2010), which is sufficient for describing the spatial home range patterns evaluated here. However, Argos location data were filtered by retaining the highest quality location per day for home range determination (following Witt et al. 2010) and mapped in ArcGIS 10.2 (ESRI, California).

Home ranges of turtles and sharks were quantified separately using Kernel Density Estimates (KDEs) applied to Argos-derived locations (WGS84 coordinate system) projected to Albers Equal Area coordinate system (meters) (KDE; quartic kernel; 25 km smoothing parameter and a $1 km^2$ grid cell) using custom script in MATLAB (The MathWorks, Inc., Natick, Massachusetts, USA). We calculated the 25, 50, 75, 90 and 95 % density volume contours from the KDEs. We then calculated the spatial overlap for 25 % KDE between sharks and turtles as an indicator of *core* home range overlap. KDEs and core home ranges were calculated for the nesting and non-nesting season separately. However, given our interest in behaviors during the nesting season, we focused subsequent surfacing analyses from November–

Table 1 Details of satellite tag deployments on tiger sharks *Galeocerdo cuvier* and green turtles *Chelonia mydas* at Raine Island including satellite tag model, location (latitude and longitude) of tagging location, total length of shark (TL), and curved carapace length (CCL) of turtles

Tag ID	Species	Tag model	Latitude	Longitude	Date tagged	Sex	TL	CCL	Tracking days	Transmit days	Transmission budget	Rep. rate (fast-slow)
79970*^	C. mydas	SPOT5	11.588	144.031	12/8/2007	F	NA	115	408	53	250	44–89
79971*^	C. mydas	SPOT5	11.588	144.031	12/9/2007	F	NA	105	89	38	250	45–90
79976^	C. mydas	SPOT5	11.588	144.031	12/10/2007	F	NA	109	151	65	250	44–89
79977*^	C. mydas	SPOT5	11.588	144.031	12/11/2007	F	NA	106	122	34	250	45–90
87898	C. mydas	SPOT5	14.432	144.960	9/6/2008	F	NA	100	134	51	250	45–90
87899	C. mydas	SPOT5	14.432	144.960	9/6/2008	F	NA	109	147	58	250	45–91
88365*	C. mydas	SPOT5	11.588	144.031	11/16/2008	F	NA	104	202	38	250	45–92
88366*	C. mydas	SPOT5	11.588	144.031	11/14/2008	F	NA	110	200	73	250	45–93
88367*	C. mydas	SPOT5	11.588	144.031	11/15/2008	F	NA	102	286	62	250	45–94
88,368*	C. mydas	SPOT5	11.588	144.031	11/14/2008	F	NA	117	156	74	250	45–95
37111	G. cuvier	Sirtrack	11.583	144.050	12/18/2002	F	327	NA	93	7	500	45–96
54738*	G. cuvier	SPOT4	11.583	144.033	11/23/2004	F	350	NA	16	5	500	45–97
62848*	G. cuvier	SPOT5	11.583	144.033	12/8/2006	F	295	NA	61	8	500	46–91
62849*	G. cuvier	SPOT5	11.589	144.031	12/18/2005	M	288	NA	356	59	500	46–91
72587*	G. cuvier	SPLASH	11.500	144.200	11/26/2006	F	350	NA	42	31	500	45–90
79972*	G. cuvier	SPLASH	11.588	144.031	12/16/2007	F	296	NA	232	25	500	43–88
79973*	G. cuvier	SPLASH	11.588	144.031	12/13/2007	F	300	NA	21	4	500	44–89
79974*	G. cuvier	SPLASH	11.588	144.031	12/10/2007	M	292	NA	408	48	500	45–90
79975*	G. cuvier	SPLASH	11.588	144.031	11/26/2007	F	368	NA	119	4	500	46–91

Tracking days is the number of days at liberty between first and last transmission, while transmit days are the number of days in which tags transmitted a position during the turtle nesting season used in spatial analyses. Tag ID with an *asterisk* (*) indicates data from animals also included in Fitzpatrick et al. (2012) and Tag ID with a *circumflex accent* (^) indicate four turtles that contained duty-cycle tags

April. Consistent with traditional home range estimates, our calculations of home range did not include depth.

Since kernel estimates and subsequent spatial analyses may be influenced by location and deployment duration (i.e., for short tracking periods, skewed data near the tagging site), we evaluated whether there was a relationship between distance from Raine Island and deployment duration for both sharks and turtles. This would need to be accounted for, if for example, animals spent more time closer to the Island at the start of the study when tagged, after which animals dispersed, so that kernel estimates and subsequent spatial analyses would be skewed. We evaluated the relationship between the number of days at liberty and distance from Raine Island for each position derived for each individual during the nesting season using a Spearman correlation since these data were non-normally distributed.

Previous published work and current research at the study site (Fitzpatrick et al. 2012) has revealed that residency patterns of sharks and turtles during the nesting season are generally consistent, with home ranges centered at Raine Island. However, we used multi-year tracking data to ensure that our estimates of movement behavior were not based on a single year alone. All shark and turtle tagging occurred during the turtle nesting season when both sharks and turtles coincide at Raine Island at highest densities. Moreover, tracking spanned long periods, so while tagging may have occurred at different times during the nesting seasons, some tracking occurred over periods of months to years in which data between sharks and turtles were compared.

Surfacing behavior proxy

In this study, we were interested in evaluating if surfacing behavior for both tiger sharks and green turtles differed in and out of the core area of home range overlap and also if surfacing behavior varied with distance from Raine Island during the turtle nesting season (November – April). Below we describe the metric we used as a proxy for relative time spent at the surface by sharks and turtles followed by a justification and assessment of this metric.

The satellite tags used in the present study could only transmit to Argos satellite receivers when the salt-water switch broke the sea surface (i.e., the tagged animal was at the surface). The number of messages transmitted by the tags and subsequently received by satellites carrying Argos receivers were thus related to (1) the duration of time the animals spend at the surface and (2) the frequency of surfacing (Doyle et al. 2015; Hammerschlag et al. 2015). Thus, we used the total number of transmissions received by Argos for each position derived from tags attached to each individual sharks and turtles as a proxy of relative time at the surface (hereafter referred to as "surfacing behavior") (Doyle et al. 2015; Hammerschlag et al. 2015). It is important to note that several factors can

impact the number of transmissions received by Argos including satellite coverage, which varies with latitude as well as tag configuration such as programmed repetition rate, daily transmission allowance, and duty cycling that can deactivate tags for varying periods of time. Moreover, tags may incur transmission loss from biofouling or battery drain near the end of tag deployment. Consequently, the surfacing proxy based on Argos messages received could not provide an absolute measure of surfacing frequency or duration, but rather it could be used as a *relative* measure for comparing surfacing behavior spatially and/or temporally as long as satellite coverage as well as tag configuration and functionality remained similar between comparison groups.

To address this issue, analyses of putative surfacing behavior were conducted on shark and turtle data separately within the nesting season (November–April). Tagging occurred in the beginning of the nesting season and tags were configured with similar standard repetition rates (~44 s) and daily transmission allowance for both turtles and sharks, respectively (Table 1). Based on published data on surfacing frequency and duration for five green turtles at Raine Island equipped with temperature-depth recorders (TDRs), it is unlikely that typical transmission allowances would generally exceed of 250 messages per day (Bell et al. 2009), given that this would require more than 3–6 h at the surface per day (based on either standard or slow (~89 s) repetition rates). However, TDRs deployed on turtles showed they spent an average of 3 h per day at the surface (Bell et al. 2009). While we do not have comparable surface duration TDR data for tiger sharks at Raine Island, number of Argos messages received (across individuals) from sharks was lower than that of turtles, yet the daily transmission allowance of shark tags were double that of turtles (500 transmissions) and thus also unlikely to be exceeded.

Tags on tiger sharks were not duty-cycled, whereas tags on four of ten turtles were programmed to only transmit from 04:00–11:00 h every day from December–April and the remaining months were duty-cycled to transmit every 3 days. The rationale in selecting the transmit hours for these four turtles was based on green turtles at Raine Island appearing to spend more time at the surface in the morning than in the afternoon (Fitzpatrick et al. 2012). Given that such programming puts a restriction on number of tag transmissions possible per day, for subsequent investigations of turtle surfacing behavior; we compared the consistency of results of two separate analyses, one of which used data from all tagged turtles and the other where the four duty-cycled turtles were omitted.

To evaluate for potential changes in tag transmission loss over time during the study period, we analyzed the relationship between total number of Argos messages received (for each individual position) and the associated number of days at liberty using Spearman correlation. However, because we were interested in spatial differences in relative surfacing

behavior, we also used logistic regression to test for differences in turtle or shark occurrence in or out of the area of core overlap versus the number of days at liberty (for each individual). Thus, if transmission loss occurred, but probability of transmitting in and out of the overlap area was consistent through the study period, then spatial differences in relative surfacing behavior could still be compared.

We used the CLS Argos overpass predictor to evaluate satellite coverage in the study area during the turtle nesting season. Pass predictions were calculated for three locations (1) the northernmost extent of all shark and turtle position in the study period [latitude −9.836° S]; (2) the southernmost extent of all positions during the study period [14.099° S]; and (3) the position of Raine Island [−11.75° S]; longitude was consistent [144.054° E]. The pass predictor was run from November through April coinciding with the turtle nesting season (same time period for each of the three prediction runs). We then calculated and compared the total number and daily mean number of passes among the three locations.

To confirm that a relationship existed between Argos transmissions and actual time at the surface, we also compared surfacing data of the five tiger sharks equipped with SPLASH tags (which recorded actual diving behavior) against the corresponding transmissions received by the Argos satellites. The data derived from the SPLASH tags provided information on the percent of total dive within eight different depth categories (ranging from 0 to 200+ m) within 6-h bins. We used Spearman correlation to evaluate the relationship between amount of time at the surface (proportion of total dive time the tag recorded 0 m, within 6-h bins) and total number of Argos transmissions received (surfacing behavior) per 6-h bin for each SPLASH-tagged shark.

For each Argos-derived location, we tested for differences in daily frequency of surfacing (number of Argos messages) by turtles and sharks in areas of core home range overlap versus non-overlap areas using Kruskal-Wallis tests (as data were non-normally distributed). We used Spearman correlation to evaluate the relationship between surfacing behavior and distance to Raine Island for both shark and turtles, correlating the number of Argos messages versus corresponding distance to the Island for each position. For statistical analysis, values for Argos messages were log transformed, whereas data values for days at liberty and distance from Raine Island were log value +1 transformed. Analyses used SAS statistical software (SAS Institute, Cary, NC, USA); statistical significance was declared at the $p < 0.05$ level.

Results

Argos satellite tags attached to tiger sharks operated for 16–408 days (mean ± SD = 150 ± 147.6 days), providing a cumulative 1896 tracking days (Table 1). Core home range for

all tiger sharks combined (based on single highest resolution location per day per individual) in the nesting season was 1090 km^2 (25 % KDE; Fig. 2). Argos tags attached to green turtles transmitted between 89 and 408 days (mean ± SD = 190 ± 94 days) for a cumulative total of 1348 tracking days (Table 1). Core home range for green turtles (25 % KDE) during the nesting season was 848 km^2 (Fig. 2). There was no overlap in core habitat home range between tracked sharks and green turtles during the non-nesting season (March–October); however, during the peak nesting season (November–April), the area of overlap of core home ranges between tiger sharks and green turtles was 848 km^2; that is the entire turtle core home range occurred within the boundary of the shark core home range (Fig. 2).

For tagged sharks, there was no significant relationship found between distance from Raine Island and days at liberty (Spearman rank correlation: $r_S = -0.07$, $N = 350$, $p = 0.19$). Similarly, for turtles, there was no significant relationship between distance from Raine Island and days at liberty (Spearman rank correlation: $r_S = 0.03$, $N = 1689$, $p = 0.29$). These results provide confidence that kernel densities were not spatially skewed by an interaction between tagging site and study duration.

For tiger sharks there was a negative correlation between number of Argos messages received (for each individual position) and days at liberty (Spearman rank correlation: $r_S = -0.15$, $N = 350$, $p = 0.007$), yet there was no significant difference in the probability of shark occurrence in or out of the overlap area versus days at liberty (logistic regression: $N = 350$, $p = 0.41$). These results indicate that although there may have been some tag transmission loss over time, it was consistent across comparison groups so that relative spatial differences in surfacing behavior could be subsequently compared. For all tagged turtles (hereafter "all turtles"), there was no correlation between the number of Argos messages and days at liberty (Spearman rank correlation: $r_S = -0.0003$, $N = 1689$, $p = 0.89$). Likewise, for analyses in which the four duty-cycle turtles were omitted (hereafter "select turtles"), there was no correlation between number of Argos messages and days at liberty during the nesting season (Spearman rank correlation: $r_S = -0.007$, $N = 1355$, $p = 0.78$). As such, turtles did not show evidence of tag transmission loss in the study period.

In terms of satellite coverage, the Argos satellite pass predictor was run for 166 days during the nesting season. The total number of passes over the 27 weeks differed by 60 total passes between the South (3764 passes) and North (3704 passes) latitudinal extremes as well as only 13 and 47 satellite pass differences between the North and South latitudinal extremes and the location of Raine Island (3717 passes). Mean daily difference in satellite passes between the North and South latitudinal extremes was only 0.36, and mean daily

Fig. 2 Map showing **a** location of study site in Northern Australia, **b** kernel density volume contours for green turtles during the nesting season, **c** kernel density volume contours for tiger sharks during the nesting season, and **d** overlap in core home range (25 % kernel density, shown as a *pink polygon*). Area of core home range overlap was 848 km^2
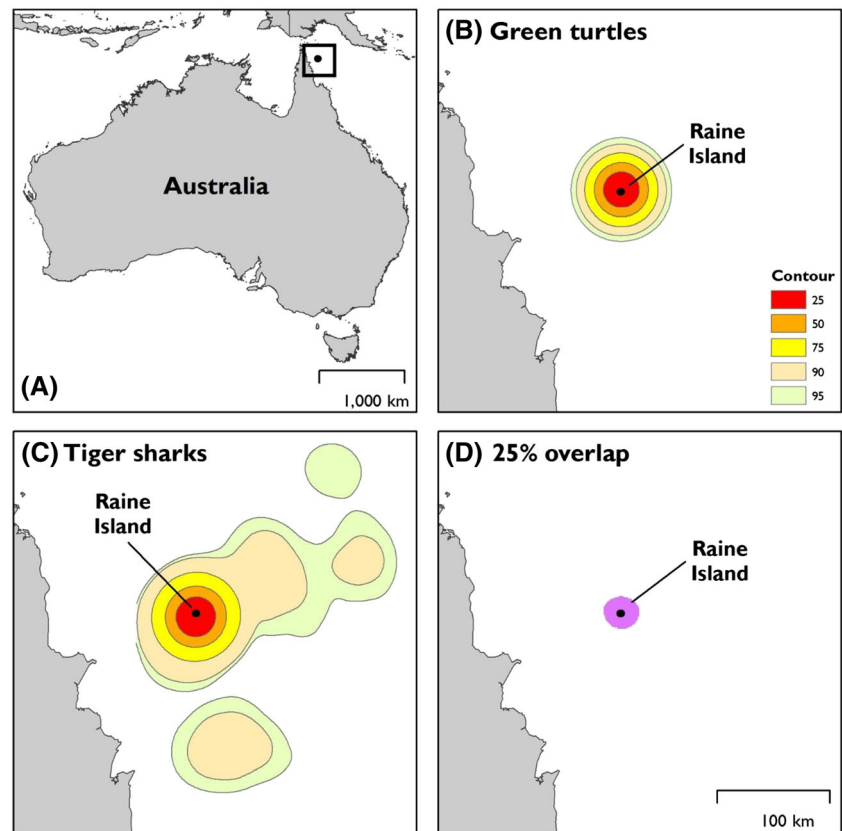
difference in satellite passes between the North and South extremes and Raine Island was only 0.08 and 0.28, respectively. Accordingly, satellite coverage was similar across the sampling area and period.

We identified a positive relationship between the proportion of time at the surface (0 m depth) and the frequency of Argos messages received per 6-h interval (Spearman rank correlation: $r_S = 0.33$, $N = 289$, $p < 0.001$) for the five sharks tagged with SPLASH tags, suggesting that total number of Argos transmissions received per day could be used as an indicator of relative time at the surface in the present study.

During the tracking of tiger sharks, 1211 messages were received by Argos satellites, ranging between 2 and 14 messages per surfacing event ($n = 351$ surfacing events). For tracked green turtles, 5505 total Argos messages were received, ranging between 1 and 17 messages per surfacing ($n = 1689$ surfacing events). Sharks spent significantly more time at the surface (i.e., number of Argos messages per day) in areas of core home range overlap with green turtles (Kruskal-Wallis test: $N = 350$, H = 11.95, $p = 0.0005$; overlap mean ± SD = 3.78 ± 2.28, median = 3.0, IQR = 2–5) than in non-overlap areas (mean ± SD = 2.85 ± 1.22, median = 2.0, IQR = 2.0–3.0, Fig. 3). Similarly, all turtles spent significantly more time at the surface in areas of core home range overlap with tiger sharks (Kruskal-Wallis test: $N = 1689$, H = 15.33, $p < 0.0001$; overlap

mean ± SD = 3.43 ± 2.11, median = 3.0, IQR = 2–4), than in non-overlap areas (mean ± SD = 2.85 ± 1.18, median 3.0, IQR = 2.0–3.0, Fig. 3). Additionally, select turtles also showed significantly higher surfacing in areas of core home range overlap with tiger sharks (Kruskal-Wallis test: $N = 1355$, H = 4.0, $p = 0.04$; overlap mean ± SD = 3.29 ± 2.07, median = 3.0, IQR = 2–4) than in areas of non-overlap (mean ± SD = 2.85 ± 1.19, median 3.0, IQR = 2.0–3.0, Fig. 3).

Surfacing of tiger sharks was negatively correlated with increasing distance from shore (Spearman rank correlation: $r_S = -0.25$, $N = 350$, $p < 0.0001$, Fig. 4). Similarly, surfacing by turtles was negatively correlated with increasing distance from shore (Spearman rank correlation: $r_S = -0.28$, $N = 1689$, $p < 0.001$, Fig. 4) and select turtle surfacing was also negatively correlated with increasing distance from Raine Island (Spearman rank correlation: $r_S = -0.2$, $N = 1355$, $p < 0.0001$).

Discussion

Hunting of marine turtles by tiger sharks likely relies on subsurface stalking and ambush (Heithaus et al. 2002, 2008; Hammerschlag et al. 2015), but here we found that sharks spent significantly more time at the surface in areas of greatest overlap with their turtle prey, closest to Raine Island where
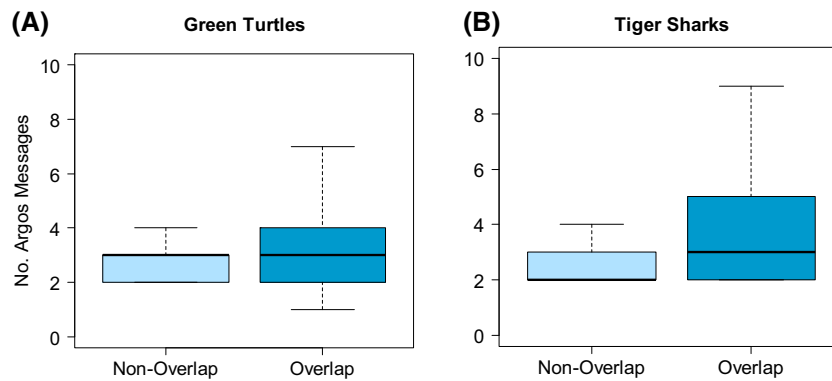
Fig. 3 Box plots of surfacing behavior (number of Argos messages received per position) in and out of areas of core home range overlap for SPOT tagged green turtles **a** and tiger sharks **b** at Raine Island during the turtle nesting season. The *box plot rectangle* represent the lower and upper quartiles; the *bold vertical line* inside indicates median value. *Whiskers* represent lowest data point within 1.5 IQR of the lower quartile, and the highest data point within 1.5 IQR of the upper quartile. Outliers not depicted

turtle density was highest. Based on these findings, we suggest that tiger sharks may patrol surface waters close to shore to maximize encounter rates with turtle carcasses that wash off the Island and to also scan the surf zone for weakened individuals suffering from exhaustion that enter the water after prolonged nesting. Our results are consistent with frequent observations of tiger shark scavenging on green turtle carcasses that wash off of Raine Island reported by

Fig. 4 Scatter plot of the number of Argos messages versus distance from shore for each position fix for **a** tiger sharks, $N = 351$ and **b** all green turtles, $N = 1690$. For both species, surfacing is higher within 20 km of shore

Limpus et al. (2003) and with our own repeated observations of sharks patrolling the Island perimeter (Fig. 1).

We found that surfacing by green turtles occurred most frequently nearest the Island, despite this area having the highest overlap with sharks. Given increased vulnerability to tiger shark predation when at the surface (Heithaus and Frid 2003), this behavior seems surprising. One interpretation might be that healthy green turtles may not perceive sharks as a primary threat and/or other factors are overriding an anti-predatory response. Similarly, in the northwest Atlantic Ocean, loggerhead turtles (*Caretta caretta*) do not appear to modify their surfacing behaviors in areas of home range overlap with tiger sharks likely because other physical (environmental conditions), biological (foraging, nesting), or anthropogenic factors (e.g., boat avoidance) outweigh predation risk responses (Hammerschlag et al. 2015). Moreover, the potential for a lack of anti-predatory response by nesting turtles may also be an endocrine-mediated physiological adaptation to maximize reproductive investment in adult green turtles. This is consistent with the work by Jessop (2001) who found that when healthy turtles are in a nesting state, their adrenocortical stress response is delayed and dampened.

While time at the surface could be an artifact of water depth (with shallower water closer to Raine Island), the reef edge adjacent to the Island is abrupt, dropping to over 300 m depths only ~200 m from shore (Bell et al. 2009) suggesting that turtles and sharks should not be constrained to shallow waters in the huge area in which they overlap (848 km^2). Additionally, shark surfacing increased with proximity to shore, despite depths of >300 m across much of the home range of both sharks and green turtles (Fig. 4). While there are likely other nearshore environmental cues closer to shore versus further away (sounds, nutrients, water quality) that could impact shark and turtle surfacing, they would likely impact these animals differently, yet both
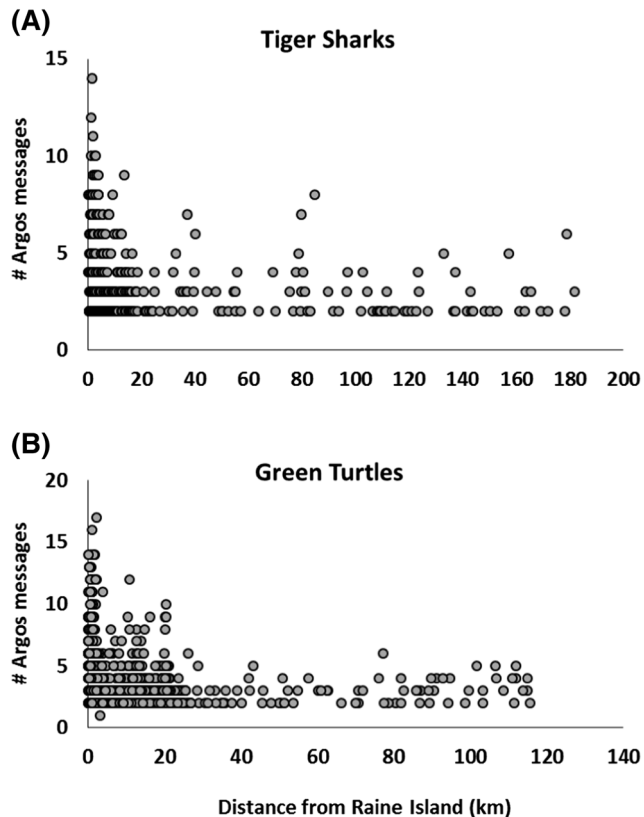
sharks and turtles exhibit a decrease of surfacing with distance from the Island. However, our interpretations are based on spatial and temporal correlation of turtles and sharks and we cannot rule out some unmeasured environmental factor influencing surfacing behavior. Conclusive validation of our interpretations would require a comparison of shark surfacing in proximity to replicate turtle nesting and control islands during the nesting season, exploring shark surfacing before/during/after turtle nesting season at turtle nesting islands, or documenting shark behavior after experimentally manipulating (limiting or supplementing) the number of dead turtles that get washed out to sea.

We calculated a proxy for relative surfacing behavior that was based on the number of transmissions received by Argos satellites. This approach was recently used by Doyle et al. (2015) for blue sharks (*Prionace glauca*) and by Hammerschlag et al. (2015) for loggerhead turtles and tiger sharks. Our surfacing proxy was supported by the positive relationship we found between surfacing data from the tiger sharks equipped with SPLASH tags and transmissions from these sharks that were also received by the Argos satellites. Given the spatial resolution of Doppler-shift location calculations made from SPOT tag transmissions, the data analyzed has varying levels of accuracy. We do not believe this presented an issue for our analysis and interpretation of results since the level of tag resolution used (250 m to 3 km) was smaller than the level of spatial analyses investigated (area of home range overlap = 848 km^2; position distance gradient from shore = 180 km). However, to minimize this potential issue, we evaluated spatial aspects of the data using two metrics (i.e., surfacing versus Island proximity and in/out overlap/non-overlap home range areas), both generating consistent results. That said, we anticipate some level of spatial inaccuracy, which we believe in large part is represented in the data variability and unexplained variation in the models. Moreover, while factors such as variability in satellite coverage, tag configuration, and transmission loss could affect the number of messages transmitted and received by Argos satellites, and thus the utility of our surfacing proxy, we were able to evaluate and likely minimize these possible confounding factors. Indeed, satellite coverage was consistent across the study area, tags did not exhibit transmission loss during the nesting season, and/or tag functionality did not differ among comparison groups.

We are certain that there are instances when sharks expecting a scavenging opportunity are just below the surface, whereby the fin does not break the surface (thus no satellite uplink). However, this study does not attempt to generate absolute values of surfacing behavior nor does it consider absolute values of time sharks spend in a scavenging mode. Rather, this study assesses the relative spatiotemporal differences in surfacing based on samples of positions in space in time.

Various studies have shown that tiger sharks normally swim in a yo-yo manner throughout the water column (e.g., Nakamura et al. 2011). Therefore, sharks spending more time at or near the surface are going to generate more satellite uplinks as compared to sharks spending less time at or near the surface. While we make inferences on animal behavior based on remotely collected from satellite tags where observation is not possible, confidence in our interpretation is that it is consistent with predictions based on ecological theory and established predator-prey interactions between turtles and tiger sharks.

Despite the great opportunities for predation on turtles by tiger sharks around Raine Island, we speculate that tiger sharks employ scavenging as their primary mode of feeding during the green turtle nesting season. For any predator, hunting and capturing prey is energetically demanding and inherently dangerous. For example, hunting costs for lions and polar bears (*Ursus maritimus*) are 2–3 times higher than predicted by the size of their prey (Carbonne et al. 2007). By contrast, at Raine Island, more than 2000 green turtles die during nesting per season in some years (Limpus et al. 2003) and it seems logical that it would be energetically advantageous for tiger sharks to scavenge on these carcasses rather than to chase live turtles, with the added possibility of wasted time and energy when predation attempts are unsuccessful. Scavenging also carries a benefit of greater safety for tiger sharks, given the potential risk of being injured by turtles during a predation attempt, for example, as has been documented with white shark (*Carcharodon carcharias*) predations on seals (Fallows et al. 2012). Similar foraging adaptations are exhibited by successful terrestrial carnivores such as spotted hyena that have evolved functional and behavioral strategies to increase their fitness as facultative scavengers (Pereira et al. 2014).

A limitation of this study is that it was not possible to directly measure predation or scavenging rates, which would allow us to definitively quantify shark feeding mode and frequency, rather we used movement and surfacing behavior as a proxy that was measured at a coarse spatial scales. Fastloc GPS tags could provide higher resolution spatial data, but the high resolution diving data required to test our hypothesis with greater precision would only be available via tag recovery, which is extremely difficult with highly mobile marine species, particularly those not tied to land (sharks). Pop-up satellite archival tags (PSAT tags) could provide valuable data on depth use throughout the water column but geolocation is based on light-level data so spatial accuracy is low and inadequate for the spatial scale of this study system (reviewed in Hammerschlag et al. 2011). Animal-borne cameras and other integrated sensors, like accelerometers, would also be extremely useful for quantifying scavenging versus predation rates (Nakamura et al. 2015), but these too would need to be recovered to generate sufficient data with high sample sizes. While mindful of the

caveats associated with our study, a novelty of our study is the use of behavioral data derived remotely from satellite tags combined with ecological theory to explore a phenomenon that is logistically challenging to study and could not otherwise be determined through direct observation.

Growing evidence from terrestrial studies has revealed that scavenging is more prevalent than traditional theory implies (DeVault et al. 2003; Wilson and Wolkovich 2011; Beasley et al. 2012). While logistically difficult to document in the ocean, facultative scavenging by apex predators is likely to be widespread (Fallows et al. 2013). Our results build on the conclusions from terrestrial studies: scavenging may shape predator-prey relationships, drive energy transfer and nutrient cycling in food webs, and can contribute to the evolutionary success of certain carnivores (DeVault et al. 2003; Wilson and Wolkovich 2011; Pereira et al. 2014). These conclusions are particularly important in the case of large marine predators, such as tiger sharks that are wide-ranging, capable of connecting disparate habitats (e.g., Hammerschlag et al. 2012; Papastamatiou et al. 2013; Werry et al. 2014; Afonso and Hazin 2015; Ferriera et al. 2015), ecologically important (Burkholder et al. 2013), vary individually and over discrete spatial areas in their allocation and use of energy for growth and reproduction (Gallagher et al. 2014), and remain vulnerable to human exploitation (Holmes et al. 2012). Our results also provide further evidence that the strength of predation risk effects on sea turtles can be context and/or geographically dependent (Heithaus et al. 2007; Hammerschlag et al. 2015). This is important since the predation risk by tiger sharks may cause turtles to alter foraging habitat use and grazing intensity on seagrass, thereby impacting seagrass communities (Burkholder et al. 2013). We suggest that our study approach, combining multi-species electronic tagging with long-term time-series demographic data and applications of ecological theory, can be valuable for investigating predator-prey interactions in situations where direct observations are limited or not possible.

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