

Intraspecific behavioral dynamics in a green turtle *Chelonia mydas* foraging aggregation

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ABSTRACT: We used animal-borne video footage to investigate the intraspecific behavioral dynamics of a green turtle *Chelonia mydas* foraging aggregation in Shark Bay, Western Australia, and test the hypothesis that the limited availability of a valuable habitat type promotes interference competition for access to these spaces. In 301 h of footage from 93 individuals, we recorded 176 turtle encounters involving between 1 and 7 turtles per encounter. The majority of encounters (55%) occurred in rare structurally complex benthic habitat (e.g. rock ledges) in deeper areas of this shallow sand-seagrass ecosystem, despite turtles spending only ca. 5% of their time at these sites. We recorded a suite of interactive behaviors nested within 3 encounter classes, which also showed habitat associations. Specifically, behaviorally diverse strongly interactive/social encounters, which represented 68% of total encounter time, occurred exclusively in structured areas. Turtle activities in these areas included solitary and group resting, self-cleaning (i.e. rubbing on hard surfaces), symbiotic cleaning by fish and other interactive behaviors including competitive contests. Competitive contests were 7 times more frequent in structured versus unstructured habitat, although turtle sightings were only twice as frequent in structured areas. In contrast, encounters in shallow habitat (e.g. seagrass beds) tended to be brief and involve limited interaction between solitary turtles. Interference competition at resting/refuge/cleaning sites could have a variety of important ecological implications, and a fuller understanding of chelonid sea turtle foraging ground behavioral ecology and habitat use (e.g. predictive habitat mapping) may require detailed knowledge of key non-foraging habitats.

KEY WORDS: Animal-borne video · Cleaning symbiosis · Competition · Contest · Marine turtle · Self-cleaning · Social behavior · Sting ray

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INTRODUCTION

The behavioral ecology of many large marine vertebrates—particularly those that are difficult to observe in the wild (e.g. sharks, sea turtles, some cetaceans)—represents an important gap in our understanding of the biology of these organisms. Over the past 2 decades, the evolution of animal-borne video and environmental data recorders has yielded a powerful new approach to behavioral research involving these large but otherwise elusive aquatic taxa (Moll et al. 2007). Video footage collected by animal-borne systems has been used to elucidate foraging strategies and fine-scale move-

ments (Davis et al. 1999, Ponganis et al. 2000, Heithaus et al. 2002a, Heaslip et al. 2012, Nifong et al. 2014), describe activity profiles (Thomson & Heithaus 2014), validate inferences made from other bio-logged data such as dive records (Seminoff et al. 2006, Thomson et al. 2011), test predictions of optimal diving theory (Heaslip et al. 2014) and generate new insight into intraspecific relationships (Reina et al. 2005, Herman et al. 2007). As the technology continually improves (e.g. smaller camera size, longer battery life, more timer control options), researchers are able to address an increasing breadth of ecological questions with growing analytical rigor when using these systems.

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Sea turtles are generally solitary animals, although they may occur in groups seasonally for courtship, mating and reproduction. Knowledge of sea turtle intraspecific interactions pertains almost exclusively to courtship and mating, which have been well documented for several species in captivity and in the wild (e.g. Booth & Peters 1972, Comuzzie & Owens 1990, Frick et al. 2000, Schofield et al. 2006). In contrast, very little is known of intraspecific interactions during other less tractable life cycle stages (e.g. juvenile pelagic, adult neritic foraging stages). During these stages, turtles may be primarily solitary but often co-occur around shared resources (e.g. food, habitat) and thus interact. Although many subadult and adult sea turtles spend extended periods on coastal foraging grounds, where they may frequently encounter other turtles, few investigations of intraspecific behavioral dynamics in coastal foraging aggregations have been undertaken. This is because turtles on foraging grounds can range widely and may be elusive or easily disturbed, which often precludes direct in-water observation. Animal-borne cameras provide a means of overcoming this challenge (e.g. Heithaus et al. 2002b, Seminoff et al. 2006, Arthur et al. 2007).

In general, the availability of resources (e.g. food, habitat) is expected to drive variation in animal distributions. However, mismatches often occur between empirical data and theoretical predictions based solely on resources (e.g. ideal free distribution under the assumption of input matching, Fretwell & Lucas 1969, Parker 1978). This is because behavioral dynamics such as interference competition and predation risk may also influence foraging and habitat use decisions (e.g. Parker & Sutherland 1986, Lima & Dill 1990, Moody et al. 1996, Tregenza et al. 1996). For sea turtles, competition for access to resources on foraging grounds has received relatively little attention. Coastal foraging grounds comprise patchy seascapes in which turtles must locate optimal sites for feeding, which often differ from sites that are optimal for other important activities such as resting or seeking refuge from predators. For example, green turtles *Chelonia mydas* in some areas transit between shallow feeding sites (e.g. seagrass meadows) and adjacent deeper, structurally complex resting sites such as coral reefs (e.g. Ogden et al. 1983, Taquet et al. 2006). However, few studies have investigated how the relative availability of different habitat types influences the frequency and nature of intraspecific interactions (e.g. competition for access to limited spaces), which could in turn influence habitat use patterns and community and population processes.

The sand-seagrass ecosystem of Shark Bay, Western Australia, provides a suitable model system for investigating such dynamics. Green turtles and loggerhead turtles *Caretta caretta* occur year round on this large (13 000 km²) coastal foraging ground (Heithaus et al. 2002c). The ecosystem is characterized by a bi-modal depth regime comprising expansive shallow (<4.5 m) seagrass beds and sand-seagrass flats, which turtles commonly use for foraging (Heithaus et al. 2002c, 2005, J. A. Thomson unpubl. data), separated and surrounded by deeper (mostly 6 to 15 m) sand-bottom channels and plains. Throughout most of this ecosystem, structurally complex habitat (e.g. rock ledges, coral heads) is rare and distributed sparsely in deeper areas. Animal-borne video footage from Shark Bay has shown that adult green turtles encountered conspecifics more often in these habitats, despite their limited availability, compared to shallow areas (Heithaus et al. 2002b). However, it was not possible to conduct a detailed investigation of intraspecific interactions across habitat types using this exploratory data set due to relatively low sample size and poor image quality.

Here, we use a large high-definition video data set to examine intraspecific behavioral dynamics in the green turtle foraging aggregation in Shark Bay. Our goals are to (1) provide a rare, detailed description of the intraspecific interactions of a chelonid sea turtle on a coastal foraging ground (lumping in rare encounters with loggerhead turtles); (2) examine factors influencing green turtle encounter rates with conspecifics; (3) statistically classify turtle encounters based on recorded behaviors and compare the frequency of encounters in different classes across habitat types; and (4) test the hypothesis that the limited availability of structurally complex benthic habitat in this system results in interference competition for access to these spaces.

MATERIALS AND METHODS

Study site and video tag deployment

Shark Bay, Western Australia, is located ca. 800 km north of the city of Perth. Shark Bay's expansive seagrass meadows (Walker et al. 1988) provide habitat for year-round aggregations of green and loggerhead turtles (Thomson et al. 2013). Here, we focus on green turtles, which were captured by hand during haphazard searches of shallow areas in a small boat. Titanium flipper tags were applied to a proximal scute of both foreflippers, and curved carapace length (CCL)

was measured (± 0.5 cm). We categorized turtle sex based on tail morphology, with turtles having large tails (extending >25 cm beyond the carapace when straightened) considered males, turtles with CCL > 95 cm and tail length ≤ 25 cm considered likely females and all others considered unclassified (Limpus et al. 1994, Heithaus et al. 2005).

Animal-borne video cameras (see Thomson & Heithaus 2014) were deployed on turtles with CCL > 70 cm between October 2011 and November 2013. Video tag deployments were primarily conducted in early summer (October to December) and winter (June to August), when mean monthly sea surface temperatures are ca. 18 to 20°C and 22 to 25°C, respectively (Thomson et al. 2015). Tags were deployed using popup links, which dissolved in seawater and released tags after 24 to 72 h. In 2011, all cameras began recording when the turtle was released. In 2012 and 2013, a subset of deployments included a timer control accessory (www.cam-do.com), which allowed the start of recording to be delayed for ca. 24 h. Here, we pool data from all deployments but test for the effects of deployment type, since we previously showed that capture stress can alter turtle activity profiles for several hours following release (Thomson & Heithaus 2014).

Behavioral data extraction

Videos were viewed in their entirety, and all turtle sightings were flagged for analysis. Several observers coded turtle behavior and made size and sex classifications (see next paragraph), but all data were checked for consistency by a single author with 10 yr of experience working with green turtles in Shark Bay (J.A.T.). We defined a turtle encounter as any period of time in which the tagged turtle was in the presence of at least 1 other turtle. If the tagged turtle was in the vicinity of untagged turtles that were stationary but could only be seen intermittently (e.g. the tagged turtle changed its orientation repeatedly), we considered the encounter to end at the last moment that the last untagged turtle was seen. In cases where the tagged turtle moved away from a location but eventually returned (e.g. to a rock ledge after surfacing to breathe), we considered sightings upon return to be new encounters because it was typically not possible to identify and keep track of individuals in this situation; there were only 7 instances in which a turtle disengaged from an encounter to surface and returned to the same spot within a few minutes, where it likely re-encountered some of the same indi-

viduals, so this error should be minimal. During each encounter, we estimated the minimum number of turtles present based on the maximum number of unique individuals seen in a short clip in which it would not be possible to double-count turtles. We thus likely underestimate the number of turtles seen in an encounter by counting only confirmed unique individuals and overestimate the number of unique individuals seen overall by counting some turtles in multiple encounters. These numbers therefore provide a useful index of turtle encounter and sightings rates but do not accurately reflect abundance.

For each turtle sighted, we recorded the species and assigned it to 1 of 3 broad size classes designed to reflect maturity status (small = likely juvenile, less than ca. 75 cm CCL; medium = likely subadult, ca. 75 to 95 cm CCL; large = likely adult, greater than ca. 95 cm, see Limpus et al. 1994). For large turtles only (i.e. likely adults), we assessed sex if the tail was clearly visible in the video. Large turtles were considered likely males if they had a large tail (estimated to be greater than ca. 25 cm) and likely females if they had a small tail. All other turtles were considered unclassified. Size and sex classifications were necessarily coarse and subjective and should be interpreted cautiously due to the potential for size misclassification. For capture-based quantitative estimates of green turtle size and sex ratios in Shark Bay, see Heithaus et al. (2002c, 2005).

During each encounter, we recorded the presence or absence of a variety of behaviors (Table 1) performed by the tagged turtle or a turtle interacting with it, along with several habitat variables. Habitat depth was classified as shallow if the bottom was clearly visible from the surface or became visible immediately after the turtle left the surface. This would include seagrass beds, sand-seagrass flats and their sloping margins (mostly less than ca. 4.5 m deep). Alternatively, habitat depth was classified as deep if the bottom only became clearly visible after the turtle made several flipper strokes downward while diving. This would include sand-bottom channels and open plains (mostly greater than ca. 6 m deep). This 2-level classification scheme is suitable for the bi-modal depth distribution of Shark Bay because even under poor visibility conditions, shallow sand-seagrass habitat is easily identified when the turtle leaves the surface. We then recorded whether the habitat where the encounter occurred was structured (i.e. rock outcrops, ledges, coral heads or large sponges present) or unstructured (sand or vegetated bottom). If an encounter occurred on a sand bottom directly adjacent to structure (i.e. within 1 to 2 m), we

Table 1. Behaviors performed by green turtles during encounters with other turtles in Shark Bay

Behavior	Description
Approach	A turtle made a directed movement toward another turtle, approaching up to a distance of ca. 1 m away
Inspect	A turtle approached another turtle within ca. 1 m. This was often accompanied by head movements suggestive of visual or olfactory inspection, such as positioning the head beneath the other turtle's carapace toward the base of the tail/cloaca (Video S1 in the Supplement at www.int-res.com/articles/suppl/m532p243_supp/)
Follow	A tagged turtle swam slowly behind a feeding or traveling turtle while maintaining a relatively consistent distance between the two
Head bump	A turtle actively bumped another turtle's head or carapace with its head (Video S2). This would not include incidental contact between a turtle's head and another turtle's body or flippers. It would also not include nuzzling or biting behavior, which were logged separately
Body/flipper contact	A turtle made contact with another turtle with its flippers, carapace or plastron
Nuzzle	Two turtles gently rubbed heads or beaks (Video S3)
Mouth gaping displays	While 2 turtles were facing each other, 1 or both opened their mouth(s), typically with heads raised, in an apparent defensive or threat display (Video S4)
Bite	A turtle bit or attempted to bite the head, flippers or carapace of another turtle (Video S5)
Chase	A turtle lunged at or swam after another turtle in a clear attempt to remove or exclude it from an area (Video S6)
Group resting/cleaning	While near 1 or several other turtles, a turtle rested or engaged in self-cleaning behavior (i.e. rubbed its head or body on a hard surface such as a rock ledge) or symbiotic cleaning by fish, in all cases by the stripey <i>Microcanthus strigatus</i> (Videos S7 & S8)
Displacement	A turtle that was initially stationary (i.e. resting, feeding or rubbing in a particular location) moved away from the area following an approach or an interaction with another turtle

considered the habitat to be structured. Post hoc, we combined depth and structure variables into a 3-level habitat variable (shallow, deep unstructured and deep structured) since no structure was observed in shallow habitat. We also noted whether encounters occurred on the bottom, in the water column or at the surface, although we did not treat this variable statistically since nearly all encounters occurred on the bottom.

Finally, we estimated the proportion of time turtles spent in structurally complex benthic habitat during a video using previously subsampled data (see Thomson & Heithaus 2014). Turtle behavior was sampled at 3 min intervals throughout each video, and we noted whether the turtle was in a structured habitat at each interval. To reduce the impact of 2 outlying data points (see Fig. 2) in statistical analyses, we converted this variable to categorical by pooling turtles that spent no time in structured habitat into 1 level ($n = 63$) and dividing the remainder ($n = 31$) into 2 levels delimited by the median proportion of time spent in structured areas (7.46%).

Analytical methods

Factors affecting turtle encounter and sighting rates

Statistical analyses were run in R v.3.0.2 (R Development Core Team 2013). We used generalized linear models with negative binomial errors in the *pscl* package (Jackman 2012) to test the effects of season (warmer = October to December, colder = June to August), deployment type (standard, delayed-start), turtle size (CCL) and the proportion of time spent in structured habitat (0, <7.46, >7.46%) on the number of encounters recorded and the number of turtles sighted in a video. We tested for season and body size effects because green turtle activity profiles in Shark Bay vary seasonally (Thomson & Heithaus 2014), which could influence turtle encounter rates, and body size

might be expected to influence the willingness of individuals to engage in certain types of intraspecific interaction (e.g. competitive contests, Parker 1974). We did not test for the effects of sex owing to the small number of videos obtained from males, particularly during the colder season ($n = 2$). The duration of each video (log-transformed) was specified as an offset in the models to account for different video lengths. After fitting the maximal models, we used

single-term deletions and likelihood ratio tests to identify the optimal models (Zuur et al. 2009).

Factors affecting the likelihood of individual behaviors occurring

We used logistic regression in the stats package (R Development Core Team 2013) to test the effects of habitat (shallow, deep unstructured, deep structured), season, deployment type and size of the tagged turtle on the likelihood of individual behaviors occurring during an encounter. For behaviors with a small number of observations, if evidence of separation was detected in the models (i.e. large standard errors), we used a bias-reduction method (Firth 1993, Heinze & Schemper 2002) to calculate penalized maximum likelihoods and standard errors in the brglm package (Kosmidis 2013). For each behavior, we ran a parallel model with the 3-level habitat variable replaced by a binary habitat variable (presence or absence of structure) to determine whether a simpler habitat classification provided a better fit (determined using Akaike's information criterion scores). Only results of the best-fitting model (i.e. with either the 2-level or 3-level habitat variable) are given. Encounters were pooled for all turtles in this analysis.

Classifying encounters based on observed behaviors

We used latent class analysis (LCA) in the poLCA package (Linzer & Lewis 2011) to classify turtle encounters and test the influence of covariates on turtle behavior. LCA is a model-based analogue to cluster analysis that assigns cases to unobserved (latent) classes based on observed (manifest) variables (Hagenaars & McCutcheon 2002). We used LCA to determine the most parsimonious number of green turtle encounter classes based on observed behaviors and assess the defining characteristics of each class and the frequency of encounters in each class occurring in different habitat types. We specified the behaviors in Table 1 as binary (presence or absence) variables in the models and also included encounter duration and the number of turtles seen during an encounter as independent variables. Since the poLCA package requires categorical variables, we assigned encounter durations to quartile groups (delimited by 9.00, 18.00 and 33.25 s). We tested the effects of habitat (shallow, deep unstructured, deep structured), season, deployment type and size of the

tagged turtle (larger: >95 cm CCL, smaller: ≤95 cm CCL) on the prior likelihood of turtle encounters falling in different classes (see Linzer & Lewis 2011).

In preliminary trials, models with 7 or more latent classes frequently did not converge. We therefore ran and compared models with 2 to 6 latent classes. We ran 100 repetitions of each model and used Bayesian information criterion (BIC) scores to identify the optimal model. We then extracted encounter class assignments and the modal posterior probability of membership in each class for every encounter to assess the degree of certainty with which encounters were assigned. We ran a parallel analysis with the 3-level habitat variable replaced by the binary habitat variable, as described previously in this section. Encounters were pooled for all turtles for this analysis.

Competitive contests

Following encounter classification, we extracted all instances in which turtles engaged in one-on-one interactions that involved apparent defensive or aggressive behaviors. This included mouth gaping displays (a putatively defensive behavior, Limpus & Limpus 2003), biting or chasing. We used these data to qualitatively assess the structure of green turtle competitive interactions and patterns of escalation in different habitat types.

RESULTS

Data summary

We obtained 301 h of video footage in 94 camera deployments on 93 individual green turtles (44 likely female, 12 male, 37 unclassified). One likely female was captured twice, approximately 3 mo apart, and had a video taken in both the warmer and colder seasons, although no turtles were seen in either video. At least 1 turtle encounter occurred in 49 of the 94 videos (52%). We recorded 176 encounters with an average encounter rate (calculated for each video and then averaged) of 0.64 h⁻¹ (1.54 SD) and a maximum of 11.84 h⁻¹ (Fig. 1a). The number of turtles seen per hour, calculated in the same manner as the average encounter rate, ranged from 0 to 29.03, with an average of 1.04 (3.46 SD). The number of turtles seen per encounter ranged from 1 to 7, with a mean of 1.52 (1.13 SD) (Fig. 1b). Nearly all turtles seen were likely subadult/adult green turtles (n = 248, 93%), with

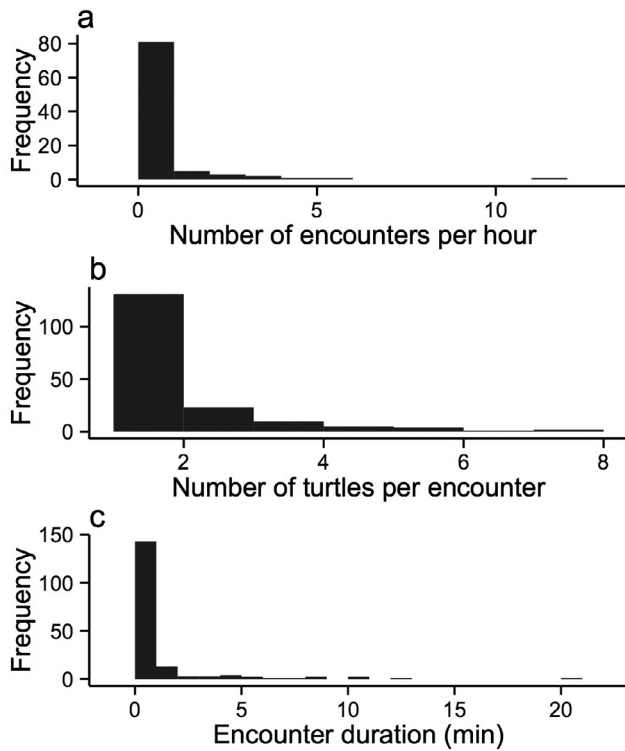


Fig. 1. (a) Number of encounters per hour, (b) number of turtles per encounter and (c) encounter duration by frequency in green turtle videos

likely subadult/adult loggerhead turtles ($n = 10$, 4%) and likely juvenile green turtles ($n = 5$, 2%) seen rarely. Four sighted turtles could not be identified due to poor visibility or distance from the tagged turtle. Of all likely adult green turtles sighted, 21 were likely male and 111 were likely female, while the remaining 109 were unknown (i.e. tail was not clearly visible). The average duration of individual encounters, which included sightings of both green and loggerhead turtles, was 64.84 s (146.35 SD), with a me-

dian of 18 s and a maximum of 20 min (Fig. 1c). The majority of turtle encounters ($n = 96/176$, 55%) occurred in deep structured habitat followed by shallow vegetated habitat ($n = 46/176$, 26%); encounter frequencies were low in all other habitats (Table 2). Most turtles encountered in unstructured habitat were solitary, while encounters in structured areas often involved 2 or more turtles, and encounters tended to be longer in deep compared to shallow habitat (Table 2). While the majority of turtle encounters and sightings occurred in deep structured areas, tagged turtles spent only an average of 4.90% (13.68 SD) of their time in this habitat type.

Factors affecting turtle encounter and sighting rates

The number of encounters occurring in a video increased with the proportion of time spent in structured habitat (Fig. 2) but was not influenced by season, turtle size or deployment type (Table 3). Similarly, the number of turtles sighted in a video increased with the proportion of time spent in structured habitat (Fig. 2) but was not influenced by season, turtle size or deployment type, although the deployment type effect was marginal (Table 3).

Factors affecting the likelihood of individual behaviors occurring

We excluded 3 encounters from subsequent analyses due to insufficient video quality for behavior classification. One other encounter, in which a male turtle briefly attempted to mount a tagged female, was excluded since no other encounter involved similar behavior.

Table 2. Turtle encounter frequencies and durations across habitat types in Shark Bay by green turtles fitted with animal-borne video cameras. NA = not applicable

Depth	Habitat type	No. of encounters	No. of turtles seen	Mean (SD) no. of turtles per encounter	Mean (SD) encounter duration (s)
Shallow	Sand bottom	2	2	1.00 (0)	5.50 (0.71)
	Vegetated	46	48	1.04 (0.21)	24.50 (22.76)
	Structured	0	0	NA	NA
	Midwater or surface	0	0	NA	NA
Deep	Sand bottom	12	14	1.17 (0.39)	37.50 (65.03)
	Vegetated	12	12	1.00 (0)	44.00 (64.03)
	Structured	96	182	1.90 (1.40)	93.95 (190.02)
	Midwater or surface	8	9	1.13 (0.35)	34.50 (51.33)

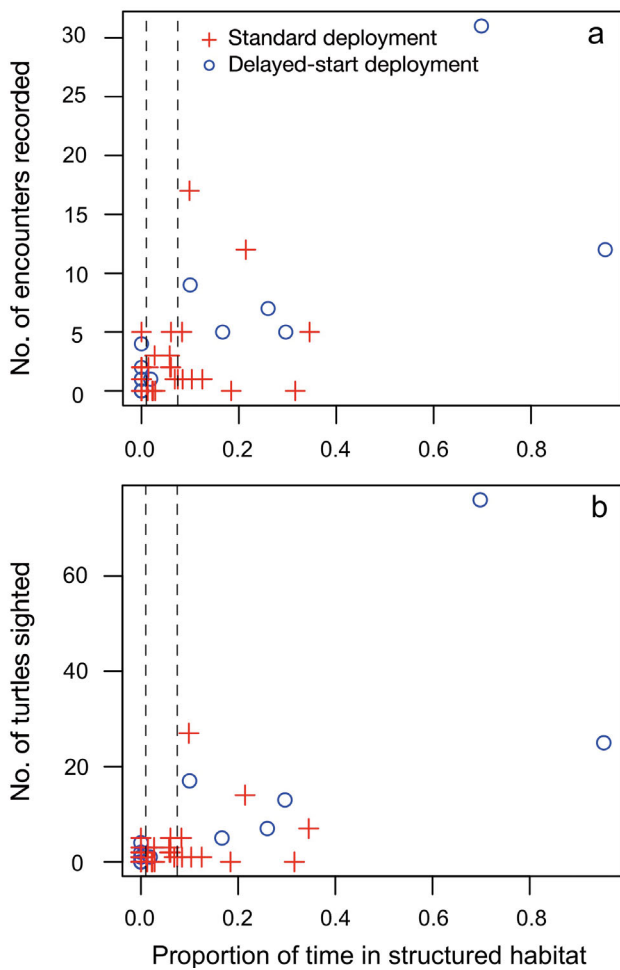


Fig. 2. Effect of the proportion of time spent in structurally complex benthic habitat on (a) the number of encounters recorded and (b) the number of turtles sighted during a video. Vertical dashed lines delineate the levels of the categorical variable to which the continuous proportion data were converted prior to modeling. Deployment type is shown because of its marginal influence on the number of turtles sighted per video ($p = 0.06$)

Table 3. Effects of habitat, season, turtle size and deployment type on the number of encounters occurring and number of turtles sighted during a video. Significant values in **bold**

Dependent variable	Independent variable	L	df	p
Number of encounters	Habitat (2-level)	55.82	2	<0.01
	Season	0.06	1	0.81
	Turtle size	0.00	1	0.97
	Deployment type	2.41	1	0.12
Number of turtles sighted	Habitat (2-level)	75.65	2	<0.01
	Season	0.00	1	0.98
	Turtle size	0.00	1	0.97
	Deployment type	3.47	1	0.06

Approaching, inspecting and following

An approach was observed in 143 of 172 encounters (83%) and was marginally more likely to occur during the warmer season than the colder season. The presence or absence of structure, size of the tagged turtle and deployment type had no effect on the probability of an approach occurring (Table 4). Inspecting was observed in 105 of 172 encounters (61%), and the likelihood of inspecting occurring did not vary with

Table 4. Effects of habitat, season, turtle size and deployment type on the likelihood of individual behaviors occurring during an encounter. Significant values in **bold**

Dependent variable (behaviour)	Independent variable	L	df	p
Approach	Habitat (2-level)	0.11	1	0.74
	Season	3.88	1	0.05
	Turtle size	0.71	1	0.40
	Deployment type	1.03	1	0.31
Inspect	Habitat (2-level)	0.10	1	0.75
	Season	2.79	1	0.09
	Turtle size	0.00	1	0.98
	Deployment type	1.14	1	0.29
Follow	Habitat (3-level)	10.44	2	0.01
	Season	1.97	1	0.16
	Turtle size	1.89	1	0.17
	Deployment type	0.05	1	0.82
Head bump	Habitat (2-level)	0.33	1	0.56
	Season	1.20	1	0.27
	Turtle size	0.07	1	0.79
	Deployment type	0.25	1	0.62
Body/flipper contact	Habitat (2-level)	1.34	1	0.25
	Season	2.00	1	0.16
	Turtle size	0.12	1	0.73
	Deployment type	2.68	1	0.10
Mouth gaping displays	Habitat (2-level)	1.93	1	0.16
	Season	2.54	1	0.11
	Turtle size	0.67	1	0.41
	Deployment type	8.80	1	<0.01
Bite	Habitat (2-level)	4.61	1	0.03
	Season	2.66	1	0.10
	Turtle size	2.41	1	0.12
	Deployment type	3.90	1	0.05
Chase	Habitat (2-level)	11.16	1	<0.01
	Season	1.40	1	0.24
	Turtle size	1.01	1	0.31
	Deployment type	0.09	1	0.76
Group resting/cleaning	Habitat (2-level)	17.49	1	<0.01
	Season	1.66	1	0.20
	Turtle size	2.61	1	0.11
	Deployment type	19.70	1	<0.01
Displacement	Habitat (2-level)	1.49	1	0.22
	Season	13.52	1	<0.01
	Turtle size	0.30	1	0.58
	Deployment type	0.80	1	0.37

season, presence or absence of structure, deployment type or size of the tagged turtle (Table 4). Following was observed in 23 of 172 encounters (13%), and the likelihood of following occurring varied by habitat type, with following most likely to be seen in deep unstructured habitat. Season, deployment type and size of the tagged turtle did not influence the likelihood of following occurring (Table 4).

Head bumping, body contact and nuzzling

Head bumping was observed in 19 of 172 encounters (11%), and the likelihood of this behavior occurring did not vary with the presence or absence of structure, season, deployment type or size of the tagged turtle (Table 4). Body contact was observed in 32 of 172 encounters (19%), and the likelihood of this behavior occurring was not influenced by deployment type, presence or absence of structure, season or size of the tagged turtle (Table 4). Nuzzling was observed in only 5 of 172 encounters (3%) and was excluded from statistical analyses.

Mouth gaping displays, biting and chasing

Mouth gaping displays were observed in 18 of 172 encounters (10%), and the likelihood of this behavior occurring was higher in delayed-start versus standard deployments but was not influenced by the presence or absence of structure, season or size of the tagged turtle (Table 4). Biting was observed in 19 of 172 encounters (11%) and was more likely to occur in structured versus unstructured habitat and marginally more likely to occur in delayed-start versus standard deployments. Season and size of the tagged turtle did not influence the likelihood of biting occurring (Table 4). Chasing was observed in 10 of 172 encounters (6%), and the likelihood of this behavior occurring was higher in structured versus unstructured habitat but was not influenced by season, deployment type or size of the tagged turtle (Table 4).

Group resting/cleaning

Group resting/cleaning was observed in 22 of 172 encounters (13%), and the likelihood of this behavior occurring was higher in structured versus unstructured habitat and in delayed-start versus standard deployments but was not affected by season or size of the tagged turtle (Table 4).

Displacement

Displacement occurred in 43 of 172 encounters (25%), and the likelihood of displacement occurring was higher in the warmer season than the colder season but was not influenced by the presence or absence of structure, deployment type or size of the tagged turtle (Table 4).

Classifying encounters based on observed behaviors

A model with 3 encounter classes was the most parsimonious, and the 3-class model with the binary habitat variable yielded a better fit than one with the 3-level habitat variable ($\Delta\text{BIC} = 10.3$, Fig. S1 in Supplement 1 at www.int-res.com/articles/suppl/m532p243_supp.pdf). Encounters in the first latent class (Fig. 3a) were most likely to involve just 1 (80%) or 2 (16%) untagged turtles. They were likely to be very short, with an 89% chance of being <18 s and a 52% chance of being <9 s. There was a 58% chance that these encounters would involve an approach and an 11% chance that they would involve inspection. However, they were very unlikely to include following (7%), body contact (3%) or displacement (3%) and never involved head bumping, mouth gaping displays, biting, chasing or group resting/cleaning. We labeled these as passing encounters.

Encounters in the second latent class (Fig. 3b) were also most likely to involve only 1 (87%) or 2 (8%) untagged turtles. However, they were likely to be longer in duration than passing encounters, with an 88% chance of being >9 s and a 64% chance of being >18 s. They were very likely to include an approach (97%) and inspection (88%) and had a moderate to low chance of including following (21%), head bumping (18%), body contact (23%), mouth gaping displays (11%), biting (13%) and chasing (8%). These encounters had a 31% chance of involving displacement but did not include group resting/cleaning behavior. We labeled these as brief interactive encounters.

Encounters in the third latent class (Fig. 3c) were most likely to involve between 2 and 7 untagged turtles and exclusively fell in the upper quartile for duration (33 s to 20 min). These encounters always included an approach, inspection and group resting/cleaning behavior. They rarely involved following (5%) but had the highest likelihood of including body contact (45%), mouth gaping displays (41%),

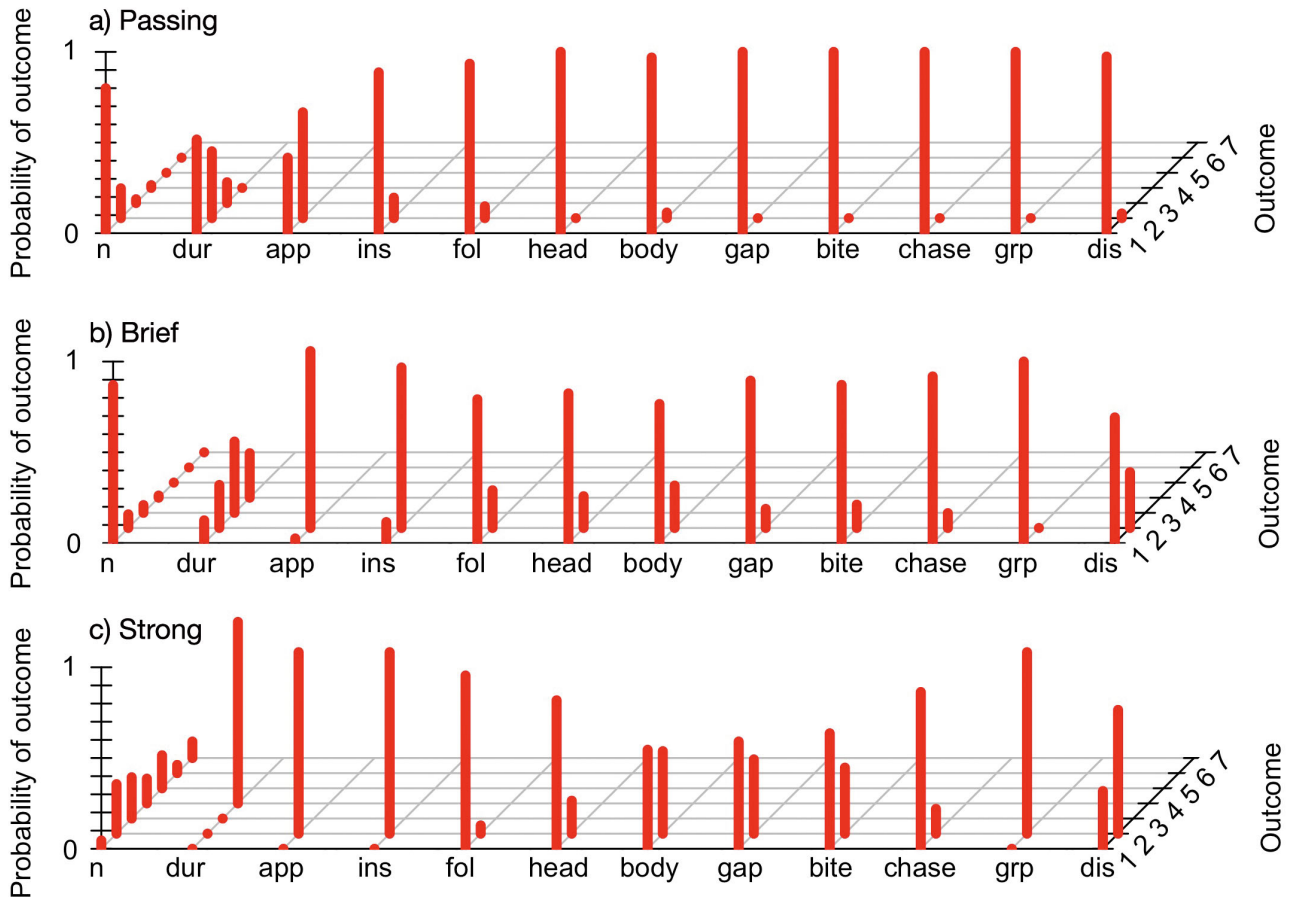


Fig. 3. Characteristics of (a) passing, (b) brief interactive and (c) strongly interactive/social encounters. Observed categorical/binary variables are plotted on the x-axis, and potential outcomes for each variable are shown as discrete levels on the z-axis. For all variables, the probability of each outcome occurring (y-axis) is represented by the vertical bars. For binary behavioral variables, outcome level 1 represents absence, and outcome level 2 represents presence. n = number of turtles in an encounter; dur = encounter duration (quartile groups); app = approach; ins = inspect; fol = follow; head = head bump; body = body contact; gap = mouth gaping display; grp = group resting/cleaning; dis = displace

biting (36%), chasing (14%) and displacement (68%). They had an 18% chance of including head bumping, equivalent to brief interactive encounters. We labeled these as strongly interactive/social encounters.

The final LCA model estimated that passing, brief interactive and strongly interactive/social encounters constituted 37, 50 and 13% of turtle interactions, respectively. Predicted class memberships based on modal posterior probabilities were similar (36, 51 and 13%, respectively), which suggests a good model fit (Linzer & Lewis 2011). Modal posterior membership probabilities in the assigned class were ≥ 0.8 for 91% of encounters (156/172) and ≥ 0.6 for all encounters; classification uncertainty arose from the overlap between passing and brief interactive encounters (Fig. S2 in Supplement 1 at www.int-res.com/articles/suppl/m532p243_supp.pdf). While brief interactive

encounters dominated the data set by frequency, strongly interactive/social encounters constituted 68% of total encounter time. Passing and brief interactive encounters constituted 6 and 26% of total encounter time, respectively. Encounters in all 3 classes occurred most frequently in deep structured habitat, although a substantial proportion of passing and brief interactive encounters also occurred in shallow vegetated habitat (Table 5). Strongly interactive/social encounters occurred exclusively in deep structured habitat.

Habitat type, deployment type and turtle size all influenced the prior likelihood of encounter class membership, while season had a marginal influence (Table 6). Encounters were more likely to fall in the strongly interactive/social class compared to the brief interactive class in structured versus unstructured habitat ($p < 0.01$), in delayed-start versus standard

Table 5. Frequency and mean duration (min) of encounters in each encounter class across habitat types in Shark Bay. Durations are given in parentheses

Habitat depth	Habitat type	Passing	Brief interactive	Strongly interactive/social
Shallow	Sand bottom	2 (0.09)	0	0
	Vegetated	16 (0.15)	28 (0.54)	0
	Structured	0	0	0
	Midwater or surface	0	0	0
Deep	Sand bottom	5 (0.21)	6 (0.88)	0
	Vegetated	2 (0.30)	10 (0.82)	0
	Structured	34 (0.18)	39 (0.41)	22 (5.76)
	Midwater or surface	3 (0.23)	5 (0.78)	0

Table 6. Effect of covariates on the prior likelihood of latent class membership. Strongly interactive/social resting encounters are the reference class against which the other 2 classes are compared. The level of each individual parameter being compared to the reference level is indicated in parentheses

Contrast	Parameter	Coefficient	SE	<i>t</i>	<i>p</i>
Brief interactive	Intercept	28.30	0.62	45.30	<0.01
	Habitat type (structured)	-14.35	0.63	-22.86	<0.01
	Deployment type (delayed start)	-3.66	1.29	-2.83	<0.01
	Turtle size	-13.22	0.60	-22.04	<0.01
	Season (warm)	2.40	1.27	1.89	0.06
Passing	Intercept	28.43	0.57	49.74	<0.01
	Habitat type (structured)	-13.53	0.55	-24.46	<0.01
	Deployment type (delayed start)	-2.64	1.28	-2.06	0.04
	Turtle size	-12.51	0.58	-21.68	<0.01
	Season (warm)	0.20	1.03	0.19	0.85

videos ($p < 0.01$) and for larger compared to smaller tagged turtles ($p < 0.01$). Encounters were marginally more likely to fall in the brief interactive class compared to the strongly interactive/social class in the warm season compared to the cold season ($p = 0.06$). Encounters were more likely to fall in the strongly interactive/social class compared to the passing class in structured versus unstructured habitat ($p < 0.01$); in delayed-start versus standard deployments, albeit marginally ($p = 0.04$); and for larger compared to smaller turtles ($p < 0.01$). However, season had no effect on the prior likelihood of membership in the strongly interactive/social class compared to the passing class ($p = 0.85$).

Competitive contests

We recorded 40 one-on-one interactions that involved mouth gaping displays ($n = 21$), biting ($n = 19$) or chasing ($n = 10$). Of these, 35 (88%) occurred

in structured habitat while 5 occurred in unstructured habitat. Of the 5 contests in unstructured habitat, 4 appeared largely passive (e.g. Video S9 in the Supplement at www.int-res.com/articles/suppl/m532p243_supp/), involving periods of slow head-tail circling (i.e. inspection), mouth gaping displays and nuzzling behavior (i.e. gentle head/beak contact) and only 1 minor bite. However, in the fifth case, a relatively small tagged turtle (76.0 cm CCL) approached a large resting turtle (likely female), which responded by swimming toward it and forcefully biting down on the tagged turtle's head. Of the 35 contests in structured habitat, passive behaviors such as slow head-tail circling and nuzzling were rarely observed (2 and 0 occurrences, respectively). Mouth gaping displays in structured areas occurred with aggression in 7 cases (e.g. Video S10 in the Supplement) and without aggression in 10 cases, and aggression occurred without displays in 18 cases.

DISCUSSION

On a shallow sand-seagrass foraging ground, we documented frequent green turtle intraspecific interactions (and rare encounters between green and loggerhead turtles) that revolved heavily around limited structurally complex benthic habitat in deeper areas. Indeed, the majority of turtle encounters (55%) and sightings (68%) occurred in structured habitat despite turtles spending only ca. 5% of their time in this habitat type overall. We recorded a suite of interactive behaviors nested within 3 encounter classes, which also showed habitat associations. Specifically, strongly interactive/social encounters, which represented 68% of total encounter time, involved up to 7 other turtles and ranged up to 20 min in length (mean = 5.76 min), occurred exclusively around benthic structure. Turtle activities in these areas were diverse and included solitary and group resting, self-cleaning (i.e. rubbing on hard surfaces), symbiotic cleaning by fish (stripey *Microcanthus strigatus*) and

other interactive behaviors including competitive displays (i.e. mouth gaping) and physical contests for access to specific sites. More frequent, longer encounters in structured areas therefore likely reflect a combination of higher turtle densities and more extensive behavioral interactions in this habitat type. In contrast, encounters in abundant shallow habitat tended to be shorter and typically involved a lower level of interaction with a solitary turtle that was travelling, feeding or resting.

Structurally complex benthic habitat in relatively deep areas is likely valuable to chelonid sea turtles on coastal foraging grounds for several reasons. First, these areas provide refuge from potential predators such as large sharks (Seminoff et al. 2006, Heithaus 2013). In Shark Bay, tiger sharks *Galeocerdo cuvier* are the primary predators of sea turtles and show preference for shallow seagrass habitat (Heithaus 2001, Heithaus et al. 2002a,c, 2005), which makes deeper areas inherently safer. Benthic structure further enhances safety by providing protective cover. Second, these areas provide hard surfaces for self-cleaning and may be home to schooling fishes that engage in symbiotic cleaning such as *M. strigatus* in Shark Bay. Both self-cleaning and symbiotic cleaning have been reported previously for chelonid sea turtles (e.g. Losey et al. 1994, Heithaus et al. 2002b, Schofield et al. 2006, 2007), and these behaviors likely confer substantial energetic benefits to these highly migratory animals by reducing epibiont loads. To pose for cleaning, green turtles in Shark Bay hovered just above the substrate with their flippers extended downward in a relaxed position (Fig. 4, see also Losey et al. 1994). Interestingly, we also recorded a large stingray posing to be cleaned next to several green turtles (Video S11 in the Supplement at www.int-res.com/articles/suppl/m532p243_supp/), which suggests that these sites are also valuable to some elasm-



Fig. 4. Tagged and untagged green turtle posing to be cleaned by *Microcanthus strigatus* (lower left) next to a rock ledge (not pictured)

branches in this system. Third, in shallow ecosystems, turtles likely select relatively deeper areas for resting because deeper water allows turtles to achieve neutral buoyancy with a larger volume of inspired air, which in turn allows for longer resting dives (Minamikawa et al. 1997, Hays et al. 2000). Fourth, the presence of vertical structure may provide shelter from strong currents, enhancing the suitability of these sites for energy conservation (Seminoff et al. 2006).

Season, body size and deployment type effects

We found no effect of season on turtle encounter or sighting rates and only marginal effects of season on turtle behavior during intraspecific encounters. Similarly, size of the tagged turtle had limited effects, although larger turtles had a higher prior likelihood of engaging in strongly interactive/social encounters versus other encounter types compared to smaller turtles (discussed in the next section). In contrast, deployment type had a substantial impact on turtle intraspecific behavior. Turtle sightings tended to be more frequent (although not significantly so), mouth gaping displays and biting were more likely to occur and turtles had a higher prior likelihood of engaging in strongly interactive/social encounters versus other encounter types in delayed-start compared to standard deployments. We previously showed that capture stress can influence turtle activity profiles for several hours following release (Thomson & Heithaus 2014), and a reduced tendency to engage in extensive intraspecific interactions may be one manifestation of this stress response. This re-emphasizes the importance of accounting for capture stress when interpreting short-term bio-logged data. We also considered the possibility that tagged turtles might seek out rugose sites to try to remove the tag by rubbing. However, no evidence of increased rubbing shortly following release was found (Thomson & Heithaus 2014), many tagged turtles did not self-clean and many untagged turtles were incidentally recorded self-cleaning, so we consider this unlikely.

Competition for access to resting/refuge/cleaning sites

Competitive displays and physical contests are common in reptiles, including some terrapins and tortoises,

but these aspects of sea turtle behavior are poorly understood (Pearse & Avise 2001). In a rare example, Schofield et al. (2007) described highly stereotyped, escalating contests between female loggerhead turtles on a breeding ground that progressed through stages comprising initial contact, passive confrontation (i.e. wide head-tail circling and mouth gaping displays), aggressive confrontation (i.e. violent contact such as biting) and separation. These contests were more aggressive when they involved benthic resting compared to surface basking or swimming turtles. Schofield et al. (2007) hypothesized that these females may have been competing over limited seabed resting space, where the lack of neighboring females would reduce the likelihood of energetically costly interactions with males. On a feeding ground in Shark Bay, we found support for the hypothesis that a limited valuable habitat type (resting/refuge/cleaning sites) promotes interference competition for access to these spaces. Indeed, biting and chasing were more likely to occur during encounters in structured habitat, and competitive contests were 7 times more frequent in structured compared to unstructured habitat, although turtle sightings were only approximately twice as frequent in structured areas. However, we did not observe a highly stereotyped contest structure, as aggression at these sites often occurred without detailed competitor inspection or passive threat displays. The difference in contest structure between studies warrants further investigation and could reflect variation in perceived resource value, competitor symmetry (e.g. relative body size), turtle residency patterns (i.e. site fidelity) or other possibly species-specific traits.

Ecological implications

Our findings raise important questions regarding chelonid sea turtle foraging ground behavior. In particular, how does the distribution of resting/refuge/cleaning sites influence the distribution of turtles within and among potential foraging locations? The proximity of cover, for example, can affect the suitability of potential feeding sites and thereby influence foraging habitat use decisions (Lima & Dill 1990). Indeed, megagrazers in Shark Bay—green turtles and dugongs *Dugong dugon*—are known to preferentially graze on the edges of seagrass banks close to deep-water refuge when predation risk from tiger sharks is high (Heithaus et al. 2007, Wirsing et al. 2007). It would be interesting to know how the structural characteristics of deep habitat in this sys-

tem affect turtle foraging site selection during shallow-water foraging bouts. More broadly, a full understanding of chelonid sea turtle habitat use in coastal ecosystems, and applications such as predictive habitat mapping, may require knowledge of non-foraging habitats in addition to prey resources. Furthermore, if such dynamics exist, the community-level impacts of turtle foraging (e.g. green turtle grazing impacts on seagrasses) may be concentrated in areas located close to high-quality resting/refuge/cleaning sites. This would be analogous to the grazing impacts of some herbivorous fish and invertebrates being concentrated in halos around reefs (Valentine & Heck 1999) and the impacts of megagrazers in Shark Bay being concentrated along seagrass bank edges (Burkholder et al. 2013). Fine-scale mapping of benthic habitat in Shark Bay and other turtle foraging grounds could provide useful insight into these putative dynamics.

Regarding competitive interference, what effects might the exclusion of less competitive turtles from optimal resting/refuge/cleaning sites have on those individuals? Competition theory (e.g. density-dependent habitat selection) often invokes interference competition (e.g. territoriality) as a driving force underlying individual habitat selection and, ultimately, fitness (e.g. Morris 1989). While sea turtles are not territorial, evidence of aggressive competition for access to space in breeding areas (Schofield et al. 2007) and on foraging grounds (Limpus & Limpus 2003, this study) leads to the question of the implications of these interactions for displaced individuals. Potential costs of repetitive exclusion from resting/refuge/cleaning sites could include increased exposure to predators and decreased swimming efficiency due to higher epibiont loads. Furthermore, it would be interesting to determine what role relative body size and condition, key components of resource holding potential (Parker 1974), play in contests for access to limited habitat or resources. While we found that larger tagged turtles in Shark Bay had a higher prior likelihood of engaging in strongly interactive/social encounters versus other encounter types compared to smaller turtles, we lacked adequate detail on the relative sizes and conditions of contest participants to test these effects. Novel research methods (e.g. marking individuals of known size and condition in a small field site and monitoring behavior with stationary or animal-borne cameras) could provide valuable new insight on this issue.

Finally, it would be interesting to determine how regional variation in turtle foraging tactics and resource availability influences intraspecific behavioral

dynamics within foraging aggregations. For example, in the Caribbean Sea, where some green turtles maintain grazing plots within seagrass meadows (Bjorndal 1980), we might expect to see evidence of exclusion competition at the margins of these plots. In systems like Shark Bay, where green turtles do not maintain grazing plots and instead feed while moving continually throughout the seascape (J. A. Thomson unpubl. data), minimal competition for access to abundant foraging sites would be expected and was indeed observed. Comparative studies of turtle intra-specific interactions across systems would therefore be valuable.

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