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Habitat use and foraging behavior of tiger sharks (*Galeocerdo cuvier*) in a seagrass ecosystem

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Abstract Understanding the foraging behavior and spatial distribution of top predators is crucial to gaining a complete understanding of communities. However, studies of top predators are often logistically difficult and it is important to develop appropriate methods for identifying factors influencing their spatial distribution. Sharks are top predators in many marine communities, yet no studies have quantified the habitat use of large predatory sharks or determined the factors that might influence shark spatial distributions. We used acoustic telemetry and animal-borne video cameras (“Critttercam”) to test the hypothesis that tiger shark (*Galeocerdo cuvier*) habitat use is determined by the availability of their prey. We also used Critttercam to conduct the first investigation of foraging behavior of tiger sharks. To test for habitat preferences of sharks, the observed proportion of time in each habitat for each individual was compared to the predicted values for that individual based on correlated random walk and track randomization methods. Although there was individual variation in habitat use, tiger sharks preferred shallow seagrass habitats, where their prey is most abundant.

Despite multiple encounters with potential prey, sharks rarely engaged in prolonged high-speed chases, and did not attack prey that were vigilant. We propose that the tiger sharks’ foraging tactic is one of stealth, and sharks rely upon close approaches to prey in order to be successful. This study shows that using appropriate analysis techniques and a variety of field methods it is possible to elucidate the factors influencing habitat use and gain insights into the foraging behavior of elusive top predators.

Introduction

Understanding patterns of habitat use and foraging behavior of top predators is important to gaining insight into the dynamics of communities. Patterns of habitat use determine the likelihood of both direct and indirect interspecific interactions, which can influence community structure and stability (e.g. Brown et al. 1999). Therefore, understanding the factors that influence spatial distributions of top predators is critical to predicting the consequences of environmental perturbations and human disturbance on these species and the communities they inhabit. Despite the importance of such studies, it is often difficult to gather data on top predators as they are frequently elusive, have large home ranges, and exist at low population densities. Thus, new methods with meaningful statistical tests could greatly enhance our understanding of top predators in diverse habitats.

Sharks are an example of top predators for which there is little information regarding habitat use and foraging behavior. Yet large sharks may be keystone predators, influencing the structure of ecosystems through predator-prey interactions (e.g. Heithaus 2001a; Simpfendorfer et al. 2001). This study was undertaken to develop methods applicable for gaining insights into their habitat use and to apply new technologies to begin to understand their foraging behavior.

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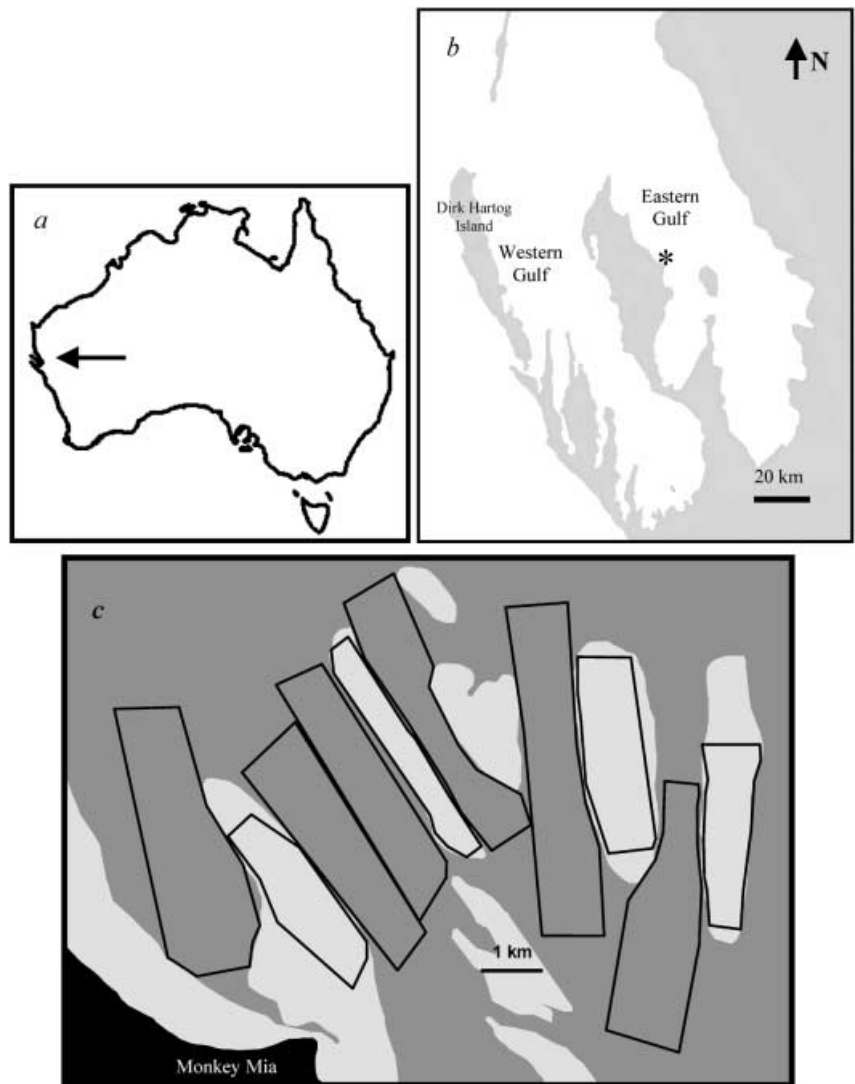
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Tiger sharks (*Galeocerdo cuvier*) are a large (up to 5.5 m total length) coastal species (Randall 1992) capable of taking large prey (e.g. Simpfendorfer 1992 ; Lowe et al. 1996 ; Heithaus 2001a; Simpfendorfer et al. 2001). In the seagrass ecosystem of Shark Bay, Western Australia, tiger sharks may be at the apex of a trophic cascade as they are the major predator on dugongs (*Dugong dugon*) and green sea turtles (*Chelonia mydas*), the bay's principal grazers (Heithaus 2001a; Simpfendorfer et al. 2001). Tiger sharks are also important in determining the habitat use and behavior of their prey species, including those that they rarely consume. For example, although bottlenose dolphins (*Tursiops aduncus*) in Shark Bay are rarely killed by tiger sharks (Heithaus 2001b; Simpfendorfer et al. 2001), dolphin habitat use is greatly influenced by tiger shark predation risk (Heithaus and Dill, in press). Because of their ability to influence the behavior and perhaps populations of their prey, gaining an understanding of tiger shark habitat use and the factors influencing their spatial distribution is required to understand seagrass ecosystems such as Shark Bay.

Previous studies of many large predators have relied on tracking data to determine movement patterns and habitat use (e.g. Mills and Gorman 1997; Goldman and Anderson 1999; Holland et al. 1999), but have generally obtained only small sample sizes. While such studies are useful in determining broad scale movements they often cannot provide reliable data on small-scale patterns of habitat use, which are critical for understanding the dynamics of spatially heterogeneous ecosystems. This is partially due to errors in determining the exact position of the animals that travel over large distances, which can result in large discrepancies between measured and actual habitat use (Heithaus et al. 2001). Large sample sizes tend to ameliorate these errors when researchers are interested in average habitat use patterns of a sample. However, even when habitat use is measured accurately, it is difficult to determine the expected values for habitat use of each individual if they have no habitat preference, and the use of appropriate techniques is critical (Porter and Church 1987; Arthur et al. 1996).

Animal habitat use can be influenced by a wide variety of factors including food availability, competition,

Fig. 1 **a** Shark Bay, Western Australia is indicated with an arrow. **b** Monkey Mia is indicated with an asterisk. **c** Location of study zones offshore of Monkey Mia. *Light shading* indicates shallow habitats and the *gray shading* represents deep habitat. Land is *black*. *Polygons* represent sample zones with transects located in the middle of the zones. Prey availability was assessed in all zones. Shark fishing did not occur in the two zones closest to Monkey Mia



predation risk, and reproductive and social behavior. For some top predators, food availability seems to be a determinant of habitat use (e.g. lions, *Panthera leo*, Mills and Gorman 1997; polar bears, *Ursus maritimus*, Stirling et al. 1993), but this is not universal. For example, wild dog (*Lycan pictus*) densities are not high in areas of high food density and appear to be influenced by the distribution of lions, which are both potential competitors and predators (Mills and Gorman 1997). Large tiger sharks in Shark Bay are unlikely to face either predation risk or interspecific competition for their primary prey. Thus, we hypothesized that tiger shark habitat use should be determined by prey availability.

The foraging behavior of many top terrestrial predators has received considerable attention, but such studies of top marine predators are rare. Knowledge about shark foraging comes largely from inferences based on stomach contents analysis (e.g. Simpfendorfer 1992; Lowe et al. 1996), anecdotal accounts (e.g. Ebert 1991), observations under baited conditions (e.g. Strong 1996), or observations immediately following an attack (e.g. Klimley 1994). These methods, while providing useful information on shark foraging, all have associated biases. These include differences in digestion rates of prey items, unnatural behavior due to baiting, and biases towards predation events that are near the surface and of extended duration. A recent technological innovation, a small animal-borne video camera ("Cittercam"), allows systematic studies of the foraging behavior of sharks and other large marine predators to be undertaken with minimal disturbance to the animal and allows recording of both predator and prey behavior throughout an encounter (Marshall 1998; Heithaus et al. 2001).

The goals of this study were to (1) develop methods for measuring habitat preferences of top predators using tracking data from acoustic transmitters, (2) quantify tiger shark movements and habitat use, (3) determine whether tiger shark habitat use is random or matches food availability, and (4) investigate tiger shark foraging behavior.

Materials and methods

Study site

Shark Bay is a large, semi-enclosed, bay 800 km north of Perth, Western Australia (Fig. 1). The bay is relatively shallow throughout (6–15 m) with extensive shallow seagrass banks (<4.0 m depth). Shark Bay contains the most extensive seagrass shoals reported in the world (Walker 1989) and supports large populations of tiger sharks and their prey (Heithaus 2001a). The study site was located in the Eastern Gulf (25°45'S, 113°44'E; Fig. 1a). For the purposes of this paper, habitats have been classified as either shallow (≤ 4.0 m) or deep (≥ 4.5 m) (Fig. 1b).

Study methods

Prey availability

Habitat differences in the availability of potential prey (dugongs, sea turtles, sea snakes, and sea birds) were determined using belt

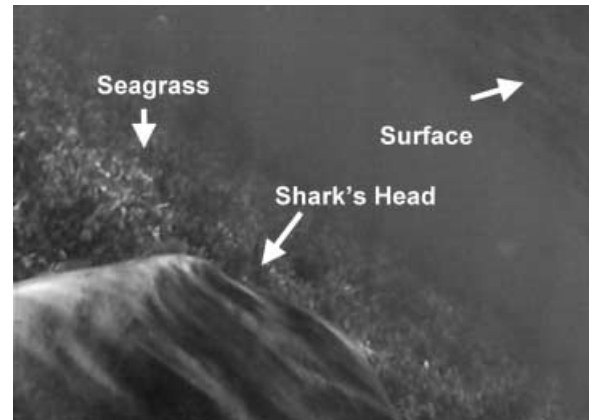


Fig. 2 Video frame from Crittercam attached to C38. Note that the shark is swimming over a shallow seagrass habitat

transects. From March 1997 to May 1999, ten transects located in various habitats (Fig. 1b) were surveyed, from a 4.5 m boat, a total of 410 times (200 deep, 210 shallow) during months that tiger sharks are present in the study area. Transect observations were made at least 2–3 times each week during this period. All turtles and sea birds at the surface within 30 m of the vessel, dugongs within 100 m, and sea snakes (1998 and 1999 only) within 5 m were recorded. Transects were only conducted in Beaufort sea state 3 or less (with most occurring in Beaufort 0 or 1) to reduce sighting biases associated with weather conditions. Due to the narrow sighting belts and good sea conditions, it is unlikely that observer error is responsible for observed patterns of tiger shark prey abundance.

Tiger shark captures

Sharks were captured using drumlines equipped with a single hook (Mustad Shark Hook size 12/0, 13/0, or 14/0) baited with Australian salmon (*Arripis truttaceus*) and fished at a depth of 0.7–2.0 m. Lines were spaced approximately 0.7 km apart and were checked every 2–4 h. Once a shark was caught, it was measured, sexed, and tagged (see Heithaus 2001a for detailed shark handling methods). Comparisons of catch rates among habitats cannot provide an accurate measure of shark habitat use due to differential bait loss and possible differences in catch radii among habitats (Heithaus 2001a). Therefore, two other methods were employed to measure shark habitat use.

Acoustic tracking

Although tracking data have several drawbacks, these can be overcome with methods for correcting position fixes (see below), large sample sizes, and appropriate analysis techniques. Only large sharks that were swimming powerfully on lines were chosen for acoustic tracking (Appendix 1). Sharks were then brought alongside the boat and inverted until they entered a state of tonic immobility, which reduces stress to the shark (Holland et al. 1999). Internal transmitters (V32, 28.5–36.0 kHz, VEMCO, Shad Bay, Nova Scotia) coated in a 7:3 mixture of bee's and paraffin wax were inserted into the peritoneal cavity of eight sharks through an approximately 10 cm incision. The incision was then closed with braided nylon string and triangle-head surgical needles for large animals. Transmitters were implanted within 5 min of a shark entering tonic immobility and all sutures ($n=6$) were completed an average of 15 min after restraint. Two of the transmitters (Appendix 1: IN7, IN8) were equipped with depth sensors to allow comparisons with depth data obtained by Crittercam (see below).

Upon release, sharks were tracked from a 4.5 m research vessel using a directional hydrophone (V11, VEMCO) and an acoustic

receiver (VR-60, VEMCO). Every 5 min we recorded the boat GPS location, direction to the shark, estimated distance to the shark (based on distance-signal strength trials conducted before implantation), and the shark's habitat. In general, we kept 200–300 m from the shark, and the position of the boat relative to the shark was changed frequently. If the estimated habitat of the shark was possibly different from that of the boat, the boat was moved to the shark's estimated position after it had moved a sufficient distance away.

Crittercam

Crittercam is an animal-borne video camera that integrates environmental data collection (temperature and depth) and acoustic tracking capabilities (Marshall 1998). A major advantage of Crittercam is that habitat use of a shark is continuously monitored by video instead of being estimated by acoustic telemetry (Fig. 2). Tiger sharks do not show any obvious behavioral reactions to Crittercam and their movements are similar to those tracked with standard acoustic tracking techniques (Heithaus et al. 2001).

As with acoustic tracking, only large sharks that were swimming powerfully on lines were selected for Crittercam deployments. Crittercams were positioned on the dorsal fin with a soft clamp (see Heithaus et al. 2001 for a detailed description of attachment method), and the shark released. Cameras were left attached to sharks for up to 11 h, with most deployments being less than 6 h ($n = 37$ deployments, 74.9 recording hours, Appendix 2). During a deployment, sharks were acoustically tracked with a Sonotronics (Tucson, Ariz.) directional hydrophone (DH-4) and receiver (USR-5 W) using the above methods. Position estimates and the habitat a shark was using at each fix were corrected using Crittercam video and depth data (Heithaus et al. 2001). Dorsal fin clamps disengaged

from the sharks at a programmed release time using a burnwire system, a backup magnesium link that dissolves in seawater, or were dislodged by the shark. Crittercams are positively buoyant and float to the surface upon release and are recovered using the signal from a built-in VHF transmitter (MOD-050, 150.0–151.0 MHz; Telonics, Mesa, Ariz.) and TR-4 VHF receiver (Telonics). During Crittercam deployments, water temperature and shark swimming depth were recorded every 2–7 s. For analyses of swimming depth, each individual shark contributed a single mean value to overall mean values.

Measuring expected habitat use, shark speed, and displacement

It is difficult to estimate the proportion of time a tracked animal should spend in each habitat if moving randomly, especially if the animal has a poorly defined home range over the tracking period (e.g. Arthur et al. 1996). This problem arises primarily because (1) the location (or habitat) in which a track is started can influence the proportion of time an animal will spend in each habitat even if it has no habitat preference, and (2) the spatial distribution of habitat patches can influence expected habitat use (Porter and Church 1987). To overcome these problems, we devised two Monte Carlo procedures that used observed tracks to generate estimates of expected habitat use if there is no habitat preference. For the first method, a correlated random walk (CRW, Fig. 3), each track was subdivided into component “moves” that were defined as the direction and distance moved between any two 5-min position fixes. We used the observed move distances (in random order), but the 45° direction bin (e.g. N-NE, S-SW, etc) of each move was selected randomly based on the probability that a move was made in a particular direction based on empirical data from all sharks (Fig. 4). The exact angle traveled within a 45° bin (e.g. 41°, 183°) was selected randomly (i.e. each angle within the bin was equally likely to be selected). Because sharks may not conform to a CRW (see Results), we also devised a randomization method (RZ) that retained the angle and distance traveled for each move. The order of moves was then randomized to create a new, random track (Fig. 5a–c).

For both RZ and CRW methods, we generated 1,000 random tracks for each individual, each using the starting point of the original track. The random tracks were mapped into a GIS

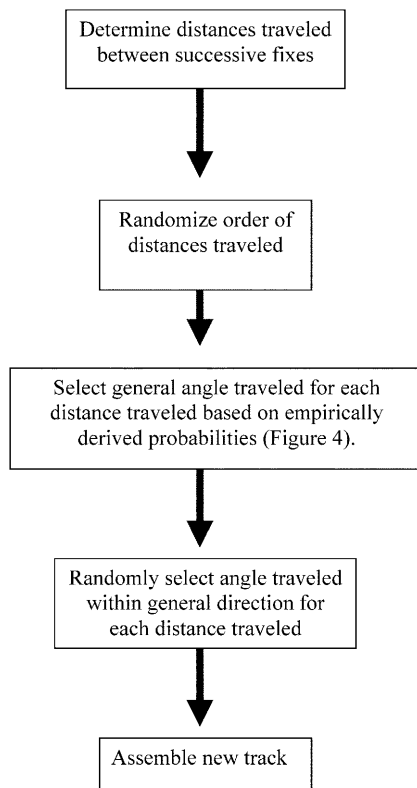


Fig. 3 Flow diagram of the method used to generate expected habitat use measures with no habitat preference for the correlated random walk (CRW) method

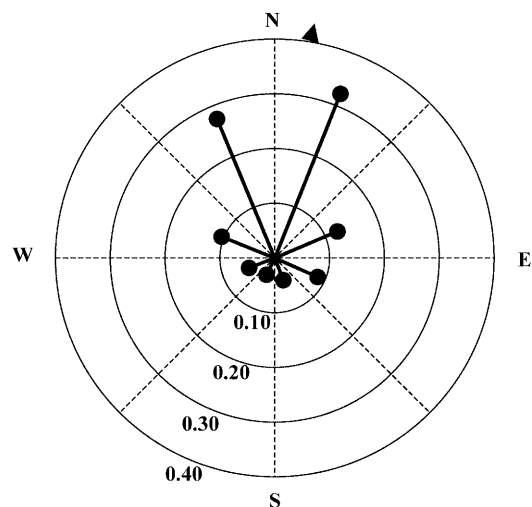


Fig. 4 Frequency distribution of mean movement directions for tiger shark moves used to generate CRW random tracks. Tiger sharks tended to move in a northerly direction with a slight bias towards moving east. To avoid pseudoreplication, each individual contributed only a single set of proportions to the overall mean. Arrow outside of circles indicates the mean direction (10.70°)

(MapInfo, MapInfo Corp.) map of the study site and a habitat designation (deep or shallow) was assigned to each fix location (defined as the endpoint of a move). The number of fixes in each habitat was determined for each random track, and we recorded the number of random tracks in which the observed proportion of fixes in (1) shallow habitats, or (2) deep habitats was greater than the observed track. If fewer than 5% of random tracks used a particular habitat more than the observed track, this individual was considered to exhibit a significant habitat preference.

The above methods are useful in different situations. The RZ method is the most conservative and assumes that the animal can only make moves of the directions and distances observed. Thus, if the observed track was generally directional, the random tracks cluster tightly along the observed track (Fig. 6a–d). Therefore, if an animal moves in a straight line through a preferred habitat, it is likely to be wrongly identified as having no habitat preference because there is no variation in movement angle to allow the animal to select another habitat. In the CRW method a “bubble” of tracks surrounds the original track (Fig. 6a, b, e, f). However, if an animal makes moves that are more directional than predicted based on a CRW, this method may not provide an accurate reflection of expected habitat use with no habitat preference. Because the RZ and CRW methods are both conservative (i.e. likely to detect no preference even if one exists), a habitat preference detected by either

method is likely to be biologically significant. Although RZ and CRW methods did not always both detect a significant habitat preference for an individual, in no cases did they detect opposite preferences.

Several analyses were carried out to determine the overall pattern of habitat use by tiger sharks. Using individuals as single data points, *G*-tests were conducted comparing the observed habitat use to the expected habitat use based on (1) habitat availability (HA) within the study area, and (2) the overall proportion of “fixes” from random tracks for each individual, for both RZ and CRW techniques. *G*-tests can be used to show a deviation from no habitat preference, but are not ideal for identifying a specific habitat preference of a sample since deviations in either direction (i.e. shallow preference or deep preference) add to the significance level of the test. To circumvent this problem, an overall sample randomization (SR) was conducted. In this procedure, the order, direction, and distance of all moves was conserved for each track, and tracks were randomly reallocated among observed starting positions of all tracks. For each iteration ($n=500$) the mean proportion of fixes in each habitat was recorded using each track as a single data point. The observed mean proportion of fixes in each habitat was compared to the distribution of means obtained from the randomizations. If less than 5% ($n=25$) of iterations generate a mean use of a habitat greater than the observed mean use, a significant habitat preference is indicated.

Average shark speed was the distance (measured by GIS) along an entire track divided by total track time. Displacement rate was

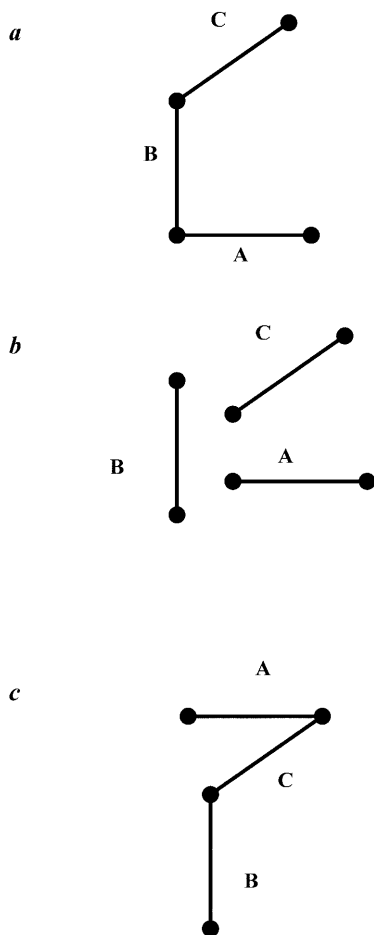


Fig. 5a–c Schematic diagram of randomization (RZ) method. **a** The original track is divided into component moves defined by the direction and distance moved between successive five-minute position fixes. **b** The moves are separated, but the direction and distance traveled are maintained. **c** The moves are reassembled in random order to generate a new track based on random movement. Closed circles indicate the location of hypothetical position fixes

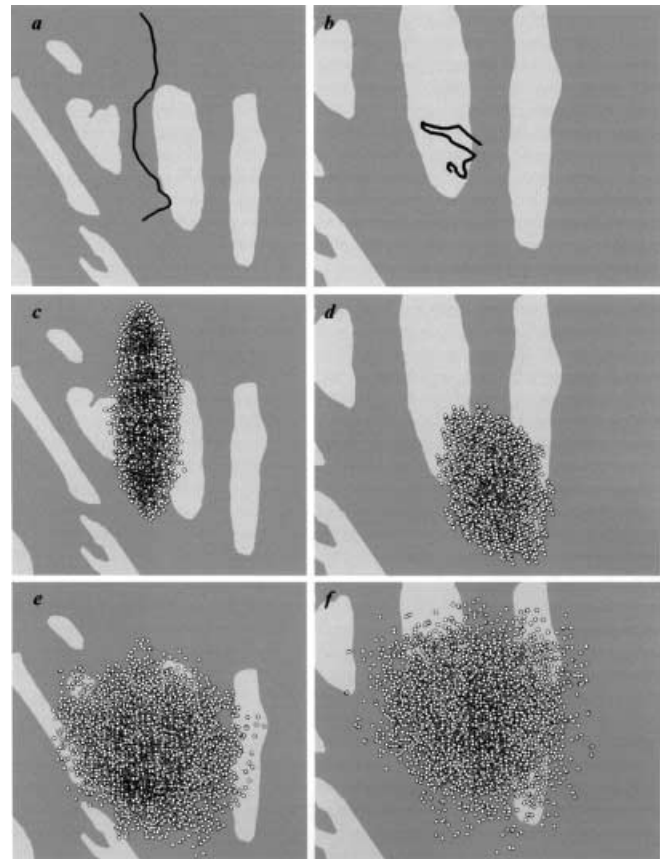


Fig. 6 GIS maps of **a, b** example original tracks (C5, C2), and random tracks based on this original for the **c, d** randomization (RZ) method, and **e, f** correlated random walk (CRW) method. Notice that for C5 the RZ method tends to retain the inherent directionality of the track while the CRW method generates tracks with much greater geographic spread. Both methods generate similar tracks for C2, which made more turns

the straight-line distance between the start and end points of the track divided by total track time. Observed net squared displacements (km) were compared to the net squared displacements predicted by the CRW model using a paired *t*-test to determine if overall shark movements could be described as a CRW or if they were highly directional. Net squared displacement increases linearly with track duration under a CRW; if the observed net squared displacement increases faster than predicted, animals are moving directionally (Turchin 1998; Bergman et al. 2000).

Foraging behavior

Tiger shark foraging behavior and prey responses to tiger sharks were investigated using 22 Crittercam deployments (49 h). Not all Crittercam deployments could be used for foraging analyses as some provided a view adequate only for measuring habitat use. A behavior was considered to be definite foraging when (1) a food item was ingested, (2) a potential prey item was encountered within 30 s of an obvious change in direction ("inspection") or during a burst swim, (3) a potential prey item was pursued, (4) audio from the Crittercam revealed that the shark had bitten prey, (5) biting motions followed a burst swim, or (6) animal material was expelled from the gills after a biting motion or burst swim. Possible foraging behavior was noted when sharks engaged in burst swims but prey could not be seen (often due to a poor camera angle) or there was no bite after a burst swim. Based on these definitions, this study probably underestimates the foraging rate of tiger sharks.

Results

Prey availability

All potential tiger shark prey species that were surveyed were found in greater density in shallow seagrass habitats than in deep ones in all years (Table 1). Sea snakes and dugongs were 3–4 times more abundant in shallow habitats than in deep ones. The relative abundance of sea birds (almost exclusively pied cormorants, *Phalacrocorax varius*) and sea turtles (both green and loggerhead, *Caretta caretta*) was more variable. Sea birds were 4.5–8.4 times and sea turtles 1.7–2.9 times more abundant in shallow habitats.

Table 1 Habitat-specific densities (sightings \times km⁻²) of potential tiger shark prey during months that tiger sharks were caught (Heithaus 2001a). χ^2 values were calculated by comparing observed counts in shallow and deep transects to expected counts based on survey effort and area in each habitat

	Shallow (<4.0 m)	Deep (>4.5 m)	χ^2	<i>P</i>
Dugongs				
1997	0.53	0.12	80.5	<0.0001
1998	0.28	0.06	20.3	<0.001
1999	0.40	0.11	49.8	<0.0001
Birds				
1997	45.2	10.0	270.5	<0.0001
1998	42.9	5.1	417.1	<0.0001
1999	41.7	6.3	805.5	<0.0001
Turtles				
1997	5.5	2.4	12.4	<0.001
1998	4.3	2.6	5.4	<0.05
1999	8.3	2.9	88.0	<0.0001
Sea snakes				
1998	12.8	4.0	20.4	<0.0001
1999	16.9	5.3	33.8	<0.0001

Tiger shark movements and habitat use

Tracks of 45 tiger sharks revealed a general pattern of northward movement (Fig. 4). Although several sharks remained in a restricted area for several hours and made many turns (Fig. 7), most sharks made relatively straight movements (Fig. 8). Net squared displacements of tiger sharks were significantly greater than predicted by a CRW (paired *t*-test, $t=2.8$, $df=44$, $P<0.01$; Fig. 9) indicating directional movements. Backwards stepwise linear regression omitted gender and water temperature as factors influencing speed or displacement, but shark length was positively correlated to both speed (linear regression, $y=0.0063x+0.6902$, $r^2=0.29$, $F=14.4$, $P<0.001$) and displacement (linear regression, $y=0.0079x+0.802$, $r^2=0.16$, $F=9.7$, $P<0.01$). However,

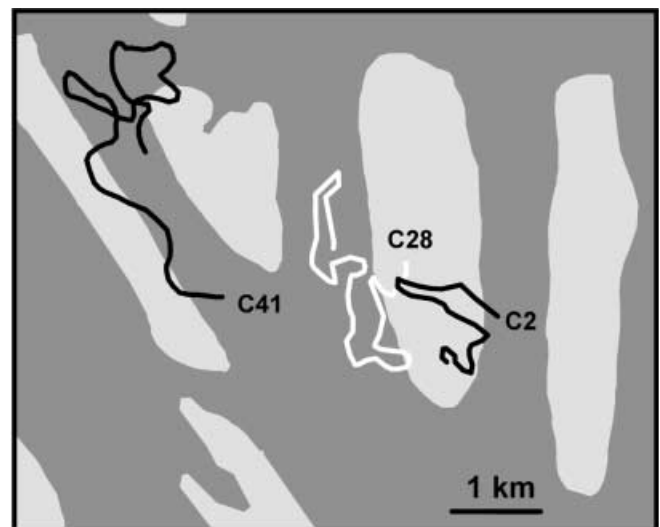


Fig. 7 Example tracks for three tiger sharks that remained in a restricted area throughout a tracking session. The shark identifications are at the beginning of the track

little of the variation in displacement per hour was explained by size variation.

Tiger sharks exhibited a preference for shallow habitats (Fig. 10). On average, tiger sharks were found to spend approximately 36% of their time in shallow habitats, which is significantly more often than expected based on habitat availability (HA, 16%, $G=325.3$, $P<0.0001$) and on predictions generated by the RZ (21%, $G=246.9$, $P<0.0001$) and CRW (27%, $G=268.0$, $P<0.0001$) techniques. The sample randomization also showed a significant preference for shallow habitats: none of the 500 iterations had a greater mean use of shallow habitats than was observed.

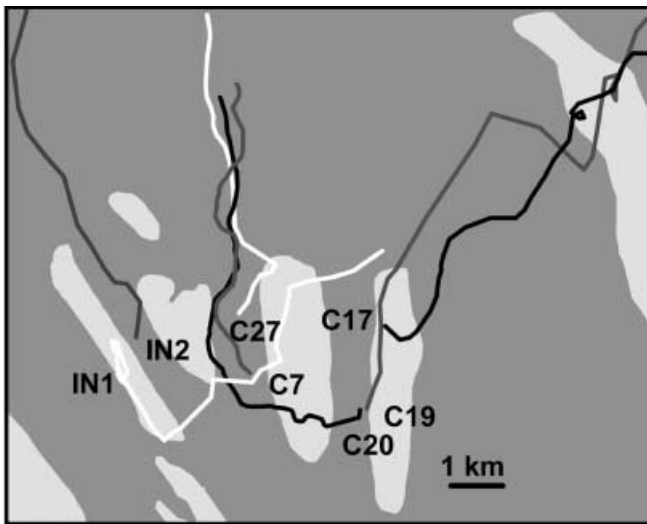


Fig. 8 Example tracks for seven tiger sharks that made generally straight line movements. The shark identifications are at the beginning of the track. Notice that despite starting in different areas, the tracks of many individuals follow similar paths (e.g. C27, C20, C7)

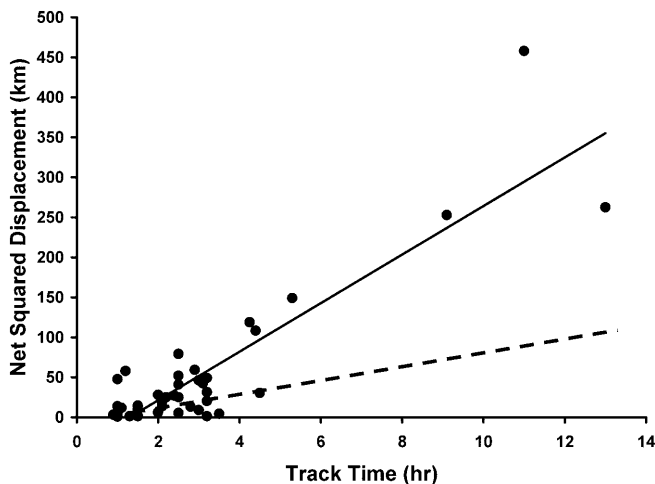


Fig. 9 Net squared displacements of tiger sharks. Observed net squared displacements were significantly greater than expected values (dashed line), indicating directional movement

There was individual variation in habitat use by tiger sharks (Fig. 11). Based on RZ, there was no habitat preference detected for 23 sharks, 19 preferred shallow habitats, and 3 preferred deep habitats. Results were almost identical for CRW (Fig. 11, Appendices 1, 2). Habitat use was not influenced by shark size (ANOVA, $F=0.6$, $df=43$, NS) or gender ($t=0.6$, $df=43$, NS).

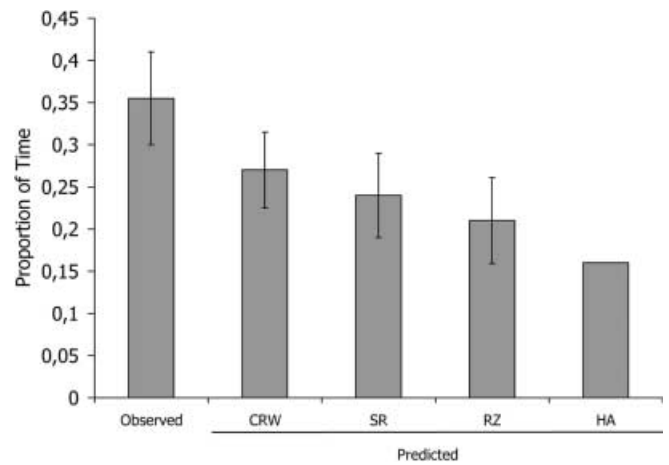


Fig. 10 Average shallow habitat use by tiger sharks. Tiger sharks use shallow habitats significantly more often than expected based on all measures of habitat use (HA: $G=325.3$, $P<0.001$; SR: $G=246.9$, $P<0.001$; CRW=268.0, SR: 0 of 500 iterations with $exp>obs$). RZ Randomization, SR sample randomization, CRW correlated random walk, HA habitat availability. Error bars represent 95% confidence intervals

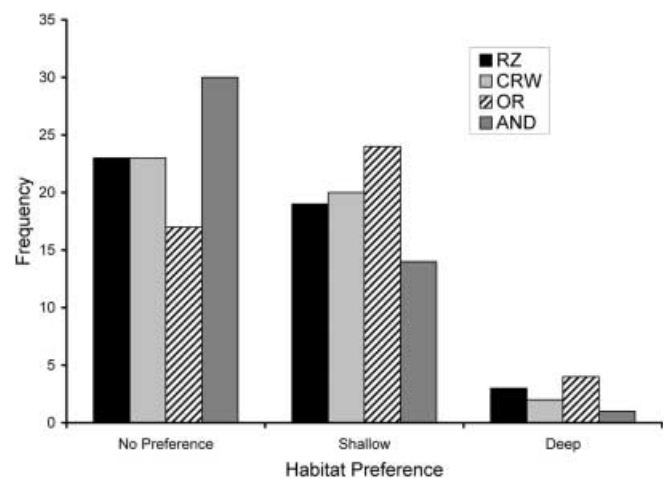


Fig. 11 Individual variation in habitat use by tiger sharks based on RZ and CRW techniques. Bars represent the number of individuals that significantly overused shallow or deep habitats ($P<0.05$) or did not significantly differ from the predictions based on random movement ($P>0.05$). OR Individuals were considered to have a habitat preference if at least one method showed a significant preference. Individuals were only considered to use habitats randomly if both methods showed random use. AND Individuals were considered to have a habitat preference only if both methods showed a significant preference. Individuals were considered to use habitats randomly if either method showed random use

Vertical movements

All tiger sharks for which swimming depth data were obtained ($n=37$ from Crittercam, $n=2$ from internal transmitters) exhibited a stereotypical swimming pattern we refer to as “bouncing” (Fig. 12). Bouncing involves a short period of swimming at a shallow depth (<2 m) followed by a relatively rapid descent ($\bar{x}=0.16$ m/s, $SD=0.03$) then a period of swimming at depth before a slower ascent ($\bar{x}=0.10$ m/s, $SD=0.02$, $t=10.1$, $P<0.001$). At the bottom of most bounces, the shark swims within a few centimeters of the substrate, but not all bounces involve a descent to the substrate. Bounces last an average of 4.3 min ($SD=0.87$) and sharks bounce an average of 14.0 times/h ($SD=3.3$). Sharks exhibited the bouncing swimming pattern even when over shallow habitats (Fig. 12). During the descent phase, all tiger sharks continued power-swimming and did not glide.

Tiger shark foraging behavior

Foraging behavior was observed in 12 of 22 tiger sharks (54%, Table 2). At least 5 sharks successfully captured prey and 1 (C37) also scavenged. Benthic foraging was observed in 2 sharks, and burst swims

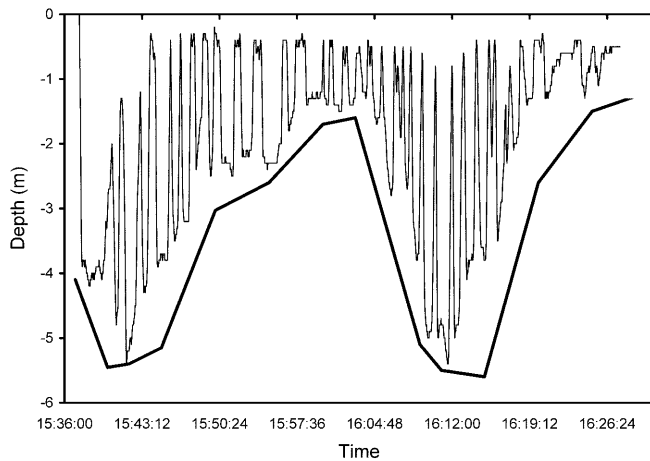


Fig. 12 Vertical movements of tiger shark C2. The thick line indicates the bottom

Table 2 Foraging behavior of tiger sharks. Bold text indicates definite foraging events and italics indicate possible foraging. Burst swims were always followed by bites in definite foraging events. However, bite was only scored if it did not follow a burst swim, and usually involved lunges towards prey. *INS* Prey inspection, *SUC* successful attempt, *UNS* unsuccessful attempt, *UNK* success unknown

Shark	Burst swim			Bite		Benthic	INS
	SUC	UNS	UNK	SUC	UNK	SUC	(see Table 3)
C4					5	1	
C5	2	2, 7	5				2
C8	3	1	<i>14</i>				
C15							1
C17							1
C19					2		2
C20				2			2, 1
C29			3				
C34							1
C37	1					1	3
C38							1
C39			1		4		

(usually <5 s) definitively associated with foraging were observed in 3 sharks (Table 2). In C5, 16 burst swims were observed, all on descents from the surface. At least 2 resulted in prey captures (flesh and blood were extruded from the gills within 2–4 s of a bite), and 2 appeared unsuccessful. In 1 of these, a shovel-nose ray (Rhinobatidae) was seen escaping.

Nine sharks encountered 19 identifiable potential food items, but very few encounters resulted in predation attempts (Table 3). Sharks did not attack vigilant prey (head up and directed towards the approaching shark) and did not initiate or continue attacks after prey began to flee.

When descending from the surface, sharks were able to approach benthic prey closely before eliciting responses. One large teleost and three rays that were encountered by a descending shark did not respond until the shark was within approximately 2 m.

Discussion

Prey availability

Tiger shark prey species were more abundant in shallow habitats. This is not surprising as the majority of seagrass, the primary food of dugongs and green sea turtles, is found in such areas. Teleosts, the principal prey of sea birds and sea snakes and another potential prey item for tiger sharks, are also more common in shallow seagrass habitats, which contain approximately 3 times more teleost biomass than do deep habitats (Heithaus and Dill, in press; Heithaus, unpublished). Bottlenose dolphins are another potential prey item, but are rarely consumed (Heithaus 2001a; Simpfendorfer et al. 2001). During months that tiger sharks are present, dolphins are most abundant in deep habitats (Heithaus and Dill, in press).

Foraging behavior

The high rate of foraging behavior observed in this study is surprising. Calculations of white shark (*Carcharodon carcharias*) energetic requirements suggest that large

Table 3 Tiger shark encounters with potential food items. Inspection is defined as a shark altering its course in order to approach a food item. *SB* Shark behavior upon detecting prey. *PB* Prey behavior at time of detection

Shark	Prey	SB	PB	Prey response	Shark response
C5	Shovelnose ray	Inspect	Rest, vigilant	Flight	Turn away
C5	Baldchin groper	Inspect	Stationary	Flight	None
C15	Shovelnose ray	Attack	Unknown	Flight	Stop attack
C15	Green turtle	Inspect	Swim, vigilant	None	Turn away
C17	Ray	Inspect	Rest, vigilant	None	Turn away
C17	Sea snake	Straight swim	Swim, vigilant	None	None
C19	Black stingray	Inspect	Rest, vigilant	Flight	None
C19	Shovelnose ray	Inspect	Rest, vigilant	Flight	Turn away
C20	Potato cod	Inspect	Vigilant	Turn towards	Turn away
C20	Green turtle	Inspect	Rest, vigilant	None	Reinspect, turn away
C34	Mackerel	Straight swim	Swim vigilant	Move away	None
C34	Loggerhead turtle	Inspect	Rest, vigilant	None	None
C37	Ray	Inspect	Rest, vigilant	None	None
C37	Mackerel	Straight swim	Swim	None	None
C37	Dead teleost	Inspect	–	–	Consume
C37	Bait on line	Inspect	–	–	Consume
C38	Garfish	Straight swim	Swim, vigilant	Flight	None
C38	Turtle	Inspect	Rest, vigilant	None	None
C41	Mackerel	Straight swim	Swim	None	None

sharks may be able to survive for periods of weeks without feeding (Carey et al. 1982). In this study, however, 10 feeding events were recorded in only 49 h of video footage (27 h from foraging sharks), and this is likely an underestimate as prey items (especially those swallowed whole) could have been consumed without being seen. Such a high rate of foraging may be due to the bias associated with catching hungry sharks which may be more likely to attack baits than sharks that have full stomachs.

Another interesting result was the relatively low frequency of fast chases after prey and the lack of attacks on prey items that were inspected (sometimes within 2 m). The lack of attacks may be due to vigilant prey or the initiation of flight. That sharks would not chase prey once they have been detected is not surprising. Despite the strong burst-swimming capabilities of tiger sharks (Compagno 1984), they have limited maneuverability (M. Heithaus, personal observation), making a successful attack unlikely once detected. Thus, the tactic used by tiger sharks appears to be one of stalking and attacking unwary prey. Stealth is a foraging tactic also used by other sharks (e.g. white sharks, Klimley 1994 ; Strong 1996 ; Goldman and Anderson 1999; sevengill sharks, *Notorynchus cepedianus*, Ebert 1991).

The tiger shark's reliance on stealth as a foraging tactic may help explain the high frequency of air-breathing animals in its diet in Western Australia (e.g. Simpfendorfer 1992 ; Heithaus 2001a ; Simpfendorfer et al. 2001). Reduced vigilance during breathing and light attenuation makes it difficult for animals at the surface to visually detect a predator below (Strong 1996), and the countershading and vertical stripes along the tiger shark's flanks provide excellent camouflage, especially when swimming over seagrass. Furthermore, a tiger shark attacking from below reduces the number of escape routes for air-breathing prey (see Strong 1996) and, by swimming near the bottom, it would increase its

search area of surface waters and its ability to visually detect silhouettes of air-breathing animals, a tactic thought to aid other marine predators (e.g. Weddell seals, *Leptonychotes weddelli*, Davis et al. 1999 ; blue sharks, *Prionace glauca*, Carey and Scharold 1990; white sharks, Strong 1996 ; Goldman and Anderson 1999).

While swimming near the bottom would be appropriate for hunting prey at the surface, tiger sharks also feed on benthic prey, including rays and air-breathing prey (e.g. dugongs, sea turtles, sea snakes) that spend most of their submerged time near the bottom (Simpfendorfer 1992 ; Heithaus 2001a ; Simpfendorfer et al. 2001). When swimming along the bottom, tiger sharks are probably more likely to be detected by benthic prey. Moving into surface waters may reduce this problem as foraging benthic prey are likely to suffer reduced search areas of surface waters while they are foraging on the bottom. Thus, the bouncing swimming pattern observed in Shark Bay tiger sharks may allow detection and capture of both benthic and air-breathing prey.

There are several alternate hypotheses for the observed tiger shark vertical movements, including enhanced olfactory detection. Detection of oils from floating or submerged carcasses may be an important way of locating scavenging opportunities, and tiger sharks may move between the surface and the bottom to detect vertically stratified scents. However, they would not be expected to bounce in shallow habitats, where water is well mixed, and should move either against or across currents to maximize the probability of detecting scents. Tiger sharks do not conform to either of these predictions. Bouncing may also represent an adaptation for minimizing the energetic costs of swimming. A bouncing swimming pattern, with a gliding descent and powered ascent, may result in an energetic saving of 50% by negatively buoyant animals like sharks (Weihs 1973). Although such a swimming pattern has been

found in both teleost fishes (e.g. yellowfin tuna, *Thunnus albacares*, Block et al. 1997) and a variety of marine mammals (Marshall 1998 ; Williams et al. 2000), Crittercam revealed that tiger sharks power-stroke as they descend, making the energetic-savings hypothesis unlikely as the sole explanation for this behavior. Also, if tiger sharks were engaging in vertical movements purely to save energy, bouncing should occur in other locations, but tiger sharks in Hawaiian waters < 100 m deep swim primarily along the bottom, rarely ascending (Holland et al. 1999). It remains unclear whether sharks realize some energetic saving with a powered descent and future studies may provide further support for the hypothesis that bounce-swimming by tiger sharks represents a foraging tactic.

Movements and habitat use

We found that tiger shark movements were primarily directional. Such movements are generally considered to be evidence for avoidance of an area (Turchin 1998; Bergman et al. 2000). Despite the apparent avoidance of the study area, tiger sharks return to it (Heithaus 2001a), indicating that it may be part of their home ranges. Thus, generally straight-line movement detected in most tiger sharks may be due to sizeable home ranges, which are common for large predators. Straight-line swimming has also been observed in scalloped hammerhead sharks (*Sphyrna lewini*; Klimley 1993) and in tiger sharks in Hawaii (Holland et al. 1999). In these studies, directional swimming was associated with round-trip excursions away from and back to a seamount (hammerhead sharks) and from coastal waters to an offshore bank (tiger sharks). In this study, tiger sharks were not followed long enough to determine whether movements were oriented towards a specific site. Future studies will be required to investigate long-term movements of tiger sharks in Shark Bay.

It is curious that sharks seldom moved to the south. This may be due to hypersaline waters (sometimes above 60 ppt) several kilometers south of the study area (Walker 1989). This may represent poor habitat for tiger sharks.

Tiger sharks used shallow seagrass habitats significantly more often than expected by all analysis methods despite the different biases associated with each method. This result supports the hypothesis that tiger shark distribution is influenced by prey availability, which is greater in shallow waters. There are several theoretical models that may explain this pattern. First, the ideal free distribution (Fretwell and Lucas 1970) predicts that the proportion of animals in a habitat will match the proportion of food available there. However, the basic ideal free distribution assumes that prey do not move among habitats in response to predation risk. These movements are likely in Shark Bay since tiger shark prey are highly mobile and should be able to switch among habitats. Theoretical models with mobile prey predict that the predators

should be distributed proportional to the food of their prey (Hugie and Dill 1994 ; Sih 1998). In Shark Bay, such a model would also predict that tiger sharks should be most abundant over shallow seagrass habitats. The results of this study qualitatively support both hypotheses, but it is impossible to test whether these models are appropriate without experimental manipulation.

The above models assume that frequency-dependent exploitation competition among sharks drives their habitat use, but the observed pattern may not require such frequency-dependence. As a shark spends more time in one habitat, prey may become more vigilant or leave the habitat (see Brown et al. 1999 for a discussion of the "ecology of fear"). Thus, an individual shark would improve its foraging success by switching among habitats. It is also possible that sharks would prefer to spend all their time in shallow habitats, but must cross deep habitats to access these areas. This seems unlikely given deep habitat preference exhibited by some individuals.

Another possibility is that tiger shark distribution is not influenced by the distribution of their prey, but by some unaccounted for and unmeasured factor. Water is well mixed among habitats and temperatures are identical (Heithaus 2001a), arguing against thermal differences influencing habitat use. There were no differences in habitat use by sharks of different sizes and genders and tiger sharks were not observed interacting with conspecifics during Crittercam deployments, removing reproductive or social considerations as likely explanations for observed patterns. The study area also does not appear to be an important mating area. Tiger sharks in other locations, like Hawaii, appear to be heavily scarred during mating attempts (e.g. Holland et al. 1999), but no such scars were observed during this study despite 270 shark captures. Finally, there are no potential predators of large tiger sharks, such as those tracked in this study, in the Eastern Gulf of Shark Bay, removing predation risk as a possible influence on habitat use. Thus, there is no support for any reasonable alternate hypotheses for the tiger shark's preference for shallow habitats.

Changes in prey availability have been proposed as an important factor influencing the large-scale movements of some shark species. For example, seasonal movements of tiger sharks in Shark Bay appear to be linked to changes in water temperature and prey availability, primarily sea snakes and dugongs (Heithaus 2001a). Temperature and prey shifts may also be the cause of seasonal onshore-offshore movements of blue sharks (Tricas 1979). At a more restricted spatial scale, basking sharks (*Cetorhinus maximus*) have been shown to concentrate their foraging effort in areas of high plankton abundance (Sims and Quayle 1998). This study is the first to show that shark habitat use is associated with prey availability.

Tiger sharks may be at the apex of not only a trophic cascade in Shark Bay (Heithaus 2001a;

Simpfendorfer et al. 2001), but an important link in behaviorally mediated indirect species interactions as well. Bottlenose dolphins are an occasional prey item of tiger sharks (Simpfendorfer et al. 2001), and dolphin habitat use is influenced by their food availability and the risk of predation from tiger sharks (Heithaus and Dill, in press). Since tiger shark habitat use is likely determined by the distribution of their principal prey species (i.e. dugongs, sea snakes, sea turtles), habitat use decisions by these species indirectly affect those of dolphins through their shared predator, the tiger shark. This situation provides a behavioral analog to the population-level process of apparent competition (Holt 1977, 1984) and stresses the importance of identifying the factors influencing habitat use decisions of top predators. Such insights are extremely valuable in elucidating the complex set of behavioral interactions within communities and provide a basis for making appropriate conservation decisions (e.g. Mills and Gorman 1997). Given the complexity of many communities (e.g. Polis 1991 ; Polis and Strong 1996), both marine and terrestrial, behaviorally mediated indirect species interactions may be a common feature of communities and should be further investigated.

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Appendix

Appendix 1

Tiger sharks tracked using internal transmitters and their habitat preferences based on correlated random

walk (*CRW*) and randomization (*RZ*) methods. *S* Shallow, *D* deep, *NP* no preference detected, *IN*=internal transmitter. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, **** $P < 0.0001$

Track no.	Date	TL (cm)	Sex	Hours	CRW	RZ
IN1	8 Dec 97	349	F	4.5	S****	S****
IN2	17 Mar 98	338	M	13.0	NP	NP
IN3	13 Mar 99	360	M	2.0	S**	S**
IN4	10 Apr 99	356	F	2.0	NP	NP
IN5	11 Apr 99	324	M	1.5	S*	S**
IN6	17 Apr 99	348	M	1.0	NP	NP
IN7	21 Apr 99	398	F	4.25	S***	S***
IN8	10 Jul 99	367	F	5.3	NP	NP

Appendix 2

Tiger sharks tracked and recorded using Crittercam (sharks tracked or recorded for >1.0 hour, 74.9 total recording hours) and their habitat preferences based on correlated random walk (*CRW*) and randomization (*RZ*) methods. *TH* Tracking hours, *RH* video hours recorded, *S* shallow, *D* deep, *NP* no preference detected. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, **** $P < 0.0001$

Crittercam no.	Date	TL (cm)	Sex	TH	RH	CRW	RZ
C1	12 Nov 97	320	M	1.5	1.5	NP	NP
C2	19 Nov 97	376	F	1.0	1.0	S*	S**
C3	23 Nov 97	350	M	1.0	1.0	NP	S*
C4	24 Nov 97	352	F	3.0	3.0	NP	S****
C5	25 Mar 98	358	M	2.5	2.5	NP	NP
C6	30 Mar 98	285	M	3.0	3.0	NP	NP
C7	4 Apr 98	319	M	3.2	3.0	NP	NP
C8	9 Apr 98	344	M	2.2	2.2	NP	S****
C9	10 Apr 98	339	M	2.8	2.8	NP	NP
C11	25 Apr 98	334	M	2.1	2.1	S*	S**
C12	26 Apr 98	380	F	3.1	1.7	NP	D***
C13	2 May 98	340	M	2.5	2.5	S**	S**
C14	4 May 98	285	F	9.1	3.0	NP	NP
C15	5 May 98	340	F	3.2	3.0	NP	NP
C16	6 May 98	393	F	1.0	0.3	S****	S****
C17	21 May 98	345	F	11.0	3.0	NP	NP
C18	24 May 98	230	F	3.0	3.0	S*	S****
C19	31 May 98	401	F	4.4	3.0	NP	D*
C20	24 Aug 98	294	F	3.2	3.0	S***	NP
C21	27 Aug 98	291	F	2.9	3.0	S**	S****
C23	16 Feb 99	310	F	1.0	1.0	NP	NP
C24	23 Feb 99	300	M	1.0	1.0	S*	S****
C25	23 Feb 99	331	F	1.5	1.5	NP	NP
C27	25 Feb 99	349	M	2.4	0.6	NP	S**
C28	27 Feb 99	271	F	3.2	0.0	D*	D**
C29	3 Apr 99	320	M	2.5	4.0	D*	NP
C30	4 Apr 99	310	F	1.0	0.0	NP	NP
C31	7 Apr 99	300	F	2.1	2.1	S*	NP
C32	12 Apr 99	280	F	1.1	2.0	NP	NP
C33	5 May 99	392	F	1.0	3.0	NP	NP
C34	10 May 99	370	F	1.5	1.5	S*	S*
C36	16 May 99	378	F	1.2	2.5	S*	S**
C37	23 May 99	302	F	1.5	1.5	S*	NP
C38	8 Jun 99	256	M	1.3	1.3	S**	S****
C39	24 Jun 99	289	F	2.5	2.9	NP	S****
C40	26 Jun 99	300	M	2.5	0.0	S****	NP
C41	8 Apr 00	309	F	3.5	3.5	S****	NP

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