M.R. Heithaus · A. Frid · L.M. Dill

Shark-inflicted injury frequencies, escape ability, and habitat use of green and loggerhead turtles

Abstract Interactions between large marine predators and their prey are difficult to observe and little is known about the risk of predation faced by sea turtles. The frequency of predator-inflicted injuries, however, has afforded insights into the predation risk faced by many taxa. We measured the frequency of shark-inflicted injuries on green (*Chelonia mydas*) and loggerhead (*Caretta caretta*) sea turtles in Shark Bay, Western Australia with a view to determining differences between species and sex-classes in the risk of predation from tiger sharks (*Galeocerdo cuvier*). Furthermore, we investigated how escape ability and habitat use might influence the probability of turtles being injured by sharks. Shark-inflicted injuries were more frequent on loggerhead than on green turtles, and most frequent on adult male loggerhead turtles. Species effects could not be attributed to differences in habitat use, since green turtles were found in habitats favored by tiger sharks more often than were loggerhead turtles. Green turtles, however, were faster and maneuvered better than loggerhead turtles, suggesting that escape ability is a factor in interspecific differences in injury frequency. The sex-class difference in injury frequency of loggerhead turtles suggests that males face greater predation risk than females and may take more risks. For green turtles, the lack of a sex difference in injury frequency might be due to greater escape ability lowering overall predation risk or to no differences between sexes in the benefits of risk-taking.

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Introduction

Predation can be important in shaping the evolution, ecology, life history and behavior of organisms. In many systems, however, predator–prey interactions are difficult to observe and researchers can only infer predation. For example, frequencies of predator-inflicted injuries and scars have been used to infer predator–prey interactions and relative predation rates for diverse taxa, including invertebrates, fishes, lizards, and marine mammals (e.g. Schoener 1979; Murtaugh 1981; Reimchen 1988; Heithaus 2001a).

Little is known about how predation risk affects the behavior and ecology of sea turtles. Sharks are the primary marine predators of adult and large juvenile sea turtles (Marquez 1990), and turtles are taken by white (*Carcharodon carcharias*), bull (*Carcharhinus leucas*), and tiger sharks (*Galeocerdo cuvier*) (Compagno 1984; Witzell 1987; Fergusson et al. 2000). Tiger sharks are the most common turtle predator and may influence turtle population sizes in some locations (Witzell 1987; Simpfendorfer et al. 2001). However, interactions between sharks and turtles are rarely observed, and little is known about the risk of predation faced by sea turtles. Loggerhead (*Caretta caretta*) and green (*Chelonia mydas*) turtles have both been found in the stomachs of tiger sharks captured in Shark Bay, Western Australia, and tiger shark tooth marks have been observed on the carapaces of both the turtle species in our study, suggesting that turtles in this area may face substantial risk of predation (Heithaus 2001b; Simpfendorfer et al. 2001). Therefore, we initiated a study of shark-inflicted injuries on turtles in Shark Bay to gain insights into interactions between sea turtles and their major predator in Shark Bay, the tiger shark (Heithaus 2001b; Simpfendorfer et al. 2001).

There are many steps in an encounter between a predator and prey where both intra- and inter-specific differences in injury frequency could arise. For example, species may differ in encounter rates with predators, or in detection and escape abilities. Therefore, understanding interspecific variation in habitat use and the ability to escape predators may be important for interpreting indirect measures of predation and estimating interspecific differences in predation rate. Gender differences may also exist; males have been found to trade-off safety for higher energetic returns or reproductive benefits in many taxa. For example, they select more dangerous habitats with richer food (Bleich et al. 1997), or incur higher encounter rates with predators while searching or advertising for mates (Kålås et al. 1995). Greater risk-taking by males is particularly likely in species with high variance in male reproductive success, particularly when body condition affects contests for mates (FitzGibbon 1990; Magnhagen 1991).

In this study, we investigate the frequency of shark-inflicted wounds (Fig. 1) on loggerhead and green turtles in the seagrass ecosystem of Shark Bay. Our goals were: (1) to analyze species and sex-class differences in injury frequencies; and (2) to determine whether differences in habitat use, substrate selection, speed and maneuverability might explain differences in injury frequencies.

Materials and methods

Study site

The study was conducted in the Eastern Gulf of Shark Bay, approximately 800 km to the north of Perth, Western Australia (25°45′S, 113°44′E; Fig. 2). The study area is relatively shallow throughout (<12 m deep), with expanses of shallow near-shore areas and offshore banks (<4 m) that are surrounded by deeper channels and open waters (6–12 m). Nearshore shallow areas include patches of sandy bottom and of seagrass cover, whereas offshore banks are predominantly covered by seagrasses (primarily *Amphibolis antarctica* and *Posidonia australis*). Deeper habitats contain some sparse seagrass stands (primarily *P. australis*), but are predominantly sand or silt bottoms with occasional rock outcrops or sponge aggregations.

The study site is a feeding ground for green and loggerhead turtles, but neither species is known to nest in the vicinity (R.I.T. Prince, Western Australia Marine Turtle Project, Wildlife Research Center, Department of Conservation and Land Management, PO Box 51, Wanneroo, Western Australia 6946, personal communication). Several loggerhead turtles captured during our study had been previously tagged on nesting beaches of Dirk Hartog Island, in the Western Gulf of Shark Bay, and one had visited an island several hundred kilometers to the northwest of Shark Bay (R.I.T. Prince, unpublished data). The nesting site of green turtles in this study is unknown, but is likely several hundred kilometers to the north (R.I.T. Prince, unpublished data).

Study methods

Fieldwork was conducted from March to July 1999 and March to June 2000. Turtles were captured in waters 0.7–9.0 m deep (Fig. 2) from a 4.5-m center-console boat with a 50-hp outboard engine. The capture method consisted of randomly searching shallow habitats and occasionally deep ones known to have a relatively high
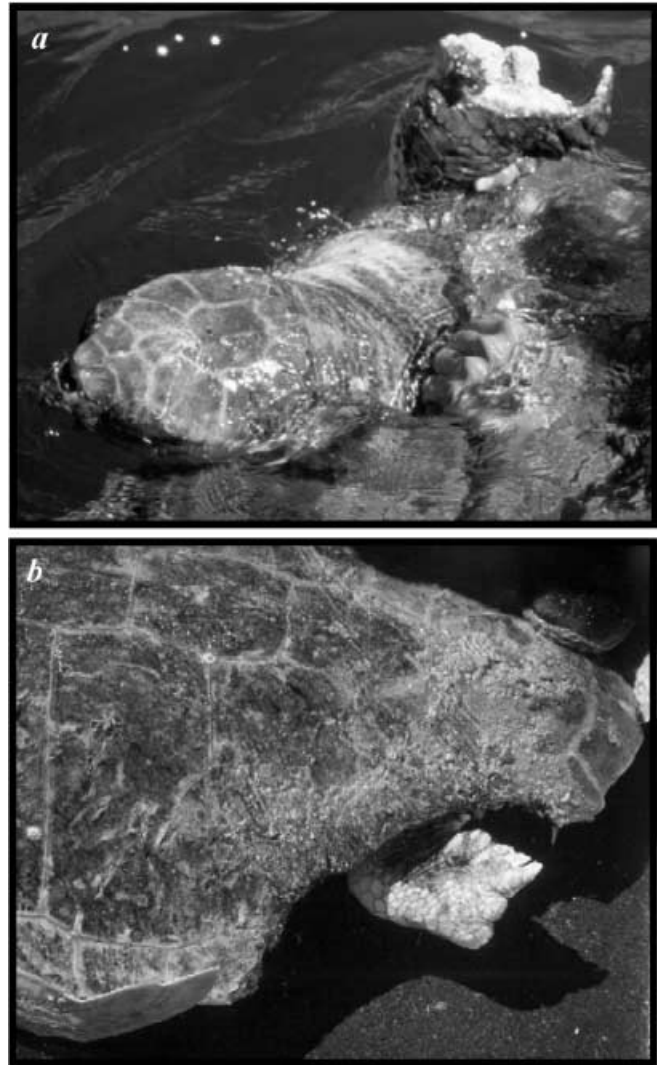

Fig. 1a, b Shark-inflicted wounds on loggerhead turtles in Shark Bay. **a** Fresh amputation of foreflipper. **b** Tiger shark (3.2–3.6 m TL) bite out of the carapace and rear flipper. Note the tooth marks anterior to the wound

turtle density. Once a turtle was spotted below the surface or breathing, the boat approached the turtle and a person jumped off the bow to catch it. Many captures involved a chase in which turtles could escape by diving, in deep habitats or, if in shallow habitats, by swimming horizontally and making sharp turns. We recorded data on escape abilities during 15 chases of green and 7 chases of loggerhead turtles in shallow habitats. These chases lasted 39.2 ± 27.7 s (mean $\pm$ SD) before the turtle either escaped out of sight or was captured. During the chase, the rate of sharp turns ($\geq 90°$) and the speed of the turtle swimming parallel to the boat were recorded on audio tape. Speed was measured with a GPS (Garmin GPS III) 1–10 times during a chase (mean $\pm$ SD = 2.5 ± 2.0) and averaged into a single measurement per chase. There was no correlation between the number of observations and mean speed recorded, suggesting that sampling frequency did not bias speed results.

Captured turtles were brought alongside the boat and tagged with titanium flipper tags provided by the Department of Conservation and Land Management of Western Australia. Data collected from captured turtles included species, sex-class, curved carapace length and width, and records of wounds. We also
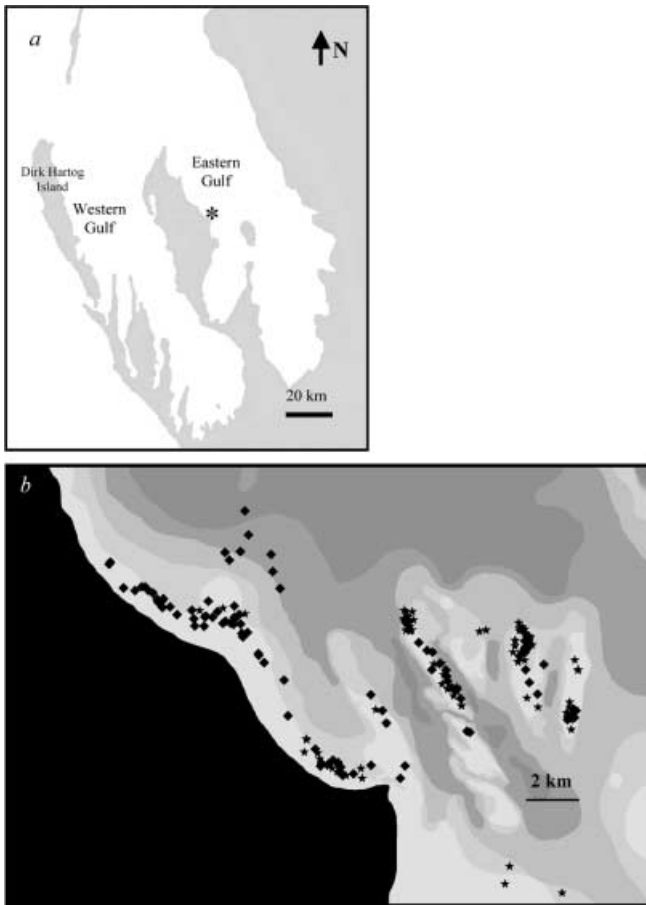
Fig. 2 Location of **a** the study site in the Eastern Gulf of Shark Bay, Western Australia (marked with an *asterisk*), and **b** all turtle captures in the study area (*stars* green turtles, *diamonds* loggerhead turtles). The lightest color represents shallow water (<2 m at MSLW) and successively darker colors represent waters 2–5 m, 5–7 m, 7–9 m, and >9 m deep. Land is *black*

recorded the depth and substrate that the turtle was occupying when sighted, as well as the GPS position of the capture location. We classified turtles as "male" if their tails were >25 cm long, or as "unclassed" if their tails were shorter (Limpus et al. 1994a, b). The latter included adult females and juveniles of both sexes, which are difficult to distinguish in the field. We considered turtles to have been wounded by sharks if: (1) they were missing at least one third of a flipper; (2) their carapace had a crescent-shaped portion removed that could only have been caused by a shark (e.g. Heithaus 2001a); or (3) obvious tooth marks or punctures from a shark were present on the carapace (Fig. 1). Turtles with wounds that did not fit the above criteria were classed as not injured.

Interspecific variation in the use of shallow and deep habitats was measured with belt transects conducted from February to July 1999. Eleven transects (5 shallow, 1.0–4.0 m; 6 deep, >6.0 m) were sampled by three observers ($n=172$ shallow passes, $n=178$ deep passes) from the boat traveling 6–9 km/h. For each turtle observed at the surface within 30 m of the vessel, we recorded water depth, GPS location, and species of turtle. Submerged turtles were not counted. Transects were conducted only in Beaufort Sea State 3 or less. Because sex-classes could not be determined during transects, sex-class differences in habitat use were investigated by comparing depths at capture locations. However, capture effort was substantially higher in shallow habitats, so capture depths do not necessarily accurately reflect average depth selection by each species.

Analyses

We assumed that, if captured by a shark, small turtles are eaten whole (M.R. Heithaus, personal observation), whereas larger turtles are more likely to escape injured. We were also inconsistent in our effort to capture small turtles (less than approximately 50 cm), so analyses exclude turtles that were <65 cm in curved carapace length. Some turtles were recaptured, but analyses include only the first capture for each individual.

The effect of species and sex-class on the probability of captured turtles having a shark-inflicted injury was analyzed with logistic regression (Hosmer and Lemeshow 1989; Trexler and Travis 1993). Analyses were executed with JMP version 3.1 (SAS Institute Inc. 1996), treating species and sex-class as dummy independent variables, and presence and absence of wounds as a binary dependent variable. The model included an interaction term and was reduced to its most significant form with backward stepping procedures (Hosmer and Lemeshow 1989). Diagnostic plots of residuals were assessed with S-PLUS version 4.5 (MathSoft, Inc.).

A function plot of the logistic regression model was generated with the equation:

$$P(\text{injured}) = \frac{e^{(\alpha + \beta_1 X_1 + \beta_i X_i)}}{1 + e^{(\alpha + \beta_1 X_1 + \beta_i X_i)}}$$

where α is the intercept, X_i is the independent variable i, and β_i is that variable's regression coefficient (Hosmer and Lemeshow 1989; Trexler and Travis 1993). Other statistical tests were common and are described in Zar (1984).

Species differences in habitat use were analyzed by comparing the number of green and loggerhead turtles sighted in deep and shallow transects. The proportion of time turtles spend at the surface might differ between habtiats, which would bias sightability. To correct for this potential bias, we divided the number of turtles sighted in each habitat by the ratio between the relative median surface time and the dive time (green turtles: shallow =1.0, deep =1.5; loggerhead turtles: shallow =2.3, deep =5.0). These correction factors were based on preliminary analysis of dive data from four green and five loggerhead turtles collected with Crittercam (Marshall 1998, A. Frid and M.R. Heithaus, unpublished data).

Results

Captured green and loggerhead turtles were of similar size. The average curved carapace length (CCL) of captured green turtles ($n=153$, $\bar{x}=86.2$ cm ± 18.2 SD) was not significantly different from that of loggerhead turtles ($n=126$, $\bar{x}=89.7 \pm 12.0$ SD; $t=1.8$, $df=277$, $P=0.07$). There was no significant difference in the CCL of green ($n=133, \bar{x}=90.7 \pm 13.2$ SD) and loggerhead turtles ($n=115$, $\bar{x}=89.7 \pm 12.0$ SD; $t=0.6$, $df=247$, $P=0.53$) included in wound analyses, since a number of small green turtles were excluded (Fig. 3).

According to the reduced regression model, the probability of a turtle having a shark-inflicted injury depended on the interaction of species and sex-class (Table 1; Fig. 4). Overall, the probability of injury was much higher for loggerhead than for green turtles, regardless of gender. The observed injury frequency was almost three times higher for unclassed loggerhead than for unclassed green turtles; similarly, half of the adult male loggerhead turtles were wounded, but none of the adult male green turtles had wounds (Fig. 4). Within species, sex-class had a strong effect for loggerhead but
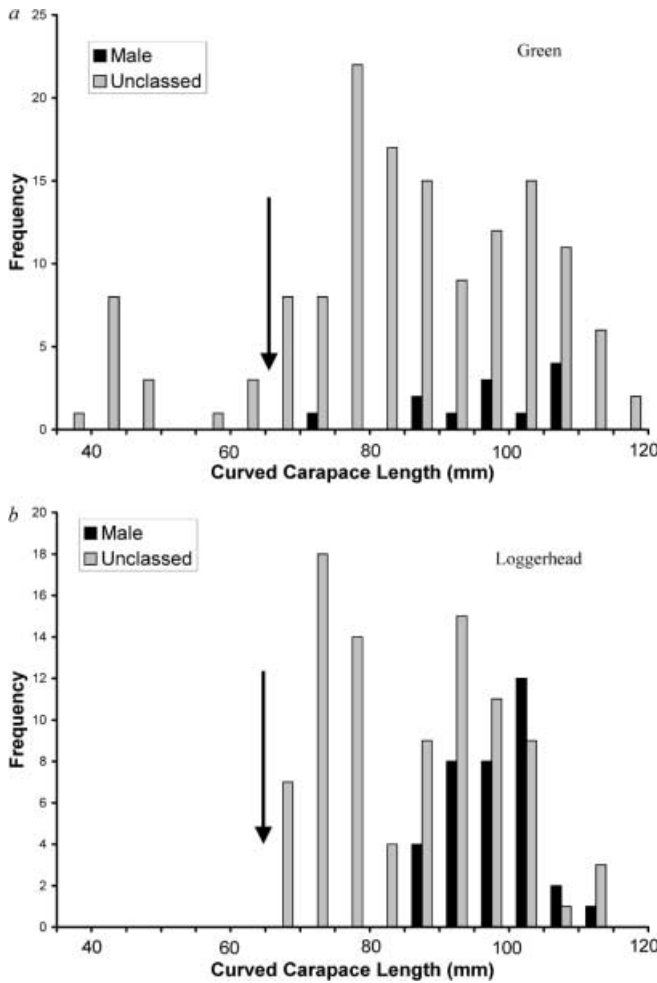
Fig. 3 Curved carapace length distributions for **a** green and **b** loggerhead sea turtles captured by hand during this study. *Arrows* indicate size cutoffs for inclusion in wound analyses
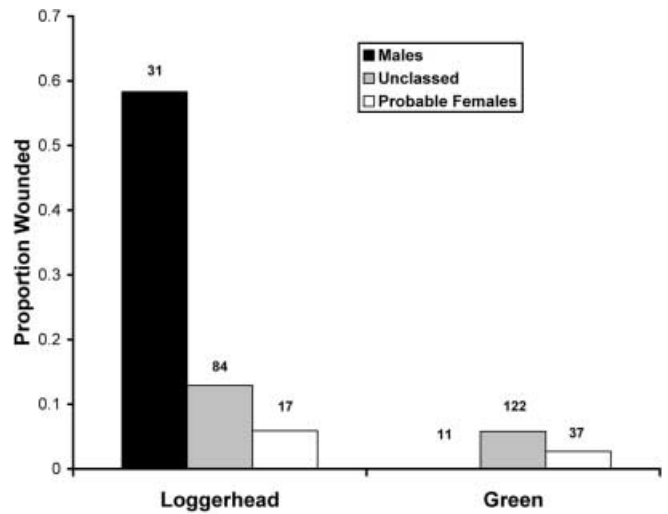

Fig. 4 Rates of shark wounds in relation to sex-class and species. *Bars* represent observed frequencies. *Numbers above bars* indicate sample sizes. Probable females are those with CCL > 100 cm and tail lengths < 25 cm while unclassed turtles are those with tails < 25 cm (and includes probable females). The latter classification was used in the logistic regression. Note that no adult male green turtles had injuries

not for green turtles (Fig. 4). Observed and estimated wound rates were over three times greater for male than for unclassed loggerhead turtles. For green turtles, however, the logistic regression model detected no difference in injury frequency between sex-classes (Fig. 4). When comparisons were made between male loggerhead turtles ($n = 36$, 58.3% injured) and probable adult female loggerhead turtles (i.e. unclassed turtles > 93 cm CCL and > 100 cm CCL), sex-class difference in injury frequency remained (> 93 cm, $n = 31$, 12.9% injured, $\chi^2 = 14.7$, $df = 1$, $P < 0.001$; > 100 cm, $n = 18$, 5.9% injured, $\chi^2 = 13.1$, $df = 1$, $P < 0.001$). Within species, CCL had no effect on the probability of a turtle

having an injury (logistic regression for loggerhead turtles: log-likelihood –64.92, $\chi^2 = 1.29$, $df = 1$, $P = 0.25$; for green turtles: log-likelihood –27.42, $\chi^2 = 0.78$, $df = 1$, $P = 0.38$).

Flipper amputations often were complete (> 80% of the flipper removed), and some turtles had more than one amputation. In one extreme case, a turtle had a large portion of both front flippers removed. In some cases, amputations were recent (i.e. skin had not grown over the amputation; Fig. 1a), suggesting that these wounds did not occur while turtles were juveniles or hatchlings.

During boat chases, green turtles were faster ($t = 6.23$, $df = 20$, $P < 0.001$) and made sharp turns twice as often (Mann-Whitney U-statistic 87, $P = 0.005$) as loggerhead turtles (Fig. 5). Unfortunately, sample sizes were inadequate for testing sex-class or size effects.

There were significant differences in habitat use by green and loggerhead turtles, with green turtles sighted in shallow transects significantly more often than loggerheads ($\chi^2 = 39.8$, $df = 1$, $P < 0.001$). This result was the same after correcting for possible habitat-differences in sightability ($\chi^2 = 10.3$, $df = 1$, $P < 0.002$). There were no sex-class differences in mean capture depth for either

Table 1 Reduced logistic regression model estimating the probability of a turtle having a wound. Species and sex (male or unclassed) were treated as dummy variables (green and unclassed = 0, loggerhead and adult males =1)	Variable	Regression coefficient			Wald test	
		Estimate	Lower 95% confidence limit	Upper 95% confidence limit	χ^2	P
	Intercept	–2.89			55.4	< 0.001
	Species	1.76	0.86	2.71	14.11	0.002
	Sex-class×species	1.19	0.25	2.21	5.88	0.015

green ($t = 0.4$, $df = 144$, NS) or loggerhead ($t = 1.2$, $df = 122$, NS) turtles, but this result may be due largely to the lack of captures in deep habitats. Similarly, there were no differences between sex-classes in substrate preference while in shallow habitats for either green ($\chi^2 = 0.03$, $P = 0.85$) or loggerhead ($\chi^2 = 2.68$, $P = 0.10$) turtles. However, loggerhead turtles were captured over sand substrates significantly more often than were green turtles, which were caught mostly over seagrass ($n = 272$ captures, $\chi^2 = 96.0$, $df = 1$, $P < 0.001$).

Discussion

The abilities of prey to modify the probabilities of being captured and killed can be grouped into three different categories. First, prey can change the cumulative probability of encountering a predator through preventative long-term behaviors, such as risk-sensitive habitat use. Second, prey can modify the conditional probability of being attacked, given an encounter, through shorter-term preventative behaviors, such as vigilance. Immediate responses to threats – such as flight initiation distance and escape speed – will influence the conditional probability of being captured, given an attack. Finally, morphological differences, such as shell thickness (which might affect the amount of damage caused by a shark bite) and foreflipper design (which would influence swimming power), could affect the probability of capture and death. Below we discuss hypotheses for the observed species and sex-class effects on injury frequencies (Fig. 6).
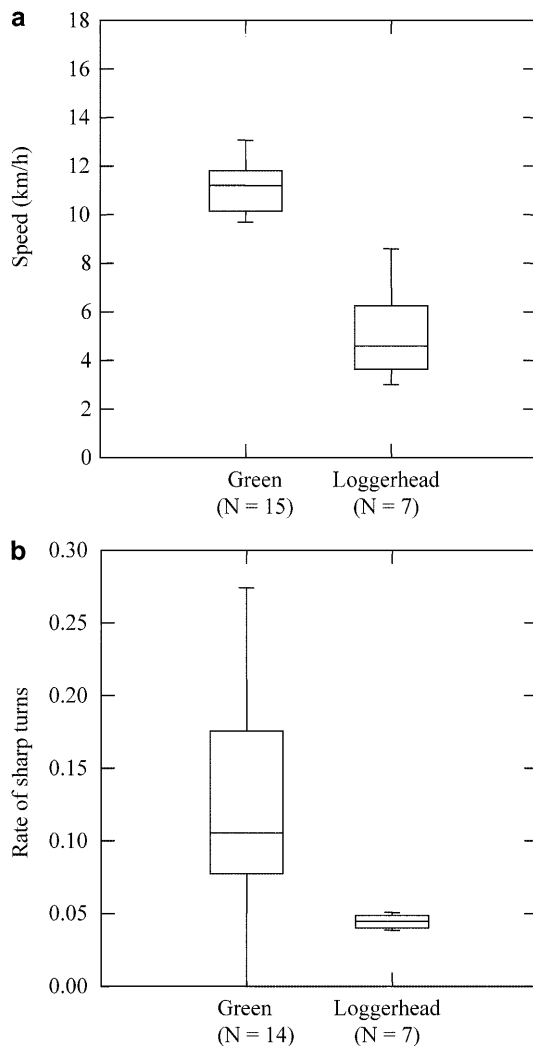
Species differences

There are at least five non-mutually exclusive hypotheses that might provide proximate explanations for species differences in injury frequencies.

1. Differences in injury frequency between green and loggerhead turtles reflect differences in their cumulative probability of encountering a predator.

   Tiger sharks in Shark Bay show a preference for shallow (< 4.0 m) habitats (Heithaus et al. in press; Heithaus and Dill, in press), so a species found in shallow habitats would encounter predators more

Fig. 5 Interspecific comparison of **a** speed and **b** rates of sharp turns ($\geq 90°$) per minute by turtles chased for capture and tagging purposes. Data apply only to shallow habitats, since in deeper habitats observations are precluded by turtles diving deeper to escape. *Boxes* enclose the median (centerline) and 25th and 75th percentiles (boundaries of the box). *Line caps* indicate 10th and 90th percentiles
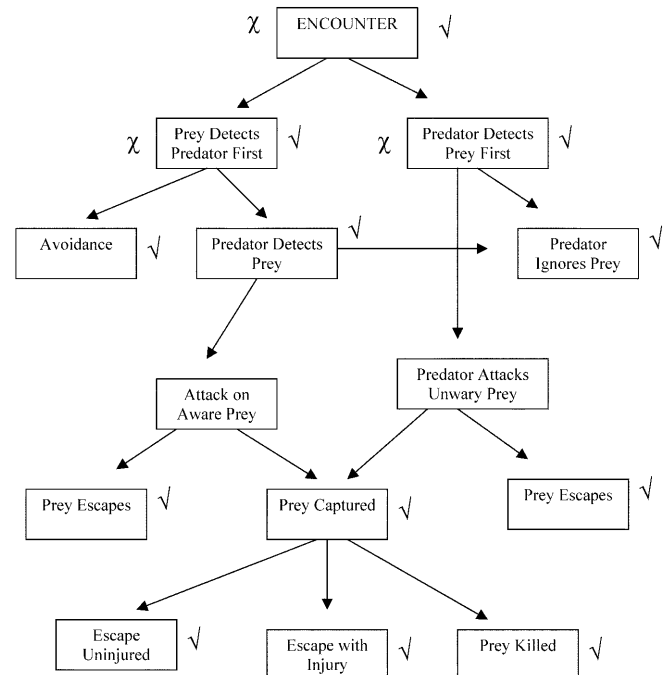

Fig. 6 Possible outcomes of a predator–prey interaction in an encounter situation (modified from Lima and Dill 1990). √ possible explanation of species differences in injury frequencies, χ possible explanation of sex-class differences in injury frequencies

frequently. However, green turtles were found in preferred tiger shark habitats more often than loggerhead turtles, so we reject this hypothesis.

2. Species differences in injury frequencies are due to variation in the probabilities of detecting or being detected by a predator.

Due to countershading and the vertical black stripes on their flanks, tiger sharks are camouflaged when swimming over seagrass habitats, but are highly visible when swimming over sand bottoms (Heithaus et al. in press). Therefore, turtles inhabiting seagrass-covered areas may be less able to detect tiger sharks along the bottom. Green turtles were captured primarily over seagrass, whereas loggerhead turtles were usually captured over sand. Therefore, differences in substrate selection do not seem to explain species differences in injury frequency. However, turtles over seagrass may be less obvious, visually, to sharks than turtles over sand, but sharks do not rely solely on vision for prey detection and it is not obvious whether camouflage of turtles would affect their probability of being detected. Differences in surface intervals between dives and in use of the water column may affect both the probability of detecting a predator and being detected by a predator, as well as susceptibility to predatory attacks (see Strong 1996). These possibilities are the focus of ongoing studies.

3. Sharks prefer a particular species and are more likely to attack it given an encounter.

If tiger sharks prefer loggerhead turtles over green turtles, a higher frequency of injuries might be expected. We have no data to address this possibility.

4. There are species differences in the conditional probability of capture, given an attack.

Differences in speed and maneuverability help explain species differences in injury frequencies. For a given approach distance by a predator, animals that have higher escape speeds are more likely to avoid capture than species with slow escape speeds, due to reduced time required to reach safety (see Ydenberg and Dill 1986; Dill 1990). Although turtles in Shark Bay do not have an absolute refuge from tiger sharks, once they accelerate and can maneuver in the water column they are effectively safe because large tiger sharks have limited maneuverability and generally do not engage in high-speed chases (Heithaus et al. in press). Also, once in the water column, turtles appear to be able to avoid being grasped by sharks by maneuvering their carapace or plastron towards the shark (Marquez 1990; M.R. Heithaus, personal observation). Therefore, the faster and more maneuverable green turtles should be more likely to escape from tiger sharks and thus may suffer fewer injuries than loggerhead turtles.

5. Species differences in injury frequency result from differences in the probability of survival following initial capture.

This problem has been discussed for odontocete cetaceans surviving shark attacks, where differences in injury frequency may be due to differences in the size of odontocetes that are attacked or the size of attacking sharks (Heithaus 2001c). In general, differences in injury frequency have been considered to reflect differences in predation risk only when comparisons are made among odontocete populations or species of similar body size that face threats from similar shark species and size classes (e.g. Heithaus 2001a, c). In this study, green and loggerhead turtles were similar in body size and faced predation threats from the same sharks. The greater swimming power of green turtles compared to loggerhead turtles may result in a higher probability of escape following capture, if the attacking shark does not catch the turtle by a foreflipper. Certainly, green turtles were much more likely than loggerheads to escape the catcher's grasp during this study (M.R. Heithaus and A. Frid, personal observation). Unfortunately, it is impossible to determine conclusively the likelihood of death after capture for either species. However, if we assume equal attack rates on green and loggerhead turtles and that the differences in injury frequencies were the result of differential survival after capture, then green turtles would have to be killed at a rate three times greater than that of loggerhead turtles. This scenario seems unlikely, since captured turtles were of similar sizes and green turtles were faster swimmers than loggerhead turtles.

Scrutiny of the above hypotheses suggests that interspecific differences in injury frequency reflect a higher capture rate for loggerhead turtles, and that better escape ability is a likely proximate explanation for the lower rate of shark injuries on green turtles. However, the question remains as to why, ultimately, green turtles spend more time in higher risk habitats than loggerhead turtles? We suspect that the answer is food. Green turtles feed on seagrass (Bjorndal 1997), which is found mostly in shallow habitats at the study site (M.R. Heithaus, unpublished data). Therefore, green turtles have to spend time in habitats preferred by sharks. Escape ability should be particularly important for turtles in shallow habitats, because there is a lesser space for evasive maneuvers (see Strong 1996), which may have selected for rapid swimming and high manuverability. In contrast to green turtles, loggerhead turtles feed largely on benthic and infaunal invertebrates (Bjorndal 1997), which are found in shallow and in deep habitats. Despite this, loggerhead turtles are attacked much more frequently than green turtles, and it is unclear why loggerhead turtles have not evolved mechanisms to reduce predation risk, such as greater escape ability.

Sex-class differences

We found that male loggerhead turtles had a higher injury frequency than did female and juvenile logger-

head turtles, and this result probably reflects a higher rate of attack on male loggerhead turtles. Males take greater risks than females in many taxa, ranging from sexually dimorphic ungulates (FitzGibbon 1990; Bleich et al. 1997) and marine mammals (Heithaus 2001a; Heithaus and Dill, in press) to insects and fish (Holtby and Healy 1990; Magnhagen 1991). As in the above species, risk-taking may be of greater benefit to the fitness of male than of female turtles. Turtles are slow-growing and long-lived animals, and females lay large clutches of small eggs in discrete nesting bouts which may be separated by several years (Van Buskirk and Crowder 1994). Longevity probably is the primary influence on the lifetime reproductive success of females. Little is known about the reproductive strategies of male loggerhead turtles, but there may be competition for females, and male–male biting and fights have been observed (M.R. Heithaus, personal observation). Therefore, body condition may influence male reproductive success substantially, and males may be willing to accept greater predation risk in order to achieve higher mating success. The following proximate hypotheses might explain differences in shark attack rates between sex-classes of loggerhead turtles:

1. Differences in injury frequencies of loggerhead turtle sex-classes may reflect attacks during reproductive activities.

   Attracting mates and copulating are risky activities for many species (see Gywnne 1989; Lima and Dill 1990, Kålås et al. 1995), and mating groups of turtles may suffer higher attack rates than individual turtles on feeding grounds. Males attempting to mate are likely to be in peripheral positions in the mating group, and consequently suffer more attacks than females at the center of the group. However, there are no data on typical mating-group sizes, so this hypothesis remains speculative. Also, while this hypothesis may explain some variation in injury frequency between sex-classes, fresh wounds observed during our study suggest that a number of attacks occur on the feeding ground.
2. Sex-classes differ in their probabilities of encountering a predator.

   On the feeding grounds, we found no differences between loggerhead turtle sex-classes in average capture depth or substrate. However, since captures were made almost exclusively in shallow water, differences in habitat use were unlikely to be detected.
3. Sex-classes may differ in the probability of detecting or being detected by sharks.

   Since loggerhead turtle sex-classes did not differ in substrate selection, it is unlikely that this would cause sex-class differences in detection probabilities. However, differences in risk-taking behavior on the feeding ground may be manifested as differences in diving behavior which could influence both energy intake rate (e.g. Kramer 1988) and susceptibility to predators (A. Frid, unpublished data).

Why were there no sex-class effects on injury frequencies of green turtles? In this species, reproductive strategies of females seem to be similar to those of loggerhead turtles (Van Buskirk and Crowder 1994), so interspecific differences in risk-taking by females would not be expected. Male green turtles do engage in scramble polygyny and several males may surround a copulating pair (Limpus 1993), but relatively few pairs have attendant males, and intermale aggression appears to be of secondary importance in mating success (Limpus 1993). Furthermore, it appears that males that have major injuries are limited in their reproductive success (Limpus 1993). Therefore, green turtle males might not enhance their reproductive success by being more risk-prone than females. Alternatively, there may be no sex differences in injury frequencies because the escape ability of green turtles generally reduces the relative riskiness of any behavior.

Conclusion

Our data indicate that loggerhead turtles are injured by sharks more frequently than are green turtles, and that male loggerhead turtles are injured more often than females. We argue that injury frequencies reflect capture rates rather than rates of survival following capture. Differences in escape ability appear to be an important proximate explanation for interspecific differences in injury frequency, since green turtles maneuver better and are faster swimmers than loggerhead turtles. The reason for sex-class differences in injury frequencies of loggerhead turtles is unclear, but may reflect greater risk-taking by males. The injury frequencies observed in this study suggest that marine turtles, especially loggerheads, may face a substantial risk of predation from tiger sharks. Since turtles have the potential to influence both the nutrient cycling and the structure of benthic communities (see Bjorndal 1997), understanding turtle responses to predators may be particularly important for understanding community dynamics of systems like Shark Bay, and should be a subject of future investigation.

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