FOOD AVAILABILITY AND TIGER SHARK PREDATION RISK INFLUENCE BOTTLENOSE DOLPHIN HABITAT USE

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Abstract. Although both food availability and predation risk have been hypothesized to affect dolphin habitat use and group size, no study has measured both factors concurrently to determine their relative influences. From 1997 to 1999, we investigated the effect of food availability and tiger shark (*Galeocerdo cuvier*) predation risk on bottlenose dolphin (*Tursiops aduncus*) habitat use and group size in Shark Bay, Western Australia. Food availability was measured by fish trapping, while predation risk was assessed by shark catch rates, acoustic tracks, and Crittercam deployments. Dolphin habitat use was determined using belt transects. The biomass of dolphin prey did not vary seasonally and was significantly greater in shallow habitats than in deeper ones. Tiger sharks were virtually absent during cold months of 1997 and 1998, abundant in warm months of all years, and found at an intermediate density during cold months of 1999. When present, shark density was highest in shallow habitats. Decreased echolocation efficiency in very shallow water and poor visual detection of tiger sharks (camouflaged over seagrass) probably further enhance the riskiness of such habitats, and the relative riskiness of shallow habitats is supported by the observation that dolphins select deep waters in which to rest. The observed dolphin group sizes were consistent with a food–safety trade-off. Groups were larger in more dangerous shallow habitats and larger during resting than during foraging. Foraging dolphins matched the distribution of their food when sharks were absent. However, during warm months, the distribution of foraging dolphins significantly deviated from that of their food, with fewer dolphins foraging in the productive (but dangerous) shallow habitats than expected on the basis of food alone. When shark density was intermediate, habitat use by foraging dolphins was more similar to the high-shark-density seasons than periods of low shark density. These results suggest that foraging dolphin distributions reflect a trade-off between predation risk and food availability. Because the distribution and abundance of tiger sharks are influenced by species other than dolphins, the distribution of the tiger sharks' primary prey may indirectly influence dolphin habitat use, suggesting that it is important to consider the community context in studies of habitat use.

Key words: alternative prey; behavior; bottlenose dolphin (Tursiops aduncus); *group size; habitat use; indirect effects; predation risk; predator–prey interactions; prey availability; seagrass ecosystems; tiger shark* (Galeocerdo cuvier).

INTRODUCTION

Understanding the spatial distribution of animals is a primary goal of ecologists, and determining the factors that are responsible for these distributions is critical to making predictions about how animals will respond to changes in their environment. Both the spatial distribution of food and habitat differences in predation risk may be important in determining animal habitat use (see Lima and Dill [1990] for a review of foraging under the risk of predation). Of particular interest are situations in which the habitats that have high food availability are also the most dangerous, so that animals may have to trade off food and safety when selecting a habitat to occupy.

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In some situations, animals may be distributed across habitats proportional to food availability (e.g., guppies, *Poecilia reticulata* [Abrahams and Dill 1989]; armored catfish, *Ancistrus spinosus* [Oksanen et al. 1995]). However, if predation risk varies among habitats, prey will not necessarily select habitats based solely on energetic return. Instead, individuals are likely to accept lower energetic returns in order to forage in habitats that are relatively safer. Both theoretical (e.g., McNamara and Houston 1990) and empirical studies have shown that this often results in animals undermatching the relative food availability in dangerous habitats (e.g., creek chubs, *Semotilus atromaculatus* [Gilliam and Fraser 1987]; guppies [Abrahams and Dill 1989]; coho salmon, *Oncorhynchus kisutch* [Grand and Dill 1997]). The specific nature of food–safety trade-offs may be influenced by the response of predators to the distribution of their prey (i.e., the foragers) (Hugie and Dill 1994, Sih 1998), the age–sex class of individuals (e.g., Cresswell 1994), and the community context of

interactions (Heithaus 2001*a*). Although the importance of predation risk and food availability have been shown both theoretically and in the laboratory, relatively few field studies, especially those of large-bodied animals, have demonstrated trade-offs between food and safety (but see Werner and Hall 1988, Cowlishaw 1997, Mills and Gorman 1997).

Trade-offs between food and safety are also known to influence the size of animal groups. In general, forming larger groups can be advantageous for reducing the risk of predation, but intraspecific competition often selects for smaller group sizes (e.g., Bertram 1978). For example, a balance of foraging costs (competition) and predation risk can explain group size in primates (Terborgh 1983, Janson and Goldsmith 1995, Hill and Lee 1998).

Risk of predation and food availability have both been hypothesized to influence dolphin habitat use and group size (e.g., Wells et al. 1980, 1987), but no studies have tested these hypotheses. This study investigates the role of tiger shark (*Galeocerdo cuvier*) predation risk and food (fish) availability in determining bottlenose dolphin (*Tursiops aduncus*) habitat use and group size in Shark Bay, Western Australia.

The population of bottlenose dolphins in Shark Bay provides an excellent field system for studying food–safety trade-offs. The dolphins in this area are long lived and are year-round residents within relatively restricted home ranges that encompass numerous habitat patches. Therefore, more than many species, dolphin individuals will have good knowledge of the food availability in various habitats. Furthermore, dolphins are frequently attacked by tiger sharks, and appear to face substantial risk of predation from them (Heithaus 2001*b*). These sharks are not present in the study area at all times (Heithaus 2001*c*) and thus dolphins are exposed to varying levels of predation risk. Finally, because dolphins have low locomotion costs (Williams et al. 1992) and there is no obvious aggression during foraging (M. R. Heithaus, *personal observation*) they should be able to move among habitats relatively freely in response to ecological conditions.

We set out to test the following hypotheses. (1) The distribution of foraging bottlenose dolphins will be determined primarily by the distribution of their food when risk is low, but dolphins will reduce their use of high-risk habitats, relative to food availability, when the risk of predation is increased. (2) Dolphins will select the safest habitats for resting, which is a particularly high-risk activity. (3) The size of dolphin groups will be larger during resting than during foraging. (4) The size of dolphin groups will be larger in dangerous habitats and during dangerous time periods. (5) Dolphin groups will be smaller in habitats with low food availability. In addition to testing these hypotheses, we investigated differences among dolphin age–sex classes in responsiveness to food availability and predation risk.
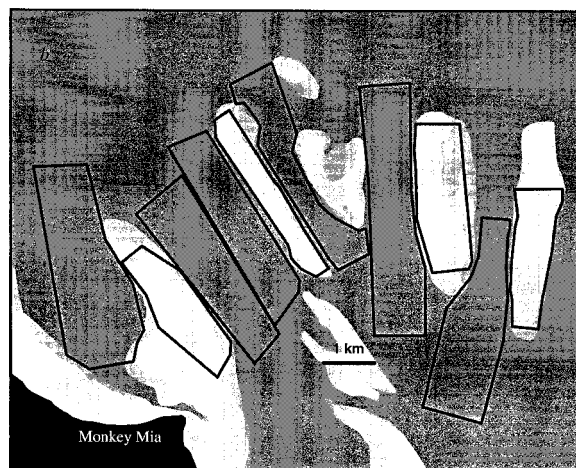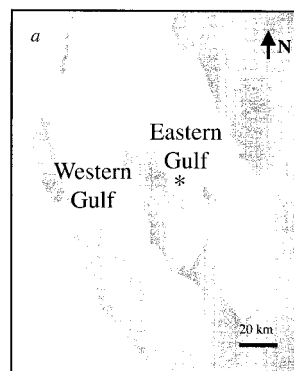

FIG. 1. (*a*) Shark Bay, Western Australia. Monkey Mia is indicated with an asterisk. (*b*) Location of focal zones offshore of Monkey Mia. Lightest shading indicates waters <2 m in depth, and darker shading indicates waters 2–4 m and >4 m. Land is black. Dolphin and fish work was conducted in all zones. Shark fishing did not occur in the two zones closest to Monkey Mia.

METHODS

Study site

Shark Bay is a large, semi-enclosed bay 800 km north of Perth, Western Australia. The study site was located in the Eastern Gulf, offshore of the Monkey Mia Dolphin Resort (~25°45′ S, 113°44′ E, Fig. 1a). It is relatively shallow throughout, with extensive shallow seagrass banks (<4 m depth) surrounded by deeper waters (6–12 m). For the purposes of this paper, habitats have been classified as either shallow (<4.0 m, 17% of study area) or deep (>6.0 m). The boundaries between habitats are generally distinct, and areas 4–6 m deep were omitted from analyses to avoid classification errors. Shallow habitats are predominantly <2.5 m deep, with the bottom covered almost entirely by seagrasses (primarily *Amphibolis antarctica* and occasionally *Posidonia australis*), while deep habitats are primarily >7.0 m and covered by sand or silt. Ten focal zones, representing replicates of these two habitat types, were defined for the purposes of this study (Fig.

1b) and were mapped into a Geographic Information System (GIS, MapInfo Professional version 4.5, MapInfo Corporation, Troy, New York).

Seasonal fluctuations in water temperature influence the community present in Shark Bay (Heithaus 2001c). Water temperatures during warm months (September–May) are generally >20°C, but drop rapidly in mid to late May to a minimum of 14°C in the winter months (June–August). Water temperatures begin to increase in late August. For the purposes of this paper, the data for "warm" (September–May) and "cold" (June–August) months are analyzed separately, and these periods were defined based on both changes in water temperature and in the abundance of many species that, along with dolphins, are prey of tiger sharks; these include dugongs (*Dugong dugon*), turtles (*Caretta caretta* and *Chelonia mydas*), and sea snakes (primarily *Hydrophis elegans*) (Heithaus 2001c). During the cold months of 1999 (June–July), patterns of dugong, turtle, and sea snake abundance were intermediate between those measured in warm months of all years and in cold months of 1997 and 1998 (Heithaus 2001c). Also, during these months in 1999, water temperatures were ~1–2°C higher than for the same dates in 1997 and 1998. There are no major differences in water temperature between habitats, due to the relatively shallow nature of the bay and water mixing by wind and tidal movement (Heithaus 2001c).

Food availability

The abundance and biomass of dolphin prey (teleost fishes) were assessed with Antillean-Z fish traps. Traps were ~1.1 m long, 0.6 m tall, and 0.6 m wide, covered with wire mesh, and had straight, conical entrances (see Sheaves 1992 for a detailed description of trap design). Traps were baited with ~250 g of cut pilchards (*Sardinops neopilchardus*). Bait was placed in a PVC capsule that had numerous 10-mm holes and was capped at both ends, which allowed water to flow easily through the capsule while preventing bait removal by fishes in the trap. Up to 10 traps were set concurrently from an 11-m catamaran. In most cases, traps were set simultaneously, in paired transects (one deep, one shallow) to avoid biases caused by tidal or diel movements of fishes. Traps were spaced ≥80 m apart to avoid overlap in catch radii, which are generally <40 m (Sheaves 1992). Traps were set for ~two hours to maximize catch rate and minimize trap saturation (Sheaves 1995).

When traps were recovered, the fork length (FL) of each fish was measured and a number of individuals of each species were weighed to generate length–mass relationships (Heithaus 2001d) that were used to determine overall catch biomass. Biomass available to dolphins was calculated using all species that dolphins are known to consume. Fish <10 cm FL were removed from biomass calculations since such small fish probably represent a relatively small proportion of dolphin

diets. However, results for seasonal and spatial variation in food available to dolphins does not change with the inclusion of small size classes and all species (Heithaus 2001d).

Predation risk

There are three shark species found in the Eastern Gulf of Shark Bay that are potential dolphin predators: tiger (*Galeocerdo cuvier*), mako (*Isurus oxyrinchus*), and white sharks (*Carcharodon carcharius*) (Connor and Heithaus 1996, Heithaus 2001c, e). Mako and white sharks are rare and probably not a major threat to the dolphins, whereas tiger sharks are common in the study area (Heithaus 2001c). Shark bite scars are found on >74% of adult dolphins in the study area and ≥11% of the dolphin population is attacked unsuccessfully each year (Heithaus 2001b). All attacks by sharks large enough to kill dolphins, where a specific attacker could be identified, were by tiger sharks. Therefore, analyses of predation risk focus on tiger sharks.

Seasonal changes in the risk of predation to dolphins were estimated from tiger shark catch rates, which appear to be an appropriate index of shark density (Heithaus 2001c). Fishing was conducted in eight focal zones (Fig. 1). Up to 10 drum lines, baited with ~1.5 kg of Western Australian salmon (*Arripis truttaceus*), were set in at least two focal zones each fishing day. Lines were spaced ~0.7 km apart and were checked every 2–4 h (see Heithaus [2001c] for a detailed description of methodology). If bait was not present at a check, the bait was considered to be lost half way between the previous check and the time when loss was detected. Because not all size classes of sharks represent a predation risk to the dolphins (Heithaus 2001b), three separate analyses were made for sharks: >300 cm TL, >275 cm TL, and all tiger sharks. These groupings correspond to the estimates of the sizes of sharks responsible for ~75, 90, and 100% of the bite scars and wounds observed on dolphins in the study area (Heithaus 2001b).

Differences in catch rates among habitats are not appropriate for determining shark relative habitat use because of habitat differences in bait removal by species other than tiger sharks and possible habitat differences in the effectiveness of odor corridors (Heithaus 2001c). Therefore, acoustic tracks of tiger sharks were used to estimate shark habitat use and habitat-specific risk to dolphins. Forty-four tiger sharks between 271 and 405 cm TL (336 ± 33.2 cm; mean ± 1 SD) were tracked. Acoustic tracks were performed on sharks using either internally implanted acoustic transmitters (*n* = 8) or an integrated video/tracking package ("Crittercam," National Geographic Special Projects, Washington, D.C., *n* = 36) attached to the dorsal fin with a temporary clamp, or using a Floy tag (Floy Tag, Seattle, Washington USA; see Marshall [1998], Holland et al. [1999], and Heithaus et al. [2001] for de-

TABLE 1. Seasonal and habitat distribution of sample effort.

Sample type	Warm	Cold 1997/1998	1999
Fish trap (sets)			
Shallow	94	70	91
Deep	159	137	93
Dolphin habitat use (transects)			
Shallow	165	102	57
Deep	209	174	88
Tiger shark			
Hours†	3474	1808	1044
Tracks	38	1	5

† Number of hours baits were set during shark fishing.

scriptions of these techniques). Sharks were tracked from a 4.5-m research vessel, using a directional hydrophone and acoustic receiver, for periods ranging from 1 to 13 h (3.0 ± 2.4 h). Boat GPS location, habitat, depth, and estimated direction and distance to the shark were recorded every 5 min. For the purposes of this paper, tracks were truncated when sharks left the study area. Shark tracks were started in both shallow ($n = 11$) and deep habitats ($n = 33$). However, many sharks that started in shallow habitats ($n = 6$) switched habitats within the first 10 min, and all sharks used multiple focal zones during tracks, so results regarding habitat use by sharks are not dependent on the starting point of tracks. Individual sharks were tracked only once.

Dolphin habitat use, behavior, and group size

Dolphin habitat use and group size were investigated using belt transects and dolphin group surveys. Transects were positioned in the middle of focal zones and a sighting belt extended 500 m to either side of the transect except where the transect line was within 500 m of another focal zone or habitat (Fig. 1b). Three observers drove along the transect in a 4.5-m boat at 6–9 km/h. Transects were only included in analyses if they were conducted in Beaufort wind conditions of 2 or less, with the majority occurring in Beaufort 0 or 1 conditions. This was done to ensure that there was minimal variation in sighting efficiency with distance from the transect and among days. Beaufort 0 conditions refer to flat water with no wind rippling. Beaufort 1 conditions are those with flat water with slight ripples caused by wind, and Beaufort 2 conditions include those with wind-induced chop but with no whitecaps visible. The order and direction in which transects were driven were haphazard, to minimize the influence of tidal and diel patterns on these data. A total of 795 transects was completed from 1997 to 1999 (Table 1).

Upon sighting a group of dolphins along a transect, the GPS position on the transect was marked, and we departed the transect line to survey the group. Data on group size, composition, and behavior were recorded along with environmental information. Individual iden-

tifications of dolphins were made using distinctive patterns of nicks and cuts out of the dorsal fin (e.g., Smolker et al. 1992). Once a survey was completed, we returned to the point of departure and resumed driving along the transect. The GPS locations of all dolphin groups were mapped into the GIS, and groups outside of focal zones were omitted from subsequent analyses.

Behavioral categories included foraging, resting, socializing, traveling, and unknown. Groups were defined by a 10-m chain rule (Smolker et al. 1992), with all dolphins within 10 m of another dolphin considered to be part of a group. When not all individuals in a group were engaged in the same behavior, the number of dolphins in each behavioral state was recorded. Dolphins making multiple dives in the same location, surfacing rapidly when not interacting with other dolphins, engaging in rapid chases of fish, or observed with a fish at the surface were considered to be foraging. Resting dolphins moved slowly, usually did not maintain a specific direction of travel, and often floated at the surface for several seconds to over a minute. Socializing was often observed in association with other behaviors, with several dolphins in the group engaging in rubbing. Only groups engaged in intense social activity, which included aggressive behavior, sexual behavior, or chasing were classified as social groups. Dolphins were considered to be traveling only when they maintained a consistent heading at a speed >2 km/h. Dolphins traveling slowly could either be resting or foraging, and thus were classified as ''unknown'' to avoid errors. Analyses of activity-specific habitat use and group size were restricted to foraging and resting, which were the least ambiguous behavioral states and the ones for which we have a priori predictions regarding predation risk–food availability trade-offs (e.g., Heithaus 2001e).

Statistical methods

For most analyses, data were combined for warm months and for cold months of 1997 and 1998, because environmental conditions and the abundance of tiger sharks and their primary prey species were similar (Heithaus 2001c). Data from the cold season of 1999 were analyzed separately from those of 1997/1998 because of both qualitative and quantitative differences in the abundance of tiger sharks and their primary prey species, and water temperature (Heithaus 2001c). Tiger shark habitat use data were analyzed both (1) pooled to increase sample size and because most tracks occurred during warm months (Table 1), and (2) with warm months and cold months of 1999 separated. Dolphin group size data were lumped into warm and cold months, which increased sample sizes to allow comparisons of activity- and habitat-specific variation in group size. Data were analyzed using JMP IN 4.0.3 (SAS Institute 2000).

Habitat and seasonal differences in the biomass of potential dolphin prey were investigated with ANOVA. Season and habitat were treated as fixed effects and

class variables. Data were $\log(x + 1)$-transformed to homogenize variances, which we checked with Bartlett's test (Zar 1984). Nonsignificant interactions ($P > 0.10$) were removed from analyses.

Seasonal changes in catch rates of tiger sharks for all three size classes were analyzed using chi-square. This was accomplished by comparing the number of sharks captured in each season with the number expected based on fishing effort. The expected number of sharks for a season (i) was generated with the equation

$$\text{Expected}_i = \frac{N \times H_i}{H_T}$$

where N is the total number of sharks caught during the seasons being compared, H_i is the number of hours that baits were set during season i, and H_T is the total number of hours baits were set for all seasons in the comparison. Tiger sharks were rarely recaptured, and we only included the first capture of an individual in analyses.

Shark habitat use was tested by comparing the relative number of 5-min location fixes inside each habitat type to the expected number of fixes based on relative availability of habitats in the study area. The first position fix of a track was excluded from analyses. Less than five fixes were expected in a particular habitat for some sharks, so a G test was used to test for a deviation from random habitat use. To avoid pseudoreplication, habitat use was measured using the number of fixes for each shark in a particular habitat as a single data point (Turchin 1998). Thus, the degrees of freedom were determined by the number of sharks tracked, not the overall number of 5-min position fixes.

Tiger sharks exhibit a ''bouncing'' pattern of swimming through the water column during which they repeatedly move between the surface and the bottom (Heithaus et al., *in press*). It is possible that sharks would not detect prey throughout the entire water column when in deep habitats, but likely would be able to do so in shallow habitats. Therefore, in calculating the relative use of habitats by tiger sharks, habitat availability was determined in two manners, surface area and volume. Volume measurement assumed that deep habitats were only twice as deep as shallow ones, on average. Since deep habitats are generally more than twice as deep as shallow ones, the availability of shallow habitats to sharks is likely overestimated, and thus, the relative use of shallow habitats is an underestimate in analyses using volume.

The effects of season and habitat on dolphin density were analyzed using ANOVA. Analyses were carried out separately for foraging and resting dolphins. Season and habitat were considered fixed effects and class variables. In order to avoid biases associated with variation in the number of passes along a transect in a season, data on dolphin densities were collapsed into a

single mean density for each transect in each season. Therefore, dolphin density was calculated by dividing the number of dolphins sighted on a transect within a season by the total area of that transect that was surveyed. In order to measure foraging-dolphin habitat use relative to food availability, we calculated dolphin density in each transect relative to habitat area and fish abundance with

$$\text{Relative Density}_i = \frac{n_i}{P_i \times A_i \times F_i}$$

where n_i is the number of dolphins sighted on a transect in a particular season, P_i is the number of times the transect was sampled, A_i is the area of the transect (square kilometers), and F_i is the relative biomass of fish caught in the transect. F_i was calculated by dividing the mean biomass of fish captured in a transect by the lowest mean biomass obtained in any transect. This measure of relative density assumes that, if food is the only factor influencing the distribution of foraging dolphins, they should be distributed across habitats relative to the standing stock of food resources. Although there is a theoretical basis for this prediction (Lessels 1995), it is not possible to determine if dolphins conform to all the assumptions of this model. However, this measure is still useful in providing a null model for comparing changes in dolphin distribution, relative to their food, with changes in the risk of predation (e.g., van Baalen and Sabelis 1993). All data were $\log(x + 1)$-transformed to homogenize variances, which were checked using Bartlett's test (Zar 1984). All nonsignificant interactions ($P > 0.10$) were removed from analyses. Tukey's test, which corrects for multiple comparisons, was used to determine significant differences among means in the case of interactions.

Although analyses included repeated sightings of the same individuals (see *Results*), this should not bias the results of this study. First, it is important to sample the same individuals in different seasons. Otherwise, any patterns observed might be due to sampling different sets of individuals, rather than to a set of individuals shifting their habitat use. Within seasons, we sampled a large number of individuals with relatively few resightings of each ($\bar{x} = 1.9$ sightings per season for an individual each year) suggesting that independence assumptions of statistical tests are unlikely to be problematic. Also, to avoid non-independence problems, no individual dolphins were counted more than once in a single day. Samples of the same individual on separate days are relatively independent, as most individuals move among focal zones several times within a single day, and group composition changes frequently throughout a day (Smolker et al. 1992; M. R. Heithaus, *unpublished data*). Finally, analyses were also carried out on the number of groups in each habitat. All patterns were identical between analyses based on the number of groups and those based on individuals, so
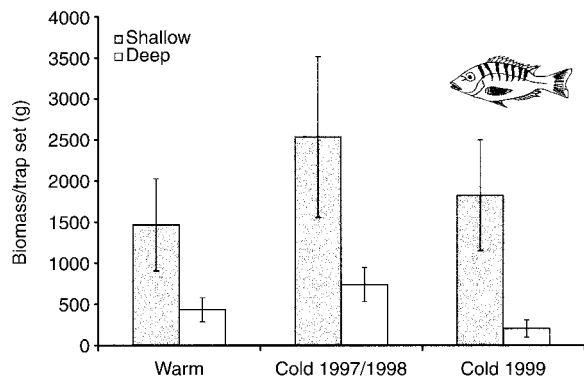
FIG. 2.   Distribution of fish biomass. Fish biomass per trap does not change seasonally but is always greater in shallow habitats. Error bars represent 95% confidence intervals.
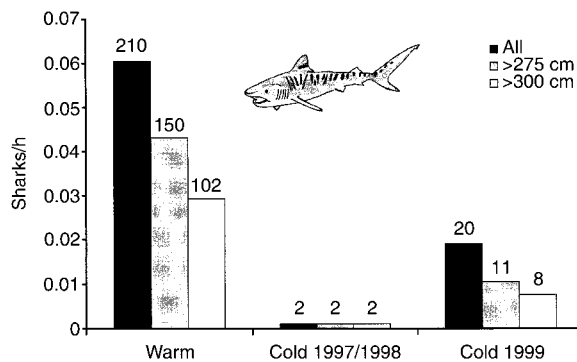

FIG. 3.   Seasonal changes in tiger shark catch rates. Note that the catch rate, and thus predation risk to dolphins, is high in warm months, very low in cold months of 1997/1998, and intermediate during the cold months of 1999. The numbers above the bars represent the number of sharks caught.

only analyses using the number of individuals are presented. However, the similarity of results suggests that nonrandom group formation by dolphins is not responsible for the habitat use patterns observed in this study.

Differences in habitat use among dolphin age–sex classes were investigated with contingency chi-square tests using the number of individuals sighted in deep and shallow habitats within a particular season. All P values were Bonferroni corrected for multiple comparisons.

The effects of season, activity, and habitat on dolphin group size were investigated with ANOVA. Data were square-root transformed to normalize and checked for homogeneity of variances. Tukey's test was used to determine significant differences among means in the case of interactions.

RESULTS

Food availability

Fish traps ($n = 644$) were set for 1347 h (Table 1). A total of 12 667 fish were captured, representing 31 species; dolphins were observed consuming 20 of these during survey observations. The biomass of potential dolphin prey was only influenced by habitat, with significantly higher biomass per trap found in shallow habitats than in deep ones (ANOVA, $n = 644$ sets, df $= 1, 619, F = 60.5, P < 0.001$; Fig. 2). There was no significant effect of season on fish biomass (ANOVA, $n = 644$ sets, df $= 2, 619, F = 1.0$, NS).

Predation risk

Shark baits were set for 6326 h (Table 1), resulting in 252 tiger shark captures. There were significant seasonal changes in catch rates within the study area for all three tiger shark size groupings. Shark abundance was extremely high during all warm seasons, very low during cold months of 1997 and 1998, and intermediate during cold months of 1999 (all: $\chi^2 = 124.6$, df $= 2$, $n = 252, P < 0.001$; >275 cm: $\chi^2 = 92.9$, df $= 2$, n

$= 163, P < 0.001$; >300 cm: $\chi^2 = 60.7$, df $= 2$, $n = 112, P < 0.001$; Fig. 3). There were significantly more sharks present during the 1999 cold months than those of 1997/1998 (all: $\chi^2 = 28.0$, df $= 1$, $n = 22, P < 0.001$; >275 cm: $\chi^2 = 12.9$, df $= 1$, $n = 13, P < 0.001$; >300 cm: $\chi^2 = 8.1$, df $= 1$, $n = 10, P < 0.01$).

Acoustic tracking of 44 tiger sharks revealed a consistent overuse of shallow habitats (Fig. 4). Tiger sharks were found in shallow habitats almost twice as often as expected based on habitat surface area, and over four times more often than expected based on the volume of available habitats (surface area: $G = 325.3$, df $= 43, P < 0.001$; volume: $G = 655.1$, df $= 43$, $P < 0.001$). Tiger sharks were found in shallow habitats significantly more often than expected during both warm months (surface area: $G = 250.2$, df $= 37, P < 0.001$; volume: $G = 517.3$, df $= 37, P < 0.001$) and the cold months of 1999 (surface area: $G = 74.3$, df $= 4, P < 0.001$; volume: $G = 137.8$, df $= 4, P <$
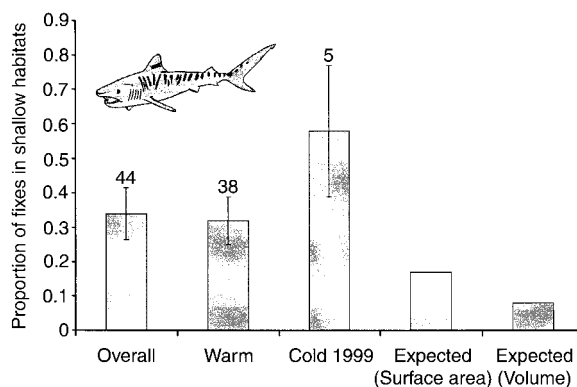

FIG. 4.   Tiger shark use of shallow habitats relative to the availability of these habitats based on surface area and volume. Tiger sharks are found in shallow habitats much more often than expected. Error bars represent 95% confidence intervals. The numbers above the bars represent the number of sharks tracked.

TABLE 2. Analysis of variance of the effect of season and habitat on the density of foraging dolphins.

Factor	df	F	P
Season	2	8.1	<0.001
Habitat	1	5.2	<0.05
Season × habitat	2	8.6	<0.001
Error	52		

Note: The analysis is based on 1205 dolphin sightings from 795 transect passes.

TABLE 3. Analysis of variance of the effect of season and habitat on the density of foraging dolphins relative to fish biomass.

Factor	df	F	P
Season	2	0.3	0.73
Habitat	1	20.5	<0.001
Season × habitat	2	5.1	<0.01
Error	52		

Note: The analysis is based on 1205 dolphin sightings from 795 transect passes.

0.001). There were insufficient data ($n = 1$) from cold months of 1997 and 1998 to address this question.

Dolphin habitat use and behavior

A total of 3826 dolphins were sighted during transects. Of these 1205 were foraging, 1713 resting, 330 socializing, and 439 traveling. There were 300 known individuals sighted (3493 sightings) and several unidentifiable individuals (333 sightings). Most individuals (232, 77.3%) were sighted during both warm and cold seasons, and those sighted in only one season were rare.

Dolphin habitat use was activity specific and changed seasonally. The density of foraging dolphins was influenced by an interaction between season and habitat (Table 2). Dolphin density was highest in shallow habitats during the cold months of 1997/1998 and lowest in shallow habitats during warm months (Fig. 5). The density of foraging dolphins relative to the biomass of potential prey was also influenced by an interaction between season and habitat (Table 3). In this case, the density of foraging dolphins relative to food was the same in shallow and deep habitats during the cold months of 1997/1998 (Fig. 6). In contrast, the density of dolphins relative to food was significantly higher in deep habitats than in shallow ones during warm months and the cold months of 1999 (Fig. 6).
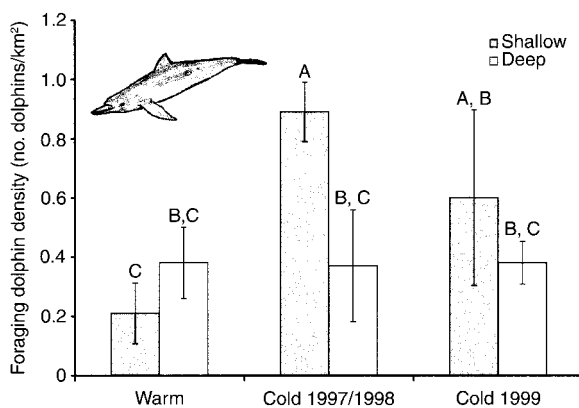
The density of resting dolphins was influenced by an interaction of season and habitat, but there was a strong effect of habitat (Table 4). During all seasons, the density of resting dolphins was significantly higher in deep habitats. The lowest densities of resting dolphins were found in shallow habitats during warm seasons (Fig. 7).

There was only one significant difference among age–sex classes in foraging habitat use during warm months. Juvenile males were found foraging in shallow habitats more often than were adults ($\chi^2 = 6.0$, df = 1, $n = 67$, $P < 0.05$). In cold months, there were no significant differences in habitat use between adult males and adult females accompanied by calves, adult males and females without calves, or between adult females with and without calves. However, juvenile males were found foraging in shallow habitats more often than adults ($\chi^2 = 7.6$, df = 1, $n = 107$, $P < 0.05$) and juvenile females ($\chi^2 = 11.9$, df = 1, $n = 88$, $P < 0.01$).

Dolphin group size

Dolphin group size was significantly influenced by habitat, with significantly larger groups found in shallow habitats ($n = 222$, 3.40 ± 0.16 dolphins; mean ± 1 SE) than in deep ones ($n = 813$, 2.91 ± 0.07 dolphins;

FIG. 5. Seasonal changes in habitat use of foraging dolphins. Bars labeled with the same letter are not significantly different ($P > 0.05$). Analysis was carried out on $\log(x + 1)$-transformed data. Error bars represent 95% confidence intervals.
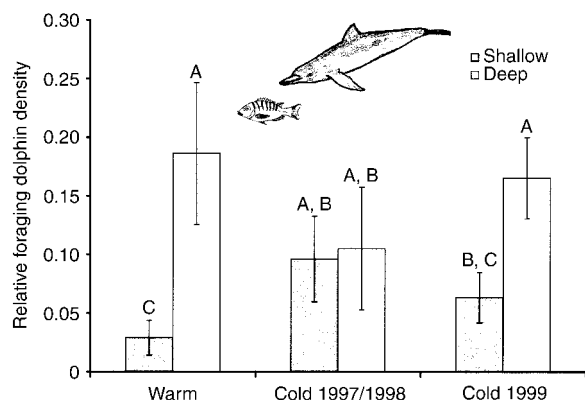
FIG. 6. Seasonal changes in habitat use of foraging dolphins relative to food availability. Relative foraging dolphin density is calculated as (no. dolphins/km² × relative fish biomass). Bars labeled with the same letter are not significantly different ($P > 0.05$). Analysis was carried out on $\log(x + 1)$-transformed data. Error bars represent 95% confidence intervals.

TABLE 4. Analysis of variance of the effect of season and habitat on the density of resting dolphins.

Factor	df	F	P
Season	2	0.7	0.51
Habitat	1	45.9	<0.001
Season × habitat	2	4.8	<0.025
Error	52		

Note: The analysis is based on 1713 dolphin sightings from 795 transect passes.

TABLE 5. Analysis of variance of the effect of season, habitat, and activity on the size of dolphin groups.

Factor	df	F	P
Season	1	5.3	<0.05
Habitat	1	9.0	<0.01
Activity	1	668.8	<0.001
Season × activity	1	4.2	<0.05
Error	1030		

Note: The analysis is based on 1035 groups.

Table 5). Group size was also significantly affected by an interaction of season and activity (Table 5, Fig. 8). Regardless of season, resting groups were larger than foraging groups (Fig. 8). There was no significant difference in the size of foraging groups found in warm and cold months, but the size of resting groups was significantly larger in warm months (Fig. 8). Within cold months, foraging groups in shallow habitats ($n = 158$, 2.1 ± 0.10 dolphins) were larger than those in deep habitats ($n = 241$, 1.4 ± 0.08 dolphins; $t = 4.42$, df $= 398$, $P < 0.001$).

DISCUSSION

We found that bottlenose dolphins faced spatial and temporal variation in predation risk, and spatial variation in the abundance of food resources. The biomass of potential dolphin prey was higher in shallow habitats during all seasons and did not vary significantly with season. However, tiger sharks were abundant during warm months, almost absent during the cold months of 1997 and 1998, and caught at intermediate rates in the cold months of 1999. When sharks were present, shark density, and thus predation risk to dolphins, was higher in shallow habitats. And although less volume must be scanned for sharks in shallow habitats (e.g., Norris and Dohl 1980a), these habitats are likely to be intrinsically riskier than deeper ones. First, tiger sharks are better camouflaged when swimming over the sea-

grass characterizing much of the shallow habitats than when swimming over the light sandy bottoms of the deep habitats. Therefore, visual detection of predators would be more difficult in the shallows than in deeper water despite slightly lower light levels in the latter. Second, dolphin echolocation is likely to be less efficient in very shallow waters due to the scattering of the clicks off the surface and bottom. Also, biological noise (e.g., sounds produced by snapping shrimp) is more frequent and louder in shallow habitats than deep habitats (M. R. Heithaus, *personal observation*), which could further reduce echolocation efficiency (Au 1993). Thus, acoustic detection of predators may be more difficult in shallow habitats than in deep ones. Finally, the probability of dolphins escaping a shark attack may be greater in deep habitats because there are more potential escape routes than in shallow habitats.

Dolphin behavior supports our conclusions regarding spatial and temporal variation in the risk of predation. Resting is probably the most dangerous activity that dolphins engage in because of reduced vigilance at this time (Würsig et al. 1994, Connor and Heithaus 1996, Heithaus 2001e) and the lack of a refuge from predators. Since dolphins have low travel costs (Williams et al. 1992), and there is no benefit to staying in dangerous areas, dolphins should rest in the safest habitats (Heithaus 2001e), especially during seasons when predators
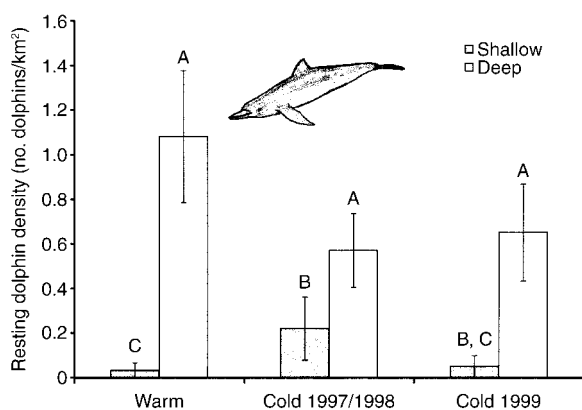
FIG. 7. Habitat use of resting dolphins. Bars labeled with the same letter are not significantly different ($P > 0.05$). Analysis was carried out on log($x + 1$)-transformed data. Error bars represent 95% confidence intervals.
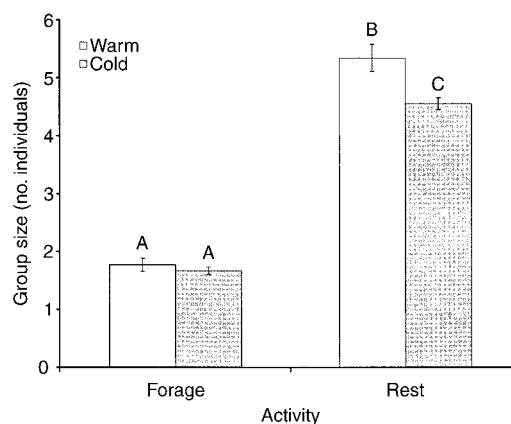
FIG. 8. Mean size of dolphin groups engaged in resting and foraging during both warm and cold months. Bars labeled with the same letter are not significantly different ($P > 0.05$). Analysis was carried out on square-root transformed data. Error bars represent 95% confidence intervals.

are common. Such activity-specific habitat use has been observed in other species. For example, desert baboons (*Papio cynocephalus ursinus*) avoid all habitats but the safest while resting (Cowlishaw 1997), and Hawaiian spinner dolphins (*Stenella longirostris*) move into shallow coves with white sand bottoms to rest during the day, probably to avoid shark predators (Norris and Dohl 1980*a*). Dolphins in this study rested almost exclusively in deep waters, suggesting that these are perceived as the safer habitats. Despite underuse of shallow habitats for resting in all seasons, the observation that dolphins increase their use of shallow habitats for resting in cold months suggests that there are no intrinsic reasons, other than risk, for dolphins to avoid shallow waters for this activity.

Both food availability and the risk of predation from tiger sharks influence habitat use by foraging dolphins in Shark Bay. During cold months, when tiger sharks are largely absent, the habitat use of foraging dolphins appears to be driven primarily by food distribution. Foraging dolphins were found in the food-rich shallow habitats much more often than in deep habitats, and the proportion of dolphins in deep and shallow habitats matched the proportion of fish biomass in those habitats.

Both theoretical and empirical studies (e.g., Abrahams and Dill 1989, McNamara and Houston 1990, Hugie and Dill 1994, Heithaus 2001*a*) lead to the prediction that dolphins should decrease their use of dangerous (i.e., shallow) habitats relative to food availability during high risk seasons if they trade off food and safety. Indeed, when tiger sharks were present in the study area, dolphins did not match the distribution of their food quantitatively or qualitatively. During warm months dolphins were found in dangerous shallow habitats much less often than expected from food availability, indicating that predation risk is an important determinant of dolphin habitat use. The cold months of 1999 provide a natural experiment to test whether dolphins trade off food and safety. While food availability, and presumably other factors, during the cold months of 1999 were similar to previous cold seasons, there were tiger sharks in the study area, presenting a regime of predation risk more similar to previous warm seasons. Dolphins increased their use of shallow habitats relative to warm months, but habitat use by foraging dolphins relative to the distribution of food resources during the cold months of 1999 more closely resembled those of warm seasons and was different from those of other cold seasons. This provides strong support for the conclusion that differences in habitat use among seasons are due to a food–safety trade-off rather that some unmeasured variable, and that dolphins are able to adaptively modify their habitat use patterns in response to changes in predation risk.

Previous studies have hypothesized a role of both predation risk and prey availability in shaping patterns of dolphin habitat use. For example, habitat use of At-

lantic bottlenose dolphins (*Tursiops truncatus*) in Sarasota, Florida has been hypothesized to reflect a trade-off between food availability and predation risk, with dolphins selecting shallow habitats to avoid encounters with bull sharks (*Carcharhinus leucas*) (Wells et al. 1980, 1987). Ours is the first study to show that both predation risk and food availability play a significant role in determining the distribution of an odontocete cetacean. Furthermore, this study shows that dolphins may adaptively switch their habitat use patterns with changes in the level of risk.

Despite abundant laboratory evidence, few field studies have shown that animals trade off predation risk and food availability, especially in systems where direct experimental manipulations are not possible. Experimental work has shown that small mammals stop foraging in risky habitats at higher remaining food availability than they do in safe habitats (e.g., Brown et al. 1992), and ontogenetic habitat shifts in bluegill sunfish (*Lepomis macrochirus*) are influenced by foraging rate and the density of predatory largemouth bass (*Micropterus salmoides*) (Werner and Hall 1988). Several observational field studies have also shown food–safety trade-offs. Desert baboons appear to trade off food availability and predation risk, and they spend less time foraging in high-risk and high-food habitats than expected from food availability alone (Cowlishaw 1997). In South Africa, wild dogs (*Lycaon pictus*) are found in low densities in areas with high food availability (small ungulates) but high predator (lion, *Panthera leo*) density (Mills and Gorman 1997). Wild dogs are found in the highest densities in areas with low predator density and lower food abundance.

Theoretical models suggest that the presence of alternative resources for top predators can have a substantial influence on the habitat use of their prey, resulting in indirect behavioral effects between prey species that do not compete with each other (Heithaus 2001*a*). This applies in the Shark Bay ecosystem. Tiger sharks in this area consume primarily dugongs, sea snakes, and sea turtles, but also include rays, sea birds, and teleosts in their diet (Heithaus 2001*c*, Simpfendorfer et al. 2001). Dolphins are a minor component of the sharks' diets despite being attacked frequently (Heithaus 2001*b*). Tiger shark seasonal abundance and habitat use are linked to both water temperature and temporal and spatial variation in the availability of their main prey (Heithaus 2001*c*, Heithaus et al., *in press*). Therefore, dolphin habitat use is at least partially influenced by seasonal movements and habitat use decisions of species with which they do not interact directly, but share a common predator (i.e., decisions made by dugongs, sea snakes, and sea turtles that influence the distribution of tiger sharks; M. R. Heithaus, *unpublished manuscript*). This situation provides a behavioral analog to apparent competition (Holt 1977, 1984).

Complex trophic interactions characterize many food

webs (e.g., Polis 1991, Polis and Strong 1996), and indirect behavioral effects on habitat use, like those described for dolphins, may be common. For example, wild dog distribution appears to be indirectly affected by the distribution of large ungulates, which influences the distribution of their shared predator, lions (Mills and Gorman 1997). Such indirect behavioral effects may function in a similar manner to trophic cascades (e.g., Pace et al. 1999). Because of the possibility of ''behaviorally mediated indirect interactions'' in many communities that contain top predators with diverse diets, field studies of animal habitat use may benefit from taking community and food web structure into account. The possibility of behaviorally mediated indirect interactions in Shark Bay and other communities is an intriguing possibility that warrants further investigation.

Juvenile male dolphins were found to enter shallow habitats more often than other age–sex classes during both warm and cold months, suggesting that juvenile males are more willing to accept higher predation risk to obtain higher energy intake rates. A similar age class difference in risk-taking behavior while foraging has been found in redshank (*Tringa totanus*) where juveniles attempt to maximize energy intake by foraging in high-risk areas of salt marshes where energy intake rate is high, while adults are found in low-risk mussel bed habitats with low energy intake rates (Cresswell 1994). Risk-taking by juvenile redshank may facilitate early breeding (Creswell 1994), and juvenile male dolphins may also gain fitness benefits from risk-taking. In Shark Bay, adult males form alliances that aggressively maintain consortships with reproductive females (Connor et al. 1992, 1999). Foraging in the energetically profitable shallow habitats may increase the growth rate of juvenile males relative to those foraging in deeper waters. Increased growth rates and larger body size may facilitate earlier alliance formation or increase ability to compete for access to females at a relatively young age. Further studies will be required to test this hypothesis.

Reproductive success of female bottlenose dolphins in Shark Bay is negatively correlated with water depth, as females found, on average, in shallow waters have more calves survive until weaning (Mann et al. 2000). Mann et al. (2000) proposed that this trend may be a result of shallow water providing some protection from predatory sharks through increased detection and avoidance. That cetaceans obtain protection from predators in shallow waters has been proposed several times (Norris and Dohl 1980*a,* Wells et al. 1987), but the relationship between water depth and risk is unclear (e.g., Heithaus 2001*e*). If predation risk were reduced in shallow habitats of Shark Bay, female dolphins with calves should be found predominantly in shallow habitats during both foraging and resting in high-risk months, but this is not the case. Instead, female dolphins accompanied by calves avoid shallow waters dur-

ing months of high shark density, suggesting that higher female reproductive success in shallow habitats in Shark Bay is not due to reduced predation risk. A more likely explanation for the trend in female success is that females found, on average, in shallower water would be able to take advantage of much higher food availability in shallow habitats during foraging, but then move into deeper and safer habitats during rest. Such adaptive switching between habitats based on activity would allow individuals to benefit from low predation risk in deeper habitats and high energy intake in shallow ones when required. Females found exclusively in deep waters are perhaps less likely to meet the energetic demands of lactation and thus have higher calf mortality rates. Also, if energy intake by mothers inhabiting deep habitats is low, this may lead to an increased predation rate on their calves. To fully understand the reasons for differential female reproductive success, it will be necessary to determine the relative frequency of the causes of calf mortality.

A fission–fusion social organization, like that of bottlenose dolphins in Shark Bay (Smolker et al. 1992), allows individuals to select their group size based on ecological conditions and activity. Predation risk has been hypothesized to be the primary reason for group formation in dolphins (Norris and Dohl 1980*b*), but food availability may also be important. Group size of bottlenose dolphins in Sarasota, Florida appears to represent a trade-off between energy intake and risk (Wells et al. 1980, 1987) and group size data from Shark Bay are generally consistent with expectations based on such a trade-off. As predicted, resting groups were larger than foraging groups, suggesting that dolphins must form smaller groups during foraging to reduce competition. Also consistent with predictions, the sizes of resting groups were responsive to changes in predation risk, as resting groups were larger in the more dangerous warm months than in the safer cold months. Dolphin group sizes in Shark Bay also appear to be responsive to food availability. In low-risk months, foraging group size was higher in the more productive shallow habitats. However, this result is also consistent with the hypothesis that groups were larger because of higher risk in shallow waters, even though overall shark density was low.

This study has several important implications for the conservation of nearshore odontocete cetaceans. Dolphins and porpoises are increasingly having to contend with human disturbance in the form of habitat alteration, reductions in prey species populations, and boating activity. This study suggests that human disturbance that changes the habitat use of species that share a common predator with dolphins may change dolphin habitat use through a behaviorally mediated indirect interaction. Also, human disturbances or activities that dolphins perceive as predation risk have the potential to alter dolphin habitat use and reduce population size, as observed in other species. For example, human dis-

turbance of Pink-footed Geese (*Anser brachyrhynchus*) results in an underuse of available resources and diminishes the number of individuals a disturbed habitat supports (Gill et al. 1996). If human disturbance, like boating activity (e.g., Allen and Read 2000), is greatest in high productivity habitats, it is possible that dolphins will not make full use of their food resources, effectively reducing the carrying capacity of the environment. Such disturbance may also cause shifts in dolphin habitat use that increase their encounter rates with natural predators and thus increase mortality rates.

This study is the first to show that both food availability and predation risk influence dolphin habitat use. Dolphins adaptively reduce their use of high-risk high-food habitats based on the presence of tiger sharks. Future studies on dolphins, in areas that differ from Shark Bay in food distribution and predation risk, can incorporate the framework and methods developed during this study to elucidate the role of predation risk and food availability in the evolution of sociality and behavior of small odontocetes.

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