

Gregarious Behavior of Nesting Turtles (*Carettochelys insculpta*) Does Not Reduce Nest Predation Risk

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Gregarious behavior among oviparous female animals just prior to oviposition can be explained by several mechanisms, including a benefit to offspring survival. By clustering eggs together in one area, females may dilute the probability of egg predation. We tested the hypothesis that nest density influences egg survival in the Pig-Nosed Turtle (*Carettochelys insculpta*) along a river in northern Australia. Beaches with multiple nests were three times more likely to experience a predation event than beaches with single nests. However, the number of nests on a beach did not influence the probability of predation of individual nests, when considering either beaches with single versus groups of nests, or when comparing beaches with single nests, small groups of nests ($n = 2-5$), and large groups of nests ($n = 6-8$). Therefore, gregarious behavior of reproductive females during the nesting period did not dilute predation risk to nests. Four other hypotheses might explain the behavior: (1) nesting areas are limited; (2) nesting in groups dilutes predation risk to nesting females; (3) nesting in groups dilutes predation risk to hatchlings; and (4) social interactions in aggregations of nesting females provide additional information on nesting beaches/sites, reducing some cost associated with independent assessments of nesting beaches/sites.

GREGARIOUS behavior among reproductive females has been observed in a variety of animals including reptiles (for a classic example in turtles, see Carr, 1967) and may be attributable to several mechanisms. First, nesting aggregations may arise incidentally if good quality nesting areas are rare relative to the density and movements of females, resulting in multiple females independently selecting the same area to be the best available to them (e.g., Shine et al., 1997). Second, females may aggregate to dilute any increase in predation risk associated with nesting (e.g., Hughes and Richard, 1974). Third, and similarly, gregarious nesting behavior may provide a mechanism by which females can ensure their nests are placed near others to dilute predation risk to nests or offspring (e.g., Robinson and Bider, 1988; Eckrich and Owens, 1995; Spencer, 2002). Finally, interactions among females in nesting aggregations may provide them with additional information about potential nesting sites via knowledge of the movements and decisions of other females, thereby reducing the costs associated with independent assessments of nesting areas.

Pig-Nosed Turtles (*Carettochelys insculpta*) often feed, thermoregulate, and nest in groups (Doody et al., 2001, 2002). During the nesting season females have been observed aggregating in groups of up to 12 in the water near a nesting beach, and such groups are also known to move together between potential nesting beaches (JSD, unpubl. data). Although typically only 1–

3 females will nest on the beach each night (Doody and Georges, 2000), over several days the group gives rise to multiple nests (up to 16) on the chosen beach (Doody et al., 2003b). Females interact with one another in the water when in these aggregations, and some females partially emerge from the water to inspect the sand at the water's edge where other females have emerged (JSD, unpubl. data).

Herein we test a prediction of the nest predation dilution hypothesis for gregarious behavior in *C. insculpta*, by determining the influence of nest density on the probability of nest predation. Support for this prediction would indicate that female *C. insculpta* may benefit from aggregations by placing their nests near other nests to reduce nest predation risk. We use survival records of a large number of nests along a large stretch of river over three years to test the influence of the number of nests on a beach on nest predation risk. We also examined any influence of nest elevation and lay date on the probability of survival, because these factors could interact with nest density. We discuss the applicability of other potential mechanisms for gregarious nesting behavior to *C. insculpta*.

MATERIALS AND METHODS

We surveyed for *C. insculpta* nests along an approximately 95 km stretch of the Daly River, Northern Territory, Australia, during 1996–1998. Two river stretches were surveyed at dif-

ferent intensities. The first “intensive” stretch (approximately 30 km) was surveyed daily for nests from July to October. The second “extensive” stretch (approximately 65 km) was surveyed 11 times in 1997 and nine times in 1998. Each two-day survey of this stretch was approximately 9–12 days apart and spanned the entire nesting season for the year. Both types of survey involved searching for nesting beaches by motorboat.

Pig-Nosed Turtles at the site lay two clutches of eggs on sandy banks and beaches during the dry season (July to October; Georges, 1992; Doody et al., 2003a,b). We searched for nests by searching for tracks in the sand and probing for eggs. Nests in the intensive stretch were conspicuous because of the presence of fresh tracks. To ensure all nests were located in the extensive stretch, all suitable nesting beaches were systematically searched with the probe. Nests were scored as destroyed by predators when both eggshells and an empty nest chamber were found. In the intensive stretch, we protected nests from predators with squares of wire mesh (0.3 m on a side). However, we scored nests as destroyed by predators when a clear attempt to excavate the nest was evident (diggings on and around the protective cover).

To examine other spatial and temporal influences on the probability of predation, we also measured height and distance from water of each nest; the lay date was estimated based on the patch size of the egg (Ewert, 1985; Beggs et al., 2000). Each nest was marked with a stake to avoid double counting. In some cases, clutches were taken for laboratory experiments. However, because most predation on turtle nests occurs within 24 h of the lay date (JSD, unpubl. data for *C. insculpta*; reviewed for other species in Spencer, 2002), and because nests were removed after this time, we considered removed nests to have escaped predation.

We used a Contingency Analysis to determine whether the probability of at least one nest predation event occurring on a nesting beach was influenced by whether the beach contained a single nest or a group of nests. We then used Student's *t*-tests to examine the influence of the number of nests on a beach on the probability of a given nest experiencing predation. First, we compared mean predation probabilities between nests that occurred singly and those that occurred in groups of up to eight nests. Next, we compared the predation probabilities among nests in three group sizes: single (1 nest), small group (2–5 nests), and large group (6–8 nests). Although these are artificial categories, visual inspection of the data indicated that these catego-

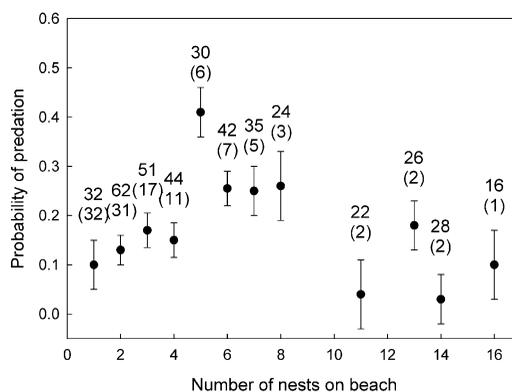


Fig. 1. The probability of nest predation as a function of nest group size. Data are means \pm 1 SD. Numbers over bars are sample sizes of nests and (beaches).

ries maximized our chance of detecting biologically significant trends. We excluded group sizes > 8 in all analyses because of low sample size of beaches for each.

We used single-factor ANOVAs to examine the influences of lay date and elevation on nest survival, and we coded lay date to facilitate those analyses. Missing data for some destroyed nests precluded the use of multivariate analyses. Data were transformed where necessary to facilitate statistical analyses.

We tested to see whether the frequency of nesting on beaches followed a random expectation. Because we were uncertain of the number of nesting banks that were suitable but not used as opposed to the number that were not used because they were unsuitable, we fitted the frequency of occurrence of nests to a zero-truncated Poisson distribution.

RESULTS

We found 412 nests on 119 beaches during the study, of which 32 beaches contained single nests and 87 beaches contained groups of nests (Fig. 1). A total of 69 nests (16.7%) were destroyed by predators (Table 1). Tracks near the destroyed nests indicated that monitor lizards (*Varanus panoptes*, *Varanus mertensi*) were the predators (see also Doody et al., 2003b).

Beaches with multiple nests were more likely to experience a predation event than beaches with single nests ($\chi^2_1 = 6.12$, $P = 0.013$). Thirty-four percent of beaches with multiple nests experienced a predation event, compared to 11% for beaches with single nests. However, group size did not influence the probability of predation of a given nest (Fig. 1), when considering either single versus group nests ($\chi^2_1 = 1.72$, P

TABLE 1. NUMBERS OF *Carettochelys insculpta* NESTS FOUND AND PROPORTION DESTROYED BY MONITOR LIZARDS DURING 1996–1998.

Year/stret	#	#	# destroyed	% destroyed
1996 intensive	13	66	15	23
1997 intensive	16	46	3	7
1998 intensive	20	75	8	11
1997 extensive	33	86	15	17
1998 extensive	34	138	28	20
Totals	116	413	69	16.7

= 0.19), or when dividing nests into single, small group ($n = 2-5$ nests), and large group ($n = 6-8$ nests; $\chi^2_2 = 3.24$, $P = 0.20$). There was good evidence of aggregation of nests, indicated by a very substantial deviation from expectation under the zero-truncated Poisson distribution ($\chi^2 = 56.97$, $df = 6$, $P < 0.0001$).

Lay date did not differ significantly between destroyed nests and intact nests (t -test using square-root transformed lay dates; $t = -1.23$, $df = 101.4$, $P = 0.22$). The probability of predation was independent of year ($\chi^2_2 = 2.36$, $P = 0.31$). Elevation of destroyed nests did not differ significantly from that of intact nests (t -test using square-root transformed elevation; $t = -0.62$, $df = 31.4$, $P = 0.54$).

DISCUSSION

The highly clumped distribution of *C. insculpta* nests indicates that some factor causes females to nest together. Beaches with groups of nests were more likely to experience a predation event than beaches with single nests. However, the number of nests on a beach did not influence the probability of a given nest being destroyed by a predator. Therefore, the probability of a monitor lizard finding a turtle nest was independent of the presence of surrounding nests, with the resulting risk reflecting the additive risk of multiple nests, each with similar risk.

The number of nests on a beach is essentially a measure of nest density at the beach scale. Burke et al. (1998) reviewed studies of nest density effects on predation rates for turtles, finding mixed results. No experimental data exist, but natural nests within 1 m of other nests experienced significantly higher predation than more isolated nests in two turtle species (*Malaclemys terrapin*, Burger, 1977; *Chelydra serpentina*, Robinson and Bider, 1988). Similarly, Spencer (2002) found that destroyed *Emydura macquarii* nests were closer to other nests than were intact nests. In a study of *Lepidochelys olivacea* not con-

sidered by Burke et al. (1998), predation of arribada (synchronous, group) nests was significantly lower than that of solitary nests (Eckrich and Owens, 1995). However, other studies on turtles found no influence of density on predation rates or the probability of predation (*Chelonia mydas*, Fowler, 1979; Brown and Macdonald, 1995; *Pseudemys concinna*, *Trachemys scripta*, *Kinosternon subrubrum*, Burke et al., 1998). The diversity of patterns may reflect variation in predator foraging strategies, including the ability of predators to habituate to nesting beaches, and locate and consume several nests. The high metabolic rate of monitor lizards (Christian et al., 1995), coupled with evidence of habituation to nesting beaches (JSD, pers. obs.), suggests that the lack of an effect of nest density on predation risk is not caused by an inability of monitors to exploit this food resource. Instead the generalist foraging strategy of monitor lizards (Vincent and Wilson, 1999) may explain the lack of an effect. Because nest density at the beach scale does not influence nest predation risk in *C. insculpta*, and indeed some other turtle species, females apparently cannot achieve benefits in nest survival by placing their nests on beaches with other nests. Therefore, the nest predation dilution hypothesis is rejected for *C. insculpta* and is unlikely to hold as a general explanation for gregarious nesting behavior in turtles.

What other mechanism could explain the gregarious nesting behavior observed in *C. insculpta*? Females at the study site typically have an average of five (range = 2–7) suitable nesting beaches within their home ranges (Doody et al., 2002), indicating that the aggregations are not a result of (nesting) resource limitations. Beach locations vary among years because of wet-season flooding, and nest suitability may change between the first and second nesting (Doody et al., 2003b), suggesting that beach homing behavior is unlikely to be important in this system. Although there is no benefit to nest survival through clumping of nests, it is possible that the behavior results in dilution of predation risk of hatchlings, as noted for mass emergences of sea turtle hatchlings (Carr and Hirth, 1961). However, unlike sea turtles, hatchling *C. insculpta* generally emerge singly (Doody et al., 2001), suggesting there has been little selection for predator swamping during hatchling emergence.

Alternatively, the behavior may be an adaptive response to reduce the risks and costs to mothers associated with nesting. Available evidence suggests it is unlikely that the behavior evolved as a mechanism to dilute predation risk to nest-

ing female *C. insculpta*. We have failed to find evidence of such predation events (e.g., remains of shells) in seven years of field study at the site, despite the fact that predators often leave behind shells (Seigel, 1980), which are resistant to postmortem deterioration (Bodie and Semlitsch, 2000). Although females are wary when on nesting beaches, indicating they perceive some risk associated with nesting (Bouksila and Blumstein, 1992), remote camera systems revealed that females seldom cluster on the nesting beach (Doody and Georges, 2000), thereby failing to dilute any terrestrial predation risk.

A final explanation for gregarious behavior near nesting predicts not only that females aggregate in the water near nesting beaches, as has been observed in a few other turtle species (Pritchard and Trebbau, 1984) but also that they interact with one another to gain information about the movements and decisions of other females. Social assessment of potential nesting areas could reduce costs associated with independent assessment of those areas, including time and energy spent searching for beaches and nest sites, and, for the highly aquatic *C. insculpta*, risk of injury on soft underparts from terrestrial excursions.

Observations of the same females moving together along the river during the nesting season, and females nuzzling the sand where other turtles have emerged onto a beach (Doody et al., 2002; JSD, unpubl. data), suggests that females may assess the movements and nesting decisions of other females. Using this socially gathered information females may reduce the number of emergences required to find a suitable nest site by (1) only emerging onto beaches that they know other females have nested upon, and (2) avoiding beaches other females have made unsuccessful emergences upon. An incidental observation made during attempts to document the nesting behavior of *C. insculpta* provides some evidence for this. The beach targeted for observations was visited repeatedly on consecutive nights by a nesting aggregation until on one night an emerging female was disturbed by an observer. The group appeared to respond to this female's assessment by disbanding, then reforming the following few nights near another beach approximately 1 km downstream, as evidenced by remote camera photographs of marked individuals (Doody and Georges, 2000). These females continued to nest at the new site over the next few nights. To our knowledge, the other females did not directly detect the observer.

Our data suggest that the nest predation dilution hypothesis does not explain gregarious

behavior associated with nesting in *C. insculpta*. Our findings reiterate the suggestion of Burke et al. (1998) that nest density is not a generalizable predictor of the probability of nest predation in turtles. We suggest that the observed social interactions in *C. insculpta* nesting aggregations lend support for the social assessment hypothesis, whereby females use information gathered about the decisions of other females, to reduce the costs associated with independent nest site assessments. Although our evidence for this hypothesis is limited, this role of social interactions in nesting aggregations of turtles needs further exploration.

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