How depth alters detection and capture of buried prey: exploitation of sea turtle eggs by mongooses

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Predators are an important source of mortality for animals that lay their eggs in buried nests. We asked how depth alters the process of predation for buried prey. We outlined a general model of predation risk where depth may alter both prey detection and subsequent capture: deeper prey are detected less often because the strength of olfactory cues decreases with burial depth and, once detected, are further protected by the costs of digging. Using this framework, we examined how burial depth influenced egg predation for critically endangered hawksbill sea turtles (Eretmochelys imbricata) by introduced mongooses (Herpestes javanicus) in Barbados. We tested the effects of nest depth on detection and subsequent predation using observational data on hawksbill nests over a 2-year period and an experiment with artificial nests. For both real and artificial nests, depth had little effect on nest detection by mongooses, but once detected, shallower nests were much more likely to be preyed on. Mongooses appear to use depth-invariant surface cues to detect nests but increase digging persistence in response to olfactory cues. We argue that excavation cost is an important but overlooked mechanism protecting deeply buried resources. For reptiles with buried nests, the relationship between depth and predation risk leads to important predictions about how changes to nesting habitat or the predator community will affect egg survival and offspring sex ratio. More generally, identifying the mechanisms by which burial depth protects prey is essential for understanding how resource burial strategies evolved and are maintained in predator–prey systems. Key words: cache recovery, conservation, hatching success, Herpestes auropunctatus javanicus, invasive species, temperature-dependent sex determination. [Behav Ecol 20:1299–1306 (2009)]

Many animals bury valuable resources. Rodents and carnivores often bury food in shallow caches for future consumption (Vander Wall 1990). Other species, including many reptiles and invertebrates, protect their reproductive investment by concealing eggs in underground nests (e.g., Cornelius 1986; Reale and Roff 2002; Iverson et al. 2004). Such buried resources become easy prey for any animal capable of locating and gaining access to them. One of the proposed benefits of burial is the reduction of predation risk without the necessity of active guarding (Vander Wall 1993). Factors that influence access to buried resources are therefore expected to have a strong effect on predation risk.

One of the principal factors expected to affect predation of buried resources is the depth of burial. There is good evidence that burial depth reduces recovery and theft of buried seed caches by rodents (Lockard RB and Lockard JS 1971; Reichman and Oberstein 1977; Vander Wall 1993; Geluso 2005), and predation of buried mollusks and other marine prey by birds is also negatively related to depth (Richardson 1985; Zwarts et al. 1996). The effect of depth on predation risk is assumed to rely on the lowered probability that predators will discover the buried resource; once detected, the resource is often very vulnerable. Effects of depth on prey detection are well supported by the literature on seed predation, where detection depends primarily on olfactory cues (Vander Wall 1998, 2000; Geluso 2005) that decrease in strength with depth (Reichman 1981). In some cases, however, the resource may be protected by the costs to the predator of excavating buried prey (Vander Wall 1993). These costs are likely to be especially important for deeply buried prey or predators with limited digging capacity. However, the possible effects of depth on aspects of foraging other than detection, including excavation, removal, and handling of buried prey, have received relatively little attention (but see Lockard RB and Lockard JS 1971; Richardson 1985; Ward and Saltz 1994). Distinguishing the underlying mechanisms relating burial depth to predation risk is important for understanding the nature of predator–prey interactions and has implications for the evolution of burial behavior. In particular, resource burial strategies and optimal burial depth are likely to depend strongly on whether depth affects the ability of predators to detect prey, to access detected prey, or both.

Viewing predation as a sequence of foraging behaviors, each with an associated probability of occurrence, provides a useful framework for exploring the roles of different possible mechanisms linking depth with predation. Lima and Dill (1990) developed a general model of the predation process, identifying several distinct components of predation risk. A simplified version of their model, adapted for predation of buried prey, considers that when a foraging predator encounters a buried prey, the probability of prey mortality, d, is the product of the probability that the buried prey is detected, q, and the probability that, once detected, the prey is successfully excavated or captured, c:

\[ d = qc. \]  

Using this framework, we identify 4 broad categories for the mechanistic relationship between burial depth and predation.
Where concealment increases with depth but prey of all depths are easily accessible, detection mechanisms will dominate. This is the likely scenario for theft of shallow seed caches by rodents of the same or similar sized species (Vander Wall 1998, 2000). On the other hand, where cues for prey detection are independent of depth, but excavation is costly, capture mechanisms will dominate. We might expect this scenario where surface cues provide a reliable indication of prey location, but deeply buried prey are more costly to excavate or more likely to evade capture (Richardson 1985; Ward and Saltz 1994). Third, where depth has no effect on prey concealment and costs of excavation are trivial, we expect no relationship between depth and predation. This type of scenario is probably common where animals use spatial memory to retrieve food from shallow caches (Devenport et al. 2000). Finally, there may be many circumstances where depth affects both detection and capture, and predation is influenced by a combination of these mechanisms.

Nest predators are an important source of egg mortality for many animals with buried nests, and this is particularly well-documented for reptiles (Stancyk 1982; Spencer and Thompson 2003). Buried eggs may remain undefended for months in some species, and protective effects of deeper burial therefore have the potential to increase nest survival substantially. However, we are aware of no studies of how depth affects the process of predation for buried eggs. Many nest predators are thought to rely primarily on smell to locate eggs (Stancyk 1982; Cornelius 1986), suggesting that burial depth may influence nest detection by obscuring olfactory cues. However, in contrast to scatter-hoarded food that is generally buried in shallow caches and requires minimal digging effort to recover, burial depth for nests is often substantial and digging may be costly. We therefore predicted that depth would affect both detection and capture of buried eggs by nest predators.

We asked how nest depth affects the process of predation for buried sea turtle eggs. We studied predation by the small Asian mongoose (Herpestes javanicus E. Geoffroy Saint-Hilaire), an introduced predator, on the nests of critically endangered hawksbill sea turtles (Eretmochelys imbricata Linnaeus) in Barbados, West Indies. Sea turtles provide an excellent model system for studying predation of buried eggs because nests are easily located by researchers and can be monitored throughout development. We measured depths of hawksbill nests over 2 nesting seasons (2004–2005) and assessed the effects of nest depth on detection and subsequent predation of hawksbill nests by mongooses. We then used artificial nests to confirm the effects of depth experimentally and to explore the role of visual and olfactory cues in nest detection and predation.

**MATERIALS AND METHODS**

**Species and study area**

The study was carried out at Bath (13.187°N, 59.476°W), the primary nesting beach for hawksbill sea turtles on the east coast of Barbados. Hawksbill nesting is confined to the area between the high water mark and barriers associated with a beachside road and cottages 10-50 m inland. Approximately 60% of the nesting area is open beach: sandy areas lacking ground vegetation or leaf litter using their clawed forepaws. Other than crabs and insects that sometimes infiltrate the nest and may damage or remove a portion of the clutch, mongooses are the sole predator of turtle eggs at our site.

**Hawksbill nest monitoring**

We collected data on hawksbill nesting at Bath in 2004 and 2005, with morning beach surveys carried out daily from May to September. Nests laid the previous night were located using fresh disturbances of sand and vegetation left by the nesting turtle. The presence of eggs was confirmed through careful excavation by hand of sand directly above the eggs following a standard international protocol (Schroeder and Murphy 1999). Nest depth was measured using a tape measure (±0.5 cm) as the distance from the sand surface to the top of the egg mass (Limpus et al. 1985). The excavated sand was replaced and the site concealed by scattering loose sand over the cavity, packs down the sand, conceals the location by scattering loose sand over the site, and returns to the ocean. Incubation lasts about 60 days and hatchlings emerge at the sand surface a few days after hatching.

The small Asian mongoose (H. javanicus) was introduced to many Caribbean islands for rat control in the late 1800s and has become an important predator of sea turtle nests (Nellis and Small 1983; Hays and Conant 2007; Leighton et al. 2008). Individual home ranges overlap extensively, and, in areas such as Bath, where anthropogenic food is abundant, local densities can exceed 10 animals/ha (Nellis and Everard 1983; Leighton 2005). Mongooses are strictly diurnal but avoid contact with humans and generally restrict their foraging to vegetated areas of the beach (Leighton et al. 2008). They have a good sense of smell and dig readily for prey hidden in sand or leaf litter using their clawed forepaws. Other than crabs and insects that sometimes infiltrate the nest and may damage or remove a portion of the clutch, mongooses are the sole predator of turtle eggs at our site.

**Artificial nest experiment**

Artificial nests were constructed by disturbing a 50-cm radius area to simulate disturbance created by a nesting turtle (crushed vegetation, displaced ground litter, and scattered sand), digging a 15-cm diameter cylindrical hole in the center of the disturbed area using a post hole digger, placing five 8-g pieces of sausage and an indicator flag in the bottom of the hole, refilling the hole using the excavated sand, packing down the sand, and applying approximately 5 ml of sausage scent (intended to provide an olfactory cue analogous to those left on the sand surface by a nesting turtle) evenly to the surface of the sand in a 30-cm radius around the hole using a plastic spray bottle. The indicator flag consisted of a 15-cm piece of orange flagging tape anchored to the bottom of the nest hole by a 60-cm piece of thin nylon string tied to a buried stick. Pilot trials showed that indicator flags sitting on top of buried bait were consistently pulled out of the nest when the bait was removed but not before. Sausage scent was created by boiling sausages in water for 1 h, removing the broth and storing it frozen in 200-ml samples that were thawed overnight at 4 °C for use the following day. Although we do not believe that...
sausage is directly related to the scent of turtles or eggs, a previous study showed that buried sausage is a useful model system for assessing patterns of predation risk for hawksbill nests (Leighton et al. 2008).

Each trial involved 20 artificial nests placed in vegetated habitat at 1 of 6 sites along the beach. Each site consisted of a continuous patch of vegetation growing along the berm (mean patch area ± standard deviation [SD]; 355 ± 63.8 m²). Each site was divided into 4 contiguous blocks, with 5 nests per block and each nest assigned a different treatment: 15-cm deep nests, 30-cm deep nests, 45-cm deep nests, “disturbance-only” (disturbance and a 30-cm hole with an indicator flag but no bait or sausage scent), and “smell-only” (sausage scent applied to undisturbed sand). Nests were assigned random coordinates within each block. All nests were created 2–10 m inland from the seaward edge of vegetation because turtles at Bath rarely nest more than 10 m into vegetation, and predation risk decreases near the edge (Leighton et al. 2008). Density of baited nests (mean ± SD; 0.035 ± 0.007 nests/m²; 0.058 ± 0.013 nests/m² with disturbance-only and smell-only treatments included) was similar to the density of incubating hawksbill nests (excluding hatched nests and failed nesting attempts) in vegetation at the peak of the nesting season (0.027 nests/m² in 2005).

Between 11 April and 5 May 2006, we ran 2 series of trials at each of 6 different sites along the beach for a total of 240 nests. All artificial nests at a given site were created the same day between 9 AM and 12 noon. Nests were deployed at a new site each day. A second series of trials was conducted at each site 10 days after the first series.

Artificial nests were checked after 6 h, 24 h, and 7 days for evidence of detection (superficial excavation < 10 cm deep), extensive digging (substantial excavation > 10 cm deep), and predation (indicator flag pulled out, bait removed) by mongooses. To measure variation in mongoose activity among sites, we used track pads, 0.7 m patches of natural sandy sub-stratum smoothed to record tracks of passing animals (Leighton et al. 2008). We created 3 track pads at each site, with pads set 1.5 m inland from the seaward edge of vegetation and 20 m apart. We cleared all track pads daily at 12 noon and checked for tracks at 5 PM. We used the total number of mongoose trails crossing the tracking surface of all 3 pads per hour of exposure as an index of local mongoose activity.

All artificial nests were removed at the end of the experimental period, and the substrate was characterized using 3 binary variables: presence of rocks (>1 cm diameter), presence of roots intersecting the nesting cavity, and high or low soil moisture as indicated by the cohesion of the sand lifted between the 2 blades of the post hole digger.

Statistical analyses

We used a series of regression models to explore the influence of nest depth on detection and predation of hawksbill nests by mongooses. We used logistic regression to test the effect of depth on predation risk (δ = the probability of nest predation over the 60-day incubation period) and the 2 components of predation risk described in Equation 1: detection (q = the probability of detection over the 60-day incubation period) and capture (ε = the probability of predation following detection). Data were coded as 1 if the event occurred and 0 if it did not. We tested the effect of depth on predation latency (days between laying and predation) and its components: detection latency (days between laying and detection) and capture latency (days between detection and predation) using ordinary least squares regression and log-transformed latency measures. In addition, we used ordinary least squares regression to test whether hawksbill nest depth was affected by microhabitat type (vegetation vs. open beach), nesting date, and year.

For artificial nests, we used generalized linear mixed models (GLMMs) to assess the influence of nest depth on predation over the 1-week monitoring period using data from the 15-, 30-, and 45-cm deep nests and including site as a random effect. As with hawksbill nests, we examined the effect of depth on predation risk and its components: detection and capture. We modeled predation risk after 6 h, 24 h, and 7 days to explore how the relationship between depth and risk changed over time. We tested the effect of depth on detection latency and predation latency using the time period in which detection or predation occurred as an ordinal response variable (1 = 0–6 h, 2 = 6–24 h, 3 = 24 h to 7 days). Distance to the vegetation edge, date of nest construction, site-specific mongoose activity during the 1-week monitoring period, and substrate characteristics (presence of rocks, roots, and moist sand) were included as additional predictors in all models. Before being included in models, predictors were tested for strong collinearity (variance inflation factor [VIF] was <3 in all cases indicating little collinearity) and standardized (mean = 0, SD = 1) to allow meaningful comparison of regression coefficients (Quinn and Keough 2002).

We assessed the relative importance of disturbance and olfactory cues during different stages of the predation process by comparing “disturbance-only”, “smell-only”, and 30-cm treatments. We used GLMMs to test the effect of treatment on the probability of detection, extensive digging (>10 cm deep), and predation after 7 days of exposure and the maximum excavation depth attained by mongooses during this period. All analyses were carried out using R v. 2.7.2 (R Development Core Team 2008).

RESULTS

Hawksbill nest depth and predation

We obtained depth measurements for 258 hawksbill nests at Bath in 2004 (n = 79) and 2005 (n = 179). Depth to the top of the egg mass ranged from 0 (eggs exposed) to 55 cm (mean ± SD; 29.5 ± 9.0 cm). Nests in vegetation were shallower than nests on the open beach (mean ± SD; vegetation: 25.9 ± 8.5 cm; open: 31.8 ± 8.6 cm; t = 4.9, P < 0.001), and the depth of nests at laying decreased slightly over the nesting season (slope = -0.032 cm/day, t = -1.2, P = 0.05). Microhabitat and date effects did not interact significantly (t = 1.0, P = 0.32), and nest depths did not differ between years (t = -0.54, P = 0.59).

Our previous research showed that risk of mongoose predation is much higher for nests in beach vegetation than for those on the open beach (Leighton et al. 2008). To ensure that the relationship between depth and predation risk was not confounded by shallower nests in vegetated microhabitats, we restricted our analyses of depth effects to hawksbill nests in vegetation (n = 101).

Mongooses detected 78 (77.2%) and preyed on 63 (62.4%) of hawksbill nests laid in vegetation. Predation risk was inversely related to egg burial depth (Figure 1), dropping from nearly 90% for exposed eggs to around 30% for 45-cm deep nests (Z = -2.56, P = 0.011, deviance explained = 5.4%, n = 101; Figure 1a). The probability of mongooses detecting a nest was not significantly related to depth (Z = -1.42, P = 0.15, deviance explained = 1.9%, n = 101; Figure 1b); however, deeper nests were less likely to be preyed on after detection (Z = -2.19, P = 0.029, deviance explained = 6.9%, n = 78; Figure 1c).

The majority of nest detection and predation events occurred early in incubation with 37 (36.6%) nests detected and 16 (15.8%) preyed on within the first 24 h, whereas
We found no significant relationship between depth and predation latency ($t = 0.86, P = 0.39, n = 62$), detection latency ($t = 0.82, P = 0.42, n = 78$), or latency to predation following detection ($t = -0.93, P = 0.35, n = 62$).

**Artificial nest experiment**

At 1 of 6 sites (site 6), both series of artificial nests remained untouched by mongooses throughout the entire experiment; therefore, only nests from the remaining 5 sites were used in analyses ($n = 200$). Track pads at site 6 received a mean ± SD of $0.19 ± 0.26$ mongoose visits per hour which was significantly lower than the mean of $0.47 ± 0.41$ for the other 5 sites (Poisson GLM: $Z = -2.80, P = 0.005, n = 266$).

Of the 120 artificial nests containing sausage, 114 (95.0%) were detected, 101 (84.2%) received extensive digging, and 51 (42.5%) were successfully preyed on by mongooses. Predation risk for artificial nests decreased sharply with nest depth (Table 1 and Figure 2). Predation increased quickly over time for 15-cm nests, reaching 97.9% after 1 week, rose more gradually to 95.6% for 30-cm nests, and remained close to 90% for 45-cm nests (Figure 2a). As with hawksbill nests, the probability of nest detection was unrelated to depth (Figure 2b) and the strongest effect of depth was in the final phase of nest predation where, once detected, shallower nests were much more likely to be reached and successfully preyed on (Figure 2c). Of the other predictors included in the model, only the position of nests relative to the seaward edge of vegetation had an important effect, with an increased risk of predation following detection for nests nearer to the edge.

As with hawksbill nests, the majority of predation on artificial nests occurred soon after the nests were created, with 20 (16.7%) preyed on within the first 6 h and 40 (33.4%) within the first 24 h of exposure (Table 1). Thus, 85.1% of all detections and 78.4% of predations occurred in the first 14.2% of the period of availability. We found no significant effect of depth on detection latency, but shallow nests were preyed on significantly more quickly than deeper nests (Table 2). Nests created in later trials were detected and preyed on more quickly by mongooses, and detection latency was lower for nests located far from the seaward edge of vegetation. Although detection tended to occur earlier when mongoose activity was higher, there was no relationship between average local mongoose activity during the 1-week monitoring period and predation risk.

Overall, mongooses did not dig in response to sausage scent in the absence of disturbance (Figure 3a, “smell-only”) but did dig in response to disturbance in the absence of olfactory cues (Figure 3a, “disturbance-only”). The probability of detection was equivalent for 30-cm and disturbance-only treatments (30 cm vs. disturbance-only: $t = 0.00, P = 1$), but the probability of detection for the smell-only treatment was significantly lower (disturbance-only vs. smell-only: $t = 6.35, P < 0.001$). The probability of extensive digging was significantly lower for the disturbance-only treatment than for 30-cm nests (30 cm vs. disturbance-only: $t = 2.31, P = 0.02$) and much lower for the smell-only treatment (disturbance-only vs. smell-only: $t = 3.92, P < 0.001$). For comparison with 30-cm nests, disturbance-only and smell-only nests were considered preyed on when mongooses dug to a depth of 30 cm. This rarely occurred, and the probability of predation for 30-cm nests was much higher than for disturbance-only and smell-only treatments (30 cm vs. disturbance-only: $t = 3.88, P < 0.001$ and disturbance-only vs. smell-only: $t = 0.00, P = 1$). The maximum depth reached by digging mongooses also differed considerably among treatments (Figure 3b). Mongooses dug to an average depth of 16 cm for 30-cm nests but averaged only 11 cm for the disturbance-only treatment (30 cm...
vs. disturbance-only: $t = 4.35, P < 0.001)$. Excavation for the smell-only treatment was rarely more than a 1-2-cm deep scuff mark (disturbance-only vs. smell-only: $t = 8.10, P < 0.001$).

**DISCUSSION**

**Deep burial protects eggs from predation**

Our study confirms that, over the range of depths at which hawksbill turtles bury their eggs, deeper burial greatly reduces the risk of mongoose predation. An increase in depth from 15 to 45 cm for a hawksbill nest corresponds to a reduction in predation risk from 78.3% to 31.9%. Although protective effects of deep burial are not surprising given similar trends in rodents exploiting scatter-hoarded seeds (e.g., Vander Wall 1993) and crows feeding on intertidal clams (e.g., Richardson 1985), our study is the first demonstration that depth reduces vulnerability of buried eggs to excavation by predators. The combination of observational and experimental data provides strong evidence of a causal link between nest depth and predation risk in this system. Similarly, 2 recent studies have found that deeper sea turtle nests also have a reduced probability of infestation by dipteran larvae (McGowan et al. 2001; Hall and Parmenter 2008).

**Effects of depth on detection**

The process of nest construction by sea turtles produces numerous potential cues that could allow mongooses to discover the nest regardless of its depth. These include visual and tactile cues from disturbance of sand and vegetation near the nest as well as olfactory cues from the turtle and from the disturbed vegetation and substrate. Artificial nest construction also produces depth-invariant physical cues from digging as well as olfactory cues from disturbed sand, from the researchers, and from spraying sausage smell. In contrast, olfactory cues from the buried eggs or sausage might reach the surface more readily in shallower nests providing cues that decrease with depth as proposed by Reichman (1981) for buried seeds. Neither natural nor artificial nests showed a significant decrease in detection with depth, suggesting that mongooses used mainly depth-invariant cues to find nests. The natural nests, however, showed a nonsignificant trend toward reduced detection of the deepest nests. Because cues arising from the eggs might play a larger role in nest detection after the cues from construction and laying had faded, we repeated our analysis including only nests that had not been detected within the first week. Even in this subset, however, we found no evidence that depth affected detection (unpublished analyses). There was clearly no relationship between depth and detection for artificial nests. It could be argued that spraying sausage smell on the surface made the artificial nests so easy

<table>
<thead>
<tr>
<th>Variable</th>
<th>Predation risk ($n = 120$, % Dev. = 66.1%)</th>
<th>Detection ($n = 120$, % Dev. = 27.6%)</th>
<th>Capture ($n = 114$, % Dev. = 70.3%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Nest depth (cm)</td>
<td>$-4.035$ 0.844 $&lt; 0.001$</td>
<td>$-0.599$ 0.477 0.209</td>
<td>$-4.542$ 1.070 $&lt; 0.001$</td>
</tr>
<tr>
<td>Distance from vegetation edge (m)</td>
<td>$-1.100$ 0.399 0.006</td>
<td>$-0.390$ 0.566 0.491</td>
<td>$-1.223$ 0.435 0.005</td>
</tr>
<tr>
<td>Presence of rocks</td>
<td>$-0.485$ 0.404 0.290</td>
<td>$-0.533$ 0.467 0.254</td>
<td>$-0.410$ 0.429 0.339</td>
</tr>
<tr>
<td>Presence of roots</td>
<td>$0.566$ 0.422 0.180</td>
<td>$0.482$ 0.468 0.303</td>
<td>$0.284$ 0.461 0.538</td>
</tr>
<tr>
<td>Presence of moist sand</td>
<td>$0.186$ 0.570 0.615</td>
<td>$0.242$ 0.537 0.652</td>
<td>$0.108$ 0.413 0.795</td>
</tr>
<tr>
<td>Date of nest construction</td>
<td>$0.405$ 0.400 0.312</td>
<td>$1.845$ 1.253 0.141</td>
<td>$0.356$ 0.424 0.428</td>
</tr>
<tr>
<td>Local mongoose activity</td>
<td>$-0.028$ 0.426 0.948</td>
<td>$0.138$ 0.441 0.755</td>
<td>$-0.374$ 0.449 0.404</td>
</tr>
</tbody>
</table>

SE, standard error. All predictors are standardized (mean = 0, SD = 1). % Dev. is the proportion of null model deviance explained.
to find that there was little potential for an additional increase in detection for shallow nests. Although artificial nests were detected more rapidly than natural nests, in both cases, the overall detection rate was high (95% for artificial nests, 77% for natural nests) and the majority of detection occurred early in incubation with a median detection time for hawksbill nests of only 2 days. In addition, the high detection rate in the disturbance-only and the low detection rate in the smell-only treatments suggest that disturbance from digging the nest was more important than sausage odor. Nevertheless, the simultaneous presence of olfactory surface cues and buried prey increased both the depth mongooses were willing to dig and the probability of successful predation, suggesting that the scent of prey acts as a reinforcing cue once digging has been initiated.

Our measure of detection assumed that shallow digging above the buried eggs or sausage reliably indicated that detection had taken place. Similar approaches have been used in previous work on seed predation (Howard et al. 1968; Lockard RB and Lockard JS 1971). However, superficial digging would be an unreliable indicator of detection if mongooses dig randomly as part of a general pattern of search for buried prey. Random digging seems unlikely because we rarely observed digging in undisturbed areas during our field work. Furthermore, the low rate of digging in the smell-only experimental treatment indicates that mongooses selectively dug where they expected to find buried prey.

The lack of a clear effect of depth on egg detection by mongooses contrasts with previous studies that have concluded that deep burial reduces predation risk primarily by making prey harder to detect (e.g., Reichman and Oberstein 1977; Johnson and Jorgensen 1981; Geluso 2005). However, most previous research has examined rodent predation on seeds buried only a few centimeters deep. It is possible that the larger surface disturbance and greater depth of turtle nests increase the relative importance of both surface cues in detection and digging costs in limiting predation. We are aware of only one study of seed predation that has attempted to differentiate between depth effects on detection versus predation: Lockard RB and Lockard JS (1971) found that bags of birdseed buried at depths greater than 10 cm were only likely to be detected by kangaroo rats (Dipodomys deserti) when additional seeds were provided on the surface, suggesting an increasing importance of surface cues for detection of deeply buried seeds. However, the same study also showed that for seeds buried greater than 6 cm, only a fraction of detected seeds were actually preyed on and seeds buried 12–20 cm deep were often detected, but digging efforts were quickly abandoned. This suggests that, even at relatively shallow depths, greater excavation costs of deeper prey can reduce the probability of predation once detection has occurred, a factor that appears to have been largely overlooked in subsequent research (but see Vander Wall 1993). In studies where only predation is measured, depth may therefore appear to protect deeply buried resources by reducing detection, but this effect could equally result from a uniform detection rate followed by selective pursuit of shallower prey. Thus, correctly distinguishing the effects of depth on detection versus pursuit of prey has potentially important consequences for understanding the ecology of predators exploiting buried resources.

### Table 2

<table>
<thead>
<tr>
<th>Variable</th>
<th>Detection latency (n = 114, % Dev. = 21.9%)</th>
<th>Predation latency (n = 51, % Dev. = 30.9%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Nest depth (cm)</td>
<td>Estimate 0.189 SE 0.209 P 0.369</td>
<td>Estimate 1.754 SE 0.688 P 0.014</td>
</tr>
<tr>
<td>Distance from vegetation edge (m)</td>
<td>Estimate -0.560 SE 0.268 P 0.039</td>
<td>Estimate -0.466 SE 0.406 P 0.257</td>
</tr>
<tr>
<td>Presence of rocks</td>
<td>Estimate 0.200 SE 0.216 P 0.357</td>
<td>Estimate -0.103 SE 0.323 P 0.752</td>
</tr>
<tr>
<td>Presence of roots</td>
<td>Estimate -0.237 SE 0.219 P 0.281</td>
<td>Estimate -0.001 SE 0.349 P 0.998</td>
</tr>
<tr>
<td>Presence of moist sand</td>
<td>Estimate 0.088 SE 0.236 P 0.789</td>
<td>Estimate 0.093 SE 0.398 P 0.816</td>
</tr>
<tr>
<td>Date of nest construction</td>
<td>Estimate -1.046 SE 0.270 P &lt;0.001</td>
<td>Estimate -1.651 SE 0.443 P 0.001</td>
</tr>
<tr>
<td>Local mongoose activity</td>
<td>Estimate -0.401 SE 0.229 P 0.083</td>
<td>Estimate 0.064 SE 0.355 P 0.858</td>
</tr>
</tbody>
</table>

SE, standard error. All predictors are standardized (mean = 0, SD = 1). % Dev. is the proportion of null model deviance explained.
Effects of depth on exploitation of detected prey

The costs in time and energy of excavating buried prey are expected to increase exponentially with burial depth (Vander Wall 1993; Ward and Saltz 1994). An individual mongoose may spend over half an hour actively removing sand before the eggs are reached (Leighton PA, unpublished data), and the energetic costs of digging for turtle nests are likely to be substantial. The costs of antipredator vigilance while digging may also be important. Mongooses frequently emerge from the excavation hole and assume a sitting-up posture, a procedure that presumably becomes more costly as digging proceeds. Finally, risk of injury or even death may increase with depth as a result of tunnel collapse. While investigating a hatched nest, members of the Barbados Sea Turtle Project found a dead mongoose buried in the nest cavity where it had presumably burrowed and been trapped (Krueger BH, personal communication). If we assume that the number of eggs is independent of depth and that costs increase with depth, foraging theory would predict that shallower nests would be more profitable and therefore preferred by predators (Vander Wall 1993). Our study provides strong support for this prediction, with shallower nests being much more likely to be preyed on by mongooses following detection. An alternative to active preference of shallower nests by predators is that deeply buried eggs may simply be more difficult to locate accurately by digging. This does not seem to be the case in our study: although mongooses typically began digging at an angle, we never observed a case of mongooses tunneling in the wrong direction or missing the egg chamber. It is likely that the column of loose sand above the egg mass and increasing strength of olfactory cues associated with the eggs help guide digging.

Many factors other than depth influence predation risk, and it is reasonable to expect that these may also affect detection and excavation of prey differently. Substrate characteristics can influence detection by altering transmission of olfactory cues through the soil (Geltuso 2005; Vander Wall 1998) but can also affect digging costs (Vander Wall 1993; Ward and Saltz 1994). At Bath, patches of beach vegetation generally occupy a transition zone between open sand and inland forest. Substrate properties vary greatly across this gradient, with loose and sandy soil nearer the water and increasingly compact soil containing more organic matter further inland. The location of nests relative to the seaward edge of vegetation had no effect on whether a nest was detected, but nests further inland were much less likely to be preyed on following detection, suggesting that denser substrate increases excavation costs. Although we found no significant effect of variation in moisture, rocks, or roots, trends approaching significance suggested that rocky soils may deter predators, whereas roots might actually facilitate predation, perhaps by loosening the sand (see Horrocks and Scott 1991).

Nellis and Small (1983) suggested that predator learning is likely to be an important factor affecting sea turtle nest predation. If learning takes place within a nesting season, we expect predation risk to increase with date in the season, and this pattern was observed in natural nests (Leighton PA, unpublished data). Although predation risk did not increase for artificial nests over the 3-week experimental period, the decreasing detection latency also supports the idea that learning may strengthen the association between surface cues and the presence of buried prey for this novel food source. The absence of predation in 1 of 6 locations used in the experiment, where hawksbill nests are nevertheless often preyed upon, could result from a failure of the local mongoose population to learn how to exploit the artificial nests.

Nest depth and conservation

Our study suggests that conservation measures for protecting individual sea turtle nests from mongoose predation should target shallow nests. Strategies for protecting individual nests in situ can be classified as functioning by reducing detection (e.g., erasing tracks of the nesting turtle) or by increasing excavation costs (e.g., physical barriers). Both approaches have many variants (reviewed in Stancyk 1982), but the optimal method may depend on how predators detect prey and whether digging cost is a major deterrent. If, as in our study, disturbance is the primary cue for nest detection, reducing surface disturbance is likely to be effective. However, if depth-mediated olfaction plays a major role, applying masking scents or replacing surface sand could be more useful. These are relevant considerations for researchers who excavate nests for data collection (see Schroeder and Murphy 1999) because this procedure could substantially increase the probability of detection. Furthermore, care must be taken that any device applied to increase excavation costs does not become an additional cue for nest detection by predators or human poachers. Because mongooses dig in response to disturbance, even in the absence of buried food, an interesting conservation strategy might be to create an abundance of artificial disturbances in nesting habitat prior to the main nesting season. If predator digging efforts rarely result in successful predation, this may weaken the association between disturbances and the presence of buried food.

Sea turtles, like many other egg-burying reptiles, show temperature-dependent sex determination with warmer nests resulting in more female hatchlings. A growing body of research has revealed an alarming bias in hatchling sex ratios at nesting beaches around the world, with projections of greater than 90% female hatchlings common (reviewed in Wibbels 2003). Depth-biased predation could affect hatchling sex ratios because of variation in temperature associated with depth (e.g., Valenzuela 2001) or with microhabitat differences that also affect depth (e.g., Oz et al. 2004). In areas like Bath where nests in densely vegetated microhabitats are shallower and more frequently encountered by predators, the coolest nests may be at the highest risk. Thus, nest predators could selectively consume the nests most likely to produce males. The important potential link between patterns of nest predation and hatchling sex ratios has received almost no empirical investigation (but see Oz et al. 2004).

A wide array of species prey on sea turtle nests (reviewed in Stancyk 1982). Identifying predator characteristics associated with different nest predation mechanisms could provide a general basis for predicting which species are likely to pose the greatest threat in a given context. If depth primarily affects prey capture costs, the impact of a given predator should depend on factors such as predator size and nest depth that affect relative digging capacity. Artificial nests could be used to establish the relationship between depth and predation risk for other predatory species.

The relationship between depth and predation risk is likely to be quite general for predator–prey systems: foragers seeking burrowing prey, nest predators seeking eggs, scatter hoarders seeking seeds, diving animals seeking prey, and parasitoids seeking buried eggs or larvae. In such systems, burial depth can be the outcome of an evolutionary game between prey and predators (Andersson and Krebs 1978; Dally et al. 2006), with optimal burial depth for prey being a function of both the cost of digging for the prey (or its parent) and the costs for the community of predators in which the behavior evolved. The introduction of exotic predators such as mongooses has the potential to create a strong selection pressure for deeper burial, whereas loss of important natural predators may favor shallower burial. Such changes can have important long-term consequences, especially where burial depth affects other processes such as seed germination rate (Vander Wall 1993), sex determination of buried eggs, or the
emergence success of young. Further research into the economics of foraging decisions made by animals that prey on buried resources would greatly improve our ability to predict how ongoing anthropogenic changes are likely to impact such communities.

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