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Nest-Site Selection in Individual Loggerhead Turtles and Consequences for Doomed-Egg Relocation

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Abstract: *Relocation of eggs is a common strategy for conservation of declining reptilian populations around the world. If individuals exhibit consistency in their nest-site selection and if nest-site selection is a heritable trait, relocating eggs deposited in vulnerable locations may impose artificial selection that would maintain traits favoring unsuccessful nest-site selection. Conversely, if most individuals scatter their nesting effort and individuals that consistently select unsuccessful nest sites are uncommon, then artificial selection would be less of a concern. During the 2005 nesting season of loggerhead turtles (*Caretta caretta*) at Mon Repos beach, Queensland, Australia, we measured the perpendicular distance from the original nest site to a stationary dune baseline for in situ (unrelocated) and relocated clutches of eggs. We observed the fate of in situ clutches and predicted what would have been the fate of relocated clutches if they had not been moved by mapping tidal inundation and storm erosion lines. In 2005 turtles deposited an average of 3.84 nests and did not consistently select nest sites at particular distances from the stationary dune baseline. Selection of unsuccessful nest sites was distributed across the nesting population; 80.3% of the turtles selected at least one unsuccessful nest site and when previous breeding seasons were included, 97% selected at least one unsuccessful nest site. Females with nesting experience selected more successful nest sites than females with little or no experience. Relocating eggs vulnerable to tidal inundation and erosion saves the progeny from a large percentage of the population and the progeny from individuals who may in subsequent years nest successfully. Our results suggest that doomed-egg relocation does not substantially distort the gene pool in the eastern Australian loggerhead stock and should not be abandoned as a strategy for the conservation of marine turtle populations.*

Keywords: *Caretta caretta*, egg relocation, loggerhead sea turtle, nest-site selection, turtle conservation

Selección de Sitios de Nidación de Individuos de Tortugas de Carey y sus Consecuencias para la Reubicación de Huevos Vulnerables

Resumen: *La reubicación de huevos es una estrategia común para la conservación de poblaciones de reptiles en declinación en todo el mundo. Si los individuos presentan consistencia en la selección de sitios de nidación y si esta es hereditaria, la reubicación de huevos depositados en sitios vulnerables puede imponer una selección artificial que mantendría la tendencia a favorecer la selección de sitios de nidación no exitosos. Por el contrario, si la mayoría de los individuos esparcen su esfuerzo de nidación y los individuos que consistentemente seleccionan sitios no exitosos son comunes, entonces la selección artificial sería menos preocupante. Medimos la distancia perpendicular desde el sitio original del nido hasta la base de una duna fija para huevos in situ (no reubicados) y reubicados durante la época de nidación de tortugas de carey (*Caretta caretta*) en la playa Mon Repos en 2005. Observamos el destino de las nidadas in situ y predijimos, mediante un mapa de la inundación de la marea y de las líneas de erosión, cual hubiera sido el destino de las nidadas reubicadas si no hubieran sido movidas. En 2005, las tortugas depositaron un promedio de 3.84*

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nidos y no seleccionaron los sitios consistentemente a distancias particulares de la duna fija. La selección de nidos no exitosos se distribuyó en la población; 80.3% de las tortugas seleccionaron por lo menos un sitio no exitoso y cuando incluimos datos de las temporadas de nidación previas, 97% de los individuos seleccionó por lo menos un sitio no exitoso. Las hembras con experiencia de nidación seleccionaron más sitios exitosos que las hembras con poca o ninguna experiencia. La reubicación de huevos vulnerables a la inundación de la marea y a la erosión salva a la progenie de un alto porcentaje de la población y a la progenie de individuos que en años subsecuentes pueden anidar exitosamente. Nuestros resultados sugieren que la reubicación de huevos vulnerables no distorsiona sustancialmente la poza génica de la población de Australia oriental y no debería ser abandonada como estrategia para la conservación de poblaciones de tortugas marinas.

Palabras Clave: *Caretta caretta*, conservación de tortugas, reubicación de huevos, selección de sitios de nidación, tortugas de carey

Introduction

Relocation of eggs is a common strategy for conservation of declining reptilian populations around the world, including crocodilians (Thorbjarnarson et al. 1992), terrestrial and freshwater turtles (Kuchling 1999; Seigel & Dodd 2000), and marine turtles (e.g., Limpus 1985; Marcovaldi & Laurent 1996; Dutton et al. 2005; Kornaraki et al. 2006). Nest relocation has also been used in bird conservation programs (reviewed in Temple 1977). In an attempt to improve survival rates of eggs and hatchlings, clutches of eggs (i.e., doomed eggs) deposited in vulnerable areas (e.g., too close to the water) are relocated away from their original nest site to a less vulnerable location. Because selection of nest sites affects the fitness of individual females through the survival and sex ratios of the offspring (Wood & Bjorndal 2000; Congdon et al. 2001), so saving eggs deposited in vulnerable locations may impose artificial selection that maintains traits favoring unsuccessful nest-site selection (Mrosovsky 1983, 2006, 2008) if nest-site selection is a heritable trait.

Concerns about distortion of gene pools through doomed-egg relocation have received the greatest attention in management programs for marine turtles (Mrosovsky 2008; Pike 2008). As a result of this debate, the validity of egg relocation as a sound conservation practice for marine turtles and management of nesting populations is currently being evaluated by the Marine Turtle Specialist Group (International Union for the Conservation of Nature [IUCN], Species Survival Commission [SSC]). For doomed-egg relocation to distort gene pools, 2 criteria must be met. First, nest-site selection must be heritable. Second, there must be consistent individual differences in nest-site selection. If individuals exhibit consistency in their nest-site selection and if nest-site selection is heritable, then relocating eggs deposited in vulnerable locations may impose artificial selection and in the long run may be unfavorable to the conservation of populations (Mrosovsky 1983, 2006, 2008). Conversely, if most individuals scatter their nesting effort and individuals that consistently select unsuccessful nest sites are uncommon, then distorting the gene pool may be less of a concern (Mrosovsky 1983; Pike 2008).

Marine turtles, because of their high site fidelity and multiple nesting events within a season, provide an opportunity to assess individual consistency in nest-site selection. In some threatened populations, 20–60% of clutches are deposited in areas vulnerable to tidal inundation and erosion, which results in a substantial reduction in hatchling production (e.g., Mrosovsky 1983; Whitmore & Dutton 1985; Eckert 1987). Distortion of the gene pools by egg relocation in such populations merits concern only if these unsuccessful nest sites are consistently selected by the same individuals. Previous researchers have investigated sequential nest placement by individual loggerheads (*Caretta caretta*) (Camhi 1993; Hays & Speakman 1993), green turtles (*Chelonia mydas*) (Bjorndal & Bolten 1992), leatherbacks (*Dermochelys coriacea*) (Eckert 1987; Tucker 1990; Kamel & Mrosovsky 2004; Nordmoe et al. 2004), and hawksbills (*Eretmochelys imbricata*) (Kamel & Mrosovsky 2005, 2006). Most report varying degrees of nest scattering, but Kamel and Mrosovsky (2005, 2006) found high consistency in nest placement by individual hawksbills (*E. imbricata*) nesting in Guadeloupe, French West Indies, which suggests that relocating doomed eggs in this population may maintain negative traits linked to poor nest-site selection. To address the consistency of nest-site selection by individual turtles further, we assessed nest-site selection by individual loggerhead turtles within a single reproductive season and across multiple seasons at Mon Repos, Australia.

The Woongarra Coast of south Queensland, including the beach at Mon Repos, supports the largest nesting aggregation of loggerhead turtles in eastern Australia and is the primary index site for monitoring population trends in the South Pacific (Limpus & Limpus 2003). Nesting of marine turtles along the Woongarra Coast has been monitored each year since 1968, and essentially all nesting loggerheads at Mon Repos and adjacent beaches have been tagged for individual recognition. Because of high site fidelity in this nesting rookery (Miller et al. 2003) since the 1982–1983 breeding season, all untagged nesting females lacking tag scars were assumed to be first-time breeders. The locations of a large proportion of clutches from almost every female in this population have been recorded.

In response to the depleted state of the current eastern Australia loggerhead population (Limpus & Limpus 2003), clutches deposited in areas judged vulnerable to inundation and erosion along the Woongarra Coast are relocated to less vulnerable sites farther from the water. To determine whether relocating doomed loggerhead eggs at Mon Repos is maintaining traits linked to poor nest-site selection, we addressed the following questions: (1) Do individuals exhibit high individual consistency (repeatability) in the distance of nest sites from a stationary baseline? (2) What percentage of the nesting females select at least one unsuccessful nest site? (3) What percentage of the nesting females select both successful and unsuccessful nest sites? (4) Are individuals consistent in their nest-site selection across multiple breeding seasons? (5) Does nesting experience affect nest-site selection?

Methods

Study Site

Mon Repos (24°48′S, 152°27′E) is a 1.54-km crescent-shaped beach and is the largest of 8 sand beaches on the Woongarra Coast, a 23-km extent of rocky coastline between the mouths of the Burnett and Elliot rivers in mainland south Queensland, Australia. Mon Repos beach is backed by relatively dense forest (*Casuarina equistifolia*), except at the southern end, where the forest is less dense due to the presence of a caravan park. Lights from the caravan park illuminate small portions of the southern end of Mon Repos; turtles rarely nest in this area.

The casuarina forest is restricted to the crest of the primary dune. Seaward of the forest line, the primary dune descends to an open, well-vegetated dune nesting area. The principal dune plants are a creeping vine, *Ipomea pes-carpe*, and a grass, *Spinefex hirsutus*. Seaward of the dune nesting area, a secondary dune with sparse vegetation descends a relatively short distance to a fluctuating tidal plane. The width of Mon Repos beach from the forest line to the base of the secondary dune ranges from 5 to 20 m. At the lowest tide, there is more than 100 m of open sand. The incubation season for loggerhead clutches at Mon Repos encompasses the summer–autumn cyclone season for the Coral Sea region. This results in intermittent storm-driven flooding and erosion of the secondary dune and seaward margin of the dune nesting habitat. In many events, sections of beach are cut away and occasionally the seaward-most clutches are washed into the sea.

Data Collection

We continued the standard methodology used by the Queensland Parks and Wildlife Service marine turtle conservation project to study this nesting population since 1975. For pre-2005 data on nesting history, we used the service's computerized turtle research database. Each turtle was examined for and, if necessary, fitted with titanium tags, one in each front flipper (Limpus 1992). On completion of a nesting event, we mapped clutches by triangulating from 70 numbered posts located approximately 25 m apart on the crest of the primary dune (the dune-post baseline). The dune-post baseline runs along the entire beach lengthwise and provides a stationary reference point to accurately locate nest sites. We assigned each nest site to 1 of 4 beach zones along the forest-to-ocean axis: dune, seaward slope, below the slope, and below the high-water mark. As part of the conservation protocol, starting in 1990, all clutches deposited on or below the seaward slope or within 1.5 m landward of the secondary dune were relocated within 2 h of being laid. Rotation of eggs was kept to a minimum (Limpus et al. 1979).

We added parameters to the standard methodology during the 2005 loggerhead turtle nesting season (October through March) for the present study. To determine the almost certain fate of relocated clutches if they had been left in situ, we measured the perpendicular distance from the original nest site to the dune-post baseline (the nest–baseline distance). With the same technique, we measured the nest–baseline distance for clutches left in situ. In addition, we measured the perpendicular distance of storm-erosion lines from each of the posts along the dune-post baseline (erosion–baseline distance). The average erosion–baseline distance from 2 adjacent posts was considered the erosion–baseline distance for that sector. Because erosion events occurred multiple times across the nesting and incubation seasons, erosion–baseline distances were measured after each event.

To predict whether clutches would have been lost to erosion if they had not been relocated out of vulnerable areas, we compared the nest–baseline distance with the appropriate erosion–baseline distance. Nests were considered to be located in an area that would have resulted in clutch loss if the erosion–baseline distances were smaller (i.e., closer to the dune-post baseline) than nest–baseline distances for a given sector and time period. Only erosion events that overlapped temporally with an estimated 60-day incubation period were considered for nest sites from clutches that were relocated. In combination with information on the success of clutches that were not relocated, these data permitted the designation of each 2005 nest site as successful or unsuccessful. Successful nest sites were either those of clutches left in situ that were not inundated or eroded (safe in situ) or those of clutches that were moved but whose original sites were not inundated or eroded (unnecessary relocation). Unsuccessful nest sites were either those of clutches left in situ that were inundated or eroded (eroded in situ) or those of clutches that were moved and whose original sites were inundated or eroded (necessary relocation).

Data Analyses

To quantify differences in nest-site selection between individual loggerheads, we calculated the repeatability (intraclass correlation coefficient) of nest–baseline distance for females that deposited 3 or more clutches in 2005 (Lessells & Boag 1987). To calculate repeatability, we used the harmonic mean of the number of observed nests per female and the mean variances from a one-factor model II analysis of variance (Lessells & Boag 1987; Sokal & Rohlf 1995). This analysis was intended to compare our results with recent repeatability analyses for leatherback and hawksbill turtles (Kamel & Mrosovsky 2004, 2005).

Next, we assessed how these initial repeatability data were related to variability of nest-site success across the population. For females that deposited 2 or more clutches, we determined the percentage of females that selected at least 1 unsuccessful nest site. We then grouped females as either selecting all successful nest sites, all unsuccessful nest sites, or both successful and unsuccessful nest sites, to determine the percentage of females that were variable in their nest-site success. To assess the nest-site success by individuals across several seasons, we analyzed a subset of turtles with at least 5 documented breeding seasons. Because data on nest-site success were collected only in 2005, we used nest placement within the beach zones as an indicator of nest-site success for past breeding seasons. Nest sites in the dune and slope zones were considered successful, whereas nest sites in the below-slope and below-high-water zones were considered unsuccessful. According to these criteria, each documented breeding season for each turtle was considered successful (all successful nest sites), unsuccessful (all unsuccessful nest sites), or variable (at least 1 unsuccessful nest site).

To analyze differences in nest-site success among females with different levels of reproductive experience on the basis of the number of documented breeding seasons and number of years since first breeding, we used chi-square tests and binomial logistic regression models for females that deposited 2 or more clutches in 2005. In addition, binomial logistic regression models were used to assess spatial (along the beach) and temporal (across the 2005 season) differences in nest-site selection among turtles with different levels of reproductive experience and to evaluate different spatial and temporal nest-site success across the population as a whole. For spatial analyses, we created 35 sectors by combining adjacent pairs of the 70 sectors to compensate for low nesting in sectors located at the far northern and southern ends of the beach. For statistical analyses the alpha level used was 0.05.

Results

We recorded 977 nesting events from 295 individually identified loggerheads during the 2005 nesting season on Mon Repos. Of these nesting events, 507 were successful (safe in situ [41%] and unnecessary relocations [10%]) and 470 were unsuccessful (eroded in situ [5%] or necessary relocations [44%]). The unsuccessful nest sites were selected by 237 turtles (80.3% of the 2005 breeding population). Forty-five nesting events that could not be attributed to an individual were excluded from our analyses.

Depending on the analysis, we focused on either the 250 turtles that deposited 2 or more clutches (45 turtles for which only 1 clutch was recorded were excluded) or the 215 turtles that deposited 3 or more clutches on Mon Repos. Of the 215 turtles, 33 had 5 or more documented breeding seasons, resulting in 910 clutches across 26 years of breeding. We used this group of 33 turtles to evaluate consistency of nest-site selection and success across multiple breeding seasons.

The 215 turtles that deposited 3 or more clutches averaged 3.84 observed nesting events (harmonic mean) during the 2005 season. These turtles did not show consistency in selecting nest sites at particular distances from the dune-post baseline; the repeatability value, r, was 0.18 ($n = 215$ turtles and 862 clutches, $p = 0.10$; Fig. 1a).

Of the 250 turtles that deposited 2 or more clutches in 2005, 169 individuals (67.6% of the 2005 breeding population) were variable in their nest-site success, selecting both successful and unsuccessful nest sites (Fig. 2). Eighty-one turtles were not variable in their nest-site success: 39 (15.6%) selected all successful nest sites and 42 (16.8%) selected all unsuccessful nest sites (Fig. 2).

The 33 turtles that deposited 3 or more clutches in 2005 and for which we documented at least 5 previous breeding seasons (5–14 breeding seasons/turtle) displayed high numbers of variable and successful seasons (Fig. 3). Not a single individual had more than 1 unsuccessful season, and most had none (Fig. 3).

Of the 250 turtles that deposited 2 or more clutches in 2005, first-time breeders selected significantly more unsuccessful nest sites (227 unsuccessful, 192 successful) than experienced breeders (194 unsuccessful, 248 successful) ($\chi^2 = 8.70$, df $= 1$, $p = 0.0032$). For binomial logistic regression models, we used p values from a chi-square approximation. Success on the basis of actual nest-site success or on the basis of beach zone was positively related to number of breeding seasons (nest site: $g[x] = -0.35 + 0.16x$, $t_{12} = 4.73$, $p < 0.001$; beach zone: $g[x] = 0.28 + 0.15x$, $t_{12} = 3.84$, $p < 0.05$) (Fig. 4a).

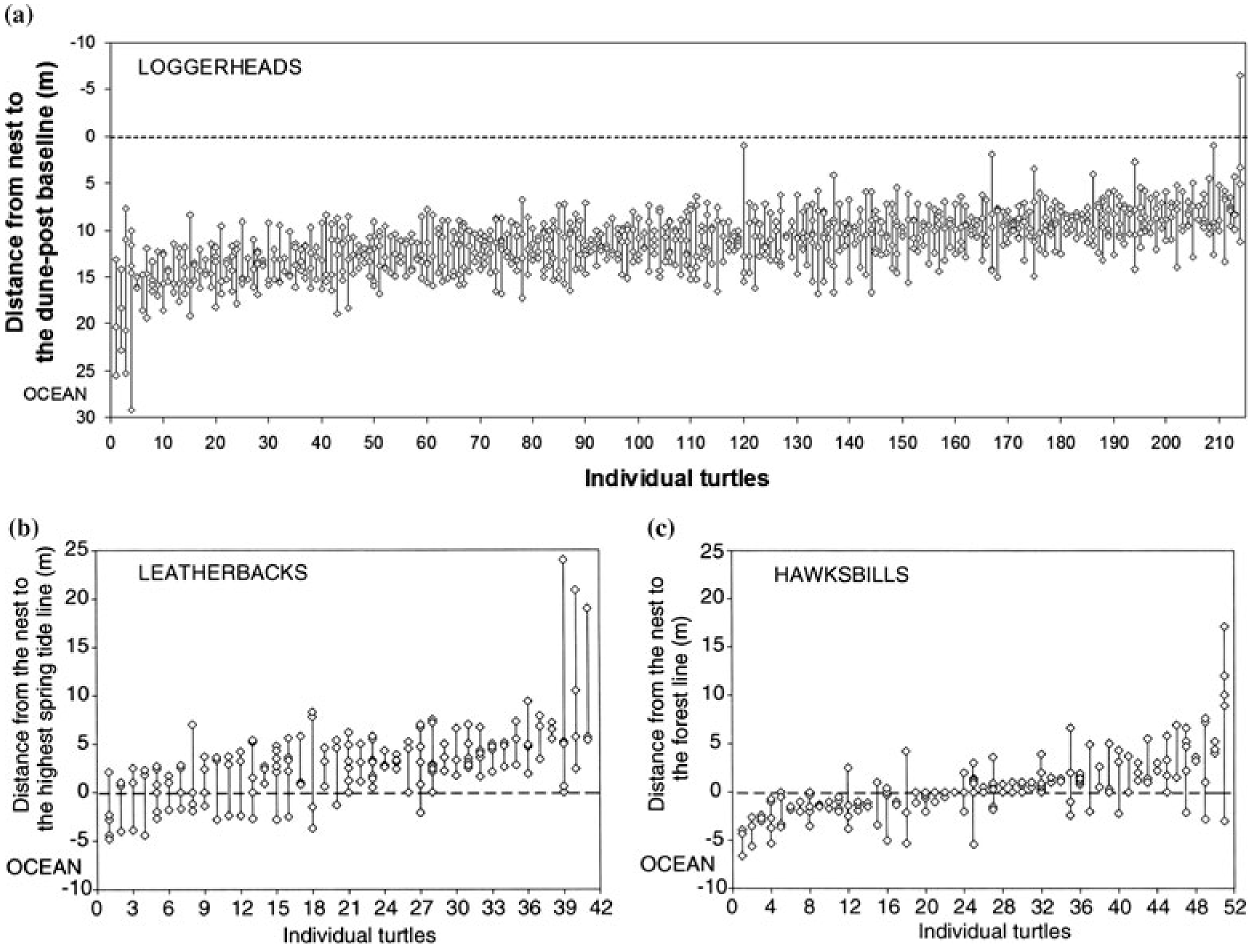

Figure 1. Positions of nest sites (diamonds) selected by individual turtles with respect to the distance from (a) the dune-post baseline for loggerheads in the present study ($r = 0.18$, $n = 215$ turtles and 862 clutches, $p = 0.10$), (b) from the highest spring tide line in leatherbacks ($r = 0.18$, $n = 41$, $p = 0.008$), and (c) from the forest line in hawksbills ($r = 0.40$, $n = 51$, $p < 0.0001$). Vertical lines link nest sites of individual turtles. In (a), turtles are ordered by the average distance of their nests from the dune-post baseline. Figures (b) and (c) are reprinted with permission from Kamel and Mrosovsky (2004, 2005), respectively.

Success was also positively related to years since first breeding (nest site: $g[x] = -0.20 + 0.05x$, $t_{25} = 4.69$, $p < 0.001$; beach zone: $g[x] = 0.43 + 0.05x$, $t_{25} = 3.59$, $p < 0.01$) (Fig. 4b). In addition, the 42 turtles that selected all unsuccessful nest sites in 2005 had significantly fewer breeding seasons than the population as a whole ($\chi^2 = 9.13$, $df = 3$, $p = 0.028$). Nesting tendencies differed spatially and temporally between first-time and experienced breeders. First-time breeders nested later in the season than experienced breeders ($g[x] = -2.30 + 0.68x$, $t_7 = 5.07$, $p < 0.01$) and distributed their nests along the beach lengthwise differently than experienced breeders ($g[x] = -0.79 + 0.04$, $t_{33} = 4.37$, $p < 0.05$). In addition, temporal ($g[x] = 0.87–0.20x$, $t_7 = -4.03$, $p < 0.01$) and spatial ($g[x] = -0.72 + 0.04x$, $t_{33} = 4.88$, $p < 0.001$) nest-site success differed across the season and along the beach lengthwise, respectively.

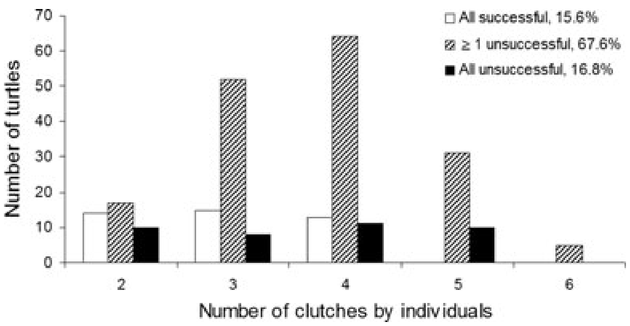

Figure 2. Consistency of nest-site success by individual loggerhead turtles that deposited 2 or more clutches in 2005 ($n = 250$).

Discussion

The validity of doomed-egg relocation as a sound conservation strategy for marine turtles has been questioned

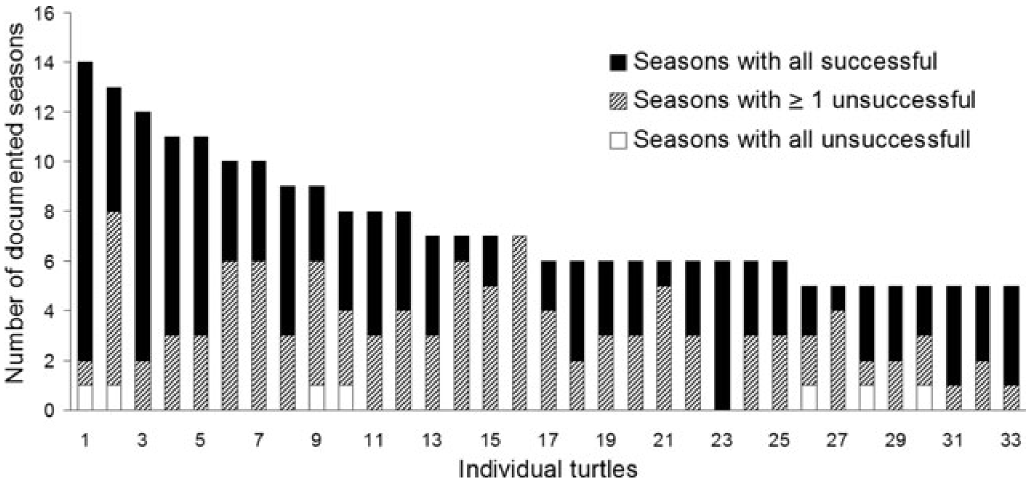

Figure 3. Consistency of nest-site success across multiple seasons by loggerhead turtles that deposited 3 or more clutches in 2005 and were documented to have deposited clutches in at least 5 previous seasons (n = *33). Selection of a particular beach zone along the ocean-to-forest axis was used as an indicator of nest-site success; dune and slope nests were considered successful, and below-slope and below-high-water nests were considered unsuccessful. Breeding seasons were considered successful (all successful nest sites), unsuccessful (all unsuccessful nest sites), or variable (≥1 unsuccessful nest site).*

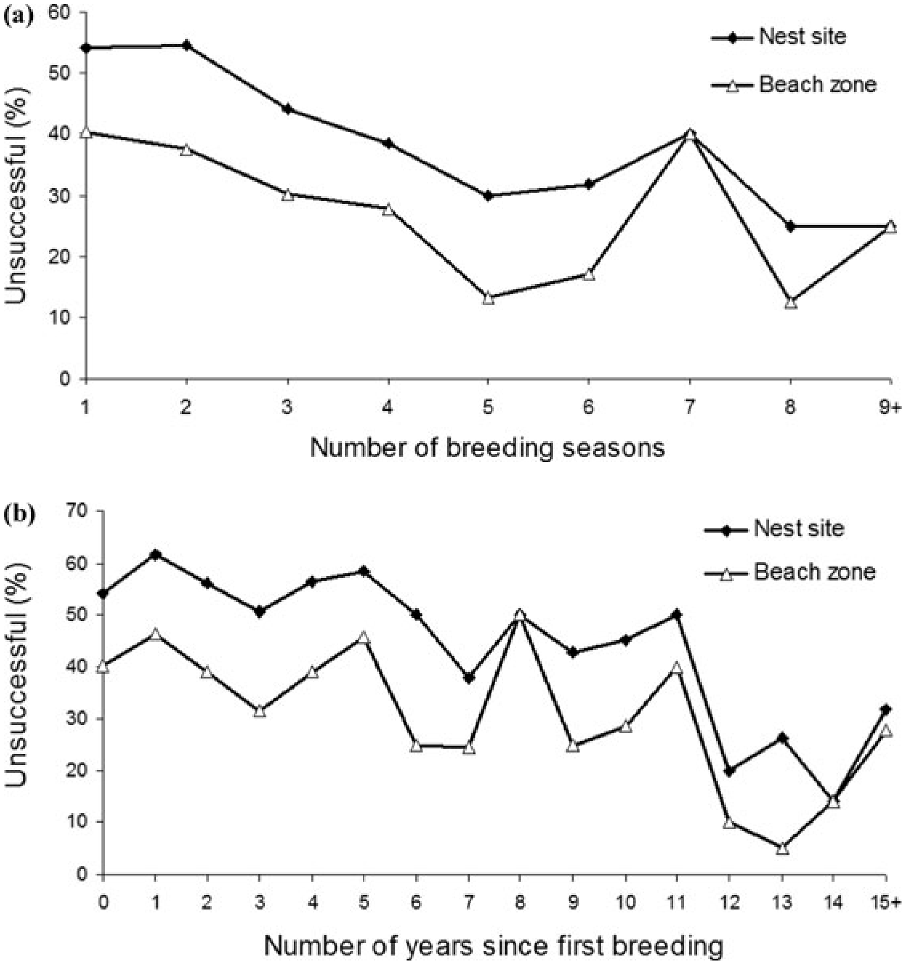

Figure 4. For loggerhead turtles that deposited 2 or more clutches in 2005 (n = *250), relationships between the percentage of unsuccessful nest sites on the basis of distance from the nest site to dune-post baseline (nest site) or beach zone placement and (a) number of breeding seasons (nest site:* $g[x] = -0.35 + 0.16x$, $t_{12} = 4.73$, $p < 0.001$; *beach zone:* $g[x] = 0.28 + 0.15x$, $t_{12} = 3.84$, $p < 0.05$) *and (b) number of years since first breeding (nest site:* $g[x] = -0.20 + 0.05x$, $t_{25} = 4.69$, $p < 0.001$; *beach zone:* $g[x] = 0.43 + 0.05x$, $t_{25} = 3.59$, $p < 0.01$)*. For the binomial logistic regression models,* p *values were from a chi-square approximation.*

(Mrosovsky 2006, 2008) and is currently a major topic of discussion by the IUCN/SSC Marine Turtle Specialist Group. Among other concerns (e.g., sex-ratio alteration and hatchling-fitness reduction), distortion of the gene pool has received considerable attention (Mrosovsky 2006, 2008; Pike 2008). Mrosovsky (2006) considers 3 options for doomed eggs: do not relocate doomed eggs and let the turtles fend for themselves; relocate, boost population numbers, and accept the potential genetic consequences; or commercialize doomed eggs and return the proceeds to marine turtle conservation. To evaluate these options, one must first understand the extent to which gene pools may be distorted, if at all.

Egg relocation may distort gene pools by targeting a nonrandom portion of the population only if certain individuals consistently select nest sites in vulnerable areas. More studies of nest-site selection across several species of marine turtles, however, suggest varying degrees of nest scattering, in which most turtles select nest sites in many different areas, some of which are vulnerable. Individual green turtles (*Che. mydas*) nesting at Tortuguero, Costa Rica, tend to scatter their nests among 3 zones along the ocean-to-vegetation axis, within and between seasons (Bjorndal & Bolten 1992). Consecutive nest placements along the ocean-to-vegetation axis are independent for individual leatherbacks (*D. coriacea*) nesting at Sandy Point, St. Croix, U.S. Virgin Islands (Eckert 1987) and Playa Grande, Costa Rica (Nordmoe et al. 2004). Individual loggerheads (*C. caretta*) nesting on the island of Cephalonia, Greece, and Cumberland Island, Georgia (U.S.A.), have high within-individual variation in distances of nests relative to the ocean (Hays & Speakman 1993) and dunes (Camhi 1993), respectively. Our results are similar: a large percentage of individual loggerheads selected both successful and unsuccessful nest sites within a single season and across multiple seasons.

Recent attention has been given to distances of nest sites from prominent features, measured on a continuous scale, for use in repeatability analyses (Kamel & Mrosovsky 2004, 2005, 2006). Such analyses maximize the chance of detecting individual differences in nest-site selection. Our low repeatability value, of 0.18, was similar to that presented by Kamel and Mrosovsky (2004) for nest position relative to the highest spring tide line in leatherbacks ($r = 0.18$, $n = 41$, $p = 0.008$; Fig. 1b), which, although showing some individual differences, tended to scatter their nesting effort. In contrast, Kamel and Mrosvosky (2005, 2006) found high individual consistency (repeatability) for hawksbill turtles in nest position relative to the forest line ($r = 0.40$, $n = 51$, $p < 0.0001$; Fig. 1c), current water line ($r = 0.23$, $p = 0.001$), and vegetative cover ($r = 0.71$, $p < 0.0001$). The contrast suggests interspecific differences in nest-site selection.

Loggerheads, and particularly leatherbacks, tend to nest on more dynamic, oceanic beaches in which the stability of the nesting beach may vary considerably across and between seasons. The inability of turtles to assess the localized instability of the nesting habitat, and therefore its suitability for egg incubation, may account for the lack of consistent patterns in nest-site selection (Bjorndal & Bolten 1992). For turtles nesting on beaches where erosion, and therefore nest loss, is unpredictable, selection should favor a strategy of scattering reproductive effort, which should increase the probability that at least some nest sites will be successful (Eckert 1987). In contrast to loggerheads and leatherbacks, hawksbills in the Caribbean tend to favor protected beaches with low wave energy, where the nesting environment remains fairly stable during a nesting season (Horrocks & Scott 1991; Mrosovsky 2006). The predictability of these more stable beaches apparently favors a strategy in hawksbills in which individuals specialize in particular nest-site choices (Mrosovsky 2006).

The stable hawksbill nesting beaches described by Kamel and Mrosovsky (2005, 2006) are narrow (1–15 m). Because the position of vegetation and width of the beaches did not vary greatly across a nesting season, hawksbills may have appeared to exhibit high repeatability simply because there was limited variation in available nest sites. In contrast, hawksbills that nest on a wider beach at Tortuguero, Costa Rica, do not select a large proportion of nest sites in dense vegetation and tend to scatter their nests (Bjorndal & Bolten 1992). Repeatability in nest-site selection in other hawksbill populations should be evaluated to assess whether doomed-egg relocation in hawksbill populations may distort the gene pools. Nevertheless, because hawksbills tend to select few nest sites in areas that are vulnerable to tidal inundation and erosion (e.g., Horrocks & Scott 1991; Hoyle & Richardson 1993; Mrosovsky 2006), the loss of eggs to inundation or the genetic consequences of relocating doomed eggs would have little influence on the population as a whole.

Individual loggerheads with long breeding histories selected all or at least some successful nest sites in many seasons and selected all unsuccessful nest sites in very few seasons. In addition, not a single turtle had more than one season of all unsuccessful nest sites. These results suggest an additional scattering in reproductive effort across multiple breeding seasons within loggerheads. Similar multiyear results were found in a 9-year study of nest placement by leatherbacks at Playa Grande, Costa Rica, in which consecutive nest-site selections were independent (Nordmoe et al. 2004). The occurrence of multiyear scattering indicates that particular individuals are not predisposed to selection of unsuccessful nest sites throughout their reproductive lives and that seasons in which individuals select some nest sites low on the beach may be important to the nesting dynamics of the population.

For those populations of marine turtles that lack consistent individual differences and display low repeatability in nest position, such as the loggerheads at Mon Repos, the large number of unsuccessful nest sites relates to the selection of unsuccessful nest sites by a large percentage of the population. In such populations, relocation of eggs vulnerable to lethal tidal inundation and erosion saves the progeny from a large percentage of the population, not from a small cohort of consistently unsuccessful individuals. Therefore, relocating doomed eggs would not substantially distort the gene pool.

We have emphasized the importance of nest placement away from the water to avoid inundation. In sea turtles, however, nest-site selection is influenced by selective forces that drive nest placement inland and those that drive nest placement seaward (Bjorndal & Bolten 1992). Nests deposited close to the ocean have a greater likelihood of inundation and egg loss to erosion, whereas nest placement farther inland results in greater likelihood of hatchling misorientation and desiccation and predation on nesting females, eggs, and hatchlings (Wood & Bjorndal 2000). These maternal trade-offs among opposing selective forces may explain the maintenance of traits in the population for nesting too low on the beach (Mrosovsky 2006).

Although loggerheads exhibit high nest-beach fidelity, genetic studies and notching hatchlings reveal that females are strongly linked to the regions where they hatched rather than to the specific beaches where they hatched (Bowen 2003; Miller et al. 2003). Even after returning to the natal region and selecting a particular nesting beach, some turtles nest on other beaches in the general area during subsequent nesting events (Bjorndal et al. 1983). Because nesting beaches differ in profile and erosion potential, nest-site selection strategies that are unfavorable at one beach may not necessarily translate to the same outcome on another beach. Variability in nest-site selection strategies has probably played a role in the long evolutionary success of these species. The strategy allows them to relocate to different nesting beaches as sea levels have changed in response to past climactic changes, and it may be needed again with the projected rise in sea level (Fish et al. 2005).

The effect of experience on nest-site selection in marine turtles is poorly studied. In our study females with nesting experience selected more successful nest sites than did females with little or no experience. That first-time breeders tended to select a higher percentage of nest sites in vulnerable areas indicates this behavior is affected by experience and is not strictly genetically hardwired. This conclusion is additional justification for the practice of doomed-egg relocation. Within the 2005 season, relocating eggs deposited in vulnerable areas saved a high percentage of the progeny of new recruits to the population, which in subsequent seasons may well select less vulnerable nest sites.

We found significant differences in the spatial and temporal positioning of nesting events between first-time and experienced breeders. Experienced breeders began nesting earlier in the season, which resulted in selection of a higher percentage of successful nest sites. Spatial differences in nest-site selection along the beach were found as well, but the difference in distributions of nest sites by experienced breeders and first-time breeders did not correspond to areas of higher nest-site success.

Marine turtles cannot assess the success of hatchling production resulting from nest-site selection and hence cannot learn to place their nests in more appropriate incubation habitats. Nevertheless, with repeated nesting crawls within and across nesting seasons, there is the potential for the nesting females to become habituated to innocuous stimuli on the beach and thus crawl farther from the sea when selecting nesting sites.

Low within-individual consistency occurred in nest-site selection, and experience affected nest-site selection in loggerhead turtles. Doomed-egg relocation does not substantially distort the gene pool in the eastern Australian loggerhead stock and should not be abandoned as a strategy for the conservation of marine turtle populations.

Because concerns over distortion of the gene pool have been a major impetus for proposing the commercialization of doomed eggs, results from our study, and several studies cited earlier, indicate that such commercialization cannot be justified on this biological basis for at least some, and perhaps most, sea turtles populations. More research on nest-site selection in other marine turtle populations is needed. Studies on beaches, such as Tortuguero, Costa Rica, where green turtles, hawksbills, and leatherbacks nest (Bjorndal & Bolten 1992) would help distinguish between species and environmental differences. In addition, further studies investigating how an organism can increase its reproductive output in later breeding seasons by selecting nest sites in less vulnerable areas without knowledge of previous nest-site success may provide valuable insights into the nesting dynamics of oviparous reptiles with limited parental care.

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