

EXPERIMENTALLY TESTING NEST SITE SELECTION: FITNESS TRADE-OFFS AND PREDATION RISK IN TURTLES

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Abstract. The nesting habitat of most freshwater turtle species has been described, but factors influencing maternal nest site selection have rarely been tested experimentally. Offspring fitness is assumed to be the major factor influencing nest site selection because habitat characteristics and nest microenvironments affect offspring survival. However, two opposing factors drive maternal nest site selection: minimizing female mortality and maximizing offspring fitness. In Australia, introduced red foxes are the major predator of turtle nests, and they also destroy nesting females. Thus, females may trade off maximizing nest survival or offspring fitness to avoid predators. In this paper, I show that the risk of predation affects maternal nest site selection and has negative effects on reproductive success in a freshwater turtle. I also show that the mechanisms behind predator detection vary between native and introduced species. From 1996 to 2000, I observed female freshwater turtles, *Emydura macquarii*, nesting around four lagoons in southeastern Australia to determine nesting habitat characteristics. During 1997 and 1998, foxes were removed from two sites, and nest predation rates declined by >50%, but remained >85% in nonremoval sites. Foxes destroyed ~3% of the female population only in high-risk areas. Female turtles nest away from shore to maximize offspring fitness when foxes are removed from an area. The dilemma in high-risk areas is that predation risk limits females from nesting in preferred areas away from shore, where nest predation is reduced. However, females may sacrifice some offspring by nesting in inappropriate substrate, where incubation conditions are not optimal, but nest predation is significantly reduced. Nesting turtles do not detect foxes by chemical recognition, but they have an innate avoidance response to the odor of a native predator. Nesting habitat affects offspring fitness, but factors affecting female survival may ultimately drive maternal nest site selection in turtles.

Key words: anti-predatory behavior; Australia; chemical recognition; *Emydura macquarii*; fitness trade-off; fox; nest site selection; predation risk; predator detection; quoll; turtles; *Vulpes*.

INTRODUCTION

Nest site selection by female turtles has long-term implications for offspring and maternal fitness. Offspring gain a selective advantage when females nesting in appropriate macro- and microhabitats because mortality is affected by high nest predation in the short term (Congdon et al. 1983, Thompson 1983, Iverson 1991, Brown and MacDonald 1995, Yerli et al. 1997, Burke et al. 1998) and offspring reproductive success can be affected in the longer term by a skewed sex ratio through temperature-dependent sex determination, TSD (Vogt and Bull 1984, Schwarzkopf and Brooks 1985, Ewert et al. 1994, Davenport 1998, Bragg et al. 2000). Maternal effects are widespread and may play an important adaptive role in evolution (Bernardo 1996, Mousseau and Fox 1998), yet the link between the locations of nests and forces influencing maternal choice are rarely tested. Turtles may be vulnerable to

terrestrial predators because nesting is the only occasion when many species leave the water, and predation risk or perceived risk will play a much greater role in nest site selection than previously acknowledged.

Predators can influence a prey population directly by injuring or killing an individual, and the threat of predation can influence the behavior of prey at different life history stages. Behavioral modifications, such as restrictions in movement, can have enormous impacts on reproductive success and may ultimately influence prey density. Kangaroos (*Macropus giganteus*) in subalpine regions of Australia forage close to forest refuges (Banks et al. 2000) when red foxes (*Vulpes vulpes*) inhabit the area. When foxes, which kill juveniles and harass females with young, are removed from the area, females feed in more open areas where they have access to better quality food. Predation on juveniles is reduced because predators are removed, but fecundity increases because females can acquire better quality food (Banks et al. 2000). The sublethal effects of predation are complex and affect prey on different levels, but their impacts on reptilian life history stages are poorly known. Eggs of the Australian freshwater turtle, *Emydura macquarii*, hatch synchronously and young emerge from a

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nest as a group to dilute predation risk (Spencer et al. 2001). Velvet geckos (*Oedura leseurii*) from populations sympatric with a snake predator (*Hoplocephalus bungaroides*) avoid retreat sites covered with snake scent, but those from an allopatric populations do not (Downes and Shine 1998). Predation on turtle nests is extremely high in most turtle populations, and strong selective pressures may influence female nest site choice.

The costs associated with predator avoidance may influence the response to the perceived danger; this adaptive decision making occurs in both invertebrates and vertebrates (for a review, see Sih 1987, Lima 1998). Foxes have replaced most native predators of turtles and their nests on the Murray River in southeastern Australia. Despite being a recent introduction to Australia (~130 yr; Saunders et al. 1995), freshwater turtles are long lived and may have associated foxes as potential predators, modifying their nesting behavior accordingly. How prey assess predation risk is extremely complex. Freshwater turtles are generally wary upon emergence from the water and will return at any slight disturbance. Thus visual recognition of a predator may play a significant part in nest site selection. Alternatively, where predators are a significant source of mortality, animals may use indirect methods, such as chemical recognition, to avoid encounters. Odor is an important means of signaling among nocturnal mammals, and a potential prey species may reduce predation risk by recognizing the presence of a predator (Weldon 1990, Ward et al. 1997). An innate response to a predator cue occurs if the two species have co-existed over evolutionary time (Ward et al. 1997), which Murray River turtles and foxes obviously have not. However, the response-provoking component in one predator's odor might invoke a similar response to other predators in prey that do not necessarily have an evolutionary association (Nolte et al. 1994). Thus turtles may respond similarly to fox odor as they may to that of native predators, which were common prior to European settlement.

In this paper, I show that sublethal impacts of predation have negative effects on the reproductive success of the Australian freshwater turtle, *Emydura macquarii*. I used a controlled and replicated fox removal experiment to determine, firstly, whether movement of nesting turtles is restricted by the threat of foxes, and secondly, whether any restriction of movement and access to resources affects hatching success and nest emergence. I then determined whether turtles respond to the presence of predators through a chemical recognition of their odor.

METHODS

Emydura macquarii and study sites

Three species of freshwater turtle inhabit the Murray-Darling system in southeastern Australia (Cann

1998). All three species are pleurodiran (suborder: Pleurodira) and belong to the Cheloniidae, which are the dominant freshwater chelonian family in Australia. *Emydura macquarii* is currently recognized as a widespread species inhabiting the Murray-Darling drainage system, west of the Great Dividing Range, and with several forms distributed throughout eastern-flowing rivers of coastal New South Wales and Queensland (Cann 1998). Females grow to a carapace length of >300 mm and are primarily confined to permanent waters in the Murray-Darling system. They are omnivorous, consuming mainly filamentous algae, fish (usually the remains of European carp, *Cyprinus carpio*), and insects (Spencer et al. 1998). Mating occurs from March to April (Cann 1998) and turtles overwinter in the water (Tasker 1991). Nesting occurs between late October and mid-December, and females generally produce only one clutch of 15–35 eggs per year (Chessman 1978, Spencer 2001).

My study sites are located in the upper Murray River near Albury-Wodonga (36° S 46° E) in southeastern Australia, and each lagoon is closed to the river except during floods. Lagoons are 12–40 ha and much of the land between Hume weir and Lake Mulwala has been subject to large-scale vegetation clearing since settlement (Smith and Smith 1990) and is now mainly grassy plain. Trees, predominately river red gum (*Eucalyptus camuldensis*), are sparse and confined to riparian zones.

Nesting habitat

Nocturnal and diurnal searches for nesting female *E. macquarii* began during storms around two areas near Albury-Wodonga (36° S, 46° E) and two areas, 100 km downstream, near Lake Mulwala (35° S, 146° E) in southeastern Australia in November 1996–1998. All effort was made to not disturb females emerging from the water or during nesting; once a turtle had begun to lay eggs, she seemed oblivious to my presence. Nesting females were observed using binoculars (Tasco 8 × 21; Tasco, Brookvale, New South Wales, Australia) or a night vision scope (Star Lazer, Lane Cove, New South Wales, Australia). Over three years, I observed 71 females until they had finished nesting and had returned to the water. Their nests were marked by placing small wooden stakes or easily recognizable sticks 5 m due north of the nest. Nests were observed daily for two weeks and again four weeks after being laid. A nest was considered successful, i.e., it avoided predation, if it had not been destroyed four weeks after being constructed. Each nest was classified as intact or destroyed, constructed at night or day, and constructed during rain or dry weather. I measured the distance of the observed nest to the closest woody vegetation, distance to the water, and distance to the nearest nest, using 50-m measuring tapes from the nest to the nearest access point. Access to land was limited to certain areas around each lagoon, because a vertical drop to the water of ≥1 m characterizes the banks of the lagoons. The soil type

of each nest was classified as either dirt or sand; there were clear boundaries between the two types of soil at each site. SYSTAT 9.0 (1999) was used for all statistical analyses in this study. Principal components analysis (PCA) was used to reduce the number of continuous (distance to water, distance to nearest nest, and distance to nearest tree) nesting habitat variables to one or two principal factors. The principal components were then placed into a general linear model with the rest of the habitat variables and ANOVA was used to determine differences between the habitat types of destroyed and intact nests.

Predator detection of nests

Two areas around Lake Mulwala were used to determine whether foxes were discovering turtle nests by the chemical cue of eggs and/or by using slight soil disturbances of a recently constructed nest. Four treatment groups were used for the study: (1) eggs with soil disturbance to represent a freshly dug turtle nest; (2) eggs with minimal disturbance, to represent an older nest; (3) disturbance without eggs; and (4) minimal disturbance without eggs. I randomly allocated 10 replicates of each treatment to each area, with "nests" ≥ 50 m apart to avoid density-dependent predation. Flask-shaped nests were dug by hand (clean gloves were worn for each treatment) and 10 eggs were placed carefully inside each nest. An earthen plug was created from the wet excavated soil, and the soil was flattened by hand in the first treatment. In the second treatment, I placed 10 eggs into each "nest," but all effort was made to not disturb the grass and topsoil, and all soil dug out from the nest was removed from the area. The third and fourth treatments were created without adding eggs, using the same methods as in the first and second treatments, respectively. This experiment was first done with quail eggs in 1996 and again with *E. macquarii* eggs in 1998.

Nesting behavior and predation risk

To determine whether female turtles alter their nesting behavior in response to predation risk, I conducted a controlled replicated fox removal experiment. The experiment was conducted around four lagoons in Albury, and each lagoon was either separated by the Murray River or by ≥ 15 km. Fox numbers were monitored in all sites from July 1996 to January 1999, using spotlight counts conducted over 4–7 consecutive nights each month between August and November, and every second month between January and May. Foxes were removed from around two lagoons (removal) after the first nesting season, whereas foxes were continually monitored around the other two lagoons (control). Each site was chosen randomly as a removal or control site. Data from the two control sites were also used to compare nesting habitat, but nests constructed in the removal sites were only used to compare nesting behavior between high and low predation risk sites.

Transects 6–8 km long around each lagoon were searched from an open car window or from the roof of a moving vehicle traveling at 5–10 km/h, with a single observer using a 100-W spotlight. Each area was searched for 4–7 consecutive nights per month between October and March and every second month throughout the rest of the year. Although transects were not straight and the habitat was open, it is unlikely that an individual would have been counted on more than one occasion per night. The spotlight areas were all relatively flat, movement of foxes could be observed for long distances, and either the lagoon or the River usually bordered the viewing area. All animals spotted per night were included in the transect count. The mean of the 4–7 nights of spotlighting each month per site was used to measure relative fox densities (Newsome et al. 1989). Estimates of the variance between nightly spotlight counts were not calculated because counts cannot be considered independent samples.

Fox numbers were reduced from the two removal sites between May 1997 (after the first turtle nesting season) and January 1999. At each of the removal sites, ~ 48 commercial 35-g FOXOFF[®] baits (Animal Control Technologies, Somerton, Victoria, Australia) were buried along most fence lines, hill ridges, or access roads at both sites, in accordance with Rural Lands Protection Board regulations, i.e., at least 200 m from public roads and households. Baits were laid 150–200 m apart and were buried 100 mm beneath a pile of loose soil to attract passing foxes (Thompson 1994). Between March and October, baits were laid for 7–10 d every second month and were checked daily, but between November and April, baits were laid monthly and were checked every three days. Once removal of foxes had begun, any foxes seen in the two removal sites were shot using a low-velocity 0.22-caliber rifle.

Each year, I measured the distance to water, to the nearest turtle nest, and to the closest tree for turtle nests constructed while I was observing females nesting around the Albury sites, as well as all other nests (destroyed or intact) discovered subsequently. In total, 2146 nests were characterized in this section of the study. Nests at removal sites in 1997 and 1998 were considered to be in areas of low predation risk and nests in nonremoval sites were in high-risk areas. Nest predation rates were determined from nests constructed during the observation period for females nesting around each lagoon. I used a series of one-way ANOVAs to test for differences in nesting habitat between years within each site. Data were ln-transformed if they failed a Levene Median test for equal variances. Student-Newman-Keuls (SNK) multiple comparison procedures were conducted to determine differences between years.

Detection of predators

To separate chemical or olfactory detection of predators from visual detection, I used islands in Lake Mul-

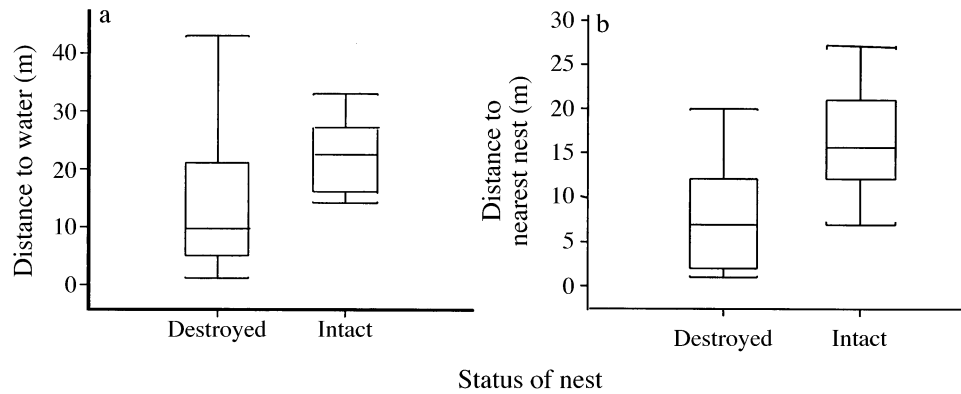


FIG. 1. (a) Box plots of the distance to water of destroyed and intact nests of the Australian freshwater turtle ($N = 71$ nests). (b) Box plots of the distance from the nearest nest (m) to destroyed and intact nests. The boxes indicate the 25th and 75th percentiles of the column, and the line inside the box marks the value of the 50th percentile. Capped bars indicate the 10th and 90th percentiles.

wala on the Murray River. Lake Mulwala was created when the river was impounded between Yarrawonga and Mulwala in 1939, resulting in a 6000-ha lake. Over 20 islands were created at the eastern end of the lake where the Ovens River joins the Murray. Some of these islands cover >10 ha and are between 100 m and 1 km from shore. Larger islands generally have some open grassland, where nesting predominantly takes place, as well as small patches of open eucalypt forest. The islands are believed to be important recruitment areas for juvenile turtles, because they may provide some relief from fox predation (Thompson 1993). In 1998, I characterized and plotted the position of nests on an enlarged topographic map for 10 of the islands. In November 2000 (<24 h prior to nesting), I dragged fox bedding and feces in a damp cloth sack around the shorelines and the main nesting areas of two of these islands. Similarly, around two other islands I dragged the bedding and feces of a native predator (Eastern Quoll, *Dasyurus viverrinus*) that was present in the area prior to European settlement. Clean bedding was placed around two other islands as controls. I used the distance to the nearest nest to compare densities of nests on each island between years.

RESULTS

Nest habitat

Of 71 turtle nests, predators destroyed 52, leaving only 19 nests intact after four weeks of incubation. The first two principal components accounted for 95% of the variance, PC1 accounting for 76% of the variation and PC2 accounting for 19%. PC1 represents increasing distance from the water (95% of the variance of PC1) and PC2 mainly represents an increasing distance from the nearest tree (82% of the variance of PC2). There is considerable overlap in habitat between intact and destroyed nests, but the majority of intact nests were not close to trees or water. Most nests destroyed by predators were close to water and trees, although

some nests away from water were also destroyed. The majority of intact nests were found in a small, distinct range 15–35 m from water (Fig. 1), as well as 10 m farther away from neighboring nests compared to nests destroyed by predators (Fig. 1).

Time of day and rainfall when the nest was constructed did not influence whether the nest was intact or destroyed, although soil type significantly influenced the predation rate ($F_{1,65} = 15.2$, $P < 0.001$). Of nests constructed in sand close to shore, $\sim 40\%$ survived nest predation, compared to $<10\%$ survival for nests constructed in soil.

Birds and foxes were the major predators of turtle nests. Birds, primarily Australian Bell Magpies (*Gymnorhina tibicen*), used their beak to create a distinct hole into the nest and usually swallowed eggs whole. On most occasions, the nest was not completely destroyed by birds, but all eggs were usually destroyed within 24 h. Birds mainly destroyed nests by swooping from trees: for nests constructed diurnally, those that were destroyed were 12.5 ± 12.7 m (mean ± 1 SD) from the nearest tree, compared to 53.4 ± 14.8 m for intact nests (Fig. 2). Nests destroyed by foxes were easily identified by a combination of tracks, feces, and

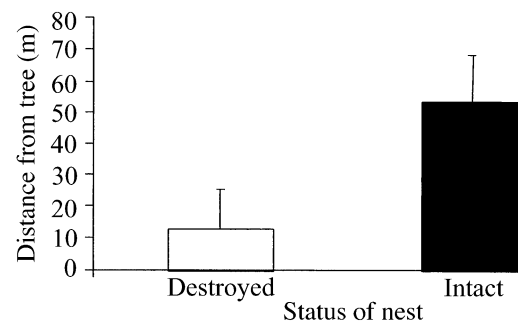


FIG. 2. Distance from destroyed and intact turtle nests constructed during the day to the nearest tree (mean ± 1 SD; $N = 22$).

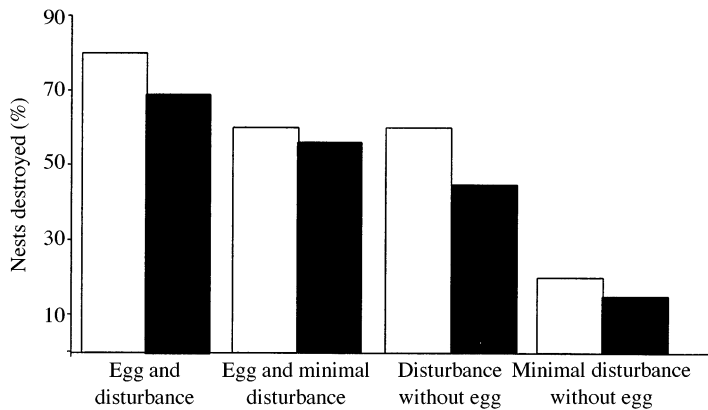


FIG. 3. Percentage of nests with turtle (open bars) and quail (solid bars) eggs destroyed in the predator detection experiments.

remaining eggshells. Foxes also left digging mounds of dirt surrounding the nest. During the study, water rats (*Hydromys chrysogaster*) destroyed two nests, leaving remains similar to the characteristics of nests destroyed by both birds and foxes: a small, circular hole surrounded by small mounds of dirt, tracks, and/or eggshells. There were no indications that snakes destroyed nests, and monitor lizards were never observed in any of the study areas.

Predator detection of nest

In the predator detection experiments, only foxes destroyed nests, with 70% of disturbed quail and 80% of disturbed turtle egg nests destroyed (Fig. 3). Similar percentages were destroyed for experimental nests with eggs and minimal disturbance and for nests with no eggs and disturbance, using both turtle and quail eggs; nests with no eggs and minimal disturbance had low rates of predation. Foxes thus appeared to find nests by both chemical detection of eggs and slight soil disturbance (Fig. 3).

Predation risk and changes in nesting behavior

Relative fox densities at all sites in 1996 were 1.5–3.0 foxes/km². Predation rates on nests that year were high, with 85–93% (93% = 27/29 nests), 85% (17/20), 91% (11/12), and 92% (23/25) of observed nests destroyed at the four nesting areas (Fig. 4).

Spotlight counts of foxes remained below 0.75/km² and were below 0.2/km² by November (the turtle nesting period) in both 1997 and 1998 at the removal sites (Fig. 4). During the same period, fox numbers remained high in nonremoval sites. In 1997 and 1998, nest predation rates declined to <50% in the removal sites, but remained >83% over the same period in the nonremoval sites (Fig. 4).

Nest site selection by *E. macquarii* also altered when foxes were removed. In 1996, female *E. macquarii* generally nested 14–18 m from water at each lagoon, but females nested much farther from water once foxes were removed (Fig. 5). In both removal sites, turtles nested significantly farther from the shoreline in sub-

sequent years than when foxes were present in 1996 ($F_{2,524} = 6.28$, $P = 0.002$ and $F_{2,621} = 20.8$, $P < 0.001$ for the two sites). Conversely, female turtles nested at similar distances, or even closer to the water, in nonremoval, high-risk sites (Fig. 5). Female turtles used larger nesting areas when foxes were removed, and thus nests were less clumped (Fig. 5b) and were farther from trees, which were generally close to the shoreline. A large proportion of nesting habitat at or close to the

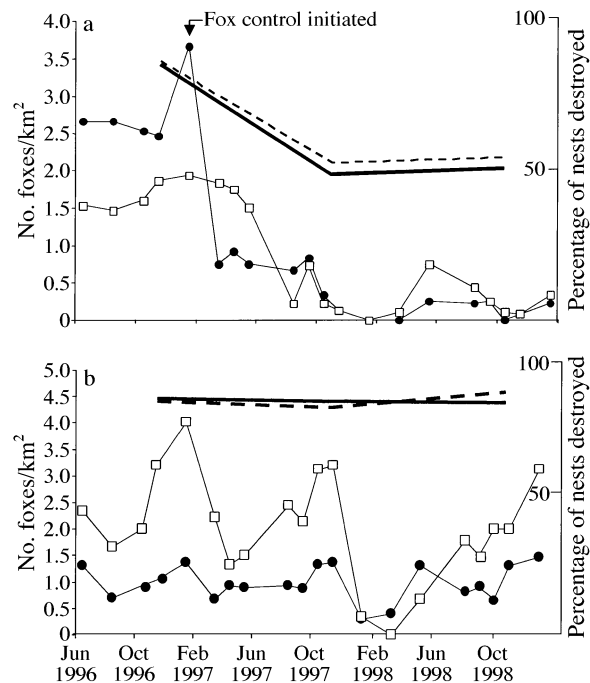


FIG. 4. (a) Fox densities and nest predation rates at sites where foxes were removed. (b) Fox densities and nest predation rates at nonremoval sites (control) and at removal sites over the same period. Open squares and solid circles are fox densities (left-hand axis scales) at the two removal or two control sites, respectively, and the dashed and solid lines are the corresponding nest predation rates at each site (right-hand axis scales).

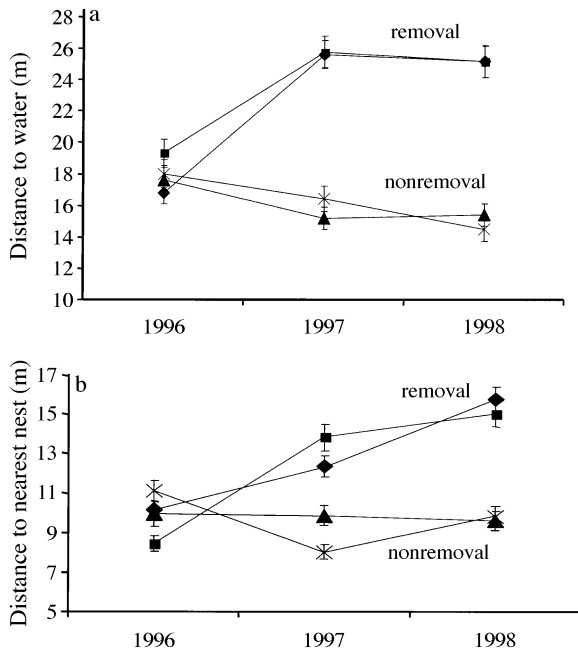


FIG. 5. (a) Distance (mean \pm 1 SE) to water for turtle nests constructed around both removal and nonremoval sites. (b) Distance (mean \pm 1 SE) to the nearest nest for turtle nests in removal and nonremoval sites. For both (a) and (b), $N = 2146$. Squares and diamonds represent fox removal sites (1997–1998), and the triangles and asterisks are nonremoval sites.

shoreline of most lagoons is river sand. Of nests not destroyed by predators, there was a higher failure of eggs and hatchlings (pooled) to complete incubation and to emerge from nests constructed in sand (4.2 ± 0.6 eggs and hatchlings, mean \pm 1 SE; $N = 24$) than from nests constructed in soil (2.6 ± 0.4 eggs and hatchlings; $N = 32$; $t = 2.37$, $df = 54$, $P = 0.02$).

Detection of predators

In total, 577 turtle nests were found on the islands in 1998 and 2000. Nest densities on the two islands in the fox treatment were not significantly different between years (for 1998, $t = 0.76$, $df = 67$, $P = 0.22$; for 2000, $t = 0.32$, $df = 87$, $P = 0.38$), and the positions of nests were also similar (Fig. 6). However, densities of nests in the quoll treatment were significantly different between years ($t = 4.65$, $df = 85$, $P < 0.001$ and $t = 6.07$, $df = 127$, $P < 0.001$) because the majority of nests constructed in 2000 (after material with quoll feces and bedding was spread throughout the island prior to nesting) were concentrated around the “easy” access points, where the majority of turtles emerged to nest (Fig. 6). Nest densities on the control islands were not significantly different between years ($t = 0.57$, $df = 92$, $P = 0.28$ and $t = 0.31$, $df = 107$, $P = 0.38$).

DISCUSSION

Numerous theories have been proposed regarding nest site selection in turtles. Thermal properties (Stone-

burner and Richardson 1981), composition and densities of vegetation (Mrosovsky 1983, Hays et al. 1995), microhabitat and slope (Mortimer 1990), interspecific competition (Whitmore and Dutton 1985), and human disturbance (Witherington 1982, Kolbe and Janzen 2001) are all factors that may influence maternal nest site choice. Even TSD (temperature-dependent sex determination) is suggested as a deciding factor in nest site selection in turtles because a female can manipulate the sex ratio of the clutch to enhance the reproductive success of her offspring (Vogt and Bull 1984, Schwarzkopf and Brooks 1985, Bobyn and Brooks 1994, Davenport 1998, Bragg et al. 2000, Janzen and Moran 2001). Although attention to nest site selection in freshwater turtles has been heavily focused on specific factors affecting offspring fitness, this study demonstrates that female turtles alter nesting behavior in response to direct predation risk. Predation is an important process in many systems (e.g., aquatic), but rarely has it been considered an important evolutionary process in reptiles (Downes and Shine 1998, 1999, Spencer et al. 2001). Selection for life history traits that minimize vulnerability occurs in most populations (Morse 1979, Vermeij 1987, Downes and Shine 1998). Nest predation is the greatest source of mortality in turtles, and selection should favor females choosing habitats that reduce the negative effects of nest predation, given the importance of reproductive success to fitness (Martin

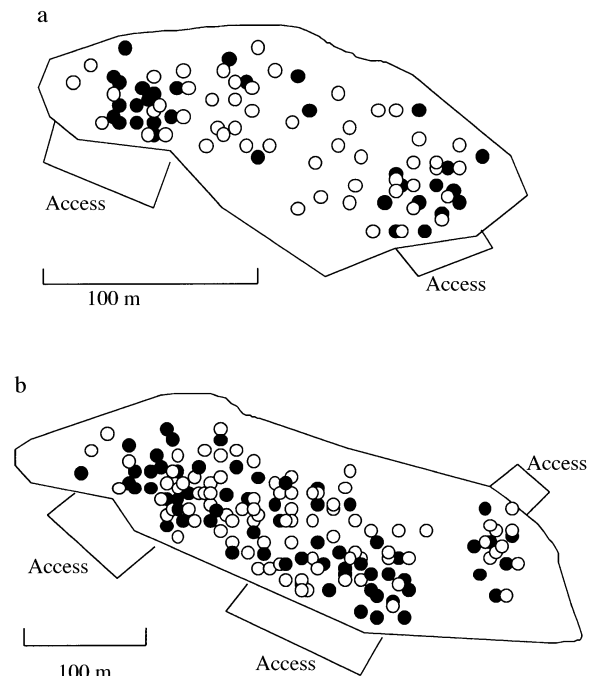


FIG. 6. Open circles indicate the position of turtle nests constructed on two islands in 1998. Solid circles are nests constructed after (a) quoll feces and bedding were scattered throughout the island and (b) fox feces and bedding were scattered throughout the island. The pattern of nesting on control islands was similar to that in panel (b).

1993). Direct predation on nesting *E. macquarii* has more immediate and dramatic effects on fitness. Thus a trade-off between avoiding predators and effectively disguising the nest may drive maternal nest site selection in *E. macquarii*.

Two relatively opposing forces drive maternal nest site selection: minimizing female mortality and maximizing offspring fitness. Foxes destroy a small percentage of nesting females (~3%) each year and many others have bite marks on their carapace and plastron, suggesting unsuccessful predation attempts (Spencer 2001). Considering that annual survivorship of adult female turtles is >99% (excluding predation on nesting females), a predation rate of 3% on nesting females is a significant source of mortality (Spencer 2001). To minimize the risk of direct predation, females could nest in or near water, but offspring fitness would be severely reduced because the clutch would drown. Nests in beach zones on the coast of Florida, USA suffered high mortality during Hurricane Andrew (Milton et al. 1994), and predation on nests generally increases closer to water or to other nests (Zimmerman 1984, Christens and Bider 1987, Martin 1988a, b, Lariviere and Messier 1998). Female *E. macquarii* locate their nests 14–18 m from shore in high-risk areas and must balance the risk of predation with maximizing clutch success. In low-risk areas, however, nests are located >25 m from shore because the risk of direct predation is eliminated and maximizing offspring fitness (i.e., reducing nest predation) may determine maternal nest site choice.

Is clutch success or offspring fitness maximized in low-risk areas? In this study, nest predation rates are extremely high, with 85–95% of nests destroyed in the upper Murray (Fig. 3), but nest predation decreases to <50% primarily because foxes have been removed from the areas. However, nest predation influences maternal nest site choice in low-risk areas because turtles consistently construct nests in areas where they are more likely to survive predation and remain intact (Fig. 1). Most predation on turtle nests occurs within a day or two after the eggs have been deposited, and often within a few hours of construction (Legler 1954, Burger 1977, Tinkle et al. 1981, Congdon et al. 1983, 1987, Christens and Bider 1987). Similarly, *E. macquarii* nests are often destroyed within seconds after the female leaves the area. Birds could only detect nests visually by observing females nesting, because they never destroyed nests constructed at night; nests not detected immediately remained intact or were later destroyed by other predators. Furthermore, the majority of nests destroyed during the day were constructed near trees, where birds could observe nesting females (Fig. 4). Nest predation by birds is increased in high-risk areas because the majority of the upper Murray River floodplain is used for agricultural practices and trees are predominantly located in riparian zones (Fig. 5). High nest predation rates in birds drive many life his-

tory traits, including clutch size and frequency, and may also drive nest site choice (Martin 1995). Tengmalm's owls (*Aegolius funereus*) respond to increased risks of nest predation by shifting their nest holes and increasing their breeding dispersal (Hakkarainen et al. 2001).

Offspring fitness is maximized in low-risk areas because female turtles construct nests in areas where nest predation, the greatest source of offspring mortality, is minimal. However, other sources of offspring mortality may also influence nest site selection. Maternal nest site choice can have consequences for the fitness of offspring because habitat characteristics and nest microenvironments are functionally linked (Weisrock and Janzen 1999). Turtles further enhance offspring fitness in low-risk areas by nesting farther away from water and avoiding river sand. More offspring fail to complete the incubation period in river sand than in soil, and reproductive success is further reduced in high-risk areas because more nests are constructed closer to shore, where river sand mainly occurs. Eggs of *Chrysemys picta bellii* in artificial nests of sand dehydrate more quickly than eggs kept in clay (Legler 1954). With very little vegetation associated with sand, the incubation temperature range may be much larger than that for nests associated with soil and grass. Embryo survival in nests of *Kinosternum baurii* without vegetative cover is considerably reduced, because temperatures reach the thermal maximum more often than in nests with cover (Wilson 1998). The threat of direct and nest predation are behind the processes of maternal nest site selection in high-risk areas. Females face a series of hierarchical decisions or trade-offs before nesting occurs. The dilemma in high-risk areas is that predation risk limits females from nesting in preferred areas away from shore, where nest predation is significantly reduced. However, females may increase their reproductive success by sacrificing some offspring and nesting in river sand, where incubation conditions may not be optimal, but nest predation is significantly lower than in the surrounding soil.

There is extensive empirical evidence demonstrating that animals adjust food quality and alter their behavior to reduce the risk of predation and increase their chance of survival (McNamara and Houston 1987). Similarly, females of *E. macquarii* adjust nesting behavior and reduce the amount of time spent on land in high-risk areas to increase their chance of survival. How do they assess potential predation risk? Avoidance of a predator odor can be species specific (Swihart 1991, Nolte et al. 1993, Downes and Shine 1998) or a general response to a carnivore (Stoddart 1982, Nolte et al. 1994). However, the preferences demonstrated in the island experiments cannot be explained as a generalized avoidance of predator odor, because female *E. macquarii* show little response to fox odor and probably detect foxes by visual recognition. Female turtles are extremely wary when they emerge to nest, and return to water

when disturbed. If foxes continually pass through the nesting area, female turtles may make several false nesting attempts before deciding on a nest site; they may assess predation risk by the amount of predator activity and the number of nesting attempts. Foxes, on the other hand, detect nests using both olfactory cues and slight soil disturbance (Fig. 3). Thus turtle nests are more susceptible to fox predation in the first few hours after nesting because the soil is freshly disturbed, enhancing olfactory recognition of eggs and female secretions. Similarly, *E. macquarii* uses olfactory senses to detect native predators. In this study, gravid females showed the same anti-predatory response to eastern quoll odor that they did in areas with high risk for fox predation. The response to quoll odor is an innate behavioral shift, because many turtles may never have been exposed to possible predation pressures by quolls. Very little is known about predation pressures by native predators prior to European settlement because foxes and land clearing on the Murray River have displaced most native predators. Native dasyurids may have harassed or destroyed nesting turtles prior to European settlement, because many prey only respond to predators that are actively dangerous (Dickman 1992).

In previous research, heavy emphasis has been placed on the habitat and microenvironment of a nest in order to explain maternal nest site selection in turtles. However, I have shown that predation risk and factors affecting female fitness may be equally important. Freshwater turtles may have evolved high levels of predator detection to reduce their vulnerability to predators and to increase their direct fitness at the expense of increased nest predation rates and reduced clutch success, which ultimately affects offspring fitness.

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LITERATURE CITED

- Banks, P. B., A. E. Newsome, and C. R. Dickman. 2000. Predation by red foxes limits recruitment in populations of eastern grey kangaroos. *Austral Ecology* **25**:283–291.
- Bernado, J. 1996. Maternal effects in animal ecology. *American Zoologist* **36**:83–105.
- Bobyne, M. L., and R. J. Brooks. 1994. Interclutch and interpopulation variation in the effects of incubation conditions on sex, survival and growth of hatchling turtles (*Chelydra serpentina*). *Journal of Zoology* **233**:233–257.
- Bragg, W. K., J. D. Fawcett, T. B. Bragg, and B. E. Viets. 2000. Nest-site selection in two eublepharid gecko species with temperature-dependent sex determination and one with genotypic sex determination. *Biological Journal of the Linnean Society* **69**:319–332.
- Brown, L., and D. W. MacDonald. 1995. Predation on green turtle *Chelonia mydas* nests by wild canids at Akyatan Beach, Turkey. *Biological Conservation* **71**:55–60.
- Burger, J. 1977. Determinants of hatching success in the diamondback terrapin, *Malaclemys terrapin*. *American Midland Naturalist* **97**:444–464.
- Burke, V. J., S. L. Rathbun, J. R. Bodie, and J. W. Gibbons. 1998. Effect of density on predation rate for turtle nests in a complex landscape. *Oikos* **83**:3–11.
- Cann, J. 1998. Australian freshwater turtles. Beaumont Publishing, Singapore, Malaysia.
- Chessman, B. C. 1978. Ecological studies of freshwater turtles in southwestern Australia. Ph.D. Thesis. Department of Zoology, Monash University, Melbourne, Victoria, Australia.
- Christens, E., and J. R. Bider. 1987. Nesting activity and hatching success of the painted turtle (*Chrysemys picta marginata*) in southwestern Quebec. *Herpetologica* **43**:55–65.
- Congdon, J. D., G. L. Breitenbach, R. C. van Loben Sels, and D. W. Tinkle. 1987. Reproduction and nesting ecology of snapping turtles (*Chelydra serpentina*) in southeastern Michigan. *Herpetologica* **43**:39–54.
- Congdon, J. D., D. W. Tinkle, G. L. Breitenbach, and R. C. van Loben Sels. 1983. Nesting ecology and hatching success in the turtle *Emydoidea blandingii*. *Herpetologica* **39**:417–429.
- Davenport, J. 1998. Temperature and the life history strategies of sea-turtles. *Journal of Thermal Biology* **22**:479–488.
- Dickman, C. R. 1992. Predation and habitat shifts in the house mouse, *Mus domesticus*. *Ecology* **73**:313–322.
- Downes, S., and R. Shine. 1998. Sedentary snakes and gullible geckos: predator-prey coevolution in nocturnal rock-dwelling reptiles. *Animal Behaviour* **55**:1373–1385.
- Downes, S., and R. Shine. 1999. Do incubation-induced changes in a lizard's phenotype influence its vulnerability to predators? *Oecologia* **120**:9–18.
- Ewert, M. A., D. R. Jackson, and C. E. Nelson. 1994. Patterns of temperature-dependent sex determination in turtles. *Journal of Experimental Zoology* **270**(1):3–15.
- Hakkarainen, H., P. Ilmonen, V. Koivunen, and E. Korpimäki. 2001. Experimental increase of predation risk induces breeding dispersal in Tengmalm's owl. *Oecologia* **126**:355–359.
- Hays, G. C., A. Mackay, C. R. Adams, J. A. Mortimer, J. R. Speakman, and M. Boerema. 1995. Nest site selection by sea turtles. *Journal of the Marine Biological Association of the United Kingdom* **75**:667–674.
- Iverson, J. B. 1991. Life history and demography of the yellow mud turtle *Kinosternon flavescens*. *Herpetologica* **47**:373–395.
- Janzen, F. J., and C. L. Moran. 2001. Repeatability of microenvironment-specific nesting behaviour in a turtle with environmental sex determination. *Animal Behaviour* **62**:73–82.
- Kolbe, J. J., and F. J. Janzen. 2001. Impact of nest-site selection on nest success and nest temperature in natural and disturbed habitats. *Ecology* **83**:269–281.
- Lariviere, S., and F. Messier. 1998. Effect of density and nearest neighbours on simulated waterfowl nests: can predators recognize high-density nesting patches? *Oikos* **83**:12–20.
- Legler, J. M. 1954. Nesting habits of the western painted turtle, *Chrysemys picta bellii* (Gray). *Herpetologica* **10**:137–144.

- Lima, S. J. 1998. Nonlethal effects in the ecology of predator-prey interactions. *BioScience* **48**:25-34.
- Martin, T. E. 1988a. Habitat and area effects on forest bird assemblages: is nest predation an influence? *Ecology* **69**:74-84.
- Martin, T. E. 1988b. Nest placement: implications for selected life-history traits, with special reference to clutch size. *American Naturalist* **132**:900-910.
- Martin, T. E. 1993. Nest predation and nest sites: new perspectives on old patterns. *BioScience* **43**:523-532.
- Martin, T. E. 1995. Avian life history evolution in relation to nest sites, nest predation, and food. *Ecological Monographs* **65**:101-127.
- McNamara, J. M., and A. I. Houston. 1987. Starvation and predation as factors limiting population size. *Ecology* **68**:1515-1519.
- Milton, S. L., S. Leone-Kabler, A. A. Schulman, and P. L. Lutz. 1994. Effects of Hurricane Andrew on the sea turtle nesting beaches of South Florida. *Bulletin of Marine Science* **54**:974-981.
- Morse, D. 1979. Behavioral mechanisms in ecology. Harvard University Press, Cambridge, Massachusetts, USA.
- Mortimer, J. A. 1990. The influence of beach sand characteristics on the nesting behavior and clutch survival of green turtles, *Chelonia mydas*. *Copeia* 1990:802-817.
- Mousseau, T. A., and C. W. Fox. 1998. The adaptive significance of maternal effects. *Trends in Ecology and Evolution* **13**:403-407.
- Mrosovsky, N. 1983. Ecology and nest-site selection of leatherback turtles *Dermochelys coriacea*. *Biological Conservation* **26**:47-56.
- Newsome, A. E., I. Parer, and P. C. Catling. 1989. Prolonged prey suppression by carnivores: predator-removal experiments. *Oecologia* **78**:458-467.
- Nolte, D. L., J. P. Farley, D. L. Campbell, G. M. Epple, and J. R. Mason. 1993. Potential repellants to prevent beaver damage. *Crop Protection* **12**:624-626.
- Nolte, D. L., J. R. Mason, G. M. Epple, E. Aronov, and D. L. Campbell. 1994. Why are predator urines aversive to prey? *Journal of Chemical Ecology* **20**:1505-1516.
- Saunders, G., B. Coman, J. Kinneer, and M. Braysher. 1995. Managing vertebrate pests: foxes. Bureau of Resource Sciences and Australian Nature Conservation Agency, Australian Government Publishing Service, Canberra, Australian Capitol Territory, Australia.
- Schwarzkopf, L., and R. J. Brooks. 1985. Sex determination in northern painted turtles, *Chrysemys picta*. Effect of incubation at constant and fluctuating temperatures. *Canadian Journal of Zoology* **63**:2543-2547.
- Sih, A. 1987. Predators and prey lifestyles: an evolutionary and ecological overview. Pages 203-224 in W. C. Kerfoot and A. Sih, editors. Predation: direct and indirect impacts on aquatic communities. University Press of New England, Hanover, New Hampshire, USA.
- Smith, P., and J. Smith. 1990. Floodplain vegetation. Pages 215-231 in N. Mackay and D. Eastburn, editors. The Murray. Murray Darling Basin Commission, Canberra, Australia Capitol Territory, Australia.
- Spencer, R.-J. 2001. The Murray River turtle, *Emydura macquarii*: population dynamics, nesting ecology and impact of the introduced red fox, *Vulpes vulpes*. Dissertation. University of Sydney, Sydney, Australia.
- Spencer, R.-J., M. B. Thompson, and P. B. Banks. 2001. Hatch or wait? A dilemma in reptilian incubation. *Oikos* **91**:401-406.
- Spencer, R.-J., M. B. Thompson, and I. D. Hume. 1998. The diet and digestive energetics of an Australian short-necked turtle, *Emydura macquarii*. *Comparative Biochemistry and Physiology, Part A* **121**:341-349.
- Stoddart, D. M. 1982. Demonstrations of prey olfactory discrimination by the short-tailed vole, *Microtus agrestis*. *Animal Behaviour* **20**:293-294.
- Stoneburner, D. L., and J. I. Richardson. 1981. Observations on the role of temperature in loggerhead turtle nest site selection. *Copeia* 1981:238-241.
- Swihart, R. K. 1991. Modifying scent-marking behavior to reduce woodchuck damage to fruit trees. *Ecological Applications* **1**:98-103.
- SYSTAT. 1999. Version 9.0. SPSS Science, Chicago, Illinois, USA.
- Tasker, E. M. 1991. Overwintering ecology and physiology of the Murray short-necked tortoise, *Emydura macquarii*. Honours thesis. University of Sydney, Sydney, New South Wales, Australia.
- Thompson, J. 1994. The management of red foxes (*Vulpes vulpes*) in the northern tablelands of New South Wales. Thesis. University of New England, Armidale, New South Wales, Australia.
- Thompson, M. B. 1983. Murray River tortoise (*Emydura, Chelodina*) populations: the effect of egg predation by the red fox, *Vulpes vulpes*. *Australian Wildlife Research* **10**:363-371.
- Thompson, M. B. 1993. Hypothetical considerations of the biomass of chelid tortoises in the River Murray and the possible influences of predation by introduced fox. Pages 219-224 in D. Lunney and D. Ayes, editors. Herpetology in Australia. Surrey Beatty and Sons, Sydney, New South Wales, Australia.
- Tinkle, D. W., J. D. Congdon, and P. C. Rosen. 1981. Nesting frequency and success: implications for the demography of painted turtles (*Chrysemys picta*). *Ecology* **62**:1426-1432.
- Vermeij, G. 1987. Evolution and escalation: an ecological history of life. Princeton University Press, Princeton, New Jersey, USA.
- Vogt, R. C., and J. J. Bull. 1984. Ecology of hatchling sex ratio in map turtles. *Ecology* **65**:582-587.
- Ward, J. F., D. W. Macdonald, and C. P. Doncaster. 1997. Responses of foraging hedgehogs to badger odour. *Animal Behaviour* **53**:709-720.
- Weisrock, D. W., and F. J. Janzen. 1999. Thermal and fitness-related consequences of nest location in painted turtles (*Chrysemys picta*). *Functional Ecology* **13**:94-101.
- Weldon, P. J. 1990. Responses by vertebrates to chemicals from predators. Pages 500-521 in D. W. Macdonald, D. Muller-Schwarze, and S. E. Natynczuk, editors. Chemical signals in vertebrates V. Oxford University Press, Oxford, UK.
- Whitmore, C. P., and P. H. Dutton. 1985. Infertility, embryonic mortality and nest-site selection in leatherback and green sea turtles in Suriname. *Biological Conservation* **34**:251-272.
- Wilson, D. 1998. Nest-site selection: microhabitat variation and its effects on the survival of turtle embryos. *Ecology* **79**:1884-1892.
- Witherington, B. E. 1982. Behavioral responses of nesting sea turtles to artificial lighting. *Herpetologica* **48**:31-39.
- Yerli, S., A. F. Canbolat, L. J. Brown, and D. W. Macdonald. 1997. Mesh grids protect loggerhead turtle (*Caretta caretta*) nests from red fox (*Vulpes vulpes*) predation. *Biological Conservation* **82**:109-111.
- Zimmerman, J. L. 1984. Nest predation and its relation to habitat and nest density in Dickcissels. *Condor* **86**:68-72.