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Source: *Herpetologica*, Vol. 69, No. 4 (December 2013), pp. 383-396
Published by: Allen Press on behalf of the Herpetologists' League
Stable URL: http://www.jstor.org/stable/24634291
Accessed: 10-01-2018 02:09 UTC

HERPETOLOGICA

VOL. 69 DECEMBER 2013 NO. 4

Herpetologica, 69(4), 2013, 383–396

SELECTIVITY AND REPEATED USE OF NESTING SITES IN A FRESHWATER TURTLE

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ABSTRACT: Understanding why turtles select specific localities to nest over others is important for management and conservation. For some species of freshwater turtle, the same localities are selected year upon year, but it is uncertain whether these localities are selected due to favored environmental conditions, or natal-site homing. The Mary River Turtle (*Elusor macrurus*) is an endangered freshwater species from Australia, and nesting data gathered between 2004 and 2011 demonstrated that female *E. macrurus* select to nest in specific localities along the Mary River. Here, we used time-lapse infrared photography and image-identification analysis to assess whether the same individuals returned to the same nesting banks over three consecutive years (nest-site fidelity), and we compared the physical and soil characteristics of nesting areas against other localities along the river where the turtles were not recorded to nest. The photography study illustrated that some females returned to nest at the same locality over consecutive years, whereas others did not; therefore, it is still inconclusive whether *E. macrurus* exhibits true nest-site fidelity. Preferred nesting areas were all northerly facing and thus exposed to higher levels of solar radiation than nonpreferred areas with similar soil and physical characteristics. Consequently, the preferred nesting areas exhibited significantly greater mean and daily fluctuations in the nest temperature compared with other areas with dummy nests. We suggest that the warmer nest temperature would speed up embryo development; therefore, female *E. macrurus* select to nest on northerly facing banks in an attempt to reduce the embryo incubation period. A possible reason for this behavior may be to reduce their exposure to nest-raiding predators. The study highlights importance of key nesting areas along the Mary River for the conservation of *E. macrurus*.

Key words: Behavior; Ecology; *Elusor macrurus*; Image analysis; Landscape composition; Nest-site fidelity; Photo identification; Soil characteristics

THE ACTIVITIES of humans are dramatically reducing turtle populations across the globe. The International Union for Conservation of Nature (IUCN) reports that 45% of the 263 identified species of freshwater and terrestrial turtles are either threatened or endangered (IUCN, 2011), and as a group the chelonians are at higher risk of extinction than birds, amphibians, elasmobranches, and mammals (Hoffmann et al., 2010). Biological information regarding the early life stages of turtles is likely to play an important role in conservation strategies because creating and preserving suitable habitat for nesting female turtles will increase recruitment into the population.

Nest-site selection by the adult female turtle may be critical in the survivorship of her offspring (Wilbur and Morin, 1988). For example, nest-site selection may influence the odds that the nest will be depredated or flooded (Kolbe and Janzen, 2002b) and the likelihood that the offspring will reach the water upon hatching (Kolbe and Janzen, 2002a). Moreover, the environmental conditions, in particular temperature and moisture,

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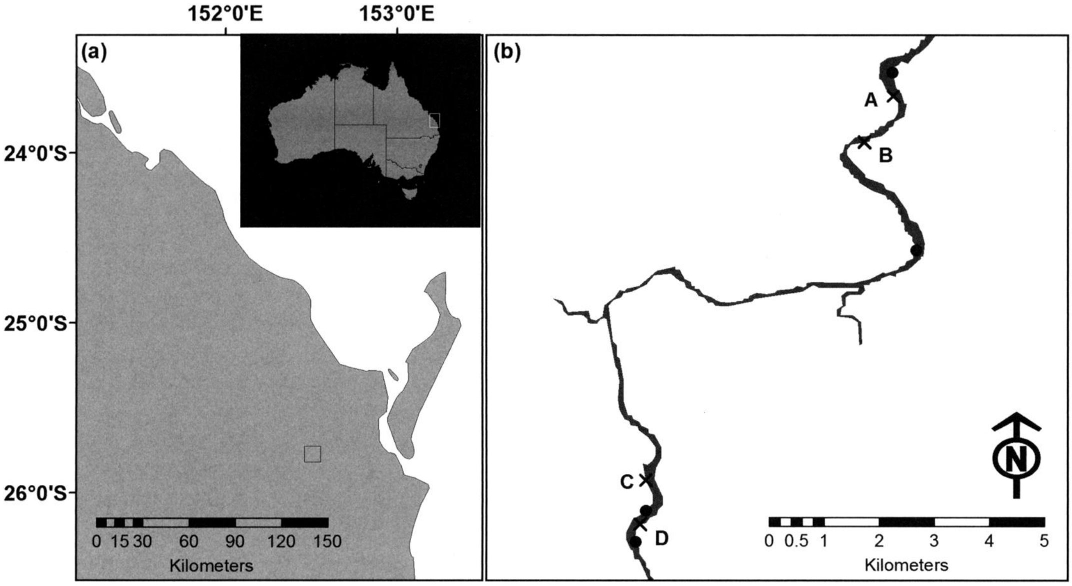


FIG. 1.—(a) Geographical location of the Mary River (Queensland, Australia). (b) The river flows southwest to northeast. Black crosses represent the location of the nesting banks monitored during the study (Nesting-banks A, B, C, and D). Black circles represent the location of the river banks where *Elusor macrurus* nests have never been recorded (nonpreferred banks).

experienced by the egg during incubation can influence embryonic development, hatching success, hatchling sex ratio, body size, locomotor performance, thermoregulation behavior, and posthatching growth rate (Miller et al., 1987; Packard et al., 1987, 1999; Janzen et al., 1990; Ackerman, 1991; Janzen, 1993; Booth, 2002, 2006; Booth et al., 2004; Micheli-Campbell et al., 2011). The temperature and moisture content within the nest are influenced by the landscape aspect and substrate characteristics of the nesting site, as well as external ambient conditions (Ackerman, 1991; Marchand and Litvaitis, 2004; Bonach et al., 2007). As a consequence, some species of turtles show homing to certain localities, returning to the nest site where they hatched (Loncke and Obbarde, 1977; Congdon et al., 1983; Jackson and Walker, 1997; Valenzuela and Janzen, 2001). Alternatively, nesting females may select nesting areas opportunistically based upon favorable environmental conditions (Roosenburg, 1996; Wilson, 1998; Restrepo et al., 2006; Ficetola, 2007).

The Mary River Turtle (*Elusor macrurus*) is the second most endangered species of freshwater turtle in Australia (IUCN, 2011). The species was scientifically described as recently as 1994, and by this date the population was estimated to be 95% depleted (IUCN, 2011). The population decline in *E. macrurus* has been attributed largely to extensive collection of the eggs from the nesting banks during the 1960s and 1970s (Cann and Legler, 1994). However, the population does not appear to have recovered since its first listing by the IUCN as endangered (IUCN, 2011). Mary River Turtle only inhabits the Mary River catchment in southeastern Queensland, Australia, and because of this limited geographical distribution, changes in land and water use within the catchment may have ramifications for the entire population. The aim of this study was to characterize the nesting biology of Mary River Turtle and to understand the nest-site selection by females. To undertake this task, we needed to understand whether females always selected the same nesting localities or whether certain localities were favored over others due to the immediate characteristics of the environment.

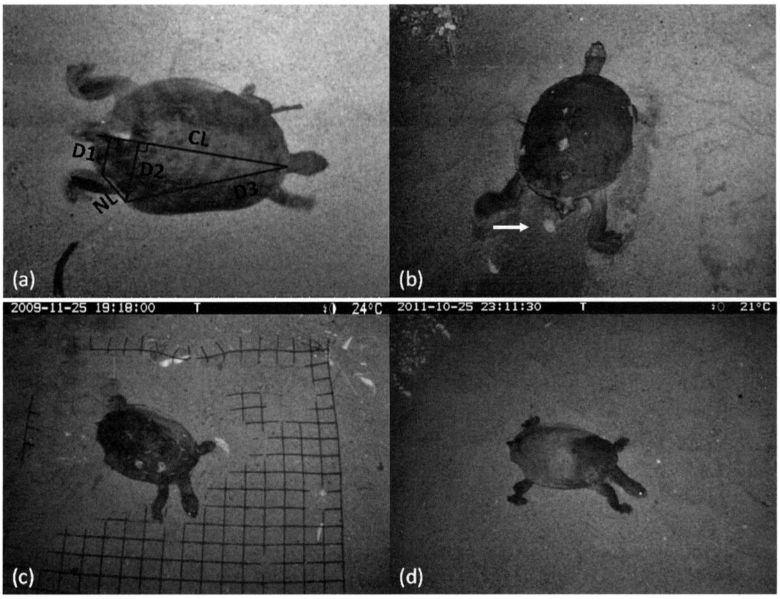


FIG. 2.—(a) Set of measurements used to identify different females. These measurements were obtained by the image-analysis software and were taken for each mark/notch present on the carapace. (b) Female *E. macrurus* laying a clutch in the view of the camera (white arrow indicates freshly laid egg). (c-d) One of the individually identified female *E. macrurus* photographed when accessing Nesting-bank B in two different years (c = 2009; d = 2011).

MATERIALS AND METHODS

Study Area

This study was conducted along a 15-km stretch of the Mary River in Queensland, Australia (Fig. 1). Female *E. macrurus* lay their eggs from October to January in moist sandy banks after periods of rainfall. The act of nesting leaves a distinct imprint that enables accurate identification of freshly laid clutches. From 2004 to 2011, sandy river banks within this section of the river were searched for the presence of *E. macrurus* nests.

Assessing Nest-Site Fidelity

To investigate nest-site fidelity, a known nesting bank (Nesting-bank B; Fig. 1b) was monitored consecutively for 3 yr with three surveillance cameras (PM75 RapidFire Mono IR, Reconyx, Holmen, Wisconsin, USA) mounted in custom-built housings ~2 m above the ground and positioned at the water's edge. Standard motion-detection cameras are developed primarily for photographing warm-blooded creatures and were not appropriate for this study because turtles do not generate sufficient external heat to trigger the infrared sensor. Instead, we used time-lapse photography and mounted the cameras above the nesting banks and oriented them to take overhead images of the turtles as they passed underneath. The cameras faced the slope of the bank, and the females were photographed as they walked through the view of the cameras when traveling from the river up the sloped bank. Each camera view covered approximately 2 m^2 of the river-bank surface. The cameras were set in time-lapse mode and took an image every 30 s. Each image displayed the date, time, air temperature, and moon phase. For each camera deployment, an image was taken of the ground covered with a plastic mesh composed of 5-cm^2 squares. These pictures were used to provide real-distance measurements and to enable the calibration of the image-analysis software.

The images containing females were identified and cataloged. These images were then analyzed with image-analysis software (SigmaScan®, Systat Software Inc., San Jose, California, USA). Identification of individual females was only possible for the turtles that had indentations (notches), naturally or artifically, on the marginal scutes. Measurements taken from each turtle image were carapace length (CL) along the midline, notch length (NL; for each notch present), perpendicular distance between the lower edge of the notch (closer to tail) to the CL line, perpendicular distance between the upper edge of the notch (farther away from tail) to the CL line, and distance between the upper edge of the notch and the beginning of the CL line (by head; Fig. 2a). A set of these measurements was taken for each notch present on a female's carapace.

Nest Data Collection

Between October and December 2009, nesting activity by female *E. macrurus* was monitored at four selected river banks located within the study area. Extensive searches for *E. macrurus* nests were conducted for three consecutive mornings after rain events. Upon the location of the clutches, slope angle (degrees, using a clinometer) and straight-line distances from the nest to the water and to the nearest vegetation edge were measured (in meters). Nest elevation was calculated as the sine of slope angle (transformed into radians) times the straight-line distance from the nest to the water (for details, see Wood and Bjorndal, 2000). Each nest was carefully excavated to expose the entire egg chamber and allow measurement of nest parameters. Egg clutch width was measured in two directions perpendicular to each other (W, widest; N, narrowest). The eggs were carefully removed from the nest and counted (clutch size), and then nest depth was measured (distance from the bottom of the clutch to soil surface) and soil samples were collected from inside the nest chamber (see details below). The eggs were then returned to original position, a temperature logger (2-cm diameter, Hobo® TidBit®, Onset, Bourne, Massachusetts, USA), programmed to record data every 40 min, was placed as close as possible to the eggs, and the clutch was then reburied.

Characterization of Nonpreferred Nesting Areas

The physical characteristics of preferred and nonpreferred nesting areas were recorded (Fig. 1b). It was necessary to select the banks based upon visual characteristics rather than just a randomized selection, because $> 95\%$ of the river banks were either rocky, vertical sided, or covered in thick vegetation; therefore, they were unsuitable for nesting by *E. macrurus*. The river banks not used by *E. macrurus* for nesting had the soil samples collected and temperature loggers ($n = 18$; Hobos TidBit) at three random locations ($\sim$20 cm in depth, the mean *E. macrurus* nest depth) across the bank. These locations were randomly chosen using the "splancs" library in R (Rowlingson and Diggle, 1993; R Development Core Team, 2011).

Measurements taken for each bank were width of the bank (straight distance between the water's edge and the top of the bank), slope angle, bank elevation (to the highest point of the bank), lengths at the top and at the bottom of the bank (by the water's edge), and bank slope aspect (i.e., the compass bearing perpendicular to the water's edge).

Soil Analysis

Soil samples were collected from both preferred (egg chambers) and nonpreferred nesting banks. First, a small sampling tube (10 cm^3) was filled with sand collected from the bottom of the chamber for quantifying soil organic matter (weight in %) by dry combustion (CNS-2000 analyzer, LECO Corporation, St. Joseph, Michigan, USA). These samples were kept refrigerated until laboratory analysis.

Second, a metal cylinder (95 cm^3) was carefully inserted into the soil surrounding the clutch, and a spatula was then used to help remove the cylinder filled with soil from the ground, aiming to minimize disturbance to the soil structure. Petri dishes were placed on both sides of the cylinder, secured by adhesive tape, and then the cylinder was placed into a zip-top storage bag. In the laboratory, these soil samples were analyzed to determine soil moisture content (MC in %), bulk density (g cm^{-3}), hydraulic conductivity (cm s^{-1}), and soil-water retention curves. MC was determined by weighing the fresh soil sample, placing it in the oven at 105°C for 24 h, and then reweighing it. The difference in mass between the wet and dry soil sample was then divided by the wet sample mass and multiplied by 100. The bulk density was calculated as the mass of the oven-dried soil sample divided by the volume of the total soil sample (95 cm^3).

A laboratory permeameter was used to measure the permeability of the soil samples by creating a difference in water pressure on both ends of a saturated soil sample and measuring the resulting flow of water. The permeameter is a closed system in which water is pumped up from a storage cistern to an adjustable level-regulator through a filter. A complete saturated cylinder filled with soil was placed in a cylinder-holder, and a sieve disc was placed on the top of it. The cylinder was then turned upside-down (so the sieve was under the sample) and then placed inside the container. A plastic siphon channeled the water oozing from the sample to a burette; this channeling released the water into a leak basin connected to the storage cistern. The siphon created a difference in water level inside and outside the cylinder-holder, inducing a continuous flow of water through the sample. The permeability coefficient (K-factor) of the samples was established by applying the following formula (derived from Darcy's law) using the volume of drained water through the burette during a fixed period:

$$K = \frac{V \cdot L}{A \cdot t \cdot h}$$

where K is the K-factor (cm d^{-1}), V is volume measured in the burette (cm^3), L is length of the soil sample (cm), A is the cross-sectional surface of the sample (cm^2), t is the time used for flow through of water volume V (measured in days), and h is the difference in water level inside and outside sample cylinder (cm).

The pressure-plate technique was used to obtain a soil-water retention curve (for details, see Otto and Alcaide, 2001; Lucas et al., 2011; Moret-Fernandez et al., 2012). Undisturbed water-saturated soil samples were exposed to 1, 2, 3, 10, 50, and 1000 kPa, and the pressure-versus-moisture points were adjusted by the van Genuchten model analyzed by RETC software (PC-Progress, Prague, Czech Republic).

Statistical Analyses

A multivariate analysis of variance (MANOVA) was used to compare the physical characteristics of the nesting banks. The MANOVA was chosen because the dependent variables may have been moderately correlated. The response variable was the number of nests on each bank, the factor was whether it was a preferred or nonpreferred nesting bank, and the covariates were slope width, slope angle, elevation above the water, and lengths at the top and bottom of the bank. Circular analysis of variance (high-concentration F-test) was performed to analyze the slope aspect of the banks in the R programming language (R Development Core Team, 2011) using the "circular" library of functions (Jammalamadaka and SenGupta, 2001). An analysis of variance with repeated measures was used to assess whether soil temperature varied among nests that were laid on preferred nesting banks and an equal, random distribution of loggers on nonnesting banks. A Kruskal–Wallis test was used to assess whether soil organic-matter content, bulk density, hydrological condition, or moisture content were different between the preferred nesting banks and an equal, random distribution of sites on the nonnesting banks. All data are presented as mean ± SE, and a difference between groups was deemed significant if $P < 0.05$ (Statistica10, StatSoft Inc., Tulsa, Oklahoma, USA).

RESULTS

Nesting and Archival Data

Data from 28 freshly laid clutches of *E. macrurus* were collected throughout the 2009 nesting season from four nesting banks (Table 1). There was large variation in the distance from the water chosen by the females to lay their eggs; some nests were as close as 1.3 m and others as far as 43.6 m from the water. Similarly, nests were constructed both close (~1 m) and far away (~15 m) from vegetation, but they were not under the shade of any plants between 800 and 1600 h. The elevation and distance to the water of a nest laid above the river level was influenced by the river-bank height and size and the water level at the time of laying. The highest nest was found ~7

Table 1.—Biological data collected from clutches of *Elusor macrurus* laid in four different nesting banks located along a 15-km stretch of the Mary River, Australia.

Nests (n = 28)	Mean ± SE	Minimum–maximum
Distance to water (m)	13.1 ± 1.9	1.3–43.6
Distance to vegetation (m)	6.1 ± 0.9	0.5–15.1
Elevation (m)	3.6 ± 0.5	0.5–6.9
Clutch size	14.9 ± 0.9	2–22
Nest depth (cm)	21.0 ± 0.6	15.5–27.0
Narrowest egg clutch width (cm)	7.6 ± 0.3	4.1–9.6
Widest egg clutch width (cm)	9.1 ± 0.3	5.5–10.9

m above the water level, and the lowest nest was 0.5 m above the water level.

The long-term nesting data from 2004 to 2011 demonstrated that females commenced nesting in mid-October and that the last clutch was laid toward the end of December. The number of clutches laid per season on Nesting-bank B was fairly consistent across the 8 yr, except for a dramatic decline in 2009 and 2010 (Table 2). Nest construction was clustered around a few nights during the nesting season, and these events were correlated with rainfall (Fig. 3). On a few occasions, however, nests were constructed independently of recent rainfall.

Nesting Females

Nesting-bank B was monitored by infrared cameras during the nesting seasons 2009, 2010, and 2011. Female *E. macrurus* accessed the bank from sunset until sunrise, with an increase in the number of recorded females between 2300 and 0300 h (Fig. 4). Females were photographed nesting in air temperatures between 12°C and 28°C (mean = 18.9 ± 0.1°C), although ambient temperature and moon phase had no significant effects on the frequency of activity on the bank or on the number of nests constructed.

Analysis of sequential images showed that females inspected the bank before finally completing nest construction, walking throughout the slope in all directions and digging sample holes in the sand multiple times. Six females were recorded laying their clutches within camera view (e.g., Fig. 2b), so it was possible to calculate nesting time (the time from when digging the nest started until the female left the nest site), which varied between 34 and 57.5 min (mean = 36.9 ± 6.3 min).

Image analysis of the infrared photographs revealed that female *E. macrurus* are likely to exhibit nest-site fidelity (example in Fig. 2c, d). Twenty-two females were individually identified over the 3 yr of study. Nine females were positively identified from distinguishable carapace marks in 2009, and nine nests were constructed on the bank. In 2010, six individuals were identified from the infrared photographs and five nests were found; 13 individuals were identified in 2011 and 20 nests were constructed (Tables 2, 3). However, several females were photographed during each year with no distinguishable marks on their carapaces. Among the nine females positively identified in 2009, three returned to the same bank in 2010 and eight returned

Table 2.—*Elusor macrurus* nesting data, collected by TDLG between 2004 and 2011, during the nesting seasons (October–December) at Nesting-bank B along the Mary River, Australia.

Year	Date of first nest	Date of last nest	Total no. of nests
2004–2005	19 October 2004	29 November 2004	23
2005–2006	14 October 2005	17 November 2005	21
2006–2007	6 November 2006	2 January 2007	26
2007–2008	12 October 2007	12 December 2007	22
2008–2009	13 October 2008	31 December 2008	18
2009–2010	14 October 2009	22 December 2009	9
2010–2011	9 October 2010	27 October 2010	5
2011–2012	17 October 2011	29 December 2011	20

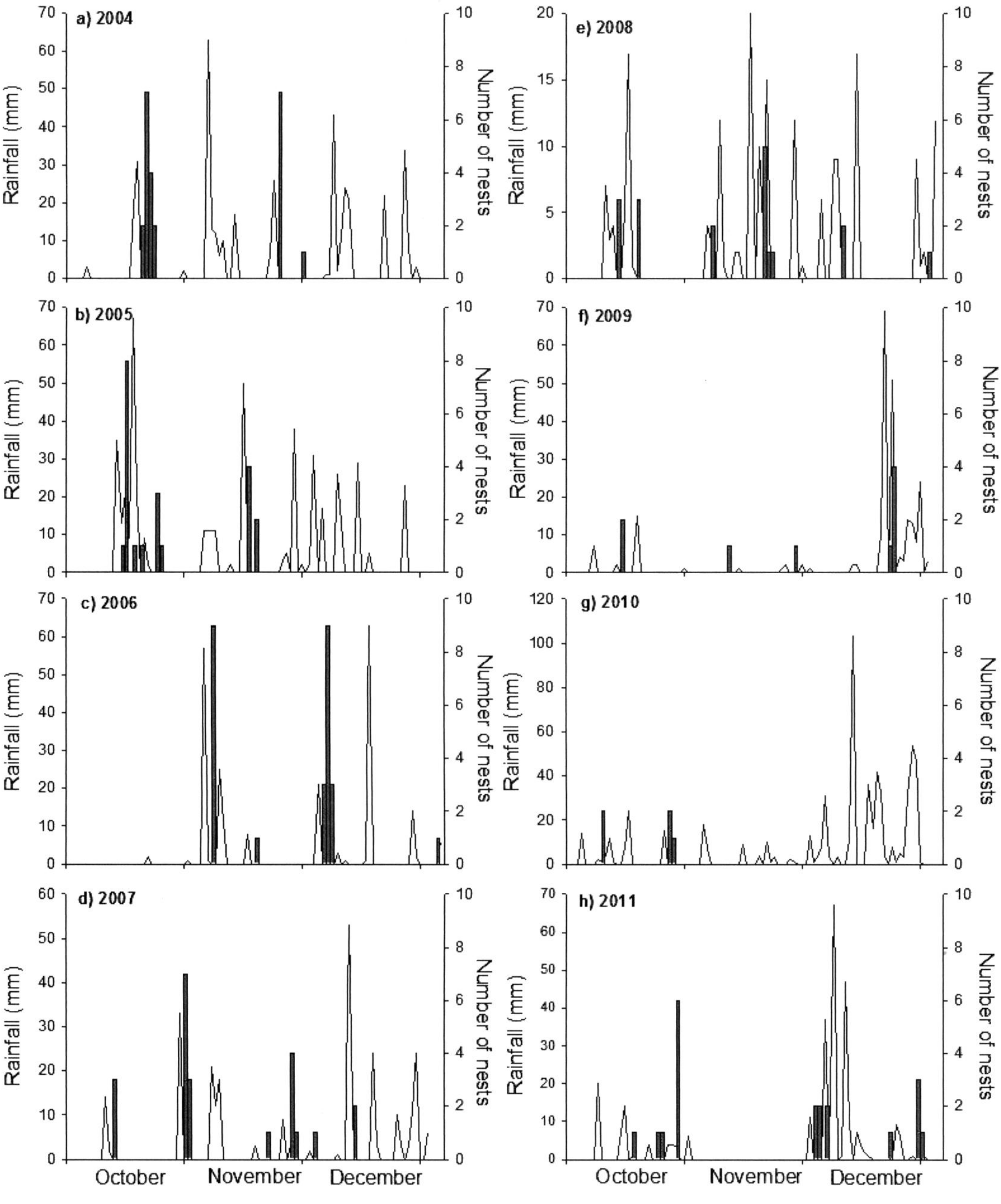


FIG. 3.—Number of *Elusor macrurus* nests constructed at Nesting-bank B (bars) and local rainfall (mm; line) recorded between October and December, 2004–2011.

in 2011 (Table 3). Two females were positively identified accessing this bank in all 3 yr. During nesting season 2010, an unusually early and large flood resulted in the cameras having to be removed from the river bank after only a few weeks of recording. Therefore, if we discount the results from 2010, almost 90% of the turtles that were positively identified in 2009 returned to Nesting-bank B in 2011. In contrast, 10 individuals positively identified in 2011 were not photographed in 2009 or 2010; in this year, however, there were many more nests found on this bank than in the previous 2 yr. The number of nests found on this bank in 2011 was similar to that recorded between 2004 and 2008.

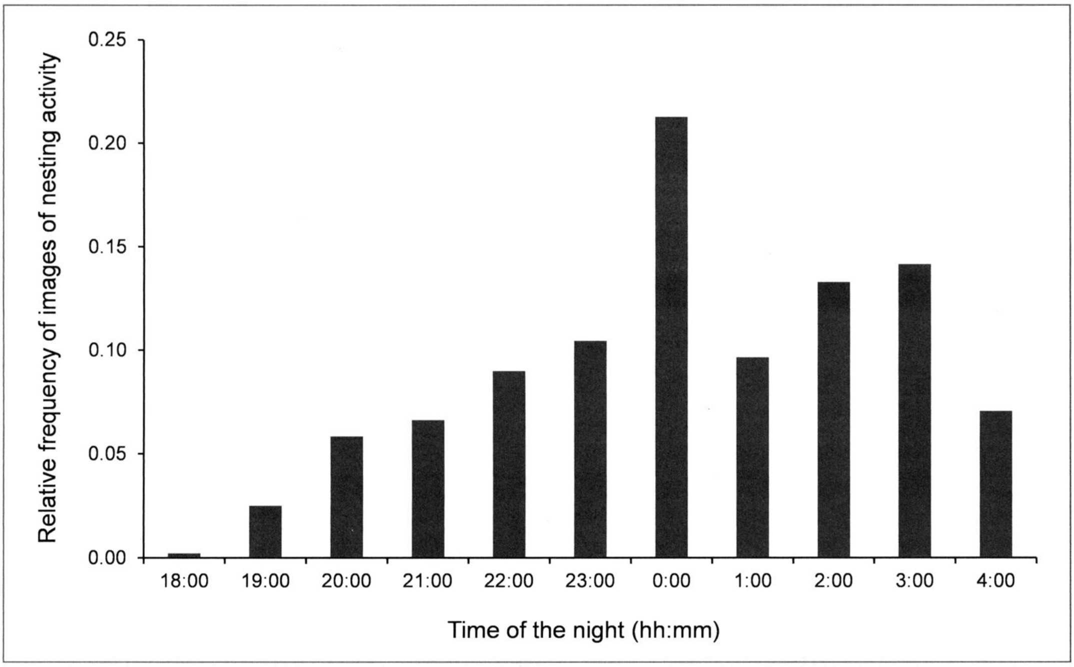


FIG. 4.—Frequency distribution of the number of images taken of female *Elusor macrurus* that accessed Nesting-bank B throughout the night over three subsequent nesting seasons (2009–2011).

Table 3.—Positive identification (X) of female *Elusor macrurus* upon a single nesting bank along the Mary River, Australia, between 2009 and 2011.

Female ID	2009	2010	2011
A		X	
B[1]	X	X	X
C[1]	X	X	X
D[2]	X	X	
E		X	
F		X	
G[2]	X		X
H			X
I			X
J			X
K[2]	X		X
L			X
M[2]	X		X
N			X
O[2]	X		X
P[2]	X		X
Q			X
R			X
S			X
T			X
U[2]	X		X
V			X

[1] Indicates turtles that were photographed in all three study years.

[2] Indicates turtles that were photographed on the bank in two separate years.

Characterization of Nesting Banks

We aimed to record temperature data from all four nesting banks. Due to an unexpected flood, however, five loggers were lost and temperature was only recorded from three banks (Fig. 5a,b). Both the mean daily temperature and the daily fluctuation in temperature were significantly higher at the banks selected by female *E. macrurus* for nesting than in a random sampling of sandy banks where no nests were found (Table 4).

The slope aspect was the only physical characteristic measured that was significantly different between preferred and nonpreferred nesting banks (Table 4). The four nesting banks preferred by female *E. macrurus* were northerly facing, whereas the aspect of the nonpreferred banks varied between east and southwest.

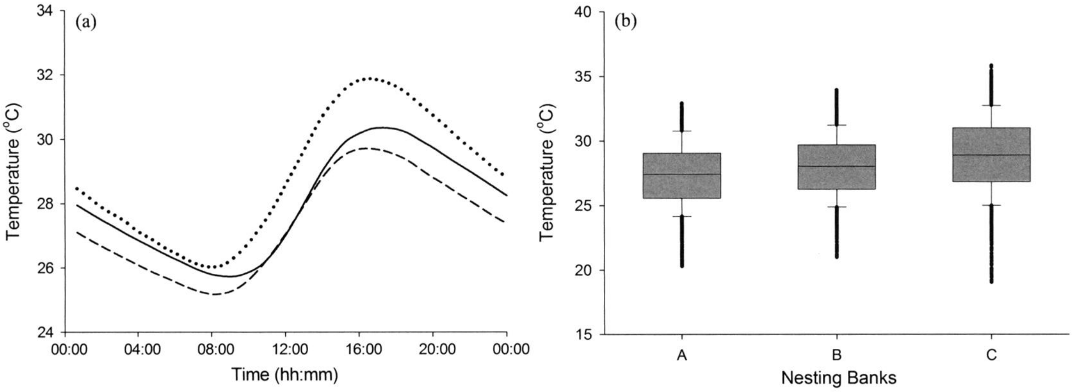
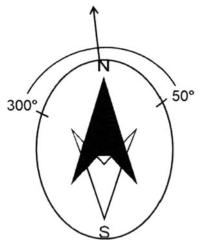
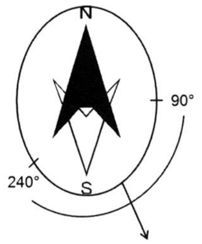


FIG. 5.—(a) Daily temperature fluctuation recorded from 16 *Elusor macrurus* nests buried in three different nesting areas (dashed line = Nesting-bank A; solid line = Nesting-bank B; dotted line = Nesting-bank C). (b) Box-and-whisker plot showing the temperature range recorded throughout the 2009 nesting season from clutches laid in three distinct nesting areas (A, $n = 6$; B, $n = 4$; C, $n = 6$; $P > 0.05$).

There was no statistical difference in organic matter, bulk density, water content, and hydraulic conductivity between soil collected from river banks selected by female *E. macrurus* for nesting and soil collected from the nonpreferred banks (Table 4). A soil water-retention curve was generated from the soil samples collected from *E. macrurus* nests (Fig. 6) and indicated that at the time of nest construction, nest water-potentials ranged between –1 and –40 kPa.

TABLE 4.—Physical features and soil characteristics recorded for eight river banks distributed along a 15-km stretch of the Mary River, Australia, used (nesting banks, $n = 4$) and not used (nonpreferred banks, $n = 4$) by female *Elusor macrurus* for nesting. Data are mean ± SE. Asterisk (*) indicates statistical differences ($P < 0.05$). temp = temperature.

Physical	Nesting banks	Nonpreferred banks	F-ratio; *P* value
Mean temp (°C)	28.5 ± 0.02	27.0 ± 0.04*	485.30; <0.01
Mean daily temp fluctuation (°C)	5.7 ± 0.1*	4.6 ± 0.2*	6.54; 0.01
Bank width (m)	6.9 ± 1.4	9.7 ± 2.0	0.78; 0.53
Bank angle (°)	25.1 ± 3.3	13.6 ± 4.0	86.0; 0.068
Bank elevation (m)	2.3 ± 0.6	1.9 ± 0.7	130.0; 0.055
Bank length at top (m)	22.2 ± 7.1	7.5 ± 2.2	0.78; 0.54
Bank length at water's edge (m)	19.3 ± 5.8	10.6 ± 3.2	0.11; 0.79
Bank slope aspect (degrees from N)	50–300°	90–240°	53.47; <0.01
			
Soil			
Organic matter (Wt %)	0.16 ± 0.03	0.16 ± 0.03	0.26; 0.61
Bulk density (g cm^{-3})	1.2 ± 0.02	1.2 ± 0.04	1.45; 0.23
Moisture content (%)	6.3 ± 0.3	10.3 ± 0.9	0.80; 0.49
Hydraulic conductivity (cm s^{-1})	0.07 ± 0.01	0.10 ± 0.02	0.60; 0.44

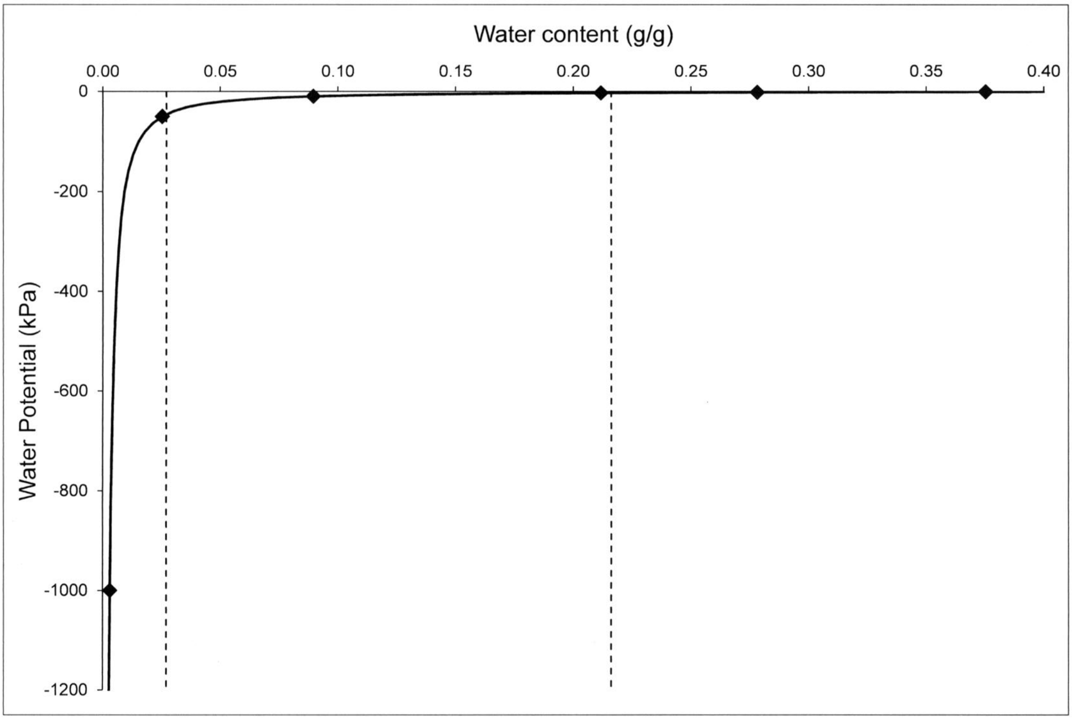


FIG. 6.—Soil-water retention curve (solid line) generated from soil samples collected from 28 nests of *Elusor macrurus* constructed in 2009. Dashed lines represent minimum and maximum values of water content present in the sand samples collected from the *E. macrurus* nests. Symbols represent the actual measured values used to generate the curve.

DISCUSSION

Female *E. macrurus* selected particular banks along the Mary River in which to lay their eggs, and many nests occurred at the same localities in consecutive years. The areas selected by the nesting *E. macrurus* were characterized by sandy soils; absence of riparian vegetation; and a steep, north-facing slope. These characteristics made the banks significantly higher than the river level within a very short distance from the water's edge. There were, however, numerous areas along the river that showed these same physical characteristics, although *E. macrurus* nests were not recorded at these localities. This study provides evidence for why female *E. macrurus* select certain areas over others in which to lay their eggs and demonstrates which areas need to be protected for *E. macrurus* conservation.

Typically, *E. macrurus* lays eggs away from the edge of the river and several meters above the river-water level. These features are shared by other freshwater turtles and are likely to reduce the chances of the nests being flooded (Booth, 2010). The females nested during the night after periods of rainfall. Other Australian freshwater turtles also nest during darkness, thereby reducing the risk of predation by visual predators and exposure to high daytime temperatures (Booth, 2010). Nesting after periods of rainfall is also a common strategy shared by other freshwater turtles and probably makes nest construction easier because moist sand gives better purchase for the female and reduces the chance of egg chamber collapse during the construction. Moreover, moist sand ensures that the eggs will be in positive water balance when first laid, and the gain of water from the environment may act as a water reserve, ensuring against fatal egg desiccation if the nest environment dries out later during incubation (Vestjens, 1969; Booth, 2010).

The nesting bank that was extensively monitored in this study showed no significant increase in the number of nests being constructed between 2004 and 2011. In fact, there was a reduction of approximately 60% in the number of clutches laid in 2009 and 2010 compared with the previous 5 yr. However, this reduction may have occurred due to unfavorable climatic conditions in these years. In 2009, there was very little rainfall during the nesting season. Although only nine nests were constructed in this season, the infrared cameras photographed numerous females throughout the season searching for suitable places to nest (including the digging of "test-holes"). The photography revealed that there were more turtles searching for nesting sites than actually laid eggs on this bank. It is likely that the females could not find suitable places to lay their eggs because of low water content in the soil. Moreover, it is possible that these females failed to nest in 2009, because other local nesting areas showed similar below-average numbers of nests.

In contrast to the drought of 2009, in 2010 the Mary River was exposed to a "once in 30-yr" extreme flood event. This flood also resulted in a low number of nests on this bank in 2010 and demonstrated that the reproductive success of *E. macrurus* is highly dependent on the seasonal rainfall. In 2011, rainfall during the nesting season was average for this time of the year, and the number of *E. macrurus* nests was comparable to archival data from 2004 to 2008.

The time-lapse infrared photography and image analysis of carapace markings proved to be a valuable strategy for observing nesting behavior in *E. macrurus*. In fact, it may be the only reliable method for recording the nesting activities of freshwater turtles that, unlike marine turtles, will not nest if there is a human presence (Cann, 1998). The limitation of this technique, however, was that the entire bank was not under surveillance, and we could only recognize females that had obvious marks or notches on their carapaces; therefore, we could not individually identify some females.

All of the female turtles positively identified in 2009 returned to the same bank to nest in subsequent years. The 2009 drought may explain why some females identified in 2011 had not been observed on this bank in 2009. Therefore, although these data suggest nest-site fidelity in *E. macrurus*, we cannot be certain that this behavior is exhibited by all individuals; more annual observations under typical climatic conditions are required to assess nest-site fidelity.

To assess which environmental characteristics may be important to nesting females, we monitored four nesting banks that consistently had a high number of *E. macrurus* nests over the past 8 yr. Although some species of freshwater turtles aggregate around nesting banks during breeding, there is no evidence that aggregation occurs in *E. macrurus*; therefore, each nest was treated as an independent event. The only difference that we detected between preferred and non-preferred nesting banks was that nesting banks faced north. Consequently, nesting banks experienced greater daily mean temperatures and were subjected to greater fluctuations in the daily temperature at the depth of the eggs in the nest. These features occur because north-facing banks receive more direct solar radiation in the Southern Hemisphere and therefore, are generally warmer than south-facing banks (Geiger, 1965). A similar preference for north-facing banks has been observed for nesting Saltwater Crocodiles (*Crocodylus porosus*) in Australia (Magnusson, 1980). In the Northern Hemisphere, the Midland Painted Turtle (*Chysemys picta marginata*) lays its eggs in southwesterly facing slopes (Hughes and Brooks, 2006), probably for similar thermal reasons. Although there is scarce documentation of this reproductive tactic in oviparous reptiles, it seems logical that egg-laying animals would seek to shorten the incubation period (Deeming and Ferguson, 1991) and thereby reduce the opportunity for nest predation and the risk of seasonal river flooding.

During this study, Lace Monitors (*Varanus varius*), plovers, and European Red Foxes (*Vulpes vulpis*) were all photographed preying on the nests of *E. macrurus*. Nesting on north-facing slopes also may be a conditioned strategy to improve the phenotype of the hatchlings, because incubation temperature can influence the phenotype of freshwater turtle hatchlings in species with genetic sex determination (Janzen, 1993; Janzen and Morjan, 2002; Ji et al., 2003; Booth et al., 2004; Micheli-Campbell et al., 2011, 2012). *Elusor macrurus* does not have temperature-dependent sex determination (Georges and McInnes, 1998); therefore, sex determination is not a driving force for nest-site selection in this species.

Implications for Management and Conservation

This study showed that female *E. macrurus* prefers specific nest sites along the Mary River. These areas were north-facing banks, and although we found no significant difference in the other measurements of the banks, we accept that other environmental features may be important that were not recorded in this study. Nevertheless, the study demonstrated that sandy, vegetation-free, north-facing river banks are important nesting areas for *E. macrurus* and should be considered for protection in future management strategies. The nonvegetated banks and sandy soils are a consequence of river-flow patterns and deposition during natural flood events (Abernethy and Rutherfurd, 1999; Dudgeon and Connell, 2001). Reduction in the intensity or frequency of floods could result in the loss of these areas; therefore, we recommend that flow regimes also be considered in the management strategies for *E. macrurus*.

Acknowledgments.—This research was funded by a Ph.D.-support scholarship to MAMC from Tiaro & District Landcare Group and by an Australian Research Council linkage grant to CEF. We thank Tiaro and District Landcare Group, F. Cortesi, H. and M. Milne, and S. Campbell for field assistance; M. Gordos and J. Cann for advice throughout; the landholders for permitting access; and V. Glenn and H. Macdermott for laboratory assistance. This study was conducted under the approval from the Department of Environment and Resource Management of Queensland (SPP-WISP 02255909) and The University of Queensland Animal Ethics Committee (AEC-SBS/076/09/TIARO&DISTRICTLANDACREGROUP).

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Accepted: 10 August 2013
Associate Editor: Michael Freake