Nest-site selection by crocodiles at a rocky site in the Australian tropics: *Making the best of a bad lot*

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Abstract Most animals select nest sites non-randomly, reflecting benefits of specific locations or incubation conditions for offspring viability as well as risks or costs to the reproducing adult. If few or no available nest sites offer suitable conditions, we expect animals to make the best of a bad lot, by selecting nest sites that provide the best conditions available. In tropical north-western Australia, freshwater crocodiles (*Crocodylus johnstoni*: Crocodylidae) in a large artificial lake (Lake Argyle) experience this challenge: the types of nest sites used by this species in other parts of its range (moist, shaded sandy soils, far from the water's edge) are scarce. Measurements of 89 crocodile nests and 89 test holes (abandoned attempts at nesting) at Lake Argyle, and 28 nests on the nearby Ord River, show that most areas along the lakeshore are too steep and rocky for nesting. Crocodiles at the lake therefore are forced to nest at sites that are sun-exposed, in dry gravelly substrates, and close to the water's edge. Comparisons of test holes and actual nests within such areas show that nesting crocodiles actively select sites that are less rocky, are suitable hydrically, and that provide stable thermal regimes. Those hydric and thermal attributes allow successful development of the offspring. The ability of freshwater crocodiles in Lake Argyle to flexibly modify their nest-site selection criteria, under severe constraints enforced by this open rocky landscape, are critical to the species' success in exploiting the opportunity created by the dam's construction.

Key words: *Crocodylus johnstoni*, hatchling survival, Lake Argyle, maternal choice, Ord River, test hole.

INTRODUCTION

A nesting female often has access to a wide range of potential sites in which she could deposit her eggs. Those sites differ in the incubation environments they offer to the developing young, as well as in costs to the nesting female in risk and energy (e.g. Burger 1991; Madsen & Shine 1999; Kolbe & Janzen 2002). Field surveys demonstrate that the nest sites used are a highly non-random subset of those available in the landscape (Shine & Harlow 1996; Brown & Shine 2004; Rodriguez-Prieto *et al.* 2010), and experimental studies show that females utilize a wide range of biotic and abiotic cues when selecting sites for oviposition (Rodewald 2004; Brown & Shine 2005; Socci *et al.* 2005). Many taxa display stereotyped species-specific choices for particular attributes when selecting nests (Furrer 1975; Brown & Shine 2007).

Nonetheless, maternal nest-site selection also needs to be flexible, because the availability of specific features may shift considerably through space and time (Dreitz *et al.* 2001; Mahon & Martin 2006; Weishampel *et al.* 2006). Nesting females respond to that variation by modifying their seasonal timing of nesting (Cargnelli & Neff 2006; Telemeco *et al.* 2009)

and/or their criteria for nest-site choice (Cornelius 2008; Chalfoun & Martin 2010). For example, females of wide-ranging species may select nests with similar thermal regimes across an extensive climatic range, by choosing shaded nest sites in hotter regions, and sun-exposed nest sites in cooler regions (Ewert *et al.* 2005; Doody *et al.* 2006a). One common problem concerns the availability of nesting sites in anthropogenically modified aquatic landscapes. Frequently, human activities create opportunities for aquatic adults of a species, but without providing terrestrial areas with the microclimates needed for egg incubation (e.g. turtles: Ficetola *et al.* 2004; Marchand & Litvaitis 2004; Eskew *et al.* 2010a,b, wading birds: White 2003, penguins: McKay *et al.* 1999, semi-aquatic lizards (e.g. *Physignathus lesueurii*): N. Pezaro, pers. com., 2011, and semi-aquatic snakes (e.g. *Xenochrophis* spp.): R. Somaweera, pers. obs., 2006). The reverse problem is encountered by flying insects with aquatic egg and larval stages (Statzner *et al.* 1997).

In the current paper, we examine an example of the phenomenon of how animals manage to reproduce in an anthropogenically modified lake landscape that provides abundant aquatic resources, but very few oviposition sites. We studied a crocodile species that utilizes consistent (and highly non-random) sites for oviposition throughout its wide geographic range. We first quantify the availability of suitable nesting

habitats at this lake system and then compare attributes of those sites to others in river systems (oviposition sites used over the rest of the species range). Finally we compare actual nests to test diggings within the anthropogenic habitat to identify the microclimatic conditions sought by nesting females.

METHODS

Species

The Australian freshwater crocodile (*Crocodylus johnstoni*: Crocodylidae) is endemic to tropical mainland Australia (Cogger 2000) and mainly inhabits watercourses upstream of tidal influence (rivers, creeks, swamps and billabongs: Webb *et al.* 1983a). Infrequently, the species penetrates into tidal waters (Messel *et al.* 1981). Females dig nests and oviposit during the annual dry season (August–September). Eggs hatch at the beginning of the wet season (November/December) after an average incubation period of 9–14 weeks (Webb & Smith 1984). Females do not attend nests during the incubation period, but return to excavate hatchlings (Webb *et al.* 1983a; Somaweera & Shine 2011). Previous fieldwork on nesting of this species has been conducted in natural lotic habitats (Webb *et al.* 1983a; Smith 1987; Cooper-Preston 1991; Chibeba 2003). Consistently, these studies have reported that female *C. johnstoni* nest in shaded, moist soil (typically, riverside sandbanks) that provide specific thermal regimes (Webb & Smith 1984; Chibeba 2003). Shade reduces overheating by solar radiation, and reduces desiccation rates; and soft soil facilitates nest excavation. Female crocodiles move long distances inland (sometimes over 200 m) if friable unvegetated, sandy substrates are unavailable closer to water (Cooper-Preston 1991). Nesting further from water also may reduce egg mortality from floods, and reduced nest densities may render it less likely that later-nesting females will open a previously laid nest.

Study sites and surveys to delineate nesting habitat

Lake Argyle in the East Kimberley region of Western Australia (16°29′S, 128°75′E) has a maximum surface area of approx. 1100 km², making it the largest man-made water body in Australia. The lake was constructed by damming the Ord River in the early 1970s. As in other parts of monsoonal northern Australia (Webb 1991) the lake experiences three main seasons: the wet season from November/December to April; the early dry season May to July/August; and the 'build-up' or the late dry season from September to December. The mean annual maximum and minimum temperatures are 35.1°C and 21.6°C respectively, while the mean annual rainfall is 796.8 mm with an average of 44.4 rainy days a year (Bureau of Meteorology 2011). The lake contains a large population of *C. johnstoni*, estimated to be over 30 000 non-hatchlings (G. Webb Pty Ltd. 1989; WMI Pty Ltd. 2005, 2010).

To map potential nesting areas within the entire lake, we surveyed the circumference of the lakeshore by boat from mid-August to late September in 2009. We located crocodile nesting sites by observing signs of nesting (disturbed gravel, depressions and slide marks), predation (egg shells, dig marks) and in 12 cases by observing adult crocodiles digging in the banks. The sites where nesting was recorded showed consistent habitat features of substrate, vegetation, slope and distance from water (see *Results* for details). To estimate overall availability of nesting habitat, we focused on sites with these characteristics. Locations of potential nesting areas were plotted on a 1:20 000 topographical map, and examined during ground-based surveys. The classification of nest sites according to these habitat features might be in error if nest sites in other habitat types were less easily detectable. To evaluate that possibility, we used data from nocturnal surveys of crocodile densities in 23 survey sectors along the lakeshore, conducted in August 2009 (WMI Pty Ltd. 2009). If our classification of sites accurately reflects nesting activity, then we expect a positive correlation between the density of hatchling-sized crocodiles and the proportion of the lakeshore within each survey section that was composed of 'nesting sites'.

Based on nest densities and ease of access we identified five main areas for further detailed studies, all in the northern part of the lake (Fig. 1). Bay of Islands is a cluster of islands separated from the mainland by a 3-km stretch of deep water; we have never found any large terrestrial predators (either mammalian or reptilian) on these islands. Bamboo Cove is enclosed by steep banks, discouraging access by terrestrial predators. Croc Bay, Gundarim Bay and BBQ Island Bay have less steep banks, and therefore harbour land predators. Banks at all of these sites mainly comprise a gravel substrate derived from Proterozoic sandstone and glacial sedimentary rocks (DME 1996). Additionally (at a sixth site) a 10-km stretch of upper Ord River (the original river that was dammed to build Lake Argyle) was scanned in 2010 for nests. The Ord River has mostly sandy banks derived from Devonian limestone, dolomite and sandstone (DME 1996; Fig. 1).

Within each site, we located nests by excavating all likely spots by hand to look for eggs, or by probing with a thin metal rod to look for nests (Webb *et al.* 1983a) in the Ord River site. We used data from our spotlight surveys in December (2008, 2009 and 2010), April and August (2009 and 2010) to monitor population structure changes at these sites during the nesting season in comparison with six other sites where little or no nesting occurs (in Matilda Creek at the lake's north-east corner; R. Somaweera, pers. obs., 2010). We conducted spotlighting, one night per site per month from a boat with a 15-hp out-board engine at night (18.00–23.00 hours; for methodology see Messel *et al.* 1981; Bayliss *et al.* 1986). Once a crocodile was sighted, we approached it and estimated its size. Crocodiles with total length >151 cm were categorized as mature, based on published data (Webb *et al.* 1983a).

Measurement of nest attributes

We excavated nests by hand, wearing rubber gloves. All eggs were temporarily removed, marked and numbered with a
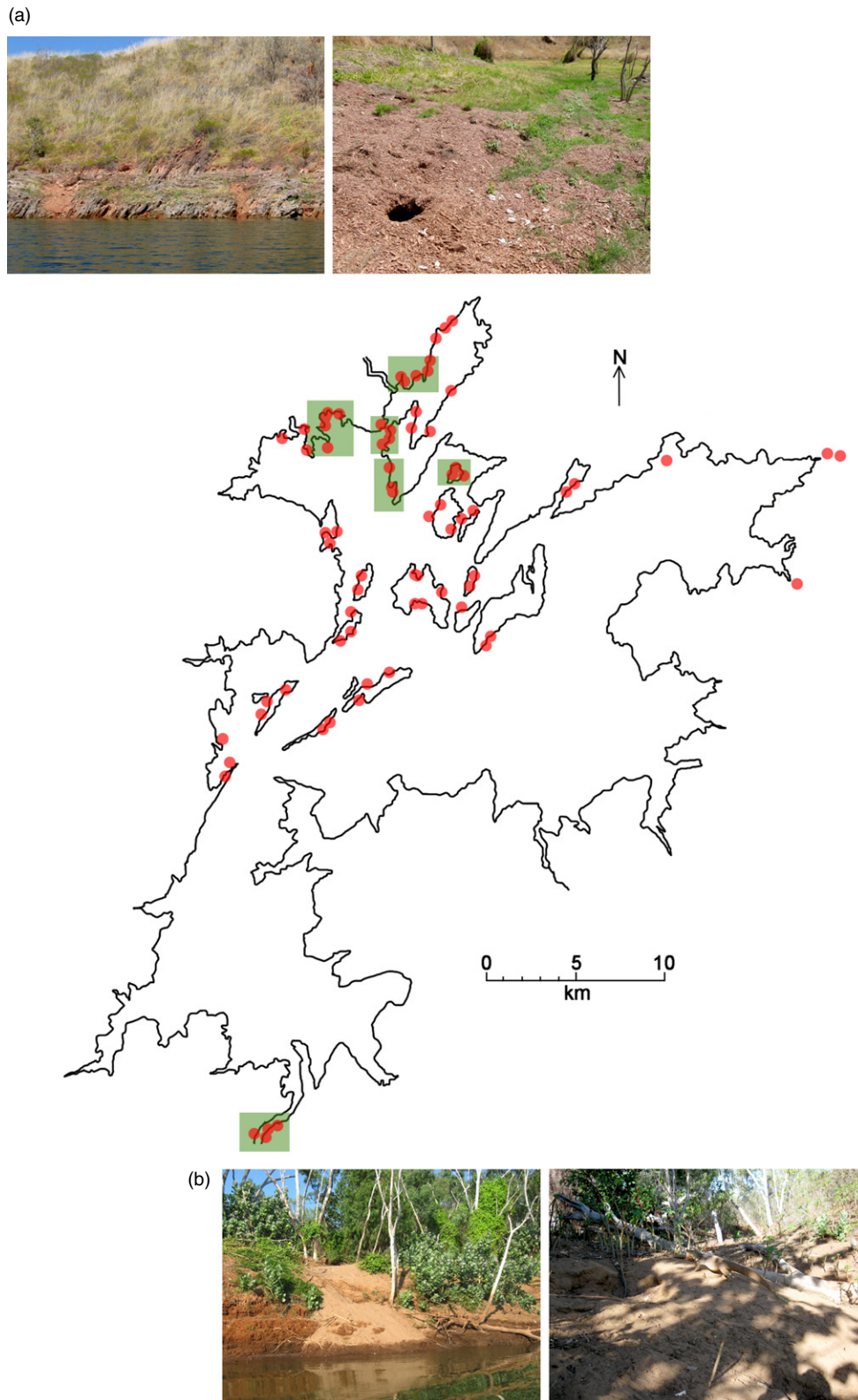
Fig. 1. The potential nest sites of *Crocodylus johnstoni* at Lake Argyle (in red dots) are located non-randomly. The lake and the Ord River (flowing into the southern end of the lake) differ in their bank and vegetation characteristics. The northern banks of the lake contain our five study sites (in green rectangles): Bay of Islands, Bamboo Cove, Croc Bay, Gundarim Bay and BBQ Island Bay. All are devoid of tall vegetation and have rocky banks with gravel substrate (a). In contrast, the Ord River (b) has sandy banks with tall streamside vegetation. As a result, most crocodile nest sites on the Ord River are well shaded.

lead pencil on the dorsal-most position to allow correct replacement and orientation within the clutch cavity. An egg map of each nest was drawn (Ferguson & Joanen 1982). The age of eggs (and hence laying date) was estimated from opaque banding (Webb et al. 1987) and mucus. We recorded the following variables at each nest:

1. Date of discovery.
2. Clutch size.
3. Depth to uppermost egg (cm).
4. Egg parameters – three randomly selected eggs from each nest were measured for length (mm) and width (mm) using a digital calliper and weight (g) using an electronic balance.
5. Substrate type – the walls of the egg chamber were classified as consisting primarily of sand, loam, fine gravel (2–5 cm) or coarse gravel (5–10 cm).
6. Substrate hardness – three penetrometer readings were taken within 10 cm of each nest.
7. Ground cover – scored as present (whether shrubs, grass, leaf litter or dead aquatic plants) or absent.
8. Distance from shore – straight-line distance of nest from water.
9. Distance from the conspicuous shore vegetation line.
10. Presence of floating vegetation along the immediate shoreline – scored as 'present' or 'absent'.
11. Aspect of bank – measured with a compass.
12. Slope of bank – measured using a clinometer.
13. Nest temperatures – thermochron iButton temperature loggers (programmed to record temperatures at 90-min intervals) were placed at mid-depth in all nests, and left until the nest was raided or hatched.
14. Sun exposure – Canopy openness and incident solar radiation over each nest were estimated with hemispherical photography and Gap Light Analyzer software (Doody et al. 2006b; Warner & Shine 2008). Photographs were taken with a super-wide fisheye lens attached to a Canon Powershot digital camera, facing directly upwards above each nest. We set the time period for analysis as 75 days, the average incubation period for *C. johnstoni*.
15. Substrate moisture content – A 100-g soil sample from within the egg pit of each nest was taken to the laboratory, and half of the material was divided into three subsamples, which were weighed, sun-dried for 5 days and then weighed again, to calculate percentage moisture content. This method may not have removed all moisture from the soil.
16. Substrate water retention capacity – The other half of the substrate sample was analyzed following a method modified from that of Warner et al. (2010). The samples were sun-dried for 5 days and three 10-mL subsamples were placed separately into circular cones of filter papers (55-mm diameter; Whatman International Ltd, Maidstone, UK, model 1001055). The filled cones were weighed to the nearest 0.01 g, and then held upright in a rack while 10 mL of tap water was added to the surface of each cone with a syringe. The cones with the soil were reweighed after 10 min at a constant room temperature (26°C). Per cent moisture content retained in the soil sample was calculated by dividing the final wet weight of the sample by the initial dry weight.

All five sites in the northern section of Lake Argyle were sampled in both 2009 and 2010, whereas the Ord River site was surveyed only in 2010. Of the above 16 variables, three (canopy openness, incident solar radiation and water retention capacity) were only measured or calculated in 2010.

After we had taken these samples and replaced eggs within the nest, we filled in the hole and sprayed the surrounding substrate with air freshener to mask scent cues (Smith 1987; Chibeba 2003; Somaweera et al. 2011). After the emergence period, nests were checked in November and December (in both 2009 and 2010) to count the number of unhatched (dead) eggs. Hatchlings from nurseries among the floating vegetation close to the nests were collected during nocturnal surveys to assess body condition and abnormalities.

Attributes of 'test holes'

Female crocodiles often dig holes close to the eventual oviposition site, but abandon the attempt before laying. These 'test holes' or 'test nests' were evident by the excavated depression and a lack of eggs. These were shallower than predated nests, and did not contain damaged eggs (see Somaweera et al. 2011). We recorded the number of test holes in a 5-m radius around each nest, and the distance to test holes.

To compare microhabitat variables of test holes *versus* actual nests, we chose one test hole per actual nest randomly by throwing a six-sided pencil (marked with a single number from 1 to 6 on each side) straight up into the air. The direction the pencil pointed when it landed determined the direction in which we looked for test holes, and the number determined how many test holes we passed by before selecting the chosen test hole. If no test holes were found in the randomly selected direction, we repeated the process. If a test hole selected by this process had been abandoned because the excavating crocodile had encountered a large rock or tree root, or saturated soil, then we gathered microhabitat data on the closest test hole to the rejected one. At each of these selected test holes, we measured the same variables as determined for actual nests (see above), and buried a thermochron iButton temperature logger at the mid-nest depth of actual nests (approx. 20 cm).

Statistical analysis

Data were analyzed using the statistical software program JMP 5.01 (SAS Institute, USA). Prior to analysis, data on crocodile numbers during surveys were ln-transformed, after adding a small arbitrary value (0.05), to maintain variance homogeneity. All percentage values were arcsine transformed before analysis. We used one-way ANOVA tests followed by Fisher's PLSD (protected least significant difference) *post-hoc* tests to compare the spatial and temporal fluctuations of crocodile densities and to compare attributes of nests in the river system *versus* the lake and the test holes *versus* actual nests. Linear regressions were used to analyze the relationship between rainfall, air temperature and nest temperature. To identify the influence of other variables

on substrate temperature, we conducted a multiple regression with canopy openness, moisture content and particle size as predictors and mean nest temperature as the dependent variable. Particle size was an ordinal variable, with the finest (clay) being 1 and coarsest (rock) being 6.

RESULTS

Availability of nesting habitat

In contrast to Ord River sites and other riverine locations where nesting of freshwater crocodiles has been studied previously (Webb *et al.* 1983a; Smith 1987; Cooper-Preston 1991; Chibeba 2003), sandy areas were rare in the rocky Lake Argyle landscape. We found sandy patches in <2% of the shoreline, mainly on islands and in Pannikin Bay. Crocodile nests were found not only in these sites, but also in gravel patches along the shoreline, a habitat type that was more common than sand (26% of the total shoreline: see Fig. 1). Most of these potential nesting beaches were located in the northern, north-eastern and western sites of the lake; the flatter eastern and southern banks consist of submerged grasslands with muddy substrate, and were not used by crocodiles for nesting.

Survey counts of crocodile densities support our classification of these gravel-bank areas as the primary nesting sites. First, the per cent of shoreline comprised of gravel banks was correlated with the density of hatchling and yearling (<60 cm) crocodiles in the 23 survey sectors ($F_{1,21} = 4.55$, $P = 0.04$), but not with the densities of larger crocodiles ($P > 0.05$ for all comparisons). Second, the numbers of large adult crocodiles in these five 'nesting sites' peaked during the oviposition season (August) whereas numbers in non-nesting areas of the lake (e.g. Matilda Creek) did not (region*season $F_{3,187} = 452.14$, $P < 0.001$; Fig. 2). At the five nesting beaches we studied in detail at northern Lake Argyle, the density of adult crocodiles
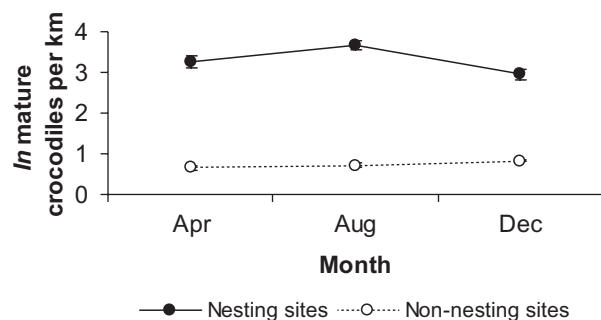
changed during survey months ($F_{6,28} = 2.94$, $P = 0.02$) with more in August (Fisher's PLSD test, $P < 0.05$) in all five sites (site*month $F_{8,20} = 0.67$, $P = 0.71$). At Matilda Creek, the number of adult crocodiles did not significantly differ among survey months ($F_{6,149} = 1.80$, $P = 0.10$).

Comparisons of nest attributes on the lakeshore compared with riverine systems

Nesting sites along rivers (including our Ord River site) were predominantly in moist sandy substrate in shaded areas (Table 1). Most of the 28 nests at Ord River were 15–20 m from the shoreline (mean 17.82 m, range 2.1–35.4 m, SE 2.12 m). Compared with these nests, the 89 lakeshore nests were on average closer to the water ($F_{1,115} = 47.43$, $P < 0.0001$) and to the shore vegetation line ($F_{1,115} = 223.04$, $P < 0.0001$) but further from forest patches ($F_{1,115} = 5.22$, $P = 0.02$). Lakeshore nests were located a mean distance of 5.74 m (range 2.8–34 m, SE 0.49 m) from water in 2009 and 7.71 m (range 2.1–20.5 m, SE 1.12 m) in 2010; this difference between years may reflect lake levels (1.72 m lower in August 2010 than in August 2009).

Most (91.0%) nests at the lake were laid in compact gravel, rather than the softer sandy substrate typical of Ord River nests, but rarely available at the lakeshore. This gravel substrate had lower water retention ability and provided greater thermal stability (lesser range between average minimum and average maximum temperatures during incubation period) than did sandy-substrate nests. Nesting sites at the lake were located in more open habitats than on the Ord River, and consequently exposed to higher levels of solar radiation (Table 2).

Comparisons of attributes of actual nests *versus* test holes (lakeshore only)

Test holes were first observed on 23 July in 2009, with the first egg-laying on 5 August. In 2010 digging began on 26 July but the first nest was not found until 17 August. Nesting was largely restricted to August, but a few nests were laid through to mid-September.

The depth of test holes ranged from 8 to 27 cm (mean 14.5 cm). Most were close to actual nests (mean distance 190 ± 106 cm, $n = 235$). Seventeen nests lacked any test holes within 5 m. Test holes were common early in the nesting season (last week of July to second week of August) and gradually decreased in number. Of the 235 test holes found, 43% apparently had been abandoned because of physical obstructions (rocks or tree roots), and another 4% after reaching wet (muddy) soil. Nests and test holes did not differ significantly in their mean distance from water ($F_{1,176} = 0.89$, $P = 0.34$).

Fig. 2. Seasonal fluctuations in the number of adult freshwater crocodiles seen in nesting and non-nesting beaches at Lake Argyle. Most nesting occurs in August. Error bars show SE.

Table 1. Comparison between attributes of freshwater crocodile nests at rivers in the Northern Territory (McKinley, Katherine, Liverpool), and the Ord River and Lake Argyle (both in Western Australia)

	Northern Territory rivers	Ord River	Lake Argyle
Substrate	77% in sand, 13% sand and humus, 7% gravel, 3% clay in McKinley (C) 100% sand in Katherine (CP)	78.6% in sand 17.6% in loam 3.6% in clay	91.1% in gravel 5.6% in sand 3.4% in loam
Shade	61% exposed, 11% partially shaded, 28% deeply shaded in McKinley (C)	67% exposed, 24.3% partially shaded, 21.7% deeply shaded 65.2 ± 34.3% canopy openness	93.6% exposed, 6.4% partially shaded 97.2 ± 4.5% canopy openness
Distance from water	1–150 m in McK (W) 3–212 m in McK (C): 58.8% within 20 m from water: only nested further inland when friable substrates unavailable close to water 2–12 m in Katherine (CP)	2–35 m with a mean of 17.82 m	2–34 m with a mean of 6.3 m
Moisture (g per 100 g soil)	4.9 ± 2.7 to 5.6 ± 3.8 (W)	5.1 ± 4.7	3.7 ± 3.0
Depth to top egg	19.6 ± 7.5 cm	13.1 ± 2.6 cm	12.2 ± 4.4 cm

W – Webb *et al*. 1983a; CP – Cooper-Preston, 1991; C – Chibeba, 2003.
SD given.

Table 2. Comparison of microhabitat variables in nests of *Crocodylus johnstoni* on the northern banks of Lake Argyle and along the Ord River (which flows into Lake Argyle)

Variable	Nest in the Lake			Nests in Ord River			Statistic
	Mean ± SE	Minimum	Maximum	Mean ± SE	Minimum	Maximum	
Soil compaction (kg cm^{-2})	1.85 ± 0.08	0.5	2.75	1.30 ± 0.12	0.25	2.75	$F_{1,115} = 13.74$, **$P < 0.05$**
Moisture (% water)	0.04 ± 0.01	0	0.11	0.05 ± 0.01	0.01	0.19	$F_{1,115} = 3.82$, $P = 0.05$
Canopy openness (%)	97.22 ± 0.89	84.79	100	65.23 ± 7.01	17.88	100	$F_{1,48} = 22.19$, **$P < 0.0001$**
Soil water retention (%)	1.42 ± 0.01	1.35	1.55	1.48 ± 0.02	1.08	1.68	$F_{1,48} = 6.86$, **$P = 0.02$**
Solar radiation (Mj m^{-2})	8.94 ± 0.02	8.64	9	6.18 ± 0.62	1.09	9	$F_{1,48} = 21.46$, **$P < 0.0001$**
Substrate on top	Predominantly (89.89%) gravel			Predominantly (78.57%) sand			$\chi^2 = 84.32$, **$P < 0.0001$**
Substrate at 20 cm depth	Predominantly (89.89%) gravel			Predominantly (78.57%) sand			$\chi^2 = 83.78$, **$P < 0.0001$**
Aspect	All directions						$\chi^2 = 10.01$, $P = 0.18$
Presence of floating vegetation	89.89% with floating vegetation along shore			10.71% with floating vegetation along shore			$\chi^2 = 64.76$, **$P < 0.0001$**
Slope	41.41 ± 1.65	0	80	37.14 ± 1.97	20	60	$F_{1,115} = 1.83$, $P = 0.18$
Temperature (°C)							
Mean	32.29 ± 0.14	29.4	34.51	32.28 ± 0.33	30.54	36.37	$F_{1,91} = 0.01$, $P = 0.99$
Minimum	24.21 ± 0.21	20.5	28	19.3 ± 0.64	15	24.5	$F_{1,91} = 82.56$, **$P < 0.0001$**
Maximum	40.29 ± 0.29	35	47	43.42 ± 0.82	37.5	49	$F_{1,91} = 17.76$, **$P < 0.0001$**

Data from 2009 and 2010 have been pooled for the analysis. Significance is based on single-factor ANOVA. Boldface *P*-value denotes statistical significance between nest sites.

Nests and test holes at Lake Argyle did not differ significantly in mean values for soil water retention of the substrate, nor in the slope and aspect of the bank, or the presence of floating vegetation close to the location ($P > 0.05$ for all comparisons). However, nests were in more exposed locations (more open canopy resulting in higher solar radiation), and were in softer and drier soils than the test holes (Table 3). Nests were never found in clay or rocky substrates, and had lower

and more stable temperatures than were recorded in test holes (Table 3, Figs 3,4a).

Daily thermal fluctuations both in nests and in test holes varied across the incubation period, driven by air temperature and rainfall events (Fig. 3). Rainfall had a significant negative influence on maximum air temperature ($r^2 = 0.05$, $F_{1,182} = 9.95$, $P = 0.002$), and air temperature was a strong predictor of mean nest temperature during the incubation period ($r^2 = 0.51$,

Table 3. Comparison of microhabitat variables in actual nests and test holes (nesting attempts) of *Crocodylus johnstoni* on the northern banks of Lake Argyle

Variable	Actual nests			Test holes			Statistic
	Mean ± SE	Minimum	Maximum	Mean ± SE	Minimum	Maximum	
Distance from water (m)	6.32 ± 0.48	2.1	34	7.04 ± 0.52	0.6	34	$F_{1,176} = 0.89, P = 0.34$
Soil compaction (kg cm^{-2})	1.85 ± 0.07	0.5	2.75	2.12 ± 0.09	0.25	4.5	$F_{1,176} = 5.56, \boldsymbol{P = 0.02}$
Moisture (% water)	0.04 ± 0.003	0	0.10	0.07 ± 0.01	0	0.39	$F_{1,176} = 8.05, \boldsymbol{P = 0.005}$
Soil water retention (%)	1.41 ± 0.01	1.35	1.55	1.42 ± 0.08	0	1.96	$F_{1,50} = 0.001, P = 0.97$
Canopy openness (%)	97.22 ± 0.8	84.79	100	88.39 ± 3.8	30.1	100	$F_{1,50} = 5.04, \boldsymbol{P = 0.03}$
Solar radiation (Mj m^{-2})	8.94 ± 0.02	8.64	9	8.12 ± 0.36	2.6	9	$F_{1,50} = 5.25, \boldsymbol{P = 0.03}$
Ground cover	85.39% without ground cover			39.33 without ground cover			$\chi^2 = 42.4, \boldsymbol{P < 0.0001}$
Substrate on top	Confined to gravel, sand and loam			Contained clay and rock in addition			$\chi^2 = 65.2, \boldsymbol{P < 0.0001}$
Substrate at 20 cm depth	Confined to gravel, sand and loam			Contained clay and rock in addition			$\chi^2 = 69.7, \boldsymbol{P < 0.0001}$
Aspect	All directions						$\chi^2 = 2.93, P = 0.89$
Presence of floating vegetation	89.89% with floating vegetation along shore			91.01% with floating vegetation along shore			$\chi^2 = 0.06, P = 0.79$
Closest forest patch (m)	21.8 ± 1.9	0	90	27.1 ± 2.5	0	100	$F_{1,176} = 2.77, P = 0.09$
Slope	41.4 ± 1.6	0	80	43.0 ± 2.1	0	90	$F_{1,176} = 0.36, P = 0.55$
Temperature (°C)							
Mean	32.3 ± 0.1	29.4	34.5	34.2 ± 0.5	26.3	47.8	$F_{1,156} = 10.6 \ \boldsymbol{P = 0.001}$
Minimum	24.2 ± 0.2	20.5	28	20.9 ± 0.4	14	27	$F_{1,156} = 54.5, \boldsymbol{P < 0.0001}$
Maximum	40.3 ± 0.3	35	47	46.3 ± 1.2	31	67.5	$F_{1,156} = 20.4, \boldsymbol{P < 0.0001}$

Data from 2009 and 2010 have been pooled. Significance is based on single-factor ANOVA. Boldface *P*-value denotes statistically significant differences (*P* < 0.05) between actual nests and test holes.

$F_{1,164} = 167.68, P < 0.0001$). Nest and test hole temperatures increased with ambient temperature, but were reduced by rainfall. Average temperature inside a nest or test hole was not significantly related to canopy openness ($F_{1,68} = 0.27, P = 0.61$) or total solar radiation ($F_{1,68} = 0.35, P = 0.56$), but nests in drier substrates were hotter (per cent moisture content of the substrate (arcsine transformed) *vs.* average substrate temperature: $F_{1,191} = 6.44, P = 0.02$). In a multiple regression, substrate temperature was more highly linked to particle size ($F_{4,47} = 3.48, P = 0.01$) than to soil moisture content ($F_{1,47} = 0.005, P = 0.09$) or canopy openness ($F_{1,47} = 1.73, P = 0.19; P > 0.05$ for all interactions).

Site selection and nest success

Overall, 66% of nests hatched successfully. This proportion differed among sites ($F_{4,83} = 12.02, P < 0.0001$) but was similar within a given site over the 2 years of the study ($F_{4,83} = 1.06, P = 0.37$). Predation was the most common cause of nest failure: predation rates differed among sites ($F_{4,83} = 14.14, P < 0.001$; none at Bay of Islands), in similar ways in the 2 years (year*site $F_{4,83} = 2.56, P = 0.08$; see Table 4). Many hatchlings from nests that hatched late in the season (after mid-December) had kinked tails and distended abdomens (indicative of overheating; Ferguson 1985), and the proportion of dead embryos and hatchlings found in a nest was positively related to its maximum

temperature ($F_{1,65} = 10.76, P = 0.001$; Fig. 4b) but not to minimum ($F_{1,65} = 0.77, P = 0.38$) or average temperatures ($F_{1,65} = 0.39, P = 0.53$). None of the other nest-site parameters we measured (distance from water, distance from shore vegetation, ground cover, substrate type, moisture content, compactness, per cent water retention ability, slope, aspect, canopy openness, nest density, clutch size, egg burial depth) was significantly correlated with hatching success ($P > 0.05$ for all comparisons).

DISCUSSION

In species with multiphasic life histories, it is often the case that different life-history stages require different habitats and/or resources. Species that are aquatic in one life-history phase but terrestrial in another, provide clear examples of this situation. In the case of our own study system, the permanent availability of water, plentiful food and lack of larger saltwater crocodiles (potential predators and competitors) have enabled freshwater crocodiles to build up considerable numbers in Lake Argyle, despite the scarcity of the kinds of terrestrial habitats used for nesting in other parts of the range.

Like some other streamside reptiles in tropical Australia (e.g. Doody *et al.* 2003), *C. johnstoni* typically lays its eggs in holes dug into moist, shaded sandbanks (Webb *et al.* 1983a; Cooper-Preston 1991). In the rocky hills around Lake Argyle,
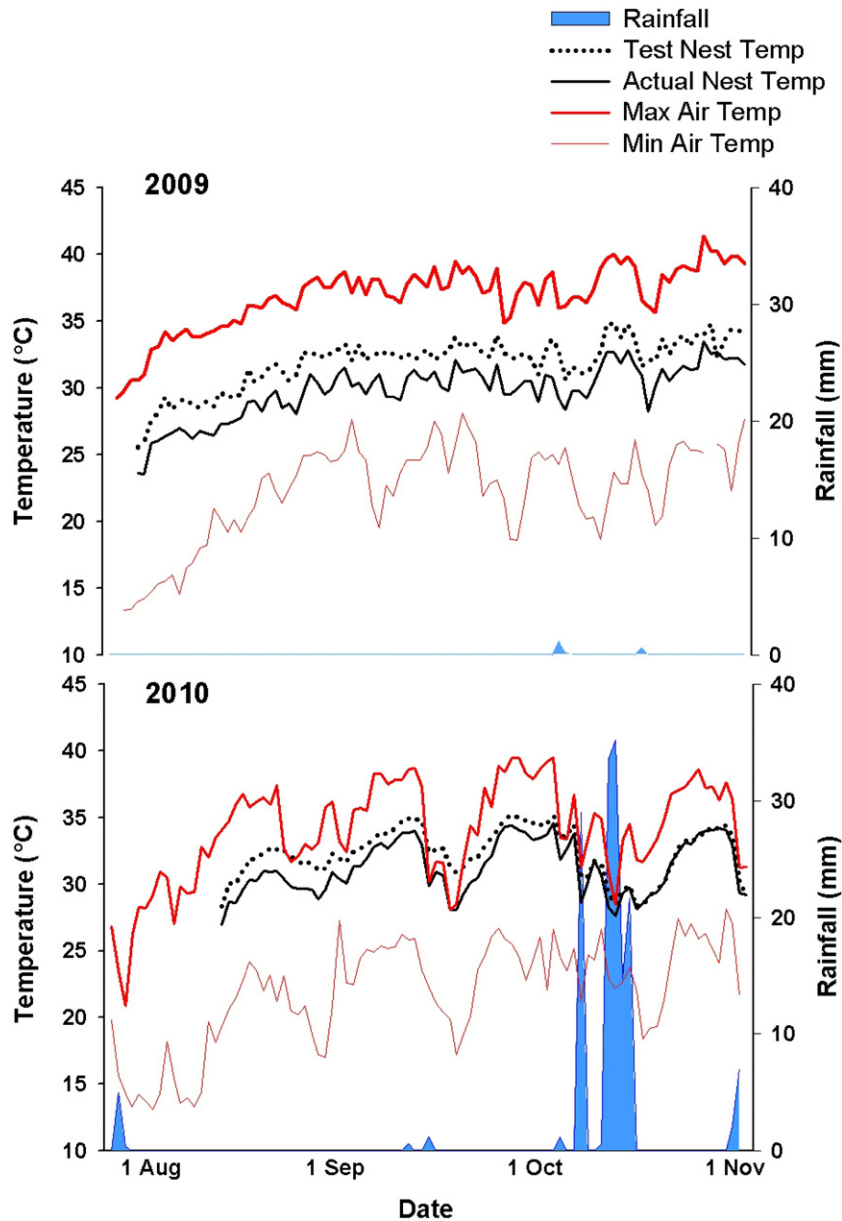
Fig. 3. Diel fluctuations of temperatures inside actual nests and test holes of freshwater crocodiles at Lake Argyle. The graph also shows air temperatures and rainfall from 1 August to 1 November in 2009 and 2010. Rainfall influences maximum air temperature, which in turn influences mean substrate temperature. Data on air temperature and rainfall are based on Lake Argyle resort (16.11°S, 128.74°E) and Kununurra Aero (15.78°S, 128.71°E) weather stations (obtained online from http://www.bom. gov.au/climate/).

however, such nesting substrates are rare. Most of the lakeshore is either muddy and weedy, or steep and rocky. Steep cliffs and dense vegetation reduce access by nesting females into areas further inland. In the absence of preferred sandy nesting beaches, the Lake Argyle crocodiles use the most friable substrate among the alternative substrates available. This flexibility in nest-site selection criteria enables females to find the conditions required for successful embryo development in this harsh landscape. A similar ability

to adjust nest-site choice to local conditions likely is widespread in crocodilian species with wide geographic distributions (e.g. *Crocodylus acutus* – Thorbjarnarson 1989; *C. porosus* – Magnusson 1980; Webb *et al.* 1983b; *C. niloticus* – Cott 1961; Modha 1967). Among other species, the Orinoco crocodile, *Crocodylus intermedius*, nests in rocky soil (Thorbjarnarson & Hernandez 1993) if sandy beaches are not available and can even switch from hole-nesting to mound-nesting if suitable substrates are not available
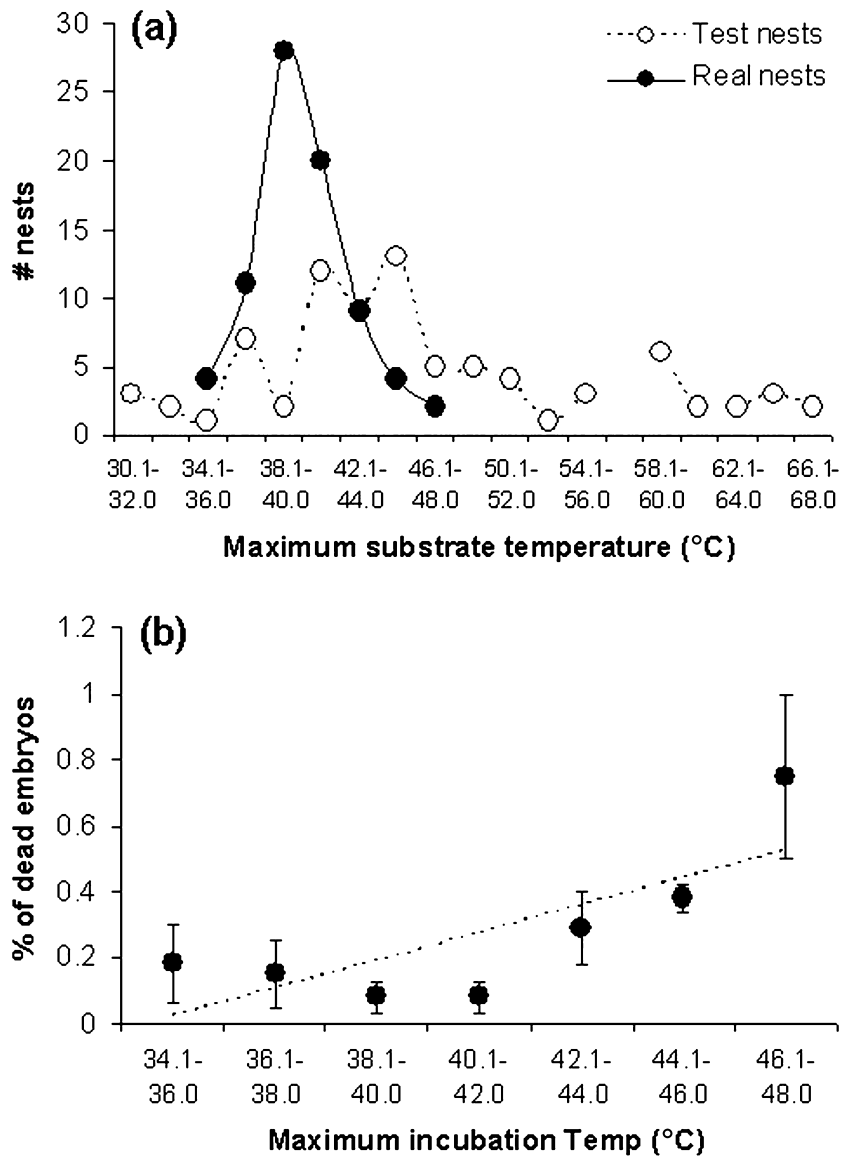
Fig. 4. The nests in which freshwater crocodiles laid their eggs were cooler, on average, than the test holes that they dug but abandoned (a). In general, nests with lower maximum temperatures had a lower proportion of malformed or dead offspring (b).

Table 4. Fate of *Crocodylus johnstoni* eggs from the northern sites of Lake Argyle in 2009 and 2010

	2009		2010	
Egg fate	n	%	n	%
Damaged by researchers	7	0.8	6	1.7
Predated	228	25.9	126	34.7
Infertile	11	1.3	6	1.7
Embryonic failure	6	0.7	18	5.0
Dead at/on hatchling	2	0.2	12	3.3
Hatched – abnormal	13	1.5	11	3.0
Hatched – normal	612	69.6	184	50.7

(Medem 1981). In the highly altered agricultural landscapes in which they live, female Chinese alligators (*Alligator sinensis*) use vegetation in small artificial ponds for nesting (Thorbjarnarson *et al.* 2001) and American crocodiles (*C. acutus*) nest on spoil berms between the cooling canals of a power plant (Gaby *et al.* 1985).

In a waterside gravel patch at Lake Argyle, the ability of a nesting female crocodile to dig a suitable chamber depends upon shore vegetation and slope characteristics, as well as substrate type. Steep slopes and thick vegetation make digging difficult (Modha 1967; Smith 1987). Within the relatively flat, unvegetated areas, our comparisons between test holes and

actual nests show that nesting females abandon sites where they encounter either physical obstructions (large rocks) or overly damp soil. It is possible, however, that nesting females abandoned at least some of the sites because of disturbance by external stimuli (e.g. predators, humans, weather extremes). Within the remaining sites, however, females appear to be selective with respect to thermal and hydric regimes. As a result, abiotic conditions within actual nests at Lake Argyle were more similar to those of nests in sandbanks at the Ord River site (>55 km away) than those in the test holes dug a few metres away on the lakeshore. The sites selected for egg deposition exhibited a narrower range of values than did test holes with respect to canopy openness, thermal regimes and soil moisture content. These comparisons support the hypothesis that nesting females test the substrate conditions, temperature and moisture of potential nests (Smith 1987; Webb & Manolis 1998).

Both the thermal and the hydric conditions in the nest environment are important; embryo survival would be enhanced by maternal avoidance of higher maximum temperatures and saturated soil (Mazzotti 1989; Roosenburg 1996). Embryo mortality increases in both overly dry and overly wet soils (Modha 1967; Mazzotti *et al.* 1988), but embryo survival may be more sensitive to the thermal environment than the hydric environment (Webb & Cooper-Preston 1989). Moreover, the variability of moisture content in response to rainfall and changes in the water table may render it an unreliable cue for nest-site selection (Wood & Bjorndal 2000).

Nesting females are faced with a complex challenge, because of covariation among relevant variables. For example, the sites chosen for egg deposition had more open canopies, and were drier and cooler than the locations of test holes. Vapour-induced heat transfer in soils depends upon substrate particle size (therefore, the extent of macropore space: Balland & Arp 2005) and the thermal conductivity of soils increases with moisture content and bulk density (Al Nakshabandi & Kohnke 1965; Ghuman & Lal 1985). Our analysis suggests that soil particle size strongly affects thermal regimes, and hence that disparities in substrate types between test holes and actual nests may have caused most of the thermal divergence between these two types of excavations.

Selection of suitable thermal regimes for incubation is important for the survival and sex-ratio of the offspring. The sex of *C. johnstoni* is determined by incubation temperatures, and hence can be influenced both by the time of nesting and by the place of nesting (Webb & Smith 1984). At Lake Argyle, some nests exhibited temperatures so high that offspring were killed or deformed. If females had laid their eggs in the

'test holes' instead of actual nests, the proportion of dead and deformed offspring would have been higher than was actually the case (Fig. 4). The very high mean and maximum temperatures of the East Kimberley (Bureau of Meteorology 2011) therefore impose a major challenge for females to find sites cool enough for embryo survival. Within a nesting beach, nest-site selection seems to be focused on avoiding hazardous microclimates (also discussed by Webb & Smith 1984).

Many factors that influence nest-site selection in other crocodilians and other regions are not applicable for *C. johnstoni* at Lake Argyle. For example, costs to the reproducing female are unlikely to be important because female *C. johnstoni* do not guard their nests; embryo vulnerability to nest flooding is similarly irrelevant because human-regulated water levels in Lake Argyle are relatively stable during the incubation period. Rates of nest predation do not appear to play a major role either, because crocodiles at Lake Argyle nest on islands that lack terrestrial predators as well as on mainland beaches where they are often predated (Somaweera *et al.* 2011). One potential explanation for this paradox is that characteristics of successful nests vary over time and space, and nest-site selection reflects long-term optima that may be neutral or maladaptive in the short term (Clark & Shutler 1999).

The restricted availability of potential nest sites at the lake is likely to have several consequences for the ecology of this crocodile population. First, the spatial distribution of nesting areas influences the spatial and temporal distribution both of adult animals and of hatchlings. Some adults presumably travel long distances from their usual home ranges to the nearest available nesting site, an energy-expensive and potentially risky migration (because of entanglement in fishing nets, etc.). Also, increased densities of adults around the nesting areas may change patterns of social interaction: we noticed an increase in injuries (puncture marks, rake marks and amputated tails) in adults during July–September (R. Somaweera, pers. obs., 2010), similar to injuries associated with breeding in other crocodilians (Cott 1961; Webb & Messel 1977). If mating occurs near nesting sites, the restricted nesting opportunities also may affect male mating success. A single large male potentially may be able to monopolize many of the local females, reducing effective population size from a genetic perspective. The aggregated nesting enforced by a scarcity of suitable substrates also may increase predation rates on nests (Somaweera *et al.* 2011), as well as the chance of nests being damaged by later-nesting females.

The ability of a species to utilize disturbed habitats depends upon satisfying the requirements of all life-history stages – and often, the egg stage will be the

weakest link. Because eggs are immobile, they need to be laid in a site that will provide suitable (thermal, hydric, gaseous) conditions for a long period (often weeks or months); and that will not be subject to predation, parasitism or fungal attack over that period. In animals whose earliest life-history stages are the only ones that require terrestrial habitats, then there is considerable potential for those terrestrial resources to be in short supply relative to aquatic resources. That decoupling between resource availability on the land *versus* water commonly will be exacerbated by anthropogenic activities. In such cases, wildlife populations may well be controlled by the limited availability of habitats required for only a short part of the life history (in freshwater crocodiles, about 3 months out of an over 50-year potential lifespan: Webb & Manolis 1998).

Many crocodilian populations are declining worldwide, at least partly because of lack of suitable nesting habitats (Thorbjarnarson & Hernandez 1993; Leslie & Spotila 2001; Villamarín *et al*. 2011). Under such conditions, the ability of females to select sites for successful nesting, and adaptive plasticity in nest-site selection criteria, could be critical to the maintenance of viable populations (e.g. Gaby *et al*. 1985; Thorbjarnarson *et al*. 2001). Our study provides a clear example of such abilities, whereby females are able to locate the most suitable nesting areas within a landscape that lacks the kinds of sites (moist, shaded, sandy banks) used for oviposition throughout the rest of the species range. This ability, and the behavioural plasticity of nesting females, have allowed this crocodile population to exploit the abundant resources available within the aquatic habitat and thrive in conditions that superficially appear utterly unsuited to breeding.

ACKNOWLEDGEMENTS

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