

Ruchira Somaweera · Jonathan K. Webb  
Richard Shine

## It's a dog-eat-croc world: dingo predation on the nests of freshwater crocodiles in tropical Australia

Received: 21 February 2011 / Accepted: 20 May 2011 / Published online: 8 June 2011  
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**Abstract** Predation on eggs is an important source of mortality for many long-lived organisms, but causes of egg mortality from specific predators remain poorly known in most cases. Understanding the identity of predators, and the rates and determinants of their effects on a cohort of recruits, can provide a valuable background for attempts to exploit, control or conserve populations. We used remotely triggered cameras to study predation on the nests of freshwater crocodiles (*Crocodylus johnstoni*) inhabiting Lake Argyle, in tropical Australia. We also supplemented our work on natural crocodile nests with artificial nests. Overall, 80 of 111 natural nests were opened by predators, and predation occurred throughout the study period (7 weeks). Unlike in other parts of the species' range, most nest-robbars were dingoes (*Canis lupus dingo*, responsible for 98% of all predator visits in the northern sites, and 54% in the Ord River site), with minimal additional predation by reptiles and birds. Contrary to expectation, rates of nest predation were not influenced by spatial clumping of nests: the probability of predation per nest did not change with total numbers of nests laid in an area, and artificially aggregated versus dispersed nests experienced similar levels of predation. Nest vulnerability was linked to abiotic features including slope of surrounding banks, compactness of nesting substrate, and distance from the nearest forest. Abundant aquatic food resources support a large crocodile population, but a lack of suitable nest-sites forces the crocodiles to concentrate nesting in small

areas readily accessible to wide-ranging nest predators. Collectively, our results suggest that distinctive attributes of the lakeside landscape alter predator guilds and fashion unique predator–prey interactions.

**Keywords** Artificial nest · Nest-site selection · Predation latency · Remote camera

### Introduction

For most species of animals, predation is a significant source of mortality, and can affect the viability of populations (Sabo 2008; Calsbeek and Cox 2010). Understanding the identity of predators, and the rates and determinants of their effects on a cohort of recruits, can provide a valuable background for attempts to exploit, control or conserve populations (West and Messmer 2004; Teunissen et al. 2008; Norbury and Heyward 2008). Intuition suggests that understanding predation in this way will be significant primarily in the case of small and highly vulnerable taxa, and unimportant for large and formidable species that are more likely to act as predators than as prey. Even for taxa where adults are relatively invulnerable, however, the early (small, undefended) life-history stages may be subject to a wide array of predators (e.g. Laurenson 1994; Loveridge et al. 2006). Accordingly, we need information on predation and its effects even in animals such as crocodilians.

Many crocodile species are threatened worldwide, usually by human activities, and information on the operation of predation on vulnerable age classes can contribute to management (Magnusson 1982; Kushlan 1988; Mazzotti 1989; Thorbjarnarson and Hernandez 1993). All crocodiles are primarily aquatic, but nest terrestrially. That situation can create a significant mismatch between the availability of suitable nesting habitat and the abundance of adult crocodilians (e.g. Leslie and Spotila 2001; Thorbjarnarson et al. 2001; Villamarín et al. 2011), and hence the numbers of nesting females. Population densities of adult crocodiles depend largely

**Electronic supplementary material** The online version of this article (doi:10.1007/s11284-011-0853-0) contains supplementary material, which is available to authorized users.

R. Somaweera · J. K. Webb · R. Shine  
School of Biological Sciences, The University of Sydney,  
Heydon-Laurence Building A08, Sydney NSW 2006, Australia

R. Somaweera (✉)  
Tropical Ecology Research Facility, University of Sydney,  
PO Box 441, Humpty Doo NT 0836, Australia  
E-mail: ruchira.somaweera@gmail.com

upon attributes (food supply, shelter, etc.) of the aquatic system, whereas nest-site availability is driven by features of the surrounding terrestrial environment. That conflict raises the possibility of a flourishing crocodile population having access to very limited nesting areas. Concentration of nesting can increase the degree of threat posed by terrestrial nest-predators (Webb et al. 1983a). We studied such a system, to document predator abundance and the rates and determinants of nest-raiding.

## Materials and methods

### Study species

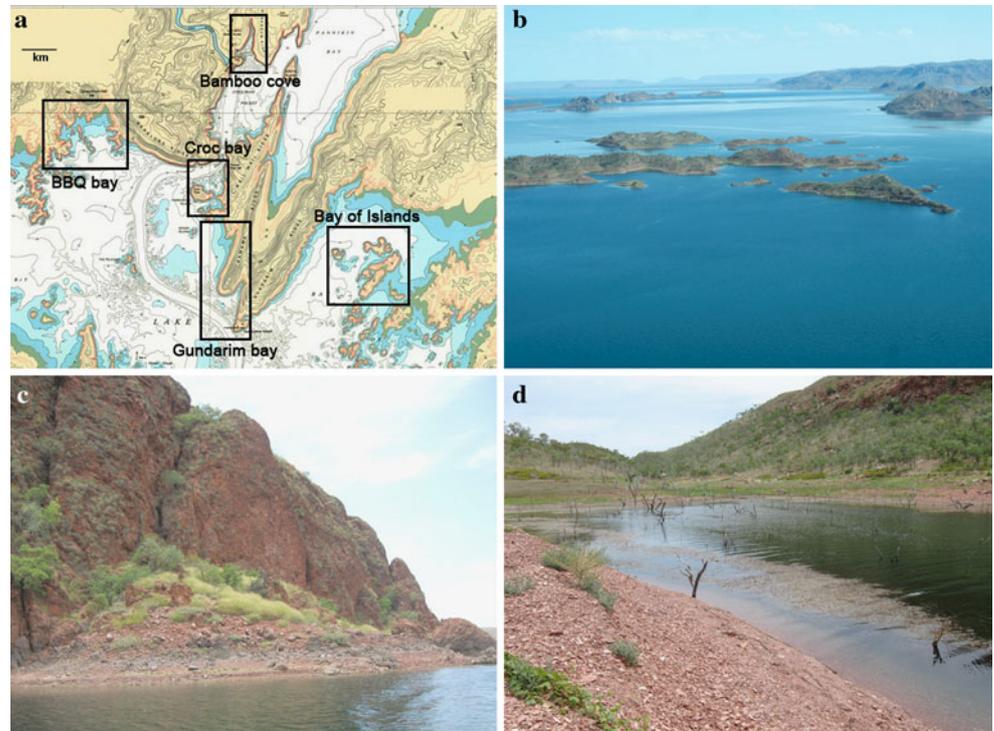
The Australian freshwater crocodile (*Crocodylus johnstoni* Krefft, 1873) is endemic to mainland northern Australia, where it occurs primarily in freshwater streams, rivers and lagoons (Webb and Manolis 1998), occasionally extending into estuarine or tidal rivers (Messel et al. 1979; Webb et al. 1983b). It is a hole-nester and oviposits during the dry season (Webb et al. 1983a). At Lake Argyle, the average clutch size of *C. johnstoni* is 14 eggs, each about 66 × 41 mm, weighing 69.4 g and hatching after an incubation period of 72–96 days (R.S., unpublished data). In the wild, *C. johnstoni* do not defend their nests (Webb et al. 1983a). In other parts of the species' range, many or most nests are raided; major nest predators include varanid lizards (*Varanus gouldii*, *V. panoptes*) and feral pigs *Sus scrofa* (Webb et al. 1983a; Smith 1987; Chibeba 2003).

### Study area

Lake Argyle is a very large (>880 km<sup>2</sup>) artificial impoundment in northwestern tropical Australia (the east Kimberley region of Western Australia, close to the Northern Territory border; 16°29'S, 128°75'E). The lake contains the largest population of *C. johnstoni* in Australia (>30,000 non-hatchlings; G Webb Pty Ltd 1989; WMI 2005, 2009), but nesting habitats are scarce. Most of the northern lakeshore consists of steep rocky ridges, whereas banks in the south and east are shallow, muddy and grassy. Occasional patches of sand and gravel within these banks serve as the only viable nesting grounds.

Our five main study sites were located in the northern part of the lake (Fig. 1). The Bay of Islands (= BOI) is a cluster of small islands separated from the mainland by >2 km of deep water. During spotlight and daytime surveys, we have seen crocodiles swimming between islands, but not between the islands and mainland. Extensive searches and camera trapping have failed to record any land predators (either predatory mammals or large reptiles) from these islands. Bamboo Cove is a steep-sided bay, precluding access by most terrestrial predators. Croc Bay, Gundarim Bay and BBQ Island Bay have less steep banks and (being parts of the mainland) harbour land predators. These study sites were selected based on the locations of the main nesting beaches in the lake and logistic reasons including regular accessibility. In 2010, we also scanned a 10 km stretch of upper Ord River (the original river that was dammed to build Lake Argyle) as a sixth site for crocodile nests.

**Fig. 1** The five main study sites are located in the northern area of Lake Argyle (a). Small islands at the Bay of Islands (BOI) are surrounded by deep water (b) whereas the other sites are parts of the mainland. Nesting beaches at Bamboo Cove (c) are surrounded by steeper banks than at the other three sites (e.g. Gundarim Bay d)



## Surveys of predator abundance

We used bait stations with remotely triggered cameras to quantify predator numbers in crocodile-nesting areas. Camera trapping is an effective method of detecting the presence of carnivores (e.g. DeVault et al. 2005; Stevens et al. 2008; but see Gompper et al. 2006). We used two bait stations per nesting site, within 200 m of the nesting beaches. At each station, we placed a motion-sensitive infrared triggered digital still camera (Bushnell Trophy Cam) 30 cm aboveground and 2–3 m from the bait. We used a 1 kg mixture of commercial cat food, cat urine in cat litter, raw chicken, raw beef and raw fish as the bait to attract an array of predators. Baits were placed on a cleared patch on the ground, and replaced every week for 4 weeks. We programmed cameras to take a photograph once per minute if triggered by movement, left to photograph 24 h a day; date and time records were stored on all photographs. The cameras were active in a non-nesting season (March–April 2010, trap hours per camera = 665) and during the nesting season (August–September 2010, trap hours per camera = 665) in the same locations.

Because pilot studies indicated that it is difficult to identify individual animals from photographs, our analysis deals with the number of visits by a given predator species to the site. Some of these visits were presumably by the same individuals. We defined a “capture” as detection of a predator in consecutive minutes at one station regardless of the number of photographs taken. For example, if a predator visited a bait station on one occasion, where it was photographed ten times during consecutive minutes, we scored this as one capture. If the same animal, or a different one, revisited the station after an interval of 5 min and remained there for 2 min, the latter set was considered as a separate capture.

## Predation of natural nests

In August 2009 and 2010, we located crocodile nests laid the previous night (based on fresh disturbance to the soil surface). Probing with a thin metal rod to look for nests was possible only in the Ord River site, where the nesting substrate is finer. The presence of eggs was confirmed through careful excavation by hand. For each nest we recorded distance to shore and distance to the closest forest patch (defined as an area  $> 1 \text{ km}^2$  with trees); nesting substrate (loam, sand or gravel); nest depth (soil surface to the topmost egg); clutch size; laying date (based on the extent of opaque banding on the eggs: Webb et al. 1983a); number of other crocodile nests located within a 10 m diameter from the focal nest; soil compaction (using a penetrometer); and characteristics of the banks surrounding the nest site (“steep” if  $> 75^\circ$ ). The excavated nest substrate was replaced and the site concealed by scattering loose soil over the nesting area.

We set up remote cameras (Bushnell Trophy Cam) in each nest site to photograph any animals moving on the entire nesting area. These cameras have a detection range of  $\sim 15 \text{ m}$  and take photographs at night using infrared night vision LEDs, thus do not omit a visible flash. We visited the sites every 2nd day for 7 weeks from 1 August to check nests for predation. When a nest had been raided, we recorded the number of eggs removed. The identity of the predator, the time of nest-opening, and the level of crocodile activity was documented through photographs from the remote cameras. Any predator scats found in nesting sites were collected, and analysed as described by Doncaster et al. (1990) to determine the percentage of different prey types. Because the study did not continue throughout the incubation period, we could not determine overall hatchling success.

## Predation on artificial nests

To understand whether a nest’s location and its proximity to other nests affect its probability of being predated, we manipulated nest distributions experimentally (see Marchand et al. 2002). Artificial nests allow for control of environmental variables, as well as increasing sample sizes (Carignan and Villard 2002; Moore and Robinson 2004; but see King et al. 1999 for a counter example). We created 20 artificial nests in each of six sites in August 2010, coinciding with nesting by *C. johnstoni* in this region. At each site, ten nests were deployed in a scattered arrangement with two nests each (at least 25 m distant from each other) at 1, 2, 5, 10 and 20 m from the water’s edge. This range corresponds to the distance of natural nests from water. The other 10 nests were placed in a group (1 m from each other) 5–6 m from the shoreline. In each artificial nest, we buried two white domestic hen eggs ( $\sim 5.5 \times 4 \text{ cm}$ ) in a hole 20 cm deep and filled with soil. An indicator flag (a 15-cm piece of pink flagging tape) was anchored to the bottom of the nest hole by a 60-cm piece of thin nylon string tied to a buried stick. Leighton et al. (2009) showed that indicator flags above buried bait were pulled out of the nest when the bait was removed, but not before. To mimic nesting behaviour we disturbed the soil and the vegetation around the holes. The locations of the nests were recorded but no markers were put on the nests. To add crocodile scent, we sprayed 10 ml of water, taken from an aquarium that had held three yearling crocodiles for 2 days, on the surface of the nest. We made all nests in a given site within the same day. The artificial nests were placed away from actual nest sites in order to avoid attracting predators to the natural nests.

The nests were checked daily after deployment and pictures from the remote cameras were scored for predator species and time of nest opening. We classified nests as predated when at least one egg was missing, or

**Table 1** Rates at which various animal species, including potential nest-predators, were recorded by camera traps at Lake Argyle sites

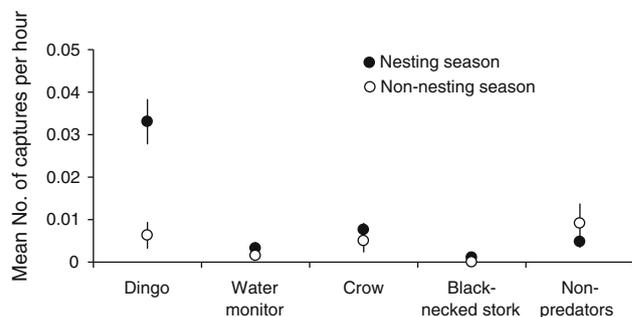
Site	Captures per hour (mean $\pm$ SD)				
	Dingoes	Mertens' water monitors	Torresian crows	Black-necked storks	Non-predators
1	0.034 $\pm$ 0.018	0.005 $\pm$ 0.002	0.007 $\pm$ 0.005	0.002 $\pm$ 0.002	0.003 $\pm$ 0.000
2	0.021 $\pm$ 0.023	0.001 $\pm$ 0.001	0.005 $\pm$ 0.005	0.001 $\pm$ 0.001	0.008 $\pm$ 0.004
3	0.012 $\pm$ 0.017	0.000 $\pm$ 0.000	0.005 $\pm$ 0.006	0.001 $\pm$ 0.001	0.019 $\pm$ 0.018
4	0.013 $\pm$ 0.010	0.003 $\pm$ 0.002	0.004 $\pm$ 0.001	0.000 $\pm$ 0.000	0.003 $\pm$ 0.002
5	0.025 $\pm$ 0.033	0.001 $\pm$ 0.001	0.008 $\pm$ 0.004	0.000 $\pm$ 0.000	0.003 $\pm$ 0.000
6	0.014 $\pm$ 0.013	0.005 $\pm$ 0.003	0.010 $\pm$ 0.012	0.000 $\pm$ 0.000	0.006 $\pm$ 0.006

when any of the eggs had beak, claw, and/or teeth marks; and considered nests to be successful when they were untouched during the 4-week period.

To reduce the possibility of predators being guided to nests by human presence, our visits were brief and the direction of approach was varied (Gunnarsson and Elmberg 2008). To minimize deposition of human scent (on both artificial and natural nests), we wore rubber boots and latex gloves, and placed equipment on a plastic drop sheet rather than on the soil surface (Whelan et al. 1994). We sprayed the nest substrate with air freshener as an odour neutraliser to mask the smells of both the turned soil and mucus on the eggs, which may otherwise attract predators (Smith 1987; Chibeba 2003). The use of scent-masking in predation studies of artificial nests has been supported by some studies (see above), and refuted by others (e.g. Skagen et al. 1999; Donalaty and Henke 2001; Burke et al. 2005) but has not been shown to increase predation levels.

### Statistical analysis

Data were analysed using the statistical software JMP 5.01 (SAS Institute, Cary, NC). The number of visits (per hour) made by each species to bait stations was calculated for each site and season (nesting and non nesting) and these numbers were compared using one-way ANOVAs. Data from one site (BOI) were omitted from analysis, because this site lacked nest predators and thus we never recorded predation there. Camera malfunction resulted in the loss of 1 week's data from each of three sites. We categorized data on rates of nest predation according to week and nest numbers (both laid and raided) and square-root transformed these data on predation rates to achieve distribution normality and variance homogeneity. We used linear regression to analyse the effect of environmental variables on predation levels; ANCOVA for the relationship between rate of nest laying and rate of nest predation; and Chi-square tests to analyse differences in weekly nest predation rates between years. The attributes of clumped versus scattered artificial nests were compared using one-way ANOVAs and linear regression.



**Fig. 2** Seasonal differences in the number of visits by different groups of animals to bait stations close to crocodile nesting sites at northern Lake Argyle. “Non-predator species” include macropods and birds other than crows and black-necked storks. Error bars Standard error

## Results

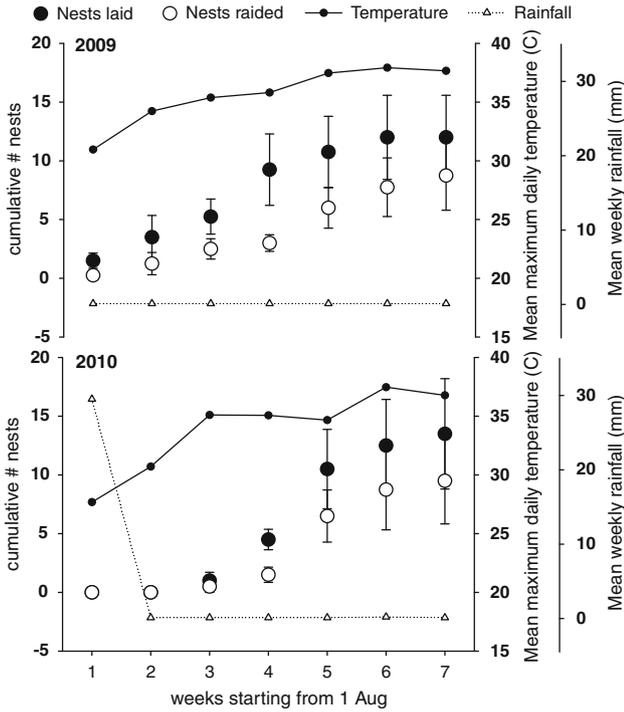
### Surveys of predator abundance

We identified 19 species of animals in 252 remote camera captures at the six baited sites over the two seasons. The average number of animal visits per bait station differed among sites ( $F_{5,252} = 3.23$ ,  $P = 0.007$ ; Table 1) but not between seasons ( $F_{1,252} = 0.59$ ,  $P = 0.44$ ). Dingoes (*Canus lupus dingo*), Mertens' water monitors (*Varanus mertensi*), Torresian crows (*Corvus orru*) and black-necked storks (*Ephippiorhynchus asiaticus*) were identified as potential nest predators. Dingoes were recorded more often in the nesting season ( $0.03 \pm 0.01$  captures per hour) than the non-nesting season ( $0.006 \pm 0.007$  captures per hour) ( $F_{1,10} = 19.76$ ,  $P = 0.001$ ; Fig. 2).

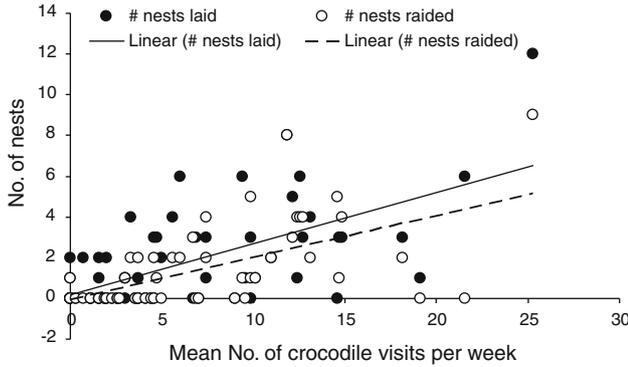
### Predation on natural nests

More nests were laid in weeks with higher maximum air temperatures ( $F_{1,75} = 72.13$ ,  $P < 0.0001$ ) and less rainfall ( $F_{1,75} = 11.95$ ,  $P < 0.05$ ; Fig. 3). The same five broad sites were used for nesting in both years of the study.

The number of crocodile visits to nesting sites (scored by remote camera) was correlated with the number of nests laid ( $R = 0.64$ ,  $F_{1,65} = 44.08$ ,  $P < 0.0001$ ). At sites with predators, the percentage of nests that were



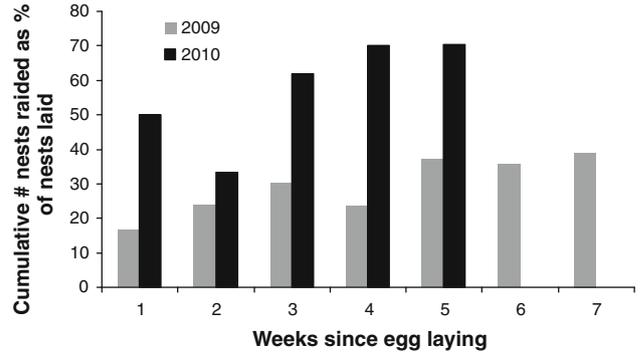
**Fig. 3** Temporal variation in the cumulative number of freshwater crocodile (*Crocodylus johnstoni*) nests laid and raided. A rainy start to the nesting season in 2010 may have delayed oviposition in that year. Error bars Standard error



**Fig. 4** The relationship between the number of crocodile visits and the number of nests laid and raided. Data from sites without predators were deleted from the analysis, and data from 2009 and 2010 were pooled

predated was not significantly related to the number of nests laid (ANCOVA with ‘eaten vs laid’ as factors and ‘# visits’ as covariate, # predated as dependent variable: interaction  $F_{1,116} = 0.71, P = 0.4$ ; Fig. 4). Predation occurred throughout the study period (Fig. 5).

The incidence of nest predation at northern sites during the first 7 weeks post-laying did not differ significantly between years ( $\chi^2 = 0.609, P = 0.435$ ) but varied between sites ( $\chi^2 = 121.06, P < 0.0001$ ): predation levels ranged from 81.8% in Gundarim Bay to 0%



**Fig. 5** Cumulative number of *C. johnstoni* nests raided as a percentage of nests laid over 7 weeks in 2009 and over 5 weeks in 2010

at BOI. None of the eggs at Gundarim Bay survived to hatch, as they were predated later in the incubation period (e.g. Video S2).

A comparison between the attributes of surviving nests versus predated nests revealed many similarities, but also some significant differences. A nest was more likely to be predated if it was close to a patch of forest, if it was laid in relatively soft soil and if the nesting beach was not surrounded by steep banks (Table 2). Predated and non-predated nests did not differ significantly in their mean distance from shore but among the predated nests, those further away from the shore were raided earlier ( $F_{1,63} = 14.03, P < 0.05$ ). However, deeper burial of eggs did not increase predation latency ( $F_{1,63} = 3.03, P = 0.09$ ).

Dingoes were the major predators of crocodile nests (98% of all predator visits noted in the northern sites, and 54% in the Ord River site). Dingo visits occurred from afternoons (~1600 hours) to the next morning (0800 hours, Fig. 7). At Gundarim Bay, up to four dingoes (including young animals) were seen together at the site (Video S1); elsewhere only one dingo was recorded at a given time. Footage from the hatching season (late November 2010) revealed that dingoes also consume hatchling crocodiles emerging from excavated nests (Video S2).

At the Ord River site, yellow spotted goannas (*Varanus panoptes*) were seen scavenging in two nests already opened by an unknown predator. Torresian Crows (*Corvus orru*) disturbed two unopened, but partially covered nests at Ord River and the two uppermost eggs in these nests were damaged. Mertens’ water monitors (*Varanus mertensi*) ( $n = 2$ ), black-necked storks *Ephippiorhynchus asiaticus* ( $n = 6$ ) and an unidentified small mammal ( $n = 1$ ) visited opened nests 1–3 days after the initial predation event. A large (~1 m in total length) *V. mertensi* was photographed carrying a crocodile egg in its mouth at Bow River, which flows into Lake Argyle (B. Dempsey, personal communication 2010); whether or not this animal had opened the crocodile nest to obtain the egg could not be ascertained.

Goannas typically ate the entire egg, leaving no trace behind. Scat samples of goannas from the Ord River site

**Table 2** Environmental and nest attributes of predated ( $n = 80$ ) and non-predated nests ( $n = 31$ ) of freshwater crocodiles at Lake Argyle. Data on nests from BOI (a site lacking terrestrial egg predators) were omitted from analysis

Factor	Non-predated nests	Predated nests	$F$ or $\chi^2$	$p$
Distance to water (m)	13.52 $\pm$ 1.77	13.94 $\pm$ 1.11	0.04	0.83
Ground cover	100% without ground cover	96.9% without ground cover	0.72	0.39
Substrate	90.32% gravel, 3.23% loam and 6.45% sand	88.75% gravel, 2.5% loam and 8.75% sand	0.19	0.91
Soil compaction (kg/cm <sup>2</sup> )	1.96 $\pm$ 0.11	1.67 $\pm$ 0.07	4.78	0.03*
Slope (°)	36.93 $\pm$ 2.45	36.5 $\pm$ 1.53	0.02	0.88
Surrounding habitat	12.9% in sites surrounded by steep banks	2.5% in sites surrounded by steep banks	4.73	0.03*
Distance to a forest patch (m)	21.61 $\pm$ 2.76	14.87 $\pm$ 1.71	4.32	0.04*
Number of nests in a 10 m diameter	2.74 $\pm$ 0.55	3.51 $\pm$ 0.43	1.41	0.24
Depth to top egg (cm)	128.94 $\pm$ 5.15	136.07 $\pm$ 3.21	1.38	0.24
Clutch size	14.29 $\pm$ 0.66	14.37 $\pm$ 0.41	0.01	0.91

\* Significant ( $p < 0.05$ ) differences between predated and non-predated nests

**Table 3** Latency to predation of freshwater crocodile nests at six sites in Lake Argyle. Mean values and associated standard deviations for the length of time (in days) between a nest being laid and being predated are shown

Site	Latency to predation in days (mean $\pm$ SD)	
	Clumped nests	Scattered nests
1	30 $\pm$ 0	23.1 $\pm$ 11.1
2	20.4 $\pm$ 12.4	30 $\pm$ 0
3	17.6 $\pm$ 10.8	18.8 $\pm$ 9.8
4	9.4 $\pm$ 0.5	14.3 $\pm$ 5.8
5	9.5 $\pm$ 7.4	9.5 $\pm$ 3.1
6	18.8 $\pm$ 9.8	18 $\pm$ 8.4

contained abundant eggshell fragments. In contrast, dingoes often left broken eggshells behind; some eggs were broken into halves or only had a single opening through which the contents had been extracted. Of 69 dingo scat samples from northern sites, none contained eggshells. The dingo scats mostly comprised lizards—mainly *Varanus acanthurus* (36% by volume of identifiable parts); birds (22%); insects—mainly grasshoppers (20%); mammals (10%); fish—mainly catfish (6%); and plant matter—mainly fruits of *Passiflora foetida* var. *hispida* (6%).

We found no evidence of predation on adult crocodiles. However, on one occasion at Crocodile Bay, two dingoes chased away a small nesting crocodile (estimated at  $\sim 1.5$  m in total length), one pursuing the crocodile into the water before raiding the nest. Three dead female crocodiles were found during the nesting season (total length from 2.1 to 2.4 m) in August/September in 2010 in northern sites, but the carcasses were too degraded to assess the cause of mortality.

#### Predation on artificial nests

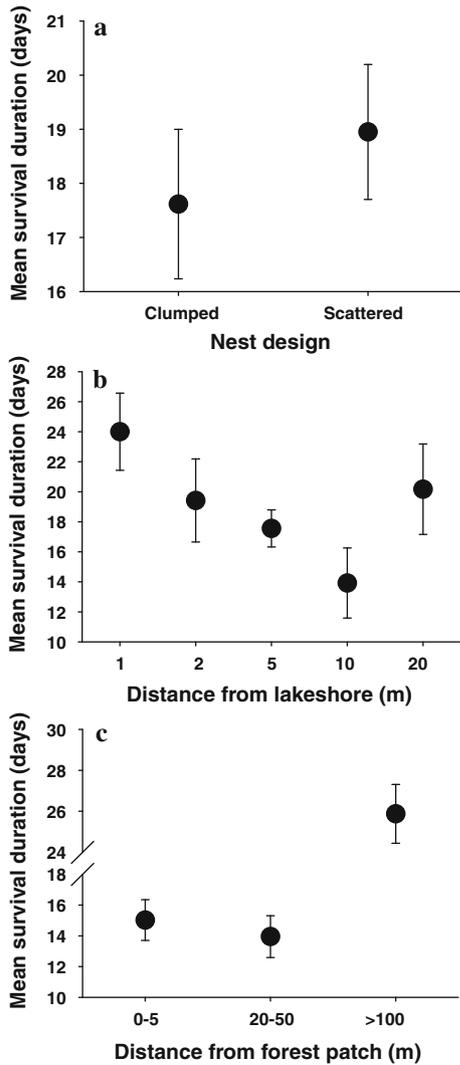
The overall mean latency to predation of the artificial nests differed among sites ( $F_{5,108} = 14.93$ ,  $P < 0.001$ )

but not between clumped versus scattered experimental distributions ( $F_{1,108} = 0.85$ ,  $P = 0.36$ ; Table 3, Fig. 6). However, the mean predation latencies of clumped versus scattered experimental nests differed among sites (interaction  $F_{5,108} = 2.47$ ,  $P = 0.04$ ), with scattered nests surviving longer than clumped nests at Croc Bay ( $F_{1,18} = 7.14$ ,  $P = 0.01$ ) and BBQ Island site 2 ( $F_{1,18} = 6.00$ ,  $P = 0.02$ ). Among artificial nests, those at Bamboo Cove survived longer than those at Gundarim Bay (posthoc Fisher's PLSD test,  $P < 0.05$ ).

A crocodile nest's distance from the water's edge did not affect its survival ( $F_{1,118} = 0.18$ ,  $P = 0.68$ ) but the pattern was curvilinear: latencies were greatest for nests that were either very close to the shoreline, or furthest away (Fig. 6). Nests that were laid closer to forest patches were predated sooner ( $F_{1,188} = 43.23$ ,  $P < 0.001$ ; Fig. 6). All initial nest excavations were done by dingoes, with peak visiting times at 0400–0500 hours and again at 1700–2100 hours (Fig. 7). Visits by predators lasted for an average of 1.47 hours. Black-necked storks ( $n = 3$ ) and crows ( $n = 8$ ) scavenged on the leftovers during the following morning. Artificial nests generally experienced high rates of survival for a short period post-construction, but then were rapidly predated. Some of the natural nests were located sooner, but the surviving nests were predated less heavily over the next few weeks (Table 4).

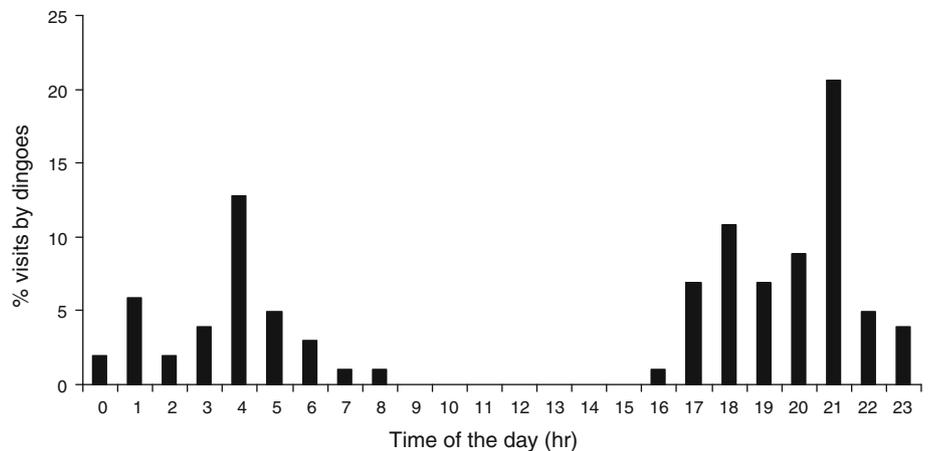
#### Discussion

Direct observations of predation on crocodile nests are rare, and many of the existing records may be affected by bias (e.g. toward diurnal and slow-moving predator species). Thus, inferences about predation on crocodile nests generally have relied on indirect evidence found at the nest site (e.g. Modha 1967; Kofron 1989; Kushlan and Mazzotti 1989; Magnusson 1982; Platt and Thorbjarnarson 2000; Chibeba 2003; Da Silveira et al. 2010). This procedure may be adequate in areas where predator



**Fig. 6** Survival duration of artificial nests in northern Lake Argyle with regard to **a** degree of clumping of nest-site locations, **b** distance from shoreline, and **c** distance from the closest forest patch. Error bars Standard error

**Fig. 7** The diel timing of visits by dingoes to sites with artificial nests, showing peaks of activity at dawn and at night



taxa are already well-known, but extrapolating to previously unstudied areas can lead to errors (Brown et al. 1998). The rocky substrates at our sites in northern Lake Argyle resulted in few overt signs (tracks, etc.), further increasing the difficulty of determining nest fates, causes of nest failure, and identity of predators (Pietz and Granfors 2000). Remote cameras overcame these problems. One potential drawback would be if the presence of cameras and the activity of researchers affected behaviour of nesting crocodiles or predators, but such effects appear to be minimal (Macivor et al. 1990; Ortega et al. 1997; Pietz and Granfors 2000; for discussion of related topics, see Macivor et al. 1990; Hernandez et al. 1997; Strickland et al. 2010).

Our camera trapping showed that dingoes are the most common predators in the nesting beaches, and that they destroy many crocodile nests. The absence of nest protection by adult crocodiles may have increased nest vulnerability. Some individuals in most species of crocodilians actively defend nests (Shine 1988; Brazaitis and Watanabe 2011). Complete lack of nest defence behaviour in wild *C. johnstoni* may reflect high nest densities, incompatible with nest attendance (Smith 1987), or the lack of mammalian egg predators in Australia over evolutionary time (Webb et al. 1983a). However, quolls (*Dasyurus* spp.), Tasmanian devils (*Sarcophilus harrisii*) and thylacines (*Thylacinus cynocephalus*) were widespread in tropical Australia over millions of years (van Dyck and Strahan 2008) and could have predated on crocodile eggs. The freshwater turtle *Emydura macquarii* avoids quoll scent when selecting nest sites (Spencer 2002). Dingoes arrived in Australia less than 4,000 years ago (van Dyck and Strahan 2008). Densities of dingoes are highly variable, reflecting intensive control campaigns against these predators in agricultural areas (Letnic and Koch 2010; Letnic et al. 2011). Previous research on nesting behaviour of freshwater crocodiles was conducted at the McKinlay River (in Northern Territory), where dingoes were scarce (Chibeba 2003;

**Table 4** Fates of artificial and natural crocodile nests, as scored 4 weeks after laying

Site	Artificial nests		Natural nests	
	Weeks after laying since predation was first recorded	Nests predated at the end of 4 weeks (%)	Weeks after laying since predation was first recorded	Nests predated at the end of 4 weeks (%)
Bamboo Cove	1	15	1	33.3
BBQ Islands	2	60	1	47.7
Gundarim Bay	1	95	1	45.5
Croc Bay	2	95	1	53.3
Pannikin Bay	2	65		
BBQ Islands site 2	1	20		

C. Manolis, personal communication 2010). This may explain why previous studies have not recorded dingo predation on crocodile nests.

Many predators move about seasonally to exploit feeding opportunities (e.g. Parks et al. 2006). Areas where a prey species lays its eggs or gives birth to vulnerable offspring are major attractants to mobile predators (e.g. racoons visiting turtle nesting beaches: Engeman et al. 2003; varanids visiting turtle nesting beaches: Blamires 2004). Camera trapping showed a large increase in dingo activity in nesting sites during the crocodile nesting season, as the dingoes moved in to exploit this highly seasonal food source in the otherwise barren rocky beaches. At other times of the year, dingoes may forage in other habitats and take a broader range of prey. Even during the crocodile-nesting season, local dingoes continue to take other prey also, based on our analyses of scat samples. Whelping in dingoes from north-western Australia takes place from mid-May to mid-August, and pups between 9 and 24 weeks of age accompany the adults on hunting journeys (Thomson 1992). We also recorded young dingoes feasting on eggs and emerging hatchling crocodiles towards the end of the incubation period.

Although eggs may be a minor component of dingo diets overall (Corbett 1995), dingoes (and feral dogs) can be major nest predators of both freshwater and marine turtles in tropical Australia (Limpus 1982; Thompson 1983; Chatto and Baker 2008). At Cape Domett in tropical Western Australia, dingoes were the sole vertebrate predators of flatback turtle *Natator depressus* nests (Whiting et al. 2008). However, other types of predators—notably varanid lizards—have been most often implicated as major causes of nest destruction for aquatic reptiles in tropical Australia (e.g. Magnusson 1982; Webb et al. 1983a; Chibeba 2003; Blamires 2004; Doody et al. 2006).

The interaction between the two major types of potential nest predators—dingoes and varanid lizards—is a complex one. Dingoes often kill and consume varanids (e.g. *V. acanthurus*, *V. brevicauda*, *V. giganticus*, *V. gouldii*, *V. panoptes* and *V. varius*: Corbett 1995; Webb 1996; Paltridge 2002; T. Newsome personal communication; current study). In our scat analysis, varanids were a popular prey item for Lake Argyle dingoes

(> 30% of identified prey). Given that varanid lizards are the main predators of *C. johnstoni* eggs identified in previous studies (Webb et al. 1983a; Chibeba 2003; Doody et al. 2009b), dingo predation on varanids may substantially reduce varanid densities and thereby remove the other large potential predator of crocodile nests. If so, then areas of Lake Argyle containing fewer dingoes may also have higher densities of varanids, and the relative importance of mammalian versus reptilian predation on crocodile nests may shift considerably. Further work is needed to explore this possibility.

Predation on nests persisted throughout our study period (~78% of the incubation period). This contrasts with the situation in *C. johnstoni* at McKinley River, where predation was substantial only soon after egg-laying (Webb et al. 1983a). Canines use visual, olfactory and acoustic cues in prey location (e.g. Simpson 1997; Irit and Joseph 2003) and may be more efficient predators than the olfactory-cued lizards (Webb et al. 1983a). Hence dingoes may be able to locate nests throughout the incubation period through odours, visual evidence (such as ground disturbance) and through calls of the hatchlings (the young crocodiles vocalize inside the egg prior to hatching). Foraging goannas appear to rely on the olfactory cues left behind by nesting females, and the odour of the mucus from fresh eggs, and thus may not be able to find nests later in the incubation period. In systems where the main nest predators are mammals, predation rates have either been consistent throughout the incubation period (Staton and Dixon 1977; Crawshaw and Schaller 1980) or greatest at hatching (Joanen 1969).

In accordance with an earlier study on a different population of freshwater crocodiles (Smith 1987), the predation rate was site-dependent. Whether or not a crocodile nest was predated was influenced by a variety of factors relating to the nest's location. Most importantly, nests that were laid in areas lacking predators (small islands, distant from the mainland) or where predator access was difficult (steep banks) were more likely to survive. Harder soil also enhanced nest survival, possibly reflecting the difficulty of opening such a nest and/or a scarcity of overt cues to reveal the nests' location. At Lake Argyle, nests that were laid closer to forest patches were predated sooner than were nests laid

further away. Nest predators frequently forage along habitat edges (Marchand and Litvaitis 2004), reducing survival of nests laid closer to such sites (Strickland et al. 2010). However, the overall benefit of nesting further away from a forest patch at Lake Argyle may be negligible, because of the large foraging range of predators like dingoes (mean home range  $> 70 \text{ km}^2$  in arid environments: Corbett 1995). Even if a more distant nest takes longer to be located by a predator, its chances of survival over the entire (7–10 week-long) incubation period may be unaffected.

Several factors reported to affect nest survival in ground-nesting species elsewhere were not significant in our study system. For example, the distance of a nest from water did not significantly influence its vulnerability to predation. Other studies have reported higher offspring mortality from nests closer to shore due to flooding (Milton et al. 1994; Standing et al. 1999), nest predation (Horrocks and Scott 1991) and inappropriate nesting substrates (Spencer 2002). Conversely, if a female nests too far from shore, her own exposure to predation increases, and her hatchlings must traverse a greater distance over land to the water (Wood and Bjørndal 2000). These factors may be relatively unimportant for *C. johnstoni* at Lake Argyle, because larger adult crocodiles have no terrestrial predators (though smaller crocodiles could be attacked by dingoes), and parents transport their hatchlings to water (R. S., manuscript in preparation). Floods are rare in this anthropogenically regulated system, so a greater distance to water may not reduce nest success. Indeed, nesting further away from water may reduce the possibility of eggs being accidentally dug up by conspecific females nesting later in the season.

In our system, deeper burial did not reduce the vulnerability of buried eggs to excavation by predators. The depth to the top egg varied from 3 to 24.5 cm (R.S., unpublished data) but such a difference may be trivial for large, formidable diggers like dingoes. In other systems where smaller and short-limbed mammals are the main egg predators, deeper nests are more likely to escape predation (e.g. Hall and Parmenter 2008; Leighton et al. 2009).

The density of nests (both natural and artificial) did not affect the final predation rates in our study. A scattered distribution of nests delayed predation in some study sites, but did not prevent it; thus, the ultimate fates of scattered and clumped nests were the same. The shortage of suitable nesting beaches in the northern part of Lake Argyle make it impossible for crocodiles to lay their eggs far from other nests. Nest aggregation may reduce the per-egg probability of predation through predator saturation or satiation (review by Doody et al. 2009a). On the other hand, nest clumping may increase rates of predation because predators concentrate their search effort in places where they encounter previous rewards (Marchand et al. 2002). At Lake Argyle, nest-clumping may have relatively little effect on nest vulnerability because: (1) dingoes roam over large areas in search of food; (2) these predators are large enough to

consume an entire clutch once found and would be difficult to satiate; and (3) consuming even a single egg is likely to result in death of the entire clutch because of destruction of the nest cavity (current study; Marchand et al. 2002; Doody et al. 2009a).

Despite high predation rates on nests (current study), the *C. johnstoni* population at Lake Argyle is large and has been increasing over recent years (WMI 2010). Thus, there is no reason to manage egg-laying sites to increase crocodile nesting success. Dingo control through sodium monofluoroacetate (1080) poison-baiting occurs in some southern parts of the Lake Argyle region, to reduce predation on livestock (T. Winnecombe, personal communication 2010). Further predator management may be necessary if invasive cane toads (*Rhinella marina*) affect the Lake Argyle crocodile population. These toxic anurans caused  $> 77\%$  mortality of adult freshwater crocodiles in an arid-zone Northern Territory population (Letnic et al. 2008), but no population declines have yet been noted at Lake Argyle (R.S., manuscript in preparation). If managers decide to manipulate the system to increase crocodile nesting success, predator exclusion from nesting areas is likely to be more productive than predator control. Reducing dingo abundance might lead to an increase of the other potential nest-predators in this system, the varanid lizards. Instead, it should be relatively straightforward to enhance nest-beach availability on island sites that lack predators (by provision of sandy substrates, and control of invasive weeds, especially *Passiflora foetida* var. *hispida*); and/or to use fencing to seasonally exclude predators from the localised mainland sites where crocodile nesting is concentrated.

**Acknowledgements** We thank Bill Stewart, Kim Hands, Scotty Hewitt, Charlie Sharpe, Greg Smith, Bill Dempsey, Mike Reed, the staff at Department of Environment and Conservation (East Kimberley office) and all our volunteers for support with the fieldwork; Charlie Manolis, Tom Newsome and Tracey Winnecombe for providing information; anonymous reviewers for their useful comments and the Australian Research Council for funding.

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