

Cryptic and Complex Nesting in the Yellow-Spotted Monitor, *Varanus panoptes*

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ABSTRACT.—Despite the general importance of nest site choice in reproductive success in taxa with little or no parental care, little is known for reptiles other than turtles. Here we report on the nesting ecology of the Yellow-Spotted Monitor, *Varanus panoptes*, a large tropical lizard that utilizes warrens (concentrated groups of burrows) in northern Australia. We used radio-telemetry, remote photography, and the complete excavation of a warren to test the hypotheses that 1) warrens are used by multiple individual *V. panoptes*; and if so, 2) they are used for communal nesting; or alternatively 3) they are used for communal aestivation during the dry season. At least six individual *V. panoptes* utilized the warren system including four females and two males, and burrows were excavated by both sexes. Excavation of the warren revealed no aestivating lizards at a time when four radio-telemetered *V. panoptes* had begun aestivation. However, we found two nests in the warren, indicative of either communal nesting or multiple clutches of the same female. Nests were deeper than that recorded for any other reptile and were structurally complex. We discuss the implications of the depth and structure of the nesting burrow for the thermal and hydric environment of the eggs and for hatchling emergence. The warren's usage by multiple individuals raises the possibility that the severe declines in *V. panoptes* caused by invasive Cane Toads (*Bufo marinus*) may have important implications for the *V. panoptes* social structure via an Allee effect.

The choice of nest site can determine the successful transition between two life stages in oviparous animals without parental care. While nesting permanently separates a mother from her eggs in these species, mothers and offspring are subject to natural selection during that period; nest site choice can be shaped by costs–benefits to both (Mousseu and Fox, 1998). Yet understanding how nesting has evolved within and among populations and species is frustrated by a multitude of knowledge gaps in certain taxonomic groups (Doody et al., 2009a).

Knowledge gaps are particularly pervasive in secretive animals, such as reptiles, particularly with regard to mating and nesting (Shine, 1988; Perry and Dmi'el, 1994; but see a vast literature on nesting in turtles). As a comparison, there is a field guide to the eggs and nests of the ~800 bird species inhabiting Australia yet the nests are unknown for the majority of the ~500 lizard spp. on the same continent (Doody et al., 2009a). Nesting in tropical reptiles is particularly under-studied. For example, nest sites are unknown for 39 of the world's 53 species of monitor lizards (Pianka et al., 2004).

One such species is the Yellow-Spotted Monitor, *Varanus panoptes*, a tropical lizard inhabiting northern and western Australia and southern New Guinea (Cogger, 2000). Despite its size and conspicuousness, knowledge of its reproduction and associated behaviors is limited to dissections and incubations in the laboratory, leading to uncertainty in the timing of reproduction and hatching, nesting behavior, and selection of nest sites (Blamires and Nobbs, 2000; Shea and Sadlier, 2001; Christian, 2004). Although the terrestrial *V. panoptes* undoubtedly lays its eggs in the ground, nests have not been described in detail (Christian, 2004; but see Vincent and Wilson, 1999 for the mention of one nest).

In some areas there are aggregations of *V. panoptes* burrows, leading Christian (2004) to hypothesize that such 'warrens' might reflect communal nesting whereby several females lay their eggs in one warren system (based on further information from local aboriginal people). He concluded that nesting in warrens would raise new questions regarding the function of communal nesting, the interconnectedness of the burrows, and social behavior among individuals using the warrens. Warrens may also be used for communal aestivation during the dry season. *Varanus panoptes* aestivates facultatively during the dry season (Christian et al., 1995; but not in all populations, see Blamires, 1999), and locals claim that the Bengal Monitor, *Varanus bengalensis*, aestivates in burrows during the hot months (March–May) in Thailand (Stanner, 2011). *Varanus panoptes* also uses burrows for foraging, thermoregulation, overnight retreat sites (Blamires, 2001), and possibly to prevent water loss, as observed in two arid-zone monitor species (Green, 1972; Vernet et al., 1988).

We used radio-telemetry, remote photography, and the complete excavation of a warren system to test the hypotheses that 1) warrens are used by multiple individual *V. panoptes*; and if so, 2) they are used for communal nesting; or alternatively 3) they are used for communal aestivation during the dry season. We also tested the idea that warrens are made up of burrows that are interconnected underground rather than being a concentration of unconnected simple burrows. We describe daily and seasonal activity at the warren and the uniqueness of *V. panoptes* nesting burrows among lizards and other reptiles. We briefly discuss implications of our findings for the social structure of *V. panoptes* and for the invasion of the Cane Toad, a poisonous prey item that decimates *V. panoptes* populations via lethal toxic ingestion (Doody et al., 2009b; Ujvari and Madsen, 2009).

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MATERIALS AND METHODS

Study Species and Study Area.—The Yellow-Spotted Monitor is a large (up to 7 kg and 1.5 m total length) terrestrial monitor lizard inhabiting savannah woodland, riparian zones, flood-

plains, and coastal mangroves in northern and western Australia and southern New Guinea (Cogger, 2000; Christian, 2004). In most of northern Australia, *V. panoptes* occurs in wet-dry tropics where there is very little rainfall between May and October and high rainfall between November and March (Taylor and Tulloch, 1985). *Varanus panoptes* aestivates underground in burrows during the mid- to late dry season (Christian et al., 1995; but see Blamires, 1999) but its timing of reproduction is uncertain. Only five ovigerous specimens with dates of collection have been examined including two with shelled eggs in April, two with enlarged ovarian follicles in May, and one with regressed ovaries in May (Shine, 1986; Blamires, 1999; Blamires and Nobb, 2000; Shea and Sadlier, 2001). However, Vincent and Wilson (1999) cite hatching in October and November and laboratory incubation periods ranging from 210–365 days, which suggests oviposition between October and March (Shea and Sadlier, 2001). It is unknown if *V. panoptes* lays more than one clutch annually in nature; however, a captive specimen deposited four clutches within 5 mo (Nabors, 1997). Interclutch periods of 42–70 d have been recorded in captive specimens (Brown, 2012).

Our study was part of a larger study assessing the spatial ecology of *V. panoptes* prior to the invasion of the Cane Toad (*Bufo marinus*). The study was conducted from 1 April–15 July 2012 in El Questro Wilderness Park, a 400,000-ha area of tropical savannah in the east Kimberley Region of tropical northern Western Australia (16°00′35.37″S, 127°58′48.11″E). The area is situated in wet-dry tropics with a summer wet season and a winter dry season (Taylor and Tulloch, 1985). The study warren was located in an ecotone between open savannah woodland and riparian vegetation along Nimmerline Creek (15°57′35.44″S, 128°01′56.19″E). The immediate area around the warren was characterized by sandy soil and was ~0.5 m higher than the surrounding area. There were scattered trees, shrubs, and grasses near the warren as well as exposed areas of mostly loamy sand.

The Onset of Aestivation.—To determine the onset of aestivation we radio-tracked nine individual adult *V. panoptes* from early April until mid-July. Lizards were captured with nooses or with cage traps baited with fresh meat and were taken to a makeshift field laboratory where they were measured, their mass determined, and all were marked with an individual number on their backs using paper correction fluid (Liquid Paper®). Lizards were fitted with radio-transmitter harnesses made from denim material and sealed with epoxy resin. Harnesses were fitted to the pelvic region and secured using a marine-grade adhesive such that the radio-transmitter was positioned on the dorsal surface with the antenna running posteriorly along the base of the tail. Each harness was secured using crimped wire loops (180-lb nylon coated wire) immediately in front of the hind legs and around the base of the tail. Each harness contained a radio-transmitter (Sirtrack ZV1G118 VHF®) with a short antenna and spring. Radio-transmitters weighed 4.5 g and included a maximum battery life of 306 d. The total weight of the harness and transmitter was approximately 16 g. Harnesses did not noticeably interfere with subsequent behavior.

Lizards were located using radio-telemetry once every 2–14 d at various times of the day. When an individual lizard was suspected to have begun aestivation, we checked the burrow and surrounding area at different times of the day to confirm inactivity, noting the lack of tracks in the sand.

Aboveground Utilization of the Warren System.—To determine if multiple individuals utilized the warren, a game camera (Moultrie® i40-IR, 4.0 megapixel) was employed in a bush above a single burrow in the warren from 13 April to 24 May. Given its large width (24 cm wide), the burrow was judged to have been excavated by a male. The motion-activated infrared camera was set to photograph animals moving in, out, or near the burrow 24 h a day. A 1-min delay separated photographs. The camera was mounted on a metal stake approximately 2 m from the burrow and 1 m above ground. Individual monitor lizards were identified from photographs by comparing overall size and patterns of ocelli on the head, back, and tail.

Belowground Utilization of the Warren System.—To determine if the warren was used for nesting and/or aestivation, we excavated the entire warren system using shovels, picks, and trowels during 20–26 June. Care was taken to photograph, map, and measure the position, width, depth, length, and interconnectivity of the burrows. We checked each burrow for any aestivating monitor lizards. We also noted the substrate type and hardness, backfilling, and rough soil moisture in the burrows and in the nests. For the nests we measured the above characteristics of the burrow leading to the nests, the chamber diameter, height, and depth below ground level.

We carefully removed, counted, and replaced the eggs and back-filled the nests to their original depths. A single egg from each clutch was taken to confirm species and to determine the developmental stage. Photographs of the embryos facilitated determination of developmental stage. The embryos and yolk were removed from the eggshell and weighed, and the embryo was measured. The entire egg contents were preserved in 80% ethanol.

RESULTS

The Onset of Aestivation.—Of the nine radio-tracked *V. panoptes*, three individuals shed their transmitters within 3 wk and two individuals were lost within 1 wk of release (and were not relocated again). Of the four remaining (3 males, 1 female), the mean date of aestivation was 15 June (range 12–25 June). Thus, most *V. panoptes* were in aestivation (or at least inactive in burrows) by the time we excavated the warren system on 20–26 June. Aestivation sites were single burrows. One of the radio-tracked animals, a large (5.7 kg) male, was initially at the warren on 6 April, released on 7 April, and observed within 200 m of the warren once a day for the next 3 d. On 10 April the lizard shed its radio-transmitter harness 0.5 km away from the warren and was not observed again.

Aboveground Utilization of the Warren System.—The warren system had 18 burrow entrances within a 15 × 5-m sandy area in open savannah woodland (Fig. 1). Because of their large size (24–26 cm wide), two of the burrows were clearly excavated by males. In mid-April there were numerous tracks of at least three individual *V. panoptes* in the sand near the burrows, but tracks were no longer present at the time of excavation on 20 June nor were there any tracks leading out of the burrows during excavation from 20–26 June. Burrow entrance widths averaged 9.5 ± 4.82 cm SD (range = 4.0–24.0 cm).

Our camera photographed *V. panoptes* 107 times at the warren between 14 April and 24 May. Individuals entered or left the burrow 74 times compared to 33 instances of individuals in front of the burrow. Based on individual patterns and body size, and including the radio-tagged male, at least six individuals utilized the warren (one burrow or the area very near the



FIG. 1. Aboveground view of part of the *V. panoptes* warren system showing three burrow entrances in the foreground and two in the background (upper right). Photo: R. Ellis.

burrow). Of the six, two were males (based on size and robustness) and three were ‘female-sized’ but could have been young males. The smallest individual appeared to be a resident, as it was photographed 80 times across the entire study period, often moving in and out of the burrow. Daily activity patterns peaked between 0700–0800 h with no activity after 1500 h (Fig. 2). Although our study period was limited to 6 wk, a reduction in activity as the dry season progressed was evident at the warren system (Fig. 2). One female-sized animal appeared to be gravid on 22 April (Fig. 3). On the morning of 27 April a male appeared at the burrow 13 min before a smaller animal (likely a female) was present. On the afternoon of 16 April a male (Fig. 3) appeared at the burrow 31 min before a smaller individual was there.

Belowground Utilization of the Warren.—Complete excavation of the warren area required removal of sand up to 2 m deep across the 15 × 5-m area (Fig. 4). There were no monitor lizards aestivating in the burrows and no tracks led away from the burrows during the 3 d of excavation. Of the 18 burrows with entrances to the surface, five were isolated tunnels that terminated within 0.5 m in length, six were isolated tunnels that terminated before 1.0 m in length, four were interconnected with other tunnels and achieved lengths from 0.7–1.6 m deep, and three were complex nesting burrows, as exhibited by deep spiraling tunnels terminating in nest chambers (see below). There were at least eight additional tunnels without surface entrances that were usually joined to tunnels with entrances that created a complex tunnel system within the warren.

The two burrows into nest chambers consisted of gently sloping sections and bends of up to 50° followed by a broad, corkscrew-shaped tunnel spiraling straight down about three complete turns before terminating into a nest chamber (Figs. 5, 6). The nesting tunnels were tightly backfilled but not completely to the entrances. The middle of the spiral was excavated by the lizards and was backfilled with loose, moist sand which seemed to be tighter-packed closer to the nest chambers. Eggs were present in two of three nesting burrows; the third chamber was identical in including a spiral that terminated in a nest chamber but without eggs. The substrate in the lower end of the spiral and nest chambers was much more compact and hardened than that above. The nest chambers were

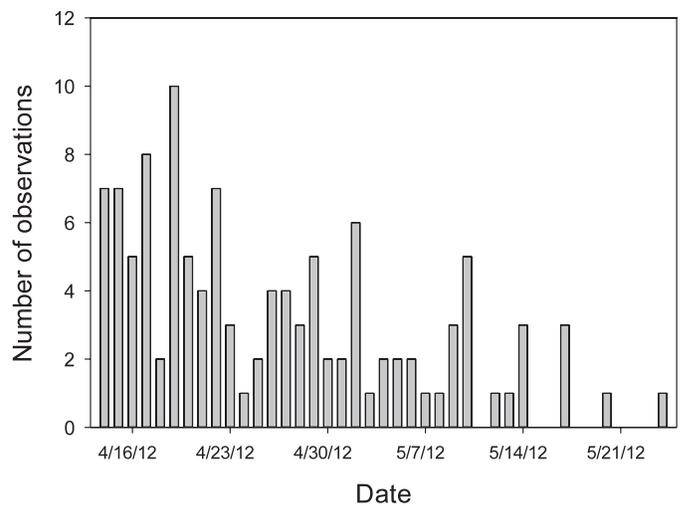
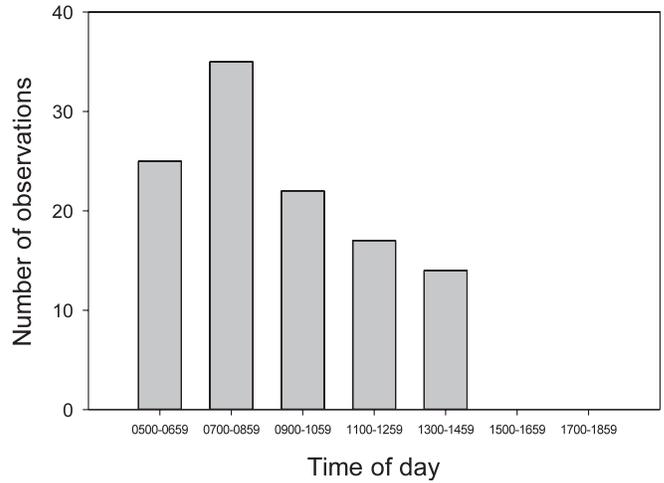


FIG. 2. Monitor lizard activity at one burrow in the *V. panoptes* warren system. (a) Variation in daily activity times; (b) seasonal variation in activity. As evidenced by its size (24 cm wide at the entrance), the burrow was excavated by a male.

partially filled with loose sand, which covered less than half of each egg, and the two nest chambers with eggs were approximately 8 m apart. Eggs were arranged in one layer at the bottom of each chamber. Clutch sizes were eight and ten eggs with respective chamber depths of 1.1 and 1.6 m below ground. If we include the empty nest chamber, the mean depth of the nests was 1.49 m below the surface.

Dissection of one egg from each nest confirmed that the eggs were *V. panoptes* and indicated fully developed embryos in one clutch, contrasting with less-developed embryos in the other clutch. The embryo from one clutch had reached developmental stage 35–36 based on the lower jaw having grown all the way to the end of the snout, the webbing between the toes had almost or completely gone, the nails were just starting to form, and the scales had not started to form anywhere on the skin (Dufaure and Hubert, 1961). The embryo from the other clutch was at developmental stage 40 based on it being fully-formed, scaled, and pigmented but not well-colored (Dufaure and Hubert, 1961). We could not definitively ascertain the difference in age between the two clutches based on developmental stage alone, but the difference is likely to have been weeks as opposed to days or months.



FIG. 3. Adult *V. panoptes* active at the warren system. (a) A smaller individual, possibly a gravid female based on her distended appearance, emerges from the burrow at around midday; (b) a larger male approaches the burrow early in the morning.

DISCUSSION

Our study describes, for the first time, a warren system that was used by multiple *V. panoptes*. Excavation of the warren revealed nests and nesting burrows that were unique for reptiles in complexity and depth. Our radio-telemetry data indicated that one possible role of warrens—the provision of suitable communal aestivation sites—could be eliminated for our warren system. Depending upon how widely such warrens are used, there are important potential implications of our findings for the nesting strategy and social behavior in this species.

Warren systems could serve to concentrate adult *V. panoptes* to facilitate mating; a pair of mating *V. panoptes* were observed at a warren in Western Australia (G. Thompson, pers. comm.). As such, warrens could provide suitable communal aestivation sites during the mid- to late dry season, prior to mating and nesting. However, radio-telemetry data during the time of aestivation, coupled with the lack of monitor lizards within the warren upon excavation, indicated that the primary function of this warren was not to facilitate group aestivation. Moreover, the decrease in activity at the warren over a 2-mo period prior to excavation (Fig. 2) supports the idea that individuals utilizing the warren dispersed to other areas to aestivate.



FIG. 4. Excavating the *V. panoptes* warren system. (a) Above view showing two areas, each of which contained a nest. (b) Side view of the top area from (a), showing the depth of the burrows. Photo: R. Ellis.

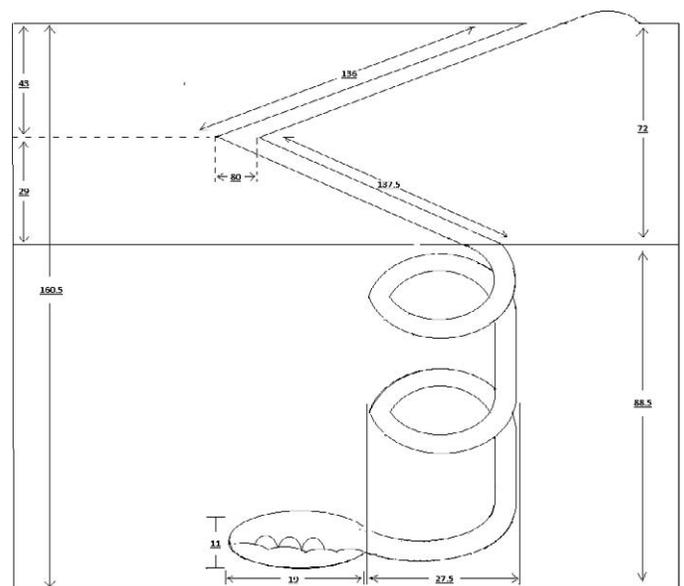


FIG. 5. Diagram of a *V. panoptes* nesting burrow (side view). The burrow was mostly plugged with soil but the egg chamber was not. Plugged soil was dry and compacted in the long burrow arms but soft and moist in the spiral section. Measurements are in centimeters.



FIG. 6. Photographs from above of an excavated *V. panoptes* nesting burrow. (a) The 'corkscrew' portion of the burrow, just above the nest chamber. (b) The corkscrew excavated out, showing the nest chamber and eggs. Photo: R. Ellis.

Alternatively, warren systems could facilitate reproduction in *V. panoptes* primarily by providing communal nesting sites. Our data support this, with three nests located within the warren system (two chambers with eggs and one without). Assuming the nests were not subsequent efforts of the same female, our warren served as a communal nesting site. Communal nesting is widespread in lizards, but the paucity of nesting data for lizards likely masks its true prevalence (Doody et al., 2009a). Of the 14 of 53 species of monitor lizards for which nests are known, the majority are based on a few nests. However, a communal nest of 50–60 eggs of *Varanus salvator* (Common Name) was discovered in a megapode nest (Gaulke, 1989). Future efforts may lead to the discovery of communal nesting in more species of monitor lizards. Alternatively, the two nests may have been subsequent clutches of the same female. Multiple clutching within a year in nature is not known in *V. panoptes*, but a captive specimen deposited four clutches within 5 mo (Nabors, 1997). Whether the clutches were fathered by a single or multiple males is unknown. The excavation of more warrens, along with genotyping to determine parentage, is needed to confirm communal nesting in this species.

The *V. panoptes* nesting burrows within the warren system were similar to those of other reptiles but unique or unusual in other ways. The burrows were mostly back-filled with soil, similar to some species of monitors (e.g., *Varanus exanthematicus* [Common Name], Bennett and Thakoordyal, 2003; *Varanus griseus* [Common Name], Tsellarius and Menshikov, 1995). However, the *V. panoptes* nests were unique among reptiles in

complexity and depth. Nests were structurally complex: an open burrow at the surface, followed by a bend, and then a back-filled, twisting tunnel that culminated in a wide, downward-spiraling chamber terminating in a horizontal nest chamber. The back-filled soil was tightly compacted in the tunnels but became moist and loose in the spiral closer to the nest chamber. The backfilling would ensure that the eggs did not desiccate and could also provide protection against olfactory-driven predators such as other monitor lizards or Dingos (*Canis lupus*). The function of the spiral is unknown but could be related to hatchling emergence. Reptile hatchlings generally emerge vertically through the ceiling of the nest chamber (e.g., Christian, 1986) rather than through the burrow entrance; nesting without a spiral would force emerging hatchlings to break through ~1.5 m of soil. Moreover, digging straight down without spiraling would cause soil to fall back into the tunnel as it was being excavated. Although some monitors and other lizards excavate complex burrows (e.g., branching tunnels, Mora 1989; Tsellarius and Menshikov, 1995), the spiral appears to be unique among reptiles. The *V. panoptes* nest chamber was not back-filled with soil but rather was open, similar to that described for *V. griseus* (Tsellarius and Menshikov, 1995).

In addition, the *V. panoptes* nests were particularly deep compared to other reptiles. Table 1 gives nest depths for numerous reptiles; this list is nonexhaustive but includes the larger reptiles because they would be expected to excavate deeper nests than do smaller species. Most reptile nests are deposited in shallow burrows <30 cm below the surface, presumably to exploit warmer temperatures associated with a thermal gradient in the ground. Our *V. panoptes* nests were much deeper than even the deepest-nesting reptile, the Leatherback Sea Turtle, *Dermochelys coriacea* (Table 1). Although our sample size is low, the values are well beyond even the maximum depths in other species (Table 1).

Why nest so deep? Apparently, temperatures at these depths are sufficient for incubation at this tropical site. However, it is puzzling why *V. panoptes* would nest considerably deeper than other large monitor lizards, especially given the similarity of incubation periods and optimal developmental temperatures (Thompson and Pianka, 2001; Horn and Visser, 1989, 1997). One possibility is that the more-stable temperatures afforded by deeper nests are necessary for successful embryonic development in *V. panoptes*. While the difference in mean temperatures between deep and shallow nests is relatively small, daily fluctuations in temperature decrease markedly with depth and virtually disappear at depths >50 cm. For example, monitor nests incubating 25–30 cm deep in termite mounds experience <3°C daily variation in temperature despite air temperature fluctuations of 10–15°C (Auffenberg, 1994; Rismiller et al., 2007). Alternatively, *V. panoptes* may nest deeper because nesting closer to the surface would result in prohibitively high temperatures for developing embryos, although other tropical reptiles nest at shallow depths in open areas. Deep nesting in *V. panoptes* may be related to the hydric environment. Reptile eggs must incubate under very high relative humidity, generally >95% (Fitch and Fitch, 1967). While this is readily achieved by nesting at greater depths, shallower depths at our site may experience humidity too low for successful development, especially during the long dry season. The idea that temperature and humidity influences burrow depth is supported by *V. griseus* using very deep burrows (up to 3 m deep) in the deserts of Egypt and Algeria, although the burrows were not known to contain nests

TABLE 1. Nest depths (to the nearest centimeter) of selected species of reptiles, especially large species, that nest underground or in materials on the surface. Depths are from the ground surface or top of materials to the bottom of the nest chamber. When available, values are means followed by number of nests in parentheses. *Denotes depth to top of top egg.

Species	Nest depth (N)	Source
Lizards		
<i>Varanus panoptes</i>	149 (3)	Present study
<i>Varanus acanthurus</i>	40 (1)	Husband, 1980
<i>Varanus bengalensis</i>	23.4 (3), 20–27 (5), 25 (2)	Auffenberg, 1994
<i>Varanus exanthematicus</i>	30**(2+), 20–25 (4)	Bennett and Thakoordyal, 2003; Bennett, 2004
<i>Varanus griseus</i>	94 (5), 70–90, 70–114	Yadgarov, 1968; Bennett, 1995; Tsellarius and Menshikov, 1995;
<i>Varanus komodoensis</i>	37, 30–40 (2)	Auffenberg, 1981
<i>Varanus rosenbergi</i>	50–60, 35–50	King and Green, 1999; Rismiller et al., 2010
<i>Varanus salvator</i>	~50 (4–5)	Gaulke, 1989
<i>Varanus spenceri</i>	70–80, ~75 (5)	Lemm and Bedford, 2004
<i>Conolophus subcristatus</i>	50–75	Christian and Tracy, 1982
<i>Ctenosaura similis</i>	31 (3), 47 (3), 51 (3), 56 (18), 56 (4)	Mora, 1989
<i>Cyclura cythlura</i>	28 (75)	Iverson, 2004
<i>Cyclura carinata</i>	<25	Iverson, 1979
<i>Cyclura cornuta</i>	54	Wiewandt, 1977
<i>Cyclura nubila</i>	43 (16), 10–40	Christian, 1986; Gerber, 2000a
<i>Cyclura pinguis</i>	67	Gerber, 2000b
<i>Cyclura rileyi</i>	22 (13)	Thornton, 2000
<i>Iguana iguana</i>	43 (2), 63 (2), 55 (6)	Mora, 1989
Turtles		
<i>Aldabrachelys gigantea</i>	30–40 (14)	Swingland and Coe, 1978
<i>Caretta caretta</i>	58 (505), 54 (82), 42 (25) 34 (10)	Kaufmann, 1971; Kraemer, 1979; Limpus, 1985; Matsuzawa et al., 1995;
<i>Chelonia depressa</i>	46–61	Bustard, 1972
<i>Chelonia mydas</i>	79	Bustard, 1972
<i>Chelonoidis nitra</i>	30	Swingland, 1989
<i>Dermochelys coriacea</i>	95 (4)	Limpus and McLachlan, 1979
<i>Eretmochelys imbricata</i>	45–50	Pritchard and Trebbeau, 1984
<i>Podocnemis expansa</i>	60 (189)	Ferreira and Castro, 2010
<i>Podocnemis unifilis</i>	16 (68)	Ferreira and Castro, 2010
<i>Pseudemys concinna</i>	16 (10)	Jackson and Walker, 1997
Crocodylians		
<i>Alligator mississippiensis</i>	20.9 (14)	Goodwin and Marion, 1978
<i>Caiman yacare</i>	18.3 (11)	Cintra, 1988
<i>Crocodylus porosus</i>	19* (21)	Webb et al., 1977
<i>Crocodylus niloticus</i>	20–50 (31), 34 (25)	Modha, 1967; Hutton, 1987
<i>Crocodylus johnstoni</i>	19–45, 20*	Smith, 1987; Webb and Manolis, 1989
<i>Crocodylus acutus</i>	38 (12), 50 (5)	Lutz and Dunbar-Cooper, 1984; Thorbjarnarson, 1989
<i>Paleosuchus trigonatus</i>	20 (2)	Magnusson et al., 1985
Snakes		
<i>Heterodon platyrhinos</i>	7–20 (21)	Peet-Pare and Blouin-Demers, In press
<i>Masticophis taeniatus</i>	39 (2)	Parker and Brown, 1980
<i>Liasis fuscus</i>	100 (1)	T. Madsen, pers. comm.
<i>Pituophis melanoleucas</i>	21 (74)	Burger and Zappalorti, 1991
<i>Tropidonophis maurii</i>	6 (1)	Brown and Shine, 2002
Tuatara		
<i>Sphenodon punctata</i>	10* (25)	Nelson et al., 2004

(Schmidt and Marx, 1957; Mammeir, pers. comm. in Bennett, 1995; Ibrahim, 2002). It is also plausible that deeper nests reduce predation risk because it is energetically more expensive (and more difficult) for a predator to reach the eggs. Egg predators of *V. panoptes* are unknown, but Water Pythons (*Liasis fuscus*) nested in *V. panoptes* burrows (Madsen and Shine, 1999) and egg cannibalism occurs in other monitor species (Rismiller et al., 2010).

Although they are used for nesting, *V. panoptes* warrens may reflect more than just a communal nesting ground as at least six individuals utilized the warren, including two males. The warren included two burrows determined (by their large size, ~25 cm wide) to have been excavated (or enlarged) by males and 16 burrows (~10 cm wide) excavated by either females or female-sized males. Similarly, four males and a female were observed at a warren in western Australia (G. Thompson, pers. comm.). Interspecific interactions led researchers to hypothesize

the existence of a complex, mammal-like social structure in the related *V. griseus* (Tsellarius and Tsellarius, 1997). Tolerance of conspecific males at nesting sites (but not warrens) has been recorded in another monitor species; female *V. griseus* defended their nesting burrows from some conspecifics for up to 4 wk but at other times were tolerant or social towards males (Tsellarius and Menshikov, 1995). Although their function is unknown, a few other species of monitor lizards excavate and utilize warrens (*V. bengalensis* and *Varanus komodoensis* [Common Name], Auffenberg, 1981, 1994). However, nests have not been located in these warrens, and there is debate on whether burrows within a warren are excavated by a single vs. multiple individual lizards (Auffenberg, 1983; Tsellarius and Menshikov, 1995). In *V. komodoensis*, warrens consisted of 5–18 burrows in soil that was softer than surrounding areas (Auffenberg, 1981). Warrens may be used for nesting by *V. komodoensis*, but the excavation of ‘many’ warren burrows revealed no eggshells or

eggs (Auffenberg, 1981). We opportunistically located only two other warren systems within 10 km of the warren in our study, but systematic surveys for warrens may reveal that they are more common than is currently appreciated.

The invasive Cane Toad causes severe, population-level declines in *V. panoptes* via lethal toxic ingestion, reducing the density of these lizards by ~90%, postinvasion (Doody et al., 2009b; Ujvari and Madsen, 2009). Although their ultimate function is unknown, it is clear that *V. panoptes* warren systems in our toad-free study system reflect social behavior. A toad-induced reduction in the density of *V. panoptes* could cause a collapse of this social system by virtue of an Allee effect (Kramer et al., 2009). An Allee effect is a positive relationship between individual fitness and population density. The mechanism of such an effect could include reduced mating encounters. For example, although no data are available for monitor lizards, most other lizards exhibit high levels of multiple paternity (Uller and Olsson, 2008). Low densities of *V. panoptes* could reduce the number of fathers siring a brood. Another possible mechanism could result in the collapse of the social system surrounding warrens because the density of lizards is too low for multiple burrow construction. Although the cause could not be determined, a *V. panoptes* warren system along the Daly River, Northern Territory, became abandoned following the arrival of Cane Toads into the area (S. Doody, pers. obs.). Future research could reveal the social system of *V. panoptes* (including the mating system) before and after toad arrival to determine if toad impacts include an Allee effect.

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