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ABSTRACT.—For 16 years, we have observed and recorded seasonal life cycles of individual free-ranging Rosenberg's Goannas, *Varanus rosenbergi*. These monitor lizards are normally solitary except during their annual summer breeding cycle. Activities and behaviors were documented from precourtship through to pairing, courtship, copulation, selecting and excavating an incubation chamber, egg laying, and finally guarding the egg mound before returning to a solitary life style. Whereas the sequence of breeding activities tends to follow a set pattern, the timing and duration of physical and physiological events vary from season to season. Courtship through to defending the egg mound occupies up to 4 months of the year, commencing just before the summer solstice and ending shortly after the autumn equinox.

Rosenberg's Goanna (*Varanus rosenbergi*) is the best studied Australian monitor (King and Green, 1999). It was once widespread across the southern parts of Australia but has now disappeared from many parts of its natural mainland range. Kangaroo Island is its last stronghold. Rosenberg's Goanna play a significant role in the island's ecology. They are the largest native terrestrial predator (Hutchinson and Tyler, 2002) and are deemed to be responsible for the unsuccessful colonization of introduced rabbits that devastatingly impacted native habitats across mainland Australia. *Varanus rosenbergi* leads a solitary life style except during their annual courtship/breeding season, and little is known about the dynamics of their dwindling populations. Even on Kangaroo Island numbers have declined in recent years due to pressures on habitat from altered land use, increased road traffic, and increased predation by feral cats and pigs (Rismiller et al., 2007).

The objective of this study is to elucidate breeding sequences and timing of reproductive events during courtship, copulation, and egg deposition for free-ranging Rosenberg's Goannas living across a wide variety of habitats and rainfall on Kangaroo Island. Long-term observations on known wild individuals provide an extensive database for comparison with other studies on field and captive varanids. This work is part of ongoing research on the population dynamics and ecology of *V. rosenbergi*, a species that has become vulnerable in its natural range.

MATERIAL AND METHODS

Study Site and Research Animals.—The study site, Kangaroo Island off the coast of South Australia, is Australia's third largest island. It is 155 km long and up to 55 km wide, covering 4,500 km². The island is characterized by 40 distinct vegetation types (Willoughby et al., 2001) distributed across 10 broad-based soil landscapes (Northcote, 2002). Island rainfall regions vary from semiarid to temperate rainforest. Monthly and annual rainfall across the island varies greatly.

Varanus rosenbergi occur across all soil types, vegetation habitats, and rainfall areas. This study presents data from two diverse field sites. The primary site, Pelican Lagoon peninsula (35°48'S, 137°47'E) is on the east end of Kangaroo Island. It is characterized by aeolian limestone, unconsolidated sand dunes with tidal salt water wetlands, fresh water wetlands, mallee woodlands, and acacia shrubland. Annual rainfall during our study (1991–2007) ranged from 383 to 787 mm, with a mean of 521.1 ± 23.4 mm (Pelican Lagoon Bureau of Meteorology station 022836).

The secondary site, Rocky River (35°53'S, 136°51'E), is located on the west end of the island in Flinders Chase National Park. Geology of the study site is limestone overlaid in parts by lateritic ironstone soils. The natural vegetation of the area consists of dry sclerophyll species, with *Eucalyptus diversifolia* as the dominant species. Annual rainfall at Rocky River between 1991 and 2007 was from 564 to 1,265 mm, with a mean of 824.4 ± 20.2 mm (Rocky River Bureau of Meteorology station 022820).

All *V. rosenbergi* in this study are part of wild, free-ranging populations. Starting in 1991, all goannas opportunistically encountered at both

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study sites were captured by hand and microchipped (Animal Electronic ID Systems, Kiama, New South Wales, Australia). Animals were weighed and the following measurements were taken: base of head-snout, parietal-snout, width across eyes, snout-vent, and vent-tail. Initially, the sex of adult goannas was determined using a combination of presence of hemipenes and width of head and confirmed when breeding or egg laying was observed. At the Pelican Lagoon study site up to 12 adults were fitted either with a small external tracking transmitters (TX1 micro, Biotelemetry Tracking, Adelaide or TXLT1, Titley Electronics, Ballina, NSW, Australia) attached to the tail or had an internal transmitter surgically inserted (IM1, Biotelemetry Tracking) in the abdominal cavity (Rismiller and McKelvey, 2000). All animals were marked using white correction fluid with a letter or number on the rump for visual identification without recapture. These markings were lost after the animals shed their skin.

Observations.—Goannas fitted with tracking transmitters were located daily for 10 to 15 consecutive days each month during 3 years of this study. In other years, routine monitoring of selected individuals was conducted, with multiple daily sightings recorded throughout the year. Each time an animal was located date, time, location, habitat/vegetation, animal behavior, and climatic conditions were recorded on tracking reports. All the information was entered into a database and on maps. Once courtship burrows were established, animals were observed from a distance using spotting scopes. In 2003, after copulation commenced we set up dawn-to-dusk remote videomonitoring on one pair. All mean values expressed in the text are shown \pm SE. All times are expressed in solar time as duration of daylight savings time can vary from year to year.

For the purpose of this study, breeding phenology was divided into the following categories: precourtship, courtship, copulation, post copulation, egg-laying, and post egg-laying periods. Monitoring activities of known individuals over many years provided opportunities to examine related questions such as frequency of egg laying in females, pair bonding/fidelity, selection of incubation termitaria, and fate of egg mounds.

RESULTS

In total, 205 goannas (71 males, 77 females, and 57 subadult or gender undeterminable) were found and tagged with microchips in the Pelican Lagoon study area between 1991 and 2007 (Table 1). In addition to new animals marked each year, there were numerous recap-

TABLE 1. Number of new male, female, and subadult (SA) or goannas of unknown gender (UK) marked each year between 1991 and 2007 at the Pelican Lagoon site. Sex ratio for each year and for the total number of known-gender animals is indicated.

Year	Male	Female	SA/UK	Male:female ratio
1991	5	6	1	1:1.2
1992	2	5	3	0.4:1
1993	5	2	4	1:4
1994	2	1	3	2:1
1995	5	0	0	5:0
1996	1	1	1	1:1
1997	2	0	1	2:0
1998	1	0	0	1:0
1999	2	2	1	1:1
2000	2	0	3	2:0
2001	4	5	4	0.8:1
2002	9	5	5	1.8:1
2003	5	4	3	1:8
2004	6	14	6	0.4:1
2005	5	9	5	1:1.8
2006	10	17	9	0.6:1
2007	5	6	8	1:1.2
Total	71	77	57	0.92:1

tures. During this study, 85 detailed instances of courtship, breeding, and egg-laying sequences were observed and recorded.

Precourtship to Copulation.—Male and female *V. rosenbergi* are normally solitary during the winter and precourtship seasons. However, in six instances a male and female were found together in a burrow during the winter. No interactions, either sexual or aggressive, were observed, and all "pairs" had returned to separate burrows before commencement of precourtship activity. Both males and females became active and began foraging from mid-August onward. Males started in the vicinity of their winter burrow and then expanded their active range to 257.5 ± 21 ha (range, 178–320 ha). At the peak of foraging activity, males established a travelling sequence, moving and using different areas and burrows on a 3-day rotation. This sequential touring (PDR and MWM, unpubl. data) was maintained with little variation until the male took up residence near a female's burrow. By late November, reproductively active females moved away from their winter refuge sites and foraged across a 96 ± 3.7 -ha (range, 85–110 ha) area. Nonbreeding adult females moved through similar sized areas using six to 30 (mean = 10.9 ± 1.3) different refuge/burrows sites during the summer.

In December, potential breeding individuals began making distinctive marks on the ground consisting of wide, deep sinuous furrows. These were produced by the goanna pressing the thorax, abdomen, and sometimes the cloaca against the ground and moving sideways while

at the same time moving forward. We designated these distinctive broad, serpentine tracks "squidge marks." Squidging was particularly noticeable around the bases of termitaria when an apron of loose soil was present. Squidge tracks radiated up to 20 m from the termite mounds, and isolated examples of squidging were recorded on walking trails.

Encounters between males during the pre-courtship period were characterized by one of two actions, posturing or physical contact. Posturing males inflated their bodies, including the gular pouch, arched their backs, and extended their legs to stand in an aggressive attitude. After some minutes of circling and tongue flicking, one male usually walked away while maintaining an aggressive body posture. In fewer instances, one male was chased off by the other.

In 16 years, we observed only eight cases of physical fighting between males. In each case, animals faced each other, adopted aggressive body postures, and lunged or wrestled until one opponent was on its back. The head of the toppled opponent was pushed from side to side until he finally managed to break free. Two fights lasted over 40 min. All fights ended with the dominant animal chasing the other. One precourtship encounter involved a marked resident female and an unknown individual of similar size but unknown sex. The female inflicted bites across the head of the opponent before it broke free and was chased off by the female. At the time of encounter, the female was within 20 m of a nuptial burrow she had used in a previous year.

From mid-December until early January, both males and females travelled extensively, leaving squidge marks around termite mounds and along trails. Animals approached a burrow of the opposite sex, placed their head inside, and then retreated. The animal in the burrow responded by coming out, tongue flicking the air and ground, and following the other. The earliest recorded date for this behavior was 2 December, but no courtship behavior was observed at this time, and animals did not stay together for longer than 2 to 3 days.

Early in January, reproductively active females remained in well-established burrows. At this time, males sought out females and courtship commenced. It was common for animals to first occupy separate burrows only a few meters apart. After 2 to 3 days, the male approached and circled the female, flicking his tongue until the female initiated the first physical contact by touching the male with her head. Within days, the male moved in with the female and her burrow was enlarged. The pair basked and spent several days in close proximity, often lying alongside each other with the

male's fore and hind limbs resting across the female's back. Within 2 to 7 days of pairing-up, animals began to copulate.

The earliest and latest dates of copulation were 27 December and 2 February, respectively. During the 16 years, we observed more than 2,000 copulations involving 60 pairs at the Pelican Lagoon site. From these, we positively documented the first and last day of copulation for 10 females. Copulation periods lasted between 7 and 17 days, with a mean of 12.4 ± 0.9 days.

During the copulation period, a male typically cohabited with a female in the nuptial burrow. The male emerged alone in the morning, basking for a period before re-entering the burrow, kicking soil from the opening as he entered. Within minutes, he backed out of the burrow followed closely by the female who emerged head first. The male rapidly licked the head and groin regions of the female while passing his head back and forth along her back and flanks. The female advanced slowly forward with her head flat to the ground while the male rapidly "pecked" the female's head and back with his snout. The male also stroked the female's head and forelimbs with his forelimbs. The head of both male and female faced the same direction when he placed a hind limb across the female's pelvis. If receptive she would raise and turn her cloaca towards his, facilitating the male's insertion of one hemipenis. The male then gave several pelvic thrusts before lying still against the female. During the next 10 to 15 min, the male gave additional pelvic thrusts until the pair separated. The female then retreated to the burrow while the male remained on the surface basking. This copulatory sequence was usually repeated several times throughout each day, with the male alternating the hemipenis in each subsequent copulation.

During the copulation period, males exhibited a range of tolerances to other males. In most cases the primary male showed territorial behavior toward the female and nuptial burrow area, chasing any intruders away from the area, though rarely engaging in physical contact. When a male left a female unattended, she frequently copulated with other males. On several occasions, two males shared a female with no aggression between any of the individuals. In one situation, two males that were sharing a female made no attempt to repel a third male that arrived and proceeded to mate with the female. Females did not display any aggressive behavior toward courting males, but in all instances she had to be receptive for successful intromission to take place. Pair bonding/pair fidelity throughout the duration of a breeding season varied from year to year. In

TABLE 2. Dates and numbers of copulations filmed on consecutive days for female Ova. am = 0630–1200 h; pm = 1200–2130 h.

	am	pm	Total
20 January		4	4
21 January	3	1	4
22 January	5	3	8
23 January	5	3	8
24 January	6	4	10
25 January	8	5	13
26 January	0	0	
27 January	14	3	17
28 January	4	2	6
29 January	0	5	5
30 January	3	3	6
31 January	9	0	9
Total			90

any given year, as few as 40% and up to 80% of pairs remained exclusively monogamous throughout the breeding period.

In 2003, we videotaped copulation behavior of one female (Ova F520D64), starting 5 days after the first copulation was observed. The camera ran daily from 0630 to 2130 h. The earliest copulation was 3.5 h after sunrise (at 0900 h) and the latest 3 h before sunset (1630 h). Table 2 summarizes the number of copulations over the 11.5-day recording period. On 26 January when no copulations occurred, 4.4 mm of rain fell and daytime temperatures did not exceed 17°C. Couplings were on average of 14 ± 4.1 min, except on 27 January when there were 14 copulations in the morning. The shortest intromission of 1 min was recorded on that morning, but other couplings were between 5 and 18 min. During the filming period, Ova mated with three different males. Her primary mate was with her before filming and was the only male present until day 8 of copulation. When the primary male left and went to another female, a second male approached and Ova mated with him. A third male appeared the same day, and the first interloper stayed within sight as they copulated. When the primary male returned on the afternoon of 29 January, there was aggressive posturing, but no contact between males. Both interlopers were gone the next day.

At the end of the copulation period, females remained relatively inactive, spending most of their time in the burrow or basking with the male. Males spent time foraging but returned regularly to the female. Females were never seen actively foraging or hunting before egg laying, but on one occasion a male dragged a fresh wallaby carcass to within 5 m of the nuptial burrow. Over a 5-day period, both male and female fed from the carcass. Two to 3 weeks

after copulation ended, males began to wander and spend less time with the female. Females generally remained at their nuptial burrow, but in nine of the observed 85 mating sequences the female moved to another burrow for up to 5 days and then returned to the nuptial burrow before egg laying. In three instances, the female moved from the nuptial burrow and did not return.

Approximately a week before egg laying, females covered a radius of 228.6 ± 16.4 m (range, 180–300 m) around their burrow, circling and scratching the surface of termitaria, seldom penetrating more than 5 to 10 mm. On subsequent days, the female returned to those mounds and tongue flicked around the surface. Sometimes, she left bands of squidge marks around the base of the mound and continued to scratch the surface. These behaviors continued up to the time of egg laying. On two occasions, females were observed leaving the burrows after sunset and following their mound circuit in the dark. Both animals were fitted with radiotransmitters that allowed them to be tracked from a distance great enough not to startle or interrupt their activities. Using night vision equipment relying on ambient starlight, we could not observe tongue flicking to determine whether the female was using scent to follow the circuit, but scratching and climbing over mounds was observed. After 2 to 2.5 h, both individuals returned to their burrows. Neither female had males sharing the burrow at the time of their night wanderings.

Termite Mounds and Egg Laying.—The duration between the last copulation and egg laying was 19 to 37 days (mean = 27.0 ± 2.0 ; $N=10$). The earliest date that a female oviposited was 29 January and the latest was 10 March. During our study, *V. rosenbergi* only laid their eggs in the mounds of *Nasutitermes exitiosus*. Time spent excavating the termite mound egg chamber was generally 2 days, but in one instance digging and oviposition was completed the same day. Excavation of the egg chamber usually began midmorning with the female clawing a hole anywhere from ground level to half way up the termite mound. Females alternated between digging and resting until approximately 1700 h when they retired to their burrows. By this time, the hole was slightly larger than the female's head, horizontally elliptical, and 10 to 15 cm deep. The next day, the female continued digging. The tunnel sloped downward, passing through the outer soil layer into the thick inner wall composed of tough cellulose carton, through to the central nursery consisting of fragile wafer-like carton. After excavating to a depth of 40 to 50 cm, the female rested outside the termite mound for 1 to 2 h before com-

mencing egg laying. Males were sighted close to a digging female 50% of the time, but we only observed a male assisting with digging on the mound on three occasions.

In three instances, females had nearly completed excavating an incubation chamber and were within hours of normal egg laying when an abrupt shift in weather patterns with unexpected thunderstorms (up to 30 mm of rain in 2 days) and a significant drop in air temperature (from 30°C to 17°C) occurred. Egg laying was not attempted during these periods. Females retreated to burrows and remained there until environmental conditions stabilized. Seven days later, one female selected a new termitarium for egg deposition and another returned to her previously excavated mound after 10 days.

When a female was ready to lay her eggs, she entered the excavated tunnel, turned her body so the head and the tip of the tail protruded, and adopted a trance-like attitude. In all but one instance, egg laying commenced between 1800 and 2100 h and was completed 2 to 4 h later. In one case, a female was observed laying eggs at 1100 h. After ovipositing all females left the mound and retired in a nearby burrow. Males were never with the female during egg laying.

Clutch size was determined directly after egg laying by counting the eggs inside 25 mounds without disturbing them. In 22 cases, 10 to 14 eggs were sighted (mean = 11.9 ± 0.2), twice we found only six and seven eggs and once 16 eggs were sighted. The latter was not included in the mean as the clutch of 16 was from an unknown female outside the normal research area and the small clutches were from older females, one of which died the following winter. No young emerged from either mound, indicating that the eggs were probably not fertile.

In active termite mounds the egg chamber and part of the excavation tunnel were plugged by the termites within 3 to 5 h after the female completed egg laying. Females returned to mounds the next morning and if the hole was not fully plugged, she scraped material from the mound's surface to backfill the entrance. In five instances, the male joined the female with back filling and closing the mound.

Females remained in the immediate vicinity of the egg mound to guard against nest marauding *V. rosenbergi* for up to 3 weeks. The primary male remained with the female for intermittent periods. Three times we observed secondary and tertiary partners assisting with guarding. A primary male remained with the female for the duration of nest guarding in only eight of 85 cases. If the egg mound was approached by an unknown male *V. rosenbergi*, the female attacked the intruder. When the

TABLE 3. Total number of egg mounds and number destroyed by marauders between 1998 and 2007.

Year	Total	Destroyed	%
1998	5	1	20
1999	15	1	6.7
2000	11	3	27
2001	17	0	0
2002	5	2	40
2003	6	0	0
2004	17	0	0
2005	17	1	6
2006	14	4	28.5
2007	26	3	12

partner male was present, he also attacked. The most aggressive fighting observed was between a defending female and a marauder, with females fighting males more than twice their body mass. Both attacker and defender sustained injuries, including dislocated or broken limbs; broken ribs; spinal injuries; and severe bites to head, throat, and abdomen. In no observed case were the attacks fatal.

Marauders were usually repelled, however when defenders were successfully displaced, the marauder excavated the eggs and either ate or destroyed them. We recorded evidence of marauding by finding open mounds and fresh eggshells outside the mounds. Between 1998 and 2007, 41 instances of mound attacking/defending were recorded. From 133 egg mounds known during this period, 15 were marauded and totally destroyed, i.e., no subsequent hatching occurred (Table 3). Six to 8 weeks after egg laying, the mound surface showed little external irregularities to suggest the presence of eggs or marauding.

Whereas sexually mature males usually bred every year, breeding cycles of females varied. Table 4 shows the breeding frequencies of 10 individual females, with a minimum of three recorded breeding seasons. Our longest known female, Ova (microchip ID F520D64, found in 1991), reproduced nine times between 1993 and 2007, with breeding intervals between 0 and 2 years. All 10 females bred in consecutive years at least once during the observation period, but intervals of 1 to 2 years between breeding events were most common.

DISCUSSION

The phenology of the *V. rosenbergi* breeding cycle (Fig. 1) begins with courtship in early to mid-December. Copulation was never observed before the summer solstice (22 December) or after mid-February. From 85 observed breeding sequences, egg laying occurred only once before

TABLE 4. Breeding frequency of known females with more than three breeding cycles. X indicates years that females mated and laid eggs. Status of females also is shown.

Name ID no:	Anna F51601E	Wungala F52120D	Leza D185A3F	Ova F520D64	Sheila B25592F	Slinky 8194792	April 8211013	May 8179357	Online 6114423	Nancy 3041540
Year										
1991	X									
1992										
1993	X	X		X						
1994				X						
1995	X		X							
1996	X	X								
1997		X	X	X						
1998	Cat kill		X							
1999		Cat kill		X	X					
2000			X			X				
2001				X	X	X	X	X	X	
2002					X				X	
2003				X		X	X	X		
2004				X	X	X		X	X	X
2005				X	Cat kill		X			X
2006							Road kill			
2007			Still alive	X		X		X	X	X

February (29 January), with most egg deposition taking place between 15 February and 10 March. Post breeding-related activities, i.e., defending the egg mound, continued up through mid-April, but in most years animals had returned to a solitary life style by the end of March.

Rismiller and McKelvey (2000) found that photoperiod was more significant than environmental temperatures for regulating Rosenberg’s Goannas body temperature. As daylight hours increased, but not necessarily environmental temperatures, so, too, did the spring daily activity levels. Our current findings suggest that the breeding phenology of female Rosenberg’s is related to the long but decreasing photoperiodic cues around the summer solstice. The significance of day length, i.e., photoperiod, on reproduction in some species of lizards has been known for a long time (Tinkle and Irwin, 1965; Underwood and Hall, 1981), but this aspect has not been examined in Australian monitors.

Precourtship through Copulation.—*Varanus rosenbergi* and *V. varius* become active in the field at similar times of the year. Rismiller and McKelvey (2000) found Rosenberg’s Goannas were least active in June and July but resumed daily activity from mid- to late August. *V. varius*, studied at the same latitude (Carter, 1992, 1999), were first recorded active on 29 August, with the last autumn sighting on 25 April. *Varanus albigularis* males became active in late July to early August, the end of the cool/dry season, approximately 4 weeks earlier than the Australian species (Philipps and Millar, 1998). At this time, males and females of all three varanid species are solitary.

Early courtship commences with all species foraging and moving. Both *V. varius* and *V. albigularis* males are described as “touring” large areas looking for females, whereas females remain in a relatively small area (Stebbins and Barwick, 1968; Philipps and Millar, 1998). All

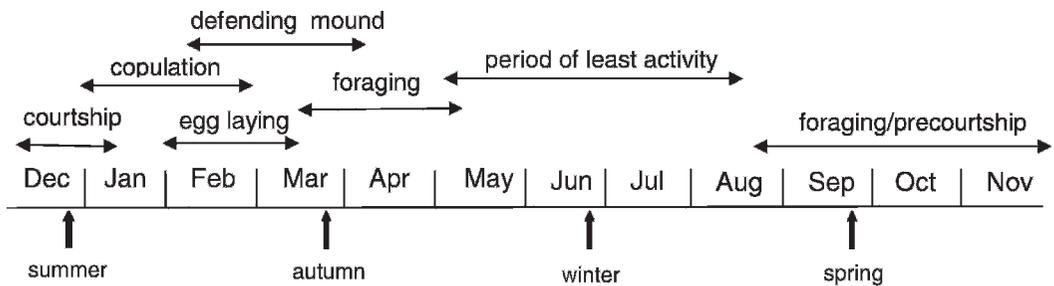


FIG. 1. Diagram showing yearly time line of activity and duration of breeding sequences for Rosenberg’s goanna on Kangaroo Island.

species display behavior that indicates scent is important in courtship; however, there have been no direct investigations on pheromonal communication in varanids. Carter (1990) and Philipps and Millar (1998) report that only the males of *V. varius* and *V. albigularis* display scent-marking behaviors, such as vent dragging (pressing the cloaca on the ground) or rubbing the head, neck, and throat on trees, rocks, or soil. In *V. rosenbergi*, both sexes engage in squidge marking as well as neck and head rubbing on the ground and rocks.

Ritual combat between males (review by Horn, 1985; King and Green, 1999), usually associated with competition for mates, have been described for several non-Australian species, such as *V. komodoensis*, *V. bengalensis*, *V. olivaceus* (Auffenberg, 1981, 1983, 1988), *V. niloticus* (Cowles, 1930), and *V. dumerili* (Davis et al., 1986), and for a few Australian species, such as *V. gilleni* (Carpenter et al., 1976) and *V. varius* (Twigg, 1988). In some accounts, there was wrestling and chasing, but neither participant sustained serious injuries, whereas in others combatants inflicted severe bites to each other. Carter (1992) noted that all large male *V. varius* had extensive scars on the back and flanks but only observed one brief fight. Physical fighting between *V. rosenbergi* males was only seen before pairing-up, as also was reported for the Savanna Monitor (*Varanus albigularis*) (Philipps and Millar, 1998).

Both *V. rosenbergi* and *V. varius* have relatively long activity periods (up to 4.5 and 3 months, respectively) before mating. This is in contrast to the subtropical *V. albigularis* that mates within 4 weeks of becoming active (Phillips and Millar, 1998). Weather patterns may be more important for breeding in the Savanna Monitor than for varanids living in cool, temperate regions. Phillips and Millar (1998) also noted that all male-male and male-female interactions were limited to a 2- to 3-week period. Carter (1990) observed *V. varius* mating over a 4-week period between 21 November and 23 December. Similarly, the copulatory period for Rosenberg's Goanna spans 4 weeks but occurs a month later, between 27 December and 26 January.

At the beginning of the copulation period, *V. rosenbergi* are together as a single pair. *Varanus rosenbergi* females were never sighted in groups before or during courtship. In contrast, Carter (1992) recorded 29 groups of two to six *V. varius* of mixed sex between 13 October and 2 January and Philipps and Millar (1998) found *V. albigularis* females in groups of two and three at the beginning of the courtship period. Pair bonding/fidelity in *V. rosenbergi* varied from 40% to 80% of pairs remaining monogamous in

a given breeding season. When multiple partnerships occurred, up to three males copulated with a single female, and an individual male copulated with up to four females. Neither Carter (1990) nor Phillips and Millar (1998) reported any evidence of pair bonding. Carter (1990) observed one *V. varius* mate with two different males over a 6-day period and another female with three different males on three consecutive days. Likewise, Phillips and Millar (1998) reported that five female *V. albigularis* mated with two males each and that on five occasions males moved up to 4.1 km to mate with different females.

Before copulation, *V. rosenbergi* males did not display head shuttering or jerky movements as described for *V. varius* (Carter, 1992). However, tongue flicking over the female's head, neck, back, and groin were recorded for both species. These behaviors also have been reported for wild *V. varius* (Carter, 1992) and *V. komodoensis* as well as captive *V. bengalensis* and *V. timorensis* (Auffenberg, 1981, 1983, 1988). *Varanus komodoensis* males seem to restrain the female during copulation to guard against her aggressive behavior. Females of other species are not aggressive towards the male; in fact, their behaviour is usually interpreted as passive. In contrast, it is clear female *V. rosenbergi* play an active role in the successful insertion of the hemipenis.

Carter (1990) observed one *V. varius* pair copulate 16 times in 3 h and another pair seven times in 1 h. Each coupling was no longer than 4 min. The most matings observed on any one day for *V. rosenbergi* was 17. Most copulation bouts lasted 5 to 15 min, but there were extremes of 1 and 30 min. This is significantly longer than the maximum 2-min courtship and intromission reported for captive *V. bengalensis* (Auffenberg, 1983) and significantly shorter than the 47-min coupling period recorded for captive *V. timorensis* (Auffenberg, 1988). The copulation period for female Rosenberg's was 7 to 17 days. The only other report on length of copulatory period in varanids is for *V. albigularis*, who were observed mating over 2 to 5 days. Because all copulations took place in trees or tree burrows, the authors did not exclude the possibility of a longer period (Phillips and Millar, 1998).

There is virtually no information about frequency of reproduction in free-ranging varanids. A study of the field energetics of *V. rosenbergi* (Green et al., 1991) postulated it would be difficult for female Rosenberg's Goanna to obtain enough energy to produce a clutch of eggs every year. Our results show that 20-year breeding cycles were more common than breeding in consecutive years. These findings are in contrast to those of Carter

(1992) for *V. varius*. Based on his field data plus information from museum specimens, he concluded that *V. varius* breed every year. From information collected on museum specimens, King and Rhodes (1982) reported that *V. acanthurus* females seem to breed every year. Long-term field studies are needed to substantiate and validate findings from captive and museum collections.

The male-to-female sex ratio of *V. rosenbergi* did not differ significantly from 1:1 when calculated for the duration of the study. Our data demonstrate that taken alone, yearly findings can result in erroneous conclusions. In Carter's (1992) 3.5-year field study, 46 males and 40 females (1:0.9 ratio) were found. King and Rhodes (1982) examined 212 *V. acanthurus* museum specimens in total and likewise found that sex ratios did not differ significantly from 1:1. These findings prove the necessity of large specimen numbers, long field studies, or both for accurate assessment of sex ratios in varanid populations.

Egg Laying through Post Egg-Laying Behavior.—Although the use of termitaria for egg deposition by reptiles is widespread (Riley et al., 1985), there is documentation for only two Australian varanid species; *V. varius* (Carter, 1992) and *V. rosenbergi* (King and Green, 1999). Both use the mounds of *Nasutitermes exitiosus*, which have been described in detail previously (Holdaway and Gay, 1948; Watson, 1988; Carter, 1992; Green et al., 2000). It is possible that other Australian varanids use terrestrial and arboreal termitaria for egg deposition, but to our knowledge no detailed reports exist.

It is not yet known how or why female *V. rosenbergi* select a specific termitarium for egg laying. Females were observed scratching on and returning to mounds before egg laying. *Varanus rosenbergi* never tunneled into a termite mounds except to ovideposit, or in the case of marauders to destroy the eggs. *Varanus varius*, in contrast, burrow extensively into termite mounds (as early as 12 September and as late as 30 March), with both males and females using termitaria as roosts (Carter, 1992). These behaviors may represent two different tactics for the females to assess termite activity in potential egg incubation mounds.

We found Rosenberg's Goanna deposited their eggs at a depth of 35 to 50 cm. This is similar to findings from Ehmann et al. (1991) in New South Wales. Carter (1992) did not specify at what depth the eggs of *V. varius* were laid but indicated some tunnels were in excess of 80 cm long.

Mean clutch size documented in this study was 11.9 ± 0.2 ($N = 23$). King and Green (1979) also found clutches of 10 and 12 eggs, but Ehmann et al. (1991) recorded only three and four eggs in *V. rosenbergi* incubation mounds.

None of the latter hatched. Two species slightly larger than *V. rosenbergi*, *V. spenceri* and *V. mertensi*, had clutch sizes from 11 to 31 eggs (mean = 19.3 eggs) (Peters, 1969; Pengilley, 1981) and from 10 to 14 eggs (mean = 12.3 eggs) (Bustard, 1970), respectively. Carter (1992) found four to 12 eggs (mean = 8 eggs) in 25 *V. varius* nests.

In this study, *V. rosenbergi* actively guarded their egg mounds against other *V. rosenbergi* marauders for periods of 1 to 3 weeks after egg laying. Ehmann et al. (1991) recorded similar behavior. Nest guarding has not been reported for other Australian varanids. Although *V. griseus*, *V. komodoensis* (Auffenberg, 1981), and *V. bengalensis* (Deraniyagala, 1957) are known to return to their nest sites, there are no detailed observations on behavior or the time spent at the nest.

There are several field observations documenting seasonal timing of egg laying in varanids, but few record the duration between last copulation and egg laying. Based on observations of breeding and finding fresh clutches, Carter (1992) estimated this period was from 2 to 4 weeks for *V. varius*. He never observed actual egg laying. Phillips and Millar (1998) reported a 33- to 43-day period between copulation and egg laying for *V. varius* and 37.1 ± 0.4 days for *V. albigularis*. Their review did not include data for the cool temperate varanid *V. rosenbergi*.

In 10 instances with precise dates, we found the duration between last copulation and egg laying in *V. rosenbergi* was 24.6 ± 1.4 days, excluding two exceptions of 36 and 37 days. Even including these longer time spans, the mean of 27.0 ± 2.0 days is shorter than periods reported for any other varanid species reviewed by Phillips and Millar (1998), except *V. mertensi*, which the authors noted as questionable. The shorter duration may represent an adaptation to living in a cooler environment.

Varanids are considered to be day-active reptiles (Cogger, 2000), but there are reports of nocturnal activity by goannas in the warmer, northern parts of Australia. Irwin et al. (1996a) sighted two *V. panoptes* walking and tongue flicking after dark. Christian (1977) recorded *V. glebopalma* foraging after sunset. In the present study, we followed gravid females moving around previously scratched termite mounds at night before excavation of an egg chamber.

This is the first study to verify nocturnal nesting in a wild population of varanids and to document the exact timing of ovipositing and duration of egg laying. Although female *V. rosenbergi* did all nest digging during the day, only one from 30 observed egg depositions occurred during daylight hours. In all other instances, egg laying commenced at dusk and was completed 2 to 4 h later, well into the night.

The nocturnal timing of egg laying in Rosenberg's Goannas coincides with the activity of the termites. Termites quickly fill the hole after the female leaves, to avoid excessive loss of heat and humidity. They continue providing a high-humidity atmosphere and maintain internal temperatures that are significantly higher than outside, throughout the incubation period (Ris-miller et al., 2007). Nocturnal nesting has been recorded for many captive Australian varanid species. Horn (1991) reported nocturnal nesting in captive *V. varius* and Irwin et al. (1996b) recorded nocturnal nesting for *V. giganteus*, *V. indicus*, *V. keithhornie*, and *V. mertensi*. It is not known whether nocturnal nesting in captive species reflects behavior in wild populations or whether it is a result of holding conditions. Clearly, more long-term field studies are needed to fully understand and compare the breeding biology of varanids.

Conclusions.—Breeding activities of *V. rosenbergi* occupy 25–30% of the annual cycle. Courtship and breeding behavior of *V. rosenbergi* are distinctively different than those formerly described for other varanids. Unlike other species, *V. rosenbergi* begin courtship with one-to-one male–female pairs. Pairs may or may not remain monogamous throughout the reproductive season. Female *V. rosenbergi* play a more active role in courtship and copulation than has been described for other varanid species. Rosenberg's Goannas defend their egg mounds against marauders, with the female playing the most significant role. These behaviors may not be unique to *V. rosenbergi* but have not been described before. Females expend a large amount of energy in both egg production and defending the mound. A female may reproduce in consecutive years, but there is often a break of 1 to 2 years between egg clutches. Long-term studies on mainland *V. rosenbergi* and other varanid populations would help clarify whether reproductive phenology and behavior documented for the Kangaroo Island population is species specific or primarily influenced by environmental conditions.

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