

Reproductive ecology and egg production of the radiated tortoise (*Geochelone radiata*) in southern Madagascar

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We studied reproduction of wild *Geochelone radiata* at the Cap Sainte Marie Special Reserve in southwestern Madagascar to gain insight into life history traits related to reproductive success. Reproductive behaviour was observed over two nesting seasons and egg production was studied by radiographing telemetered females at regular intervals. We captured and marked 1438 radiated tortoises of which 26% were adults. Mating and nesting coincided with the rainy season, and mating events peaked in December, shortly before females started nesting in January. The incubation period was approximately 263–342 days, and hatchlings emerged after the onset of the rainy season when new plant growth became available. Hatching success was high and incidental destruction by humans rather than predation had the greatest impact on tortoise nests. Individual females produced from 0–3 clutches per season with 1–5 eggs per clutch. Body size had a weak effect on clutch size, but clutch size was lower in the dry year (2000) than in the wet year (1999) and appears to reflect resource availability. Mean egg size per clutch increased significantly with increasing body size. These findings emphasize that protection of large females should be considered in the conservation of this species.

Key words: radiated tortoises, *Geochelone radiata*, reproduction, eggs, nests, Madagascar.

INTRODUCTION

Radiated tortoises or Sokatra (*Geochelone radiata*) are one of four species of tortoises endemic to Madagascar (Juvik 1975; Ernst & Barbour 1989). Their natural distribution is limited to xeric spiny forest of southwestern Madagascar (Iverson 1992a) in the regions of the Mahafaly and Karimbola Plateaus; however, they have been introduced to the islands of Mauritius and Réunion (Gonzalez 1993).

The IUCN Red List (Hilton-Taylor 2000) classifies *G. radiata* as 'Vulnerable'. Primary threats to the radiated tortoise's survival are collection and habitat loss (Durrell *et al.* 1989; Nussbaum & Raxworthy 2000). Although a local taboo against eating or touching radiated tortoises affords them protection, exploitation by immigrants and people from different regions has increased in recent years (Lewis 1995; Nussbaum & Raxworthy 2000). Significant habitat loss and destruction occur through forest clearing for agricultural use, charcoal production and overgrazing by livestock

(Nussbaum & Raxworthy 2000). Additionally, protected areas such as Cap Sainte Marie Special Reserve and Lake Tsimanampetsotsa Strict Nature Reserve have free-ranging cattle and goats, which probably compete for food with wild tortoise populations.

Although Andriamampiany (1987) examined the bio-ethology of radiated tortoises at the Beza-Mahafaly Special Reserve; Bloxam (1988) investigated temperature and activity rhythms; Lewis (1995) reported on population densities and Young (1997) studied demography at Cap Sainte Marie, no study has examined reproduction and hatchling survivorship of wild *G. radiata*. Existing information on reproduction is based on studies of captive animals: egg development (Schweizer 1965), reproduction (Zovickian 1973), courtship and breeding behaviour (Auffenberg 1978), captive management (Burchfield *et al.* 1980) and captive breeding (Peters 1969; Behler & Iadecola 1991).

Their vulnerable status, scarcity of ecological information, and threats to *G. radiata* populations necessitate studies to gather baseline life-history data from healthy, natural populations. Effective

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conservation requires a thorough understanding of reproductive parameters. We examined sexual dimorphism, sex ratio, mating, nesting behaviour, clutch size and nest survivorship in a natural radiated tortoise population in southwestern Madagascar. This information can be used to address established life history theory with regard to a long-lived iteroparous species, and is necessary for the development of management plans (e.g. Judd & Rose 1989) for radiated tortoises.

MATERIALS & METHODS

Study area

The study area is located on the Cap Sainte Marie Special Reserve (CSM; 25.594S; 45.164E), a 1750 ha reserve, in the extreme southern portion of the Province of Tulear, Madagascar. Sandy soils and 100 m tall limestone cliffs characterize the area. Vegetation in the reserve is xeric spiny forest that typifies southwestern Madagascar. Dominant plant species include *Didieracea*, *Euphorbia* and *Opuntia*, which become dwarfed closer to the ocean. The climate in southwestern Madagascar is arid and the rainfall season extends from November to April. The reserve had no weather station. Hence, we recorded air temperature and precipitation with a Tidbit Data Logger (Onset Corp., Bourne, MA) and a rainfall gauge, respectively.

Measurements

We collected data over two rainy seasons from November 1998 to the end of April 1999 and from January to the end of May 2000. Tortoise activity was monitored daily from 07:00 to 12:00 and again from 14:00 to 18:00, by the authors and two CSM park rangers using structured and random searches.

We captured tortoises by hand and gave each individual a unique mark by filing notches in their marginal scutes (Cagle 1939). Body mass was recorded (to the nearest 1.0 g, 10.0 g, 50 g and 500 g) with Pesola spring scales (four sizes of 100.0 g, 1000.0 g, 5.0 kg and 50.0 kg, respectively), and straight carapace length (SCL) was recorded (to the nearest 0.1 cm) with vernier callipers (two sizes of 15.0 and 50.0 cm). We measured SCL from the nuchal to supracaudal scutes. We used secondary sexual characteristics of the plastron (concavity), anal opening and tail length (Auffenberg 1978) to categorize each tortoise as juvenile, male, or female. The age of a tortoise was estimated by counting

annuli (Zug 1991; Germano & Bury 1998), shell wearing as measured in desert tortoises (Burke & Cox 1988), and most importantly by size class (Zug 1991; Congdon *et al.* 1993).

Mating and nesting

Observations of mating behaviour such as duration, time of day, location, behaviours observed (e.g. biting, circling, ramming, lifting), and vocalizations were noted. Whenever nesting females were encountered, we collected information on the female and the nest. In addition, we collected information from nests found opportunistically; in such cases, we had no information on the female. The location of the nest was recorded with a hand-held Garmin GPS II plus, and marked with flagging tape in adjacent vegetation. Percentage over-storey density of vegetation surrounding nests was estimated using a desmometer (Bellow & Nair 2003). For each nest we recorded clutch size, and when possible, individual egg length, width and mass. Caution was taken during handling not to roll or turn the eggs. The depth and diameter of the nest cavity along with substrate type (sand/rock), orientation relative to cover, and distance to the nearest vegetation were recorded. We measured incubation temperatures ($\pm 0.1^\circ\text{C}$) for one nest in 1999 and five nests in 2000 using Tidbit Data Loggers buried in the nest cavities. Loggers were placed centrally and above the eggs and recorded temperatures every 12 min for 270 days.

Egg production

We attached carapace-mount radio-transmitters (AVM Instrument Company, Livermore, CA) to 11 *G. radiata* females and tracked them every second week from 13 February to 27 May 2000 to take radiographs to determine clutch size, clutch frequency, clutch interval and egg size (Gibbons & Greene 1979; Turner *et al.* 1986; Hinton *et al.* 1997). In addition, we opportunistically radiographed 2–4 female tortoises daily. One non-telemetered female was radiographed at regular intervals during the study; her data were included in the analysis of the telemetered females. Females were radiographed dorsoventrally with a HF 80+ portable X-ray machine (MinXray Inc, Northbrook, IL) set at 80 kV (15 mA), at a focus to film distance of 73 cm.

We inspected radiographs for calcified eggs and determined clutch size for gravid females. It was easy to distinguish new from previous clutches

when clutch size differed. When two subsequent clutches had the same number of eggs, we distinguished clutches by the progression of calcification shown on the radiographs. Newly calcified eggs appear faint and as calcification progresses, the eggshell becomes prominent and increases in thickness. We used a ruler to measure the length and width of all eggs on the radiograph. Since egg images on radiographs are larger than the actual eggs, we used the Graham & Petokas (1989) method to apply a correction factor to radiograph egg measurements. For calculating a correction factor, we incorporated a focus to film distance of 73 cm and estimated egg to film distance as one-quarter the shell height of the tortoise. We based this estimate on the position of eggs determined from carcasses. The corrected egg length and width of radiograph images were used to estimate egg volume: $\text{volume} = \pi(L)(W^2)/6$, where L and W are egg length and width, respectively (Coleman 1991).

Statistical analyses

Statistical tests were completed using SigmaStat 2.0 and were considered significant at $\alpha = 0.05$. Data were tested for normality and homoscedasticity before using a parametric test or the non-parametric equivalent. We used a Student's t -test or Mann-Whitney rank-sum test to compare group averages and a paired-sample t -test for related observations. When the means of more than two samples were compared, we used an ANOVA, and for multiple measurements on the same subject, we used repeated measures ANOVA or the Friedman test. Correlations were evaluated using Pearson's product-moment correlation, Spearman's rank correlation, or linear regression analysis. We used multiple regression analysis to simultaneously consider more than two variables when one of the variables was assumed functionally dependent upon the others (Zar 1999).

RESULTS

Climate data

At CSM, rainfall was exceptionally high in 1999 while in 2000, southern Madagascar suffered from severe drought (Fig. 1).

Size and sexual maturity

We captured and marked 1438 radiated tortoises of which 26% were adults. The smallest morphologically distinguishable male based on secondary

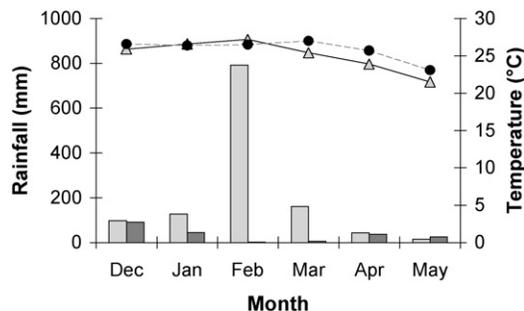


Fig. 1. Monthly rainfall (bars) and temperature (lines) recorded at Cap Sainte Marie, Madagascar, in 1999 and 2000. Grey shaded bars and grey triangles represent records for 1999, while darker bars and black circles represent records for 2000.

sexual characteristics had a SCL of 23.8 cm and all smaller individuals were classified as juveniles. Male SCL ranged between 23.8 and 39.5 cm (31.8 ± 3.19 cm, $n = 191$) and male mass was 6.063 ± 1.631 kg (2.6–10 kg, $n = 191$). Female SCL ranged from 24.0 to 36.0 cm (29.1 ± 3.22 cm, $n = 188$) and female mass was 5.129 ± 1.529 kg (2.0–9.6 kg, $n = 188$). Males were significantly larger and heavier than females (SCL: $T = 28264.5$, $P < 0.000001$; mass: $t_{372} = -5.71$, $P < 0.000001$). Male secondary sexual characteristics were clearly distinguishable at a SCL of 26.0 cm, yet the smallest male observed mating had a SCL of 29.6 cm. We used the presence of eggs (nesting females and eggs detected through radiography; $n = 39$) to identify size at maturity in females. The smallest gravid female had a SCL of 28.0 cm. The adult male to female ratio at CSM based on secondary sexual characteristics was 1:0.98 ($n = 379$).

Mating

Mating behaviour was observed on 54 occasions from December to May over two field seasons. Since November, December and May were only covered in one of the two field seasons, search effort for these months was about half the effort of January to April. Despite lower search effort, mating frequency was highest in December and slowed considerably by March (Fig. 2). For all mating pairs, males ranged from 29.6–38.3 cm SCL (33.85 ± 2.33 , $n = 31$) and females from 20.0–36.0 cm SCL (29.97 ± 3.71 cm, $n = 31$). In mating pairs, males were significantly larger than female partners (paired test: $t_{30} = 5.26$, $P = 0.00001$).

Courtship started with the male tortoise circling a female while sniffing or biting her legs, neck or tail region. Male tortoises often rammed, pushed,

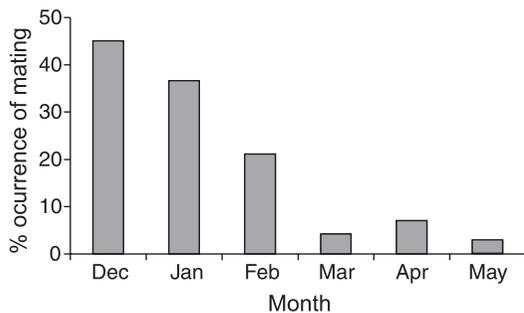


Fig. 2. Percentage occurrence of mating behaviour for *Geochelone radiata* from December to May in southwest Madagascar.

and lifted females with their gular scutes. For the most part, female tortoises tried to escape from males, keeping their tails and cloacae as close to the ground as possible. In less than 25% of the observations ($n = 11$), females lifted the posterior end of their carapaces, by extending their hind limbs, to allow males to copulate. Individual tortoises were seen courting repeatedly (especially males) but never with the same partner. Although courting behaviour occurred at all times of the day, 70% of observations were between 15:00 and 18:00. Courtship lasted from 10–107 minutes (43.11 ± 33.78 min, $n = 11$). Males emitted grunting noises during copulation.

Nesting

We observed 14 nesting females and never saw the same female nesting twice. Local people who encountered nesting females reported the location, date and time for 10 additional nests. All telemetered females with nesting observations ($n = 5$), moved several hundred metres from the centre of their usual daily range to nest.

Ninety-two per cent of nest excavations began between 07:00 and 10:00 and females required on average 127.5 minutes (range = 119–133 min, $n = 4$) for excavation, oviposition and closing/covering. All nest cavities were dug in well-drained sandy soil, and had a mean depth and diameter of 11.6 ± 1.1 and 9.0 ± 1.7 cm ($n = 19$), respectively. On two occasions, nests were abandoned when the female encountered roots or rocks while digging. On six occasions we found individual, intact eggs abandoned on the surface; the shell of these eggs often had a latticework of cracks.

Tortoises nested near vegetation adjacent to open canopy areas. Seventy-seven per cent of nests ($n = 22$) were adjacent to footpaths, which

were generally south, southwest, or southeast of the nests. Nests were made adjacent to a variety of plants including *Euphorbia* spp., *Phytenna sessiflora*, *Fernando madagascariensis*, *Operculicarya pachypus* and *Ruellia poissonii* (together 31.8% of nests), but they were most commonly associated with *Opuntia* sp. (36.4% of nests). Over-storey vegetation density of the nests ranged from 0.2 to 65.7% ($30.0 \pm 24.2\%$). Nest temperatures for all nests ranged from 14.6–42.9°C during incubation and the mean nest temperature varied from 22.2 ± 4.6 to 26.1 ± 4.5 °C.

Nest survivorship

Hatching success is unknown for two of the 11 nests located in 1999. Of the remaining nine nests, two were destroyed, one did not hatch, two-thirds of the eggs of one nest hatched, and all eggs of the remaining five nests hatched. For these nine nests, 65.6% of the 32 eggs hatched. Five nests were located in 2000 and hatching success for two of these nests is not known. One of the remaining three nests did not hatch, while four of five eggs of one nest, and all eggs in the third nest hatched. Of these three nests, 66.7% of the nine eggs hatched.

It was not always possible to determine the exact date of hatching, and for some nests we know only that the nests hatched before our arrival. However, the nests still appeared fresh and the eggs probably hatched within the previous month. Incubation period for the nests located in 1999 ranged from less than 276 days to a maximum of 340 days. For 2000, the incubation period ranged from less than 263 days to a maximum of 342 days. We had approximate hatching dates for nine of the nests and all nests hatched in January to early February. No nest predation was observed during this study, but on one occasion in 1999 and one in 2000, humans tampered with nests.

Egg production

The eggs of radiated tortoises are nearly spherical with a brittle calcareous shell. For a summary of egg and clutch statistics, see Table 1. We also compared differences between nest and radiographed eggs, between years [e.g. when nests and radiographs were both considered, clutch size was significantly larger in 1999 (median = 3) than in 2000 (median = 2)], and in clutch order (Table 2). Relative clutch mass is often used as an estimate of reproductive effort (Seigel & Fitch 1984; Barron 1997) and was 0.013 ± 0.0056 ($n = 7$) for radiated tortoises at CSM.

Table 1. Summary statistics of egg and clutch parameters for *Geochelone radiata* at Cap Sainte Marie, Madagascar.

	Mean ± S.D.	Range	n
Individual eggs			
Egg length (cm)	4.09 ± 0.41	(1.59)* 3.28–4.70	145
Egg width (cm)	3.80 ± 0.39	(1.50)* 2.30–4.59	145
Egg volume (cm ³)	31.77 ± 7.59	(1.87)* 15.84–51.65	145
Egg mass (g, nests)	39.02 ± 5.94	28.0–55.0	56
Clutch			
Egg length (cm)	4.12 ± 0.32	3.05–4.64	57
Egg width (cm)	3.83 ± 0.29	2.95–4.40	57
Egg volume (cm ³)	32.25 ± 6.78	13.89–47.05	57
Egg mass (g, nests)	40.05 ± 6.35	29.0–53.0	18
Clutch size	2.53 ± 1.11	1–5	62
Clutch mass (g)	122.8 ± 41.5	49–198	18
SCL (cm)	31.89 ± 1.90	28.0–35.6	49
Body mass (kg)	6.21 ± 1.14	4.30–8.400	49

*One clutch of four eggs contained two abnormally small eggs.

Body size (SCL) significantly influenced clutch mean egg parameters (width: $F_{1,42} = 11.41$, $P = 0.002$, $r^2 = 0.21$; length: $F_{1,42} = 5.67$, $P = 0.02$, $r^2 = 0.12$; volume: $F_{1,42} = 10.93$, $P = 0.002$, $r^2 = 0.21$), and mean egg size per clutch increased with body size. Body size had no effect on clutch size ($P = 0.17$, $n = 57$) and clutch size was not correlated with mean egg volume ($P = 0.34$, $n = 56$). However, after removing the effect of body size (through multiple regression), mean egg volume (MEV) increased as clutch size (CS) decreased (MEV = 1.54 SCL – 2.12

CS – 12.07, $r^2 = 0.23$, $F_{2,42} = 6.27$, $P = 0.004$, SCL $P = 0.004$, CS $P = 0.040$). This effect was not strong and when the data for one clutch (four eggs) with two abnormally small eggs were removed, clutch size was no longer correlated with egg volume ($P = 0.17$), although body size ($P = 0.001$) and the overall regression ($P = 0.003$) were still significant.

In the 1998/1999 field season, we observed no nesting events between November and late January and reports from local inhabitants indicated a similar paucity of nesting before February for

Table 2. Statistical appraisal of egg and clutch parameters comparing nests and radiographs, years (1999/2000), and clutch sequence for *Geochelone radiata* at Cap Sainte Marie, Madagascar.

Parameter	P	Statistic
Nests vs radiographs		
Uncorrected egg length	0.0026	$T_{58,87} = 3487$
Uncorrected egg width	<0.000001	$T_{58,87} = 3151$
Uncorrected egg volume	<0.000001	$T_{58,87} = 3196$
Corrected egg length	0.23	$T_{58,87} = 4535$
Corrected egg width	0.97	$T_{58,87} = 4224$
Corrected egg volume	0.57	$T_{58,87} = 4374$
Between years		
Clutch size (nest)	0.47	$t_{19} = 0.73$
Clutch size (nest + X-ray)	0.0051	$T_{11,51} = 499$
Mean egg length of clutches	0.64	$t_{55} = 0.47$
Mean egg width of clutches	0.71	$t_{55} = 0.37$
Mean egg volume of clutches	0.75	$t_{55} = 0.32$
Clutch sequence		
Sequence vs clutch size	0.75	$F_{2,19} = 0.30$
Sequence vs egg volume/clutch	0.36	$\chi^2 = 2.67$, d.f. = 2

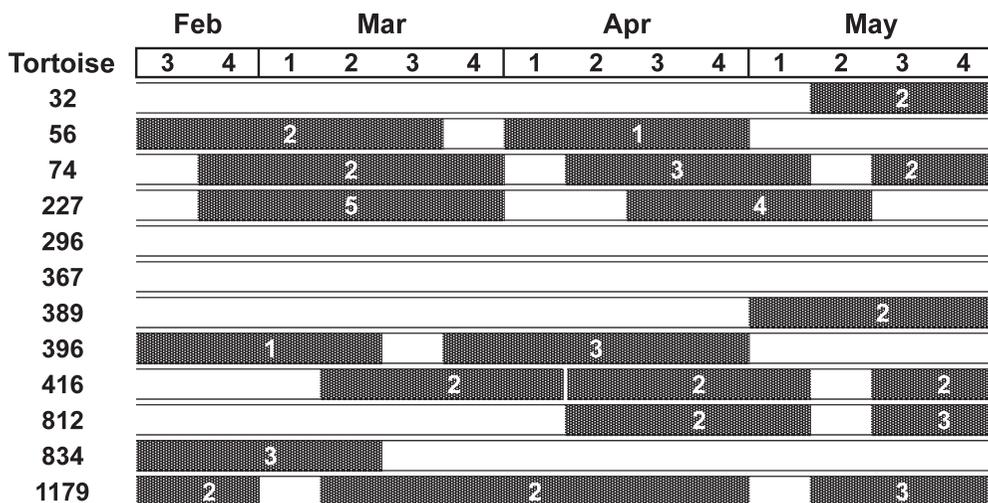


Fig. 3. Egg production (based on bi-weekly radiographs) of 12 *Geochelone radiata* at Cape Sainte Marie, Madagascar, from February to May 2000. Horizontal bars show when individuals were gravid and the number of eggs for that clutch.

1999/2000. We radiographed radiated tortoise females from mid-February 2000 and in February 6 of 11 females (55%) were gravid. The percentage gravid females increased to 7 of 12 animals (58%) in March and remained there in April and May 2000. Two telemetered females formed their first clutch in May while two others produced no eggs during the study. The number of clutches produced between February and May 2000 ranged from 0–3 clutches (1.7 ± 1.1 , $n = 12$; Fig. 3). The interval between oviposition and shelling of the next clutch (when eggs are visible in radiographs) was approximately 7–15 days (Fig. 3). Available data indicate that female radiated tortoises started nesting in late-January to February. Since females were still gravid in May, the nesting season in 2000 extended beyond this date.

DISCUSSION

Sexual maturity and mating

Most chelonians show pronounced sexual size dimorphism (Berry & Shine 1980; Gibbons & Lovich 1990). Sexual selection will favour larger males if a larger size facilitates successful mating and/or affords superiority in male–male encounters (Berry & Shine 1980; Gibbons & Lovich 1990). The larger size of male *G. radiata* probably contributes to mating success since male partners of mating pairs were significantly larger than the females. The importance of body size in mating success is supported by the size difference between sexually

active males and the size when sexual dimorphism becomes established. As in *G. gigantea* (Swingland & Coe 1978), male radiated tortoises always initiated courtship behaviour. Nevertheless, females often did not cooperate and both sexes thus influenced mating success.

Since many chelonian females store sperm, the timing of mating and ovulation need not coincide (Kuchling 1999). In *G. radiata*, however, mating behaviour occurred most frequently a month before the commencement of nesting and coincided with the onset of the rainy season. In several other *Geochelone* species, mating also coincided with the rainy season: *G. ynniphora* in northwestern Madagascar (Smith 1999), *G. gigantea* on Aldabra, 400 km NW of Madagascar (Bourn 1976; Swingland & Coe 1978) and *G. pardalis* on the African mainland in Zambia (Wilson 1968).

Nesting and incubation

The nesting period of *G. radiata* started in the warmest month of the year. Many turtle and tortoise species (e.g. *Kinixys spekii*, Hailey & Coulson 1997; *G. gigantea*, Swingland & Coe 1978) excavate their nests in the morning or late afternoon to avoid high midday temperatures and solar radiation (Meek 1988). Radiated tortoises prefer to nest near open areas with relatively low canopy cover. While nesting, females are vulnerable to overheating and *G. radiata* females generally initiated and completed nesting in the mornings. One female that nested between 12:00 and 13:00

made her nest in the shade of a *Euphorbia* tree.

The nests of radiated tortoises were often placed on the southern side of vegetation, which affords more shade to nesting females and their nests in the southern hemisphere. Temperatures in nests at an average depth of 11.6 cm fluctuated much less than ground surface temperatures, yet we still recorded nest temperatures up to 42.9°C. Ewert (1979) reported soil temperature extremes of 4.9°C for *Chelodina expansa* and 46°C for *Malaclemys terrapin*. In radiated tortoises, exposure to 42.9°C was not lethal since the eggs in this nest hatched successfully.

The incubation period of wild radiated tortoise nests (<263 to 342 days) was longer than in captives (71–197 days, Durrell *et al.* 1989; 79–273 days, Behler & Iaderosa 1991), and exceeded the incubation time reported for wild *G. yniphora* (197–281 days, Smith 1999; Pedrono *et al.* 2001), and several other chelonians (as reviewed in Ewert 1979). Prolonged incubation periods in natural nests may result from arrested development. Reptilian diapause can occur in an environment that is normally conducive to development and some turtle species require stimuli, such as temperature (e.g. *Deirochelys reticularia* and *Chelodina expansa*), or moisture, to reinstate development (Ewert 1991). The Gladys Porter Zoo in Brownsville, Texas, uses refrigeration to stimulate development of *G. radiata* eggs that have not gone beyond membrane adhesion (C. Adams, pers. comm.). Many chelonians need an environmental trigger for hatching and emergence from the nests (Kuchling 1999). The timing should ensure that hatchlings emerge during the most favourable season when food and water are readily available (Zug 1993). In southern Madagascar, the rainfall season generally starts in November and lasts to April. *Geochelone radiata* hatchlings emerged in January/February, when new plant growth was established and food was available. The hatchlings of many tropical tortoises and turtles emerge during the rainy season (Kuchling 1999). Several African *Geochelone* species (*G. yniphora*, Pedrono *et al.* 2001; *G. pardalis*, Wilson 1968; *G. gigantea* Bourne, 1976; Swingland & Coe 1978) also hatch in the rainy season.

Survivorship

Given our small sample size, hatching success of wild *G. radiata* (c. 66%) was high compared to the low success (<30%) reported for captive radiated tortoises (O'Brien 2002). O'Brien (2002) regarded a

clutch of five eggs as optimal and reported that clutches of one or 11 eggs never hatched. At CSM, one of the nests contained a single egg, which never hatched but contained a fully formed embryo.

The lack of nest predation at CSM is unusual compared to the high nest predation reported for species such as *Emydoidea blandingii*, *Chrysemys picta* and *Chelydra serpentina* in North America (Congdon *et al.* 1987; Congdon *et al.* 1993). Although fossas (Viverridae) and tenrecs (Afrosoricida) are found at CSM (Garbutt 1999) it is not known if they prey on eggs or even adults. Smith (1999) and Pedrono *et al.* (2001) also reported that nests of *G. yniphora* in Baly Bay, Madagascar, were rarely depredated. For *G. radiata*, incidental human disturbances had the greatest impact on nests. Female tortoises preferred to make nests in open areas used by local fishermen, and in paths where oxcarts travel.

Egg production

Clutch size in wild radiated tortoises (2.53 ± 1.11 eggs) was smaller than reported for captives: mean clutch size of 5.1 with a range of 2–9 eggs (Behler & Iaderosa 1991); clutch size of 4.97 ± 1.64 and a range of 1–11 eggs (O'Brien 2002). Since resource availability has a pronounced effect on tortoise growth rate and egg production (Swingland & Coe 1978; Turner *et al.* 1986; Henen 1997), the larger clutch size of captive radiated tortoises can be ascribed to their diet in captive conditions. A difference in resources might also explain the lower clutch size of radiated tortoises in 2000 compared to 1999. Although no long-term annual rainfall data exist for CSM, our rainfall records for the study periods (Fig. 1) show that 2000 was much drier than 1999, which probably influenced the quality and quantity of the food available to *G. radiata*.

Since our study did not cover a full annual cycle, we have to use circumstantial evidence to infer clutch frequency and the duration of the nesting season for wild radiated tortoises at CSM. Our first record for nesting was in late January and females were still gravid in May when the study was completed. The nesting season may start prior to this and extend to July, since Young (1997) reported a radiated tortoise nesting on 30 July 1996 at CSM. In Madagascar, wild *G. yniphora* females at Baly Bay have a clutch size of 1–6 eggs (mean = 3.2 ± 0.9) and lay a maximum of four clutches from January to May (Pedrono *et al.* 2001). It appears as

if the nesting season of wild *G. radiata* might be slightly longer than that of *G. yniphora*, and if radiated tortoises produced more clutches after May, they might have a larger maximum clutch frequency than *G. yniphora*. However, it is highly unlikely that wild radiated tortoises will produce seven clutches, as has been reported for captives (Behler & Iadecosa 1991).

Body size effects

Many chelonians grow throughout their lives and a correlation between body size and reproductive output has been demonstrated for several species (Moll 1979; Iverson 1992b; Wallis *et al.* 1999). Additional resources can be allocated to make larger eggs, to producing more eggs, or to both. In *G. radiata*, larger females produced bigger eggs, but body size had no effect on clutch size. Several chelonians show a trade-off between egg size and clutch size (Elgar & Heaphy 1989). In radiated tortoises, clutch size was not correlated with egg size, but after correcting for the effect of body size on egg size, a weak correlation was shown between egg size and clutch size; clutch size decreased with increasing egg size. In radiated tortoises, larger females allocate more resources to reproduction and these resources are mainly invested in larger eggs. Larger eggs produce larger hatchlings and larger hatchlings have a higher chance of survival than smaller hatchlings (Janzen 1993). When observing nesting in females, we noticed on one occasion that the diameter of the egg was too large to pass through the caudal gap between the carapace and plastron. This phenomenon has also been reported for *Sternotherus odoratus* by Clark *et al.* (2001). We suspect that in *G. radiata* such eggs eventually become dislodged through movement and desiccation and may explain the origin of eggs with a lattice-work of cracks found uncovered on several occasions.

Larger eggs and hatchlings are probably of particular importance to species that live in unpredictable environments. In 2000 when rainfall was low compared to 1999, radiated tortoises did not produce smaller eggs but rather exhibited reduced clutch size relative to the clutch size of 1999. It thus appears that large eggs are particularly important in the life history strategies of *G. radiata*. These findings emphasize that the protection of large females should be given special consideration in the conservation of this species.

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