

Nesting ecology of the critically endangered Fijian Crested Iguana *Brachylophus vitiensis* in a Pacific tropical dry forest

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Tropical dry forest (TDF) ecosystems occur throughout tropical and subtropical zones and one of their primary characteristics is that they are structurally and functionally constrained by seasonal fluctuations in moisture levels. Organisms within them synchronize growth and reproduction with water availability and many exhibit adaptations to drought conditions. We examined the previously unknown nesting ecology of the Critically Endangered Fijian Crested Iguana *Brachylophus vitiensis* a TDF specialist, on the Fijian island of Yadua Taba over two field seasons. In Fiji, the TDF and the endemic Crested Iguanas are threatened on a national level by anthropogenic factors and Yadua Taba Island remains the only protected site. Evaluation of adult female reproductive status revealed that only 52% of adult females reproduced in a given year. We suggest that female Crested Iguanas have adopted a biennial mode of reproduction in response to resource limitation. We found no evidence for communal nesting or nest site defence by females. All nest burrows were constructed on the forest floor in shaded areas. Mean nest temperatures (24.5°C), levels of site openness (10.9%) and total incident radiation (2.57 MJ m² day) recorded at nest sites were less than those reported for other Iguaninae. Mean egg size (17.9 g) was large relative to most Iguaninae and was independent of the small mean clutch size (2.9 eggs). Mean incubation period was extremely long (256 days) and spanned the eight-month dry season. Mean hatching success also was high (87%). We examine reproductive strategy in relation to the environmental conditions of the TDF habitat on Yadua Taba. This research provides a broader understanding of Crested Iguana nesting ecology and is a step towards the successful implementation of the Species Recovery Plan for this species.

Keywords: Iguana; Nest site selection; Clutch size; Egg size; Incubation length; Biennial reproduction; Tropical dry forest; Fiji

INTRODUCTION

TROPICAL dry forests (TDF) are generally described as occurring globally in frost-free areas where mean annual temperatures exceed 17°C and mean annual precipitation lies between 250–2000 mm (Holdridge 1967; Murphy and Lugo 1986). They are distinctly seasonal, with dry periods lasting from one to eight months, and can experience considerable variability in the amount and timing of annual rainfall (Murphy and Lugo 1986). Moisture availability plays a dominant role in shaping forest structure and dynamics, and many of the plant taxa inhabiting tropical dry forests have adapted to survive drought conditions (Murphy and Lugo 1986). While tropical dry forest flora is generally less diverse and structurally complex than wet forests, the foliage exhibits increased defences against water loss and herbivory, including dry-season leaf loss, increased toughness and high levels of secondary metabolites (Lugo *et al.* 1978; Medina *et al.* 1990; Coley and Barone 1996). Consequently many folivores preferentially select the readily digestible new growth, flowers and fruits, the bulk of which are produced during the wet season (Coley and Barone 1996; Cooper and Vitt 2002). This nutritional necessity could influence reproductive strategies of the animals that live in these environments.

Virtually all TDF habitats have evolved with large folivores and this role is generally occupied by medium-large mammals, but on many Pacific islands this niche is occupied by large lizards, and to a lesser extent, tortoises (Steadman 2006). The “true iguanas” in the subfamily Iguaninae (*Amblyrhynchus*, *Brachylophus*, *Conolophus*, *Ctenosaurus*, *Cyclura*, *Dipsosaurus*, *Iguana*, *Sauromalus*), comprise a diverse group of large, herbivorous lizards (Wiewandt 1982). As specialized herbivores Iguanines have a number of adaptations to herbivory, including leaf cutting dentition, colic compartmentalisation, and large size (Van Devender 1982; Cooper and Vitt 2002).

While Iguanines occupy a range of habitats, including deserts in the temperate zone, dry subtropical islands, and moist tropical and subtropical areas, around one third of all species are found on xeric islands. As reptile reproduction and investment is intimately linked with environmental conditions (Pough 1973), the reproductive strategies used by Iguanine species are likely to vary across environments. All Iguanines are oviparous and there is no investment in the young after hatching. However, females can influence the survival of offspring through direct input into egg size and yolk stores as well as through nest site selection and defence (Rauch 1988; Sinervo 1990). It has

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been demonstrated in lizards that females allocate energy differently between maintenance, storage, growth and reproduction on the basis of energy availability (Olsson and Shine 1997; Niewiarowski 2001). Therefore, studies focusing on nesting ecology and reproductive effort provide insight into maternal adaptations to natural environmental constraints and the trade off between reproductive output and maternal survivorship. We were particularly interested in how the seasonally variable and sometimes harsh environment of the Fijian TDF influences the reproductive effort and investment in the largest herbivore in the ecosystem, the Fijian Crested Iguana *Brachylophus vitiensis*.

Iguanines are primarily distributed in the new world tropics and subtropics with the exception of the three species in the genus *Brachylophus*. *Brachylophus* occur in the South Pacific Ocean archipelagos of Fiji and Tonga and are the sister clade to the rest of the Iguaninae (Keogh *et al.* 2008). In a group where the majority of taxa are large and terrestrial, the surviving *Brachylophus* species instead are medium sized and arboreal with *B. fasciatus* (Lau Banded Iguana) occupying dry forests in Tonga and eastern Fiji, *B. bulabula* (Fijian Banded Iguana) occupying mesic forests in central Fiji, and *B. vitiensis* (Fijian Crested Iguana) occurring in dry forests in western Fiji (Harlow and Biciloa 2001; Morrison *et al.* 2007; Keogh *et al.* 2008). The nationally protected Fijian island of Yadua Taba is one of the most important dry forest sites in the Pacific (Keppel and Tuiwawa 2007; Olson *et al.* in press) and it is the last stronghold of the critically endangered (IUCN 2007) Fijian Crested Iguana. While > 10,000 individuals survive on this reserve, elsewhere in Fiji populations are small and declining rapidly (Harlow and Biciloa 2001; Harlow *et al.* 2007). Prior to the current study no field data were available on the nesting ecology of *B. vitiensis* and our understanding of the nesting behaviour, reproductive frequency and clutch parameters of these iguanas was based almost exclusively on captive animals (Gibbons and Watkins 1982; Boylan 1989; Bach 1998). Even from data on captive animals it is apparent that *B. vitiensis* is unusual among the Iguaninae. One of the most remarkable traits is the extremely long incubation period (18-30 weeks in captivity, Gibbons and Watkins 1982), rivalled by very few other terrestrial vertebrates. Tuatara *Sphenodon*, and Chameleon genera *Chamaelo* and *Furcifer* top the scale with maximum incubation periods exceeding 12 months (Nelson *et al.* 2002; Andrews and Donoghue 2004). *Brachylophus vitiensis* also have large eggs and a small clutch size relative to other Iguanines (Iverson *et al.* 2004). Are these unique reproductive characteristics adaptations to specific TDF environmental conditions?

Our two major aims were to elucidate the patterns and processes of *B. vitiensis* nesting in the wild and examine these in light of their adaptive significance to the TDF habitat. Knowledge of reproductive patterns and nesting requirements is integral to the successful conservation of this species by way of informing future translocation, ecosystem preservation or captive breeding efforts.

MATERIALS AND METHODS

Study site

Yadua Taba lies in the northwestern region of the Fiji island group (16°50'S, 178°20'E) (Fig. 1). It is a small (70 ha) eroded volcanic island rising to a height of 117 m with prominent rocky cliffs on the eastern side. Yadua Taba is uninhabited, but it is separated by less than 150 m from the larger island of Yadua (1360 ha), which supports a village of approximately 200 inhabitants. The iguana is not known to occur on neighbouring Yadua Island, nor do any local stories or traditions suggest its recent historical presence. Humans introduced a number of mammal species to Yadua and Yadua Taba. Pacific Rats *Rattus exulans* occur on both islands while Domestic Cats *Felis catus*, Dogs *Canis lupus familiaris*, Goats *Capra aegagrus hircus*, Pigs *Sus scrofa domestica*, and a Horse *Equus caballus*, occur only on Yadua. Goats were introduced to Yadua Taba in ~1972 and there were an estimated 200 on the island in 1979 (Gibbons 1984). In 1980, Yadua Taba became Fiji's first wildlife sanctuary and the majority of Goats were removed, though a small number (~7-10) remained until 2003 when they were finally eradicated, facilitating TDF regeneration. TDF is the main vegetation type on Yadua Taba, but the island also has *Casuarina*, beach or littoral, rocky cliff, and grass/open shrubland habitats (Gibbons 1984; Laurie *et al.* 1987; Olson *et al.* 2002; Morrison *et al.* 2007). On Yadua Taba the dry season generally occurs from May through to October and is characterized by decreased temperature, increased winds, infrequent precipitation and often months at a time with no rainfall. Conversely, the wet season spans the months of November through April and is a time of increased temperature and rainfall with the potential of severe storms and occasional cyclones. The timing and intensity of the wet season can vary greatly from year to year. Fieldwork for this study was conducted on Yadua Taba during the wet season months of February to April 2006 and November 2006 to March 2007.

Nesting and clutch parameters

Nest sites were located by daytime surveys in forested areas and relied on sighting gravid

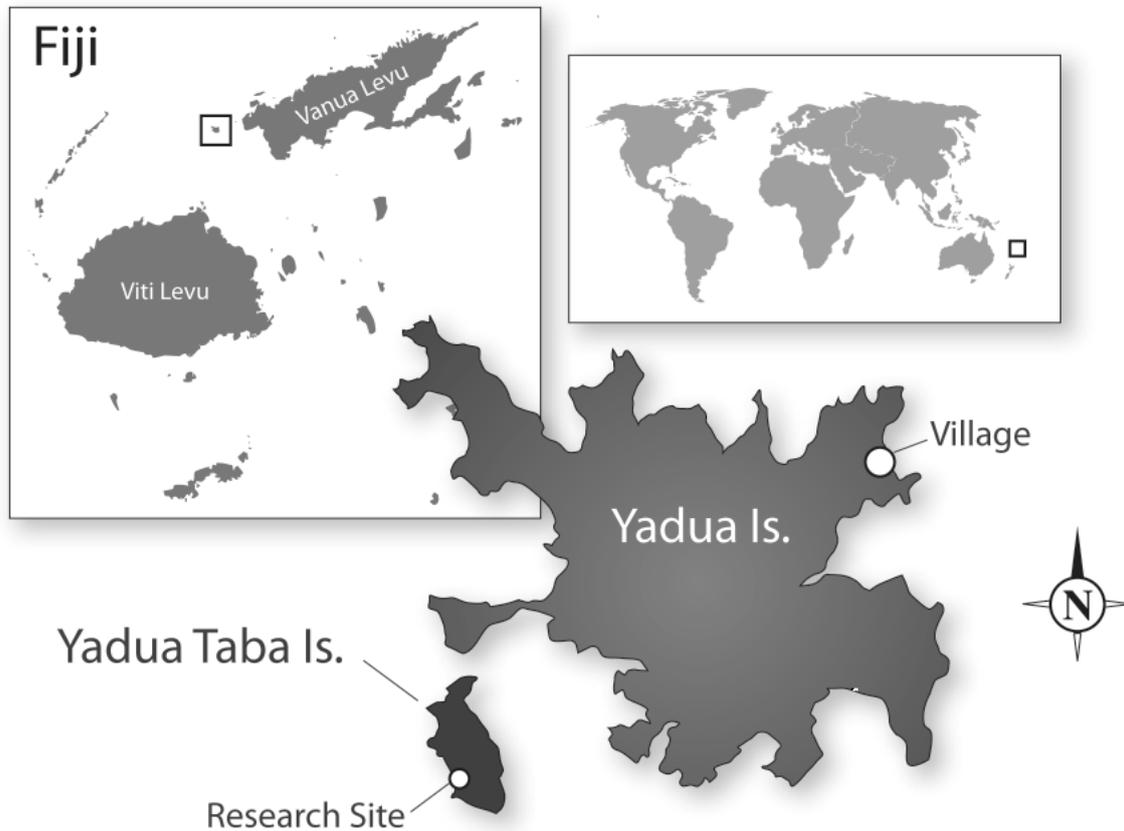


Fig. 1. Location of Yadua and Yadua Taba Islands, Fiji, (Denimanu village on Yadua = \emptyset , Main field camp on Yadua Taba = \circ).

females digging nesting burrows. The time and duration of the searches was opportunistic and all vegetation types, except for sparsely-vegetated rocky cliff zones, were included in the surveyed areas. Female *B. vitiensis* rarely come out of the trees except when nesting so once a female was detected on the ground the immediate area was scanned for any evidence of nest site excavation. A nesting female may dig a number of "test" burrows before locating a suitable nest site and will readily abandon an incomplete nest burrow if disturbed. Therefore, once located, the area was flagged and the female was left to complete the nest and lay her eggs. This prevented us from timing the individual phases of nesting, and as females did not remain at the nest sites after oviposition we were unable to link individual females to clutches. After oviposition females refill the burrow and then camouflage the site by scraping debris across the entrance. The following morning the nest was excavated and the eggs removed to record clutch size, egg mass (to the nearest 0.1 g), and egg length (to the nearest mm). We report means and standard deviations unless otherwise indicated. The dimensions of the burrow entrance and nest chamber were recorded along with burrow length and the depth of the nest chamber from the surface.

The eggs were replaced in their original positions within the nest chamber and a temperature data logger (Thermochron iButton® DS1921G) was placed alongside the middle egg, approximately central to the nest, before the burrow was carefully refilled and the site disguised. Temperature loggers were deployed in nests within 48 hrs of oviposition and were recovered from the nests within a week of hatching. The temperature within the nest was recorded every four hours for the duration of incubation.

Habitat variables associated with nests

Data were recorded for a range of habitat variables at each nest site including: location, elevation (Garmin GPS 60™), aspect, dominant forest type, plant species within 3 m, and soil type (classified into one of five categories: sandy, organic-sandy, organic-friable, organic-clay and clay). Hemispherical photography and a computer programme were used to quantify canopy openness and incident radiation (Doody *et al.* 2006b). A hemispherical photograph of the canopy was taken with a digital camera (Nikon Coolpix E8800™ 8MP) and fish eye lens (Opteka superwide angle 0.22x™) oriented north and levelled directly above each nest

chamber. Each image, containing information on the size, shape and location of canopy gaps, was analysed using GLA software (Gap Light Analyser v.2.0, Frazer *et al.* 1999) to determine incident radiation at each nest throughout the year.

Rainfall and ambient air temperature data were collected throughout the incubation period. Rain gauges were installed and rainfall was measured on the western side of Yadua Taba as well as 5.5 km northeast, on the eastern side of Yadua Island in the village of Denimanu. Records were taken regularly throughout the fieldwork seasons and opportunistically at other times by the local village. Ambient air temperature was recorded every four hours by two fully shaded iButtons® situated in dry forest on the western side of Yadua Taba Island. Additional meteorological information was obtained from the Nabouwalu Weather Station approximately 50 km east of Yadua on the large island of Vanua Levu.

Incubation, nest success and survivorship

The island was revisited from November 2006 to March 2007 and the nests relocated with the aid of GPS waypoints. As hatching approached the nests were checked weekly, increasing to daily during periods of rain. Hatching was apparent in organic and clay based soil types by the presence of a small hole above the nest chamber, while nests in sandy soil had to be carefully uncovered to determine the status of the eggs. Nests from previous years were located by the presence of an emergence hole, and often eggshells near the entrance, and the nest chamber was excavated to recover all additional eggshells. Egg number and depth of the chamber from the surface were recorded. After the hatching of monitored nests all eggshells were recovered and examined for signs of successful hatching (indicated by clean slashes through the shell left by the egg tooth), embryo mortality or predation. We recorded the number of eggs in each nest, hatching success and date of hatching for the monitored nests. Seven hatchlings from two monitored clutches were captured at the time of hatching in order to obtain data on snout vent length (SVL) and body mass (BM) of wild hatchlings.

Based on night surveys of iguanas we located an area of TDF with particularly high densities of iguanas and iguana food plants. At this site we established a 50 × 50 m plot, situated 50 m behind the beachfront and sheltered from it by a strip of littoral vegetation. Data on SVL, BM, and reproductive status of iguanas from this plot, collected as part of a larger demographic survey (S. Morrison unpublished data), were used to assess female reproductive frequency. For

all captured animals we measured SVL to the nearest 5 mm, BM to the nearest gram, and inserted a passive integrated transponder (PIT) tag subcutaneously on the left flank. Female reproductive status was determined by abdominal palpitation throughout the initial wet season field trip and recorded as gravid, spent, or non-gravid. While non-gravid females had girths similar to males, eggs were immediately apparent in the distended abdomens of gravid females, and spent females retained distended abdomens after oviposition, maintained by large amounts of ingested vegetation.

RESULTS

Nesting and clutch parameters

We divided iguana nesting behaviour into three phases: 1) digging, 2) oviposition, and 3) filling in the burrow. We were unable to quantify the number of test sites each female excavated before choosing a final nest site. However, based on the large number of incomplete or abandoned nest excavations it is clear that many females test at least one alternate site before completing a successful burrow. These trial nest sites can be as little as 10 cm apart and the vast majority were abandoned due to rocks or roots blocking the excavation. Once a suitable nest chamber is excavated the female positions herself above the entrance to deposit her eggs. After oviposition the female fills in the nest burrow with loose soil, packing the soil at the entrance with her snout and forelimbs before kicking and scraping debris over the site to camouflage it. Completed nest sites were virtually indistinguishable from the surrounding forest floor. Nests were abandoned after burrow completion and we saw no evidence of nest defence by females.

Fourteen nest sites were identified and flagged during burrow construction phase. All 14 were completed within 12 hrs of diurnal activity between the 25th of February and the 22nd of April 2006. The structure of nest burrows was simple and highly conserved, consisting of a single short entrance burrow culminating in a slightly widened nest chamber. Using data from the monitored nests, mean entrance width was 69 ± 3.2 mm ($n = 10$, range 60–80 mm), mean chamber width was 72 ± 3.4 mm ($n = 13$, range 35–50 mm) and mean burrow length was 163 ± 8.2 mm ($n = 13$, range 91–390 mm). For nest depth we combined data from monitored nests with nests hatched from previous years and mean depth to the bottom of the egg chamber was 131 ± 6.1 mm ($n = 31$, range 85–200 mm).

Nesting frequency was determined by tallying the total number of gravid and non-gravid adult females in the marked population captured during the 2006 wet season field trip (23rd of

February to the 24th of March). Approximately half of the adult females (52%) were gravid. Mean SVL for gravid females ($\bar{x} = 208 \pm 7.76$ mm, $n = 32$, range 190–225 mm) and non-gravid females ($\bar{x} = 205 \pm 8.7$ mm, $n = 29$, range 190–220 mm) did not differ ($t = 1.13$, $P = 0.27$), but as expected, mean body mass for gravid females ($\bar{x} = 282 \pm 46.5$ g, $n = 32$, range 185–370 g) was significantly greater than for non-gravid females ($\bar{x} = 255 \pm 36.33$ g, $n = 29$, range 190–330 g) ($t = 2.5$, $P = 0.02$) (Fig. 2).

Evaluation of 18 nests from previous years resulted in a mean of 2.8 ± 0.97 eggs per nest (range 2–4), comparable to the mean clutch size for the monitored nests ($\bar{x} = 2.9 \pm 0.8$ eggs, $n = 14$, range 2–4) in 2006 (Fig. 3). Eggs measured within 24 hrs of oviposition had a mean length of 46.7 ± 0.3 mm ($n = 33$, range 42–53 mm), a mean width of 25.5 ± 0.3 mm ($n = 33$, range 23–29 mm), and a mean mass of $17.9 \text{ g} \pm 1.3 \text{ g}$ ($n = 33$, range 15.3–20.7 g). Mean clutch mass was 54.5 ± 3.14 g ($n = 14$, range 32.8–74.5 g). Clutch mass was highly positively correlated with clutch size (Fig. 3) ($r = 0.93$, $P < 0.001$) but not with egg mass ($r = 0.421$, $P = 0.133$). Egg size was highly conserved, regardless of clutch size, so larger clutches were not comprised of smaller eggs. We calculated relative egg mass (mean egg mass per clutch/mean female body mass $\times 100$; REM = 6.7) and relative clutch mass (mean clutch mass/mean female body mass $\times 100$; RCM = 20.3) using the mean mass of all adult females ($\bar{x} = 268.5$ g).

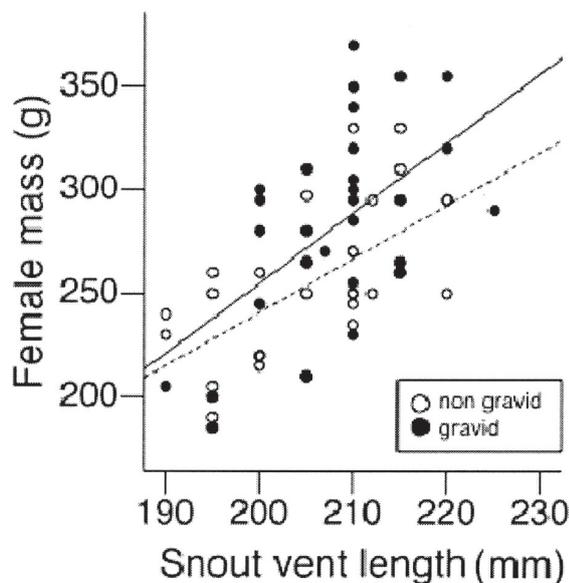


Fig. 2. Relationship between snout vent length and mass in gravid and non-gravid adult females. The regression equations are, gravid (—) mass = $3.39 \text{ SVL} - 422.4$ ($r = 0.57$, $P = 0.001$, $n = 32$), non-gravid (---) mass = $2.58 \text{ SVL} - 274.39$ ($r = 0.62$, $P < 0.001$, $n = 29$).

Habitat variables associated with nests

The three plant species most commonly found within 3 m of iguana nests were *Vavaea amicorum*, *Diospyros elliptica*, and *Glocidion vitiense* (found at 64.3, 50.0, and 35.7% of nest sites respectively). *Vavaea amicorum* and *D. elliptica* are the two species most commonly utilized by iguanas as food and perch plants (Morrison *et al.* 2007).

Nest sites were equally distributed between the organic-sandy, organic-friable, and organic-clay soil types, but no nests were found in purely sandy or clay soils despite their availability to nesting iguanas. Differences in soil type are likely to determine vegetation patterns across

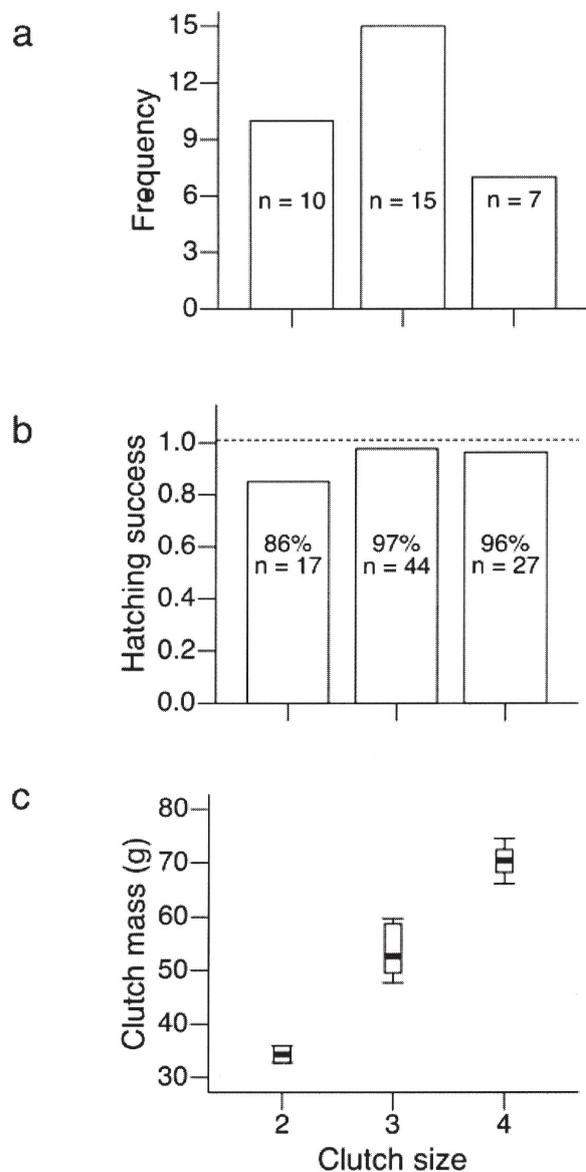


Fig. 3. (a) Clutch size in FCI, and its relationship with (b) hatching success of eggs; and (c) clutch mass. Clutch mass data were restricted to 'monitored' nests (see text; $N = 14$).

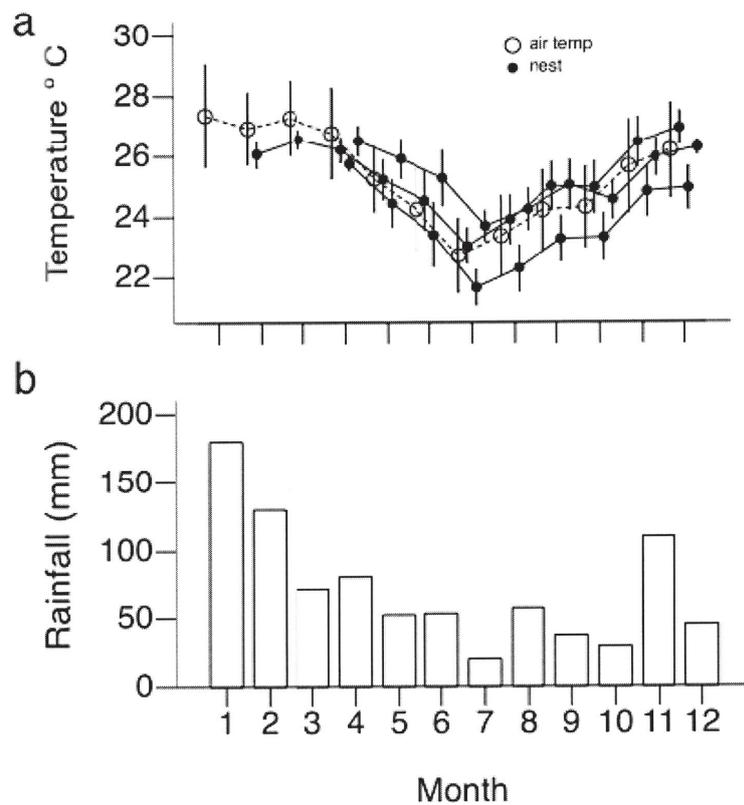


Fig 4. Monthly fluctuations in 2006 (where 1 = Jan, 2 = Feb, etc) for a) nest and air temperature (with the three nests displayed representing the min, max and mean of those monitored), and b) rainfall on Yadua Taba Island.

the island, which in turn may influence canopy cover and thus levels of incidental radiation and site openness. Soil types differed in the levels of incidental radiation received (ANOVA: $F_{2,24} = 3.79$, $P = 0.037$) and in site openness (ANOVA: $F_{2,25} = 3.76$, $P = 0.037$). Sites with organic-friable soil had greater incidental radiation than sites with organic-sandy ($t = 2.26$, $P = 0.037$) or organic-clay soil types ($t = 2.56$, $P = 0.021$). Soil type was not related to clutch size ($r = 0.26$, $P = 0.15$), hatching success ($r = 0.16$, $P = 0.12$) or nest depth ($r = 0.15$, $P = 0.4$) in monitored and previously hatched nests ($n = 32$). The mean percentage of open sky (vs. canopy) at nest sites was $10.9 \pm 0.07\%$ ($n = 28$, range 0.72–26.7%) and was positively correlated with clutch mass ($r = 0.62$, $P = 0.019$) and total incident radiation ($r = 0.92$, $P < 0.0001$). The mean total incident radiation was 2.57 ± 1.73 MJ m² day ($n = 27$, range 0.28–5.77 MJ m² day) across nest sites and was also correlated with clutch mass ($r = 0.67$, $P < 0.0001$). Nest depth was not correlated with total incident radiation ($r = -0.19$, $P = 0.35$) or site openness ($r = -0.23$, $P = 0.24$).

The mean depth of temperature data loggers in the nests was 10.6 ± 2.2 cm ($n = 14$, range 7.5–12 cm). The data from each logger was taken to represent the temperature range for that nest as the eggs lay side by side in one or

two layers, rather than end to end, and consequently were within 5 cm of the logger. The mean incubation temperature for all nests was $24.5 \pm 0.59^\circ\text{C}$ ($n = 12$, range 23.48–25.18°C) with a mean minimum temperature of $21.25 \pm 0.92^\circ\text{C}$ ($n = 12$, range 20–22.5°C) and a mean maximum of $27.43 \pm 0.52^\circ\text{C}$ ($n = 12$, range 26.5–28.5°C). We also calculated the mean daily range in temperature for all nests, $0.97 \pm 0.14^\circ\text{C}$ ($n = 12$, range 0.75–1.22°C). Mean nest temperatures were negatively correlated with the temperature range ($r = -0.52$, $P = 0.043$), so that nests with more stable temperatures were warmer than those with more variable temperatures. While sample sizes are small, mean nest temperature was not correlated with the total incident radiation reaching the nest site ($r = 0.56$, $P = 0.074$) or the depth of the nest chamber from the surface ($r = 0.04$, $P = 0.89$). Although the mean daily temperature range in nests was also unrelated to incident radiation ($r = -0.21$, $P = 0.543$), it was negatively related to nest depth ($r = -0.6$, $P = 0.039$).

In addition we buried three data loggers (at depths of 5, 10 and 15 cm) at 16 sites close to the areas in which nests were found. Loggers were buried adjacent (2 m) to nest sites and at 50 and 100 meters along four transect lines (encompassing the three main vegetation types). While the soil temperatures recorded from these

additional sites did not differ significantly from ambient air temperature, the maximum temperature was significantly higher at all three depths than those recorded within nests (5 cm, $t = -2.88$, $P = 0.008$; 10 cm, $t = -3.64$, $P = 0.001$; 15 cm, $t = -2.88$, $P = 0.008$), with minimum temperatures at the 5 cm depth also significantly lower than minimum nest temperatures ($t = -2.49$, $P = 0.02$). Maximum air temperature was significantly greater than the maximum temperature recorded inside nests ($t = 2.56$, $P = 0.021$). Therefore, temperatures within nests were slightly cooler ($\bar{x} = 24.5^{\circ}\text{C}$) than those from the 16 additional soil sites ($\bar{x} = 24.7^{\circ}\text{C}$) and the ambient air temperature ($\bar{x} = 25.4^{\circ}\text{C}$).

Mean air temperature based on monthly averages for 2006 was $25.4 \pm 1.58^{\circ}\text{C}$ ($n = 12$, range 22.7 – 27.4°C). The coolest month was July, ($\bar{x} = 22.7 \pm 1.22^{\circ}\text{C}$, range 19.5 – 26.5°C) and the warmest was January ($\bar{x} = 27.4 \pm 1.7^{\circ}\text{C}$, range 24 – 32°C). Monthly rainfall was positively correlated with mean air temperature ($r = 0.72$, $P = 0.009$), with a monthly maximum of 180 mm in January 2006 and a minimum of 20 mm in July. However, while seasonal temperatures rose and fell in a steady progression, rainfall was always less predictable (e.g., 110 mm in November, 45 mm in December). Rainfall < 100 mm was recorded in 9 of the 12 months, 8 of these consecutively (March–October), and total annual precipitation was 889 mm (Fig. 4).

Incubation, nest success and survivorship

Egg laying began at the end of February 2006, with hatching of the last monitored nest on 21 December 2006. Mean incubation period for eggs in the monitored nests was 256 ± 5.4 days ($n = 11$, range 225–285 days) and was not correlated with number of eggs in the clutch ($r = 0.04$, $P = 0.91$), hatching success ($r = -0.23$, $P = 0.45$), total incident radiation ($r = 0.19$, $P = 0.56$) or site openness ($r = 0.06$, $P = 0.85$). Incubation length was negatively correlated with mean egg mass for each nest ($r = -0.68$, $P = 0.011$), and positively correlated with both mean temperature ($r = 0.68$, $P = 0.014$) for each nest, and maximum nest temperatures ($r = 0.69$, $P = 0.014$), though not with minimum nest temperatures ($r = 0.38$, $P = 0.22$).

Hatching activity, indicated by recently hatched eggshells and muddy hatchlings, was observed from early December through to early March. Hatchlings and young-of-the-year (85 to 125 mm) were observed in all months of fieldwork, across the three years of the broader study. However, sightings were much more common during the wet season ($\bar{x} = 17 \pm 1.6$ hatchlings / month, $n = 4$; range, 7 (December

2006) — 23 (February 2006)). Only a single individual was recorded in each month of the dry season (May–October).

Hatching success was high ($\bar{x} = 87 \pm 0.01\%$) in the 14 monitored nests and 11 of these had 100% hatching success. One clutch failed with both eggs perishing apparently early in development while the other two clutches ($n = 3$ and 4 eggs) each had one failed egg. We were able to calculate survivorship to emergence for a number of excavated nests from previous years based on eggshell counts. The survivorship for these clutches ranged from 50 to 100% with a mean of $97.2 \pm 0.1\%$ ($n = 18$ nests, 49 eggs). Hatchlings captured at emergence from nests had a mean SVL of 82.6 ± 1.1 mm ($n = 7$, range 79–86 mm) and a mean body mass of 16.4 ± 0.5 g ($n = 7$, range 15–18.5 g).

DISCUSSION

Novel field data on the nesting ecology of the endangered Fijian Crested Iguana (FCI) in its tropical dry forest habitat revealed a female reproductive strategy unique among the Iguaninae and highly unusual among reptiles. These iguanas lay small clutches of large eggs every second year, and incubation is particularly prolonged. We discuss the reproductive biology of FCI in light of their unusual reproductive patterns and their tropical dry forest habitat.

Why biennial reproduction in a tropical dry forest?

Females of most lizard species, and, indeed, most iteroparous animals, reproduce at least once annually (Bull and Shine 1979, Dunham *et al.* 1988), but as understanding of lizard reproduction grows, a number of exceptions have been identified (Huey *et al.* 1974; Hasegawa 1984; Schwarzkopf 1992; Cree 1994; Iverson *et al.* 2004). Our data demonstrate a less-than-annual reproductive rate on Yadua Taba, with only about half of the adult female FCI reproducing in one season. Why would half of the adult females skip opportunities for reproduction?

Bull and Shine (1979) found that reptiles with less-than-annual reproduction rates were long-lived and often had an energy-expensive activity (such as migration, egg brooding or live-bearing) associated with reproduction. They also observed that reproductive frequency diminished with a reduction in habitat quality or growing season, independent of any behaviours associated with reproduction (Bull and Shine 1979; Van Wyk 1991). FCI do not exhibit any obvious (fecundity-independent) cost linked with reproduction. Gibbons (1981) reported that local Fijians told him of female migration to nesting

sites, but we found no suggestion of this and nests were distributed throughout the forested areas. Nor do FCI egg brood, live-bear, defend nest sites, or dig extensive nest burrows, leading us to look at environmental energy-limitation rather than behavioural energy-expenditure.

Studies from cool climate reptiles, where limited activity-seasons have been found to restrict the rate of fat accumulation and thus reproduction, highlight the impact environment alone can have on reptile reproductive patterns (Van Wyk 1991; Ibarguengoytia and Casalins 2007). Less commonly, in tropical climates where reptiles are active throughout the year a general paucity of resources or an annual period of limited resources can have a similar effect. Pig-Nosed Turtles *Carettochelys insculpta* are folivores in the wet-dry system of northern Australia and despite exhibiting no obvious behavioural cost associated with reproduction they are biennial breeders (Doody *et al.* 2003). It is suggested that the low available energy content of the dry season diet of this turtle provides insufficient energy accumulation for an annual reproduction rate (Doody *et al.* 2003).

Many Iguanines have to contend with the low digestive efficiencies associated with herbivory (Iverson 1982), and with xeric habitats and strong seasonality, both of which decrease available resources. On Yadua Taba FCI must cope with a prolonged and harsh dry season that can result in considerable adult mortality (pers. obs.). Wiewandt (1982) postulated that for Iguanines to breed successfully in any given year they must have sufficient energy reserves stored from the previous year. While some members of the Iguaninae, such as *Iguana iguana*, occupy mesic habitats and are known to reproduce annually (Rand and Dugan 1983; Brock *et al.* 1985), less than annual reproduction and low annual reproductive output have been reported for Chuckwallas (*Sauromalus obesus*, Berry 1974, Case 1982, Abts 1987), Marine Iguanas (*Amblyrhynchus cristatus*, Nagy and Shoemaker 1984, Laurie 1990), and Rock Iguanas (*Cyclura cyclura inornata*, Iverson *et al.* 2004), all of which inhabit seasonal, xeric environments. The epigenetic nature of less-than-annual reproduction is supported by data from Green Sea Turtles *Chelonia mydas* which skip years of reproduction in the wild (Mortimer and Carr 1987; Limpus and Nicholls 1988) and exhibit an annual reproductive pattern when in captivity and well-fed (Wood and Wood 1980). FCI and Banded Iguanas also reproduce up to twice annually in captivity (P. Felsted, pers. comm.) and while the present study reported a mean clutch size of 2.9 in the wild, with a maximum of four eggs, in well-fed captive populations clutch sizes can reach six eggs (Bach 1998). This demonstration of phenotypic plasticity in

reaction to changes in resource availability supports the hypothesis that resource limitation is restricting reproductive effort in wild FCI.

An alternative explanation is that the biennial reproductive pattern we observed could be modal and not accurately represent the behaviour of all females. If this were the case, it would require that young adult females reproduce less than annually when small with a transition to annual reproduction when a threshold body size is crossed. This was suggested to explain less-than-annual reproduction in *Cyclura cyclura inornata* (Iverson *et al.* 2004). However, our data show that within a wide range of adult female body sizes there is no significant difference in body size between reproductive and non-reproductive females in any one year and so is not consistent with this argument.

Are Fijian Crested Iguanas choosy about nest sites?

Most iguanas nest in open areas (Wiewandt 1982), but in the FCI most nest sites were under extremely high levels of canopy cover (~ 90%) compared to those reported for other Iguanines (*Cyclura cyclura inornata*, 22%, Iverson *et al.* 2004, *Cyclura rileyi rileyi*, 19%, Hayes *et al.* 2004). Open sites and low levels of canopy cover do occur on Yadua Taba and were originally assumed to be preferred nesting areas (Gibbons 1981), but no iguana nests were found in these sites. Instead iguana nests were seemingly randomly distributed in shaded areas within TDF or littoral forest where soil depth was > 10 cm. Surprisingly, nests that received more sunlight were not any warmer than other nests nor did amount of sunlight influence the depth of the burrow. Similarly, mean nest temperatures were not related to radiation in nests of the agamid lizard *Physignathus lesueurii* (Doody *et al.* 2006a,b). Instead, mean daily range in temperature was positively related to radiation in that species. We did not find this to be the case for FCI, though increasing mean daily temperature range was linked to decreasing burrow depth. Females may be selecting shaded nest sites that are cooler and more stable overall than the air and surrounding soil temperatures. Nests were equally distributed between three soil types and only clay and pure-sand soils were avoided. While areas with "organic friable" soil received more sun, this did not translate to changes in burrow depth or hatching success.

Prior to the current study it was not only suggested that female FCI migrated to areas of minimal canopy cover but that they nested communally (Gibbons 1981). Communal nesting (burrow aggregation) in Iguanines is commonly reported and may arise from a scarcity of

suitable nesting sites (Rand and Rand 1976; Rand and Dugan 1983; Vogel 1994; Radder and Shine 2007). While many nest excavations were aborted in dry forest areas due to obstruction by rocks and roots, incidental observations suggest no greater aggregation of nests in areas where digging was unhampered, such as in deep sandy soil under littoral vegetation. Despite the high density of iguanas (Harlow and Biciloa 2001; Morrison *et al.* 2007), it appears that FCI on Yadua Taba are not constrained by a lack of suitable nesting sites. This may explain the lack of nest guarding and female aggression in FCI on Yadua Taba. These behaviours are common among other Iguanines where competition for sites can be fierce and nest defence can last up to a month (Christian and Tracy 1982). Iverson *et al.* (2004) suggests that given the appropriate stimuli all iguanids may exhibit nest defence and this may explain female aggression associated with nesting observed in captive FCI (Gibbons 1981; Gibbons and Watkins 1982).

Is producing few large eggs a mechanism to survive the long incubation period?

Brachylophus species are unusual in several aspects of their reproduction. In addition to laying biennially, females have a small mean clutch size of only three eggs, there is no trade-off between clutch size and egg size with equal investment in each egg, the eggs and hatchlings are large and the incubation period is extremely long. In each of these attributes, *Brachylophus* are unlike all or most other members of the Iguaninae (Iverson *et al.* 2004). For example, *Brachylophus* is towards one end of a reproductive continuum with a small clutch size, a large relative egg mass (REM = 6.7) and a large relative clutch mass (RCM = 20.3), while *Iguana iguana* lies towards the other end with large clutches of up to 70 eggs, a low REM (1.1) and high RCM (29) (Iverson *et al.* 2004). Most female FCI produce a clutch of three large eggs, and large females may lay four eggs. While egg size commonly increases with maternal body size in many reptiles (Rowe 1994; Madsen and Shine 1996), there is little variation in egg size relative to clutch size or maternal body size in this species. This strongly suggests either that there is a minimum egg size necessary to survive the long incubation period or that large egg size is necessary to produce sufficiently large hatchlings to improve hatchling survival, or both. A well-founded assumption of optimal offspring size models is that selection operates primarily on size and secondarily on number of offspring (Lloyd 1987). That female FCI produce few, large eggs suggests that selection has favoured quality, rather than quantity, of offspring. Life-history theory provides multiple hypotheses that could provide explanations for each of these

particular reproductive traits, and we consider the most likely scenarios.

In dry environments large eggs are advantageous because low surface-to-volume ratio increases the ability to store more water within the egg, which may prevent desiccation and assist in the survival of the young through the extended dry season incubation (Brockelman 1975; Parker and Begon 1986; McGinley *et al.* 1987). FCI spend a vastly extended period of time in the egg compared to other Iguanine species, with incubation in the wild spanning around 256 days as opposed to the typical Iguanine incubation period of 70–98 days (Wiewandt 1982). Species with comparable adult or hatchling SVL and BM complete their incubation period in as little as a third of the time (Iverson 1979; Abts 1987; Cyril 2001; Hayes *et al.* 2004). Although FCI inhabit a tropical environment, the average temperatures for FCI nests in the wild (\bar{x} = 24.5°C) were much lower than those reported for other Iguanines (30°C–32.8°C, Wiewandt 1982). While this lower temperature may contribute to the long incubation period, another method by which hatching can be delayed is through embryonic diapause, where development of the embryo is temporarily suspended. This strategy is uncommon among lizards, occurring mainly within the Chamaeleonidae where it is thought to be an adaptation to climatic seasonality, facilitating the synchronization of hatching with a period of maximum resources (Andrews and Donoghue 2004). A lab based developmental study is required if the questions surrounding the extended incubation in FCI, together with cues for hatching, are to be answered. Hatching in reptiles may be triggered by any of a suite of environmental factors including temperature, water potential, movement, day length and barometric pressure, (Shine and Olsson 2003; Andrews and Donoghue 2004; Radder and Shine 2006). While there were 63 days between the laying of the first and last monitored FCI clutches, there were only two days disparity in the hatching dates of these two clutches, approximately two weeks after substantial rains (50 mm in 48 hrs). While the trigger for hatching in FCI remains unresolved our results show the time of hatching occurs early in the wet season and is more conserved than time of oviposition. A counterintuitive finding was that nests with longer incubation periods had higher overall temperatures. This is most likely due to nests with the longest incubations being laid earlier and experiencing more of the higher, late wet season, temperatures. Having extended incubation and hatching early in the season has been suggested to contribute to increased offspring locomotor performance, growth and survival in other lizards (Shine and Olsson 2003; Warner and Shine 2007).

Even with this long incubation through a harsh seasonal environment we found that hatching success of monitored nests was high (87%) (Fig. 3). From a total of 82 eggs, from monitored and previously hatched nests, we only recorded three shells exhibiting signs of predation (in the form of gnaw marks by Pacific Rats) and these may have occurred after hatching. Thus, egg mortality seems more likely to occur through environmental effects, but even this was minimal with only five eggs failing. The 97% hatching success in unmonitored nests does not account for nests that failed completely and so were not identified through a hatching burrow or eggshells. Therefore, while it does support high within-clutch hatching success it does not provide a complete picture and overall hatching success is likely to be slightly lower and similar to monitored nests. The combination of an extended incubation period and high hatching success found in this study suggests that incubation is a relatively safe period in the FCI life cycle, a way of bridging the resource-limited dry season.

Is producing large hatchlings a mechanism for reducing predation on hatchlings?

Predation on hatchlings is a major cause of mortality in a number of Iguanine species (Rand and Robinson 1969; Wiewandt 1977; Werner 1983; Vogel 1994) and survivorship of eggs is lower for mainland iguana populations where predators are more common. While large offspring may be an adaptation to harsh environments, high predation rates on hatchlings and juveniles may favour selection for more, smaller, offspring in these environments (Christian 1986; Vogel 1994). For example, while both genera of Galapagos iguana occupy a similarly harsh environment, *Conolophus* hatchlings suffer disproportionately high predation rates, and are smaller and hatch from larger clutches than *Amblyrynchus* hatchlings (Werner 1983; Laurie 1990; Iverson *et al.* 2004). Hatchlings on Yadua Taba were at no stage in development distinctly vulnerable to predation by their main potential predators; Swamp Harriers *Circus approximans* and Pacific Rats *Rattus exulans*. While iguanas accounted for the vast majority of prey items of the Fijian Swamp Harrier they were overwhelmingly adults and subadult individuals (P. Harlow unpublished data). Although research from New Zealand demonstrates that Pacific Rats can reduce reptile populations through predation (Towns and Broome 2003) their impact on this system remains unresolved. During our broader three year study on iguanas we observed no evidence of predation on any post-hatching iguana by Pacific Rats, and while rats were regularly (incidentally) seen on night surveys they were

never observed near iguanas, and very rarely in vegetation above the height of ~ 2 m. While the impact of the, relatively recently arrived, Pacific Rat deserves more study it appears that neither FCI eggs nor hatchlings experience high predation levels in their natural environment and as such their large size may be related to lack of, rather than pressure from, predators.

Is producing large hatchlings necessary because of the constraints placed on body size and growth through herbivory?

This is a difficult question to answer without detailed physiological and nutritional information on juvenile FCI, but the large size of the hatchlings is likely to be advantageous to their primarily herbivorous diet. Herbivory in lizards has been linked to large size (Cooper and Vitt 2002) and it has been proposed that small lizards (< 50 g), with their relatively higher metabolic rates, cannot meet their energy needs solely with plants (Pough 1973). It follows on that juvenile herbivores may not have the gut capacities required for processing a fully herbivorous diet and thus they may need to deal with this issue in various ways. In FCI, hatching is synchronous with the wet season flush of new growth, fruit and flowers, which are lower in fibre than mature leaves and can be more rapidly digested to obtain nutrients. An additional problem is that proteins necessary for growth in juvenile vertebrates occur in relatively low abundances in plants (Stevens and Hume 1995; Durtsche 2004). Some Iguanines overcome this difficulty by going through an ontogenetic shift from juvenile insectivory to adult herbivory (Van Devender 1982; Cooper and Vitt 2002; Durtsche 2004). Juvenile FCI consume a wide range of plant species and, while there are no published data suggesting insectivory (Morrison *et al.* 2007), incidental observations suggest juveniles are ingesting caterpillars, either purposefully or accidentally while feeding on plants during the wet season (pers. obs.). It is likely that large hatchlings can ingest more food (plant and animal), lay down more fat reserves and attain sizes that facilitate the folivory that will sustain them as adults more rapidly than smaller individuals. In FCI this may be the key to hatchlings surviving their initial dry seasons.

Conservation implications

The value of detailed reproductive information to reptile conservation programmes has long been recognized (Cree and Thompson 1988), but prior to this study, virtually all our knowledge of FCI reproduction was based on captive animals living under completely different conditions to wild animals in their natural habitat. Our study has demonstrated

that energy appears to be a limiting factor in the reproduction of wild FCI. This result has important implications for any future head-starting and translocation programmes in Fiji because the habitat quality, and in particular the changes in annual food quality, of any potential translocation site must be carefully evaluated. Yadua Taba has the only protected and secure population of FCI and it is one of the last prime tropical dry forest sites in Fiji. The Species Recovery Plan (IUCN/SSC Iguana Specialist Group 2008) suggests, among other things, captive breeding of unique genetic lineages and relocation or translocation of populations from the one secure population to a number of additional secure sites. Before any such translocations can happen, a detailed assessment of vegetation composition needs to be conducted on all potential translocation sites to maximize not only the survival but also the reproduction of translocated animals.

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