REPRODUCTIVE ECOLOGY OF THE MOUNTAIN DRAGON, *RANKINIA (TYMPANOCRYPTIS) DIEMENSIS* (REPTILIA: SQUAMATA: AGAMIDAE) IN TASMANIA

by Jemina Stuart-Smith, Roy Swain and Andrew Welling

(with three tables and two text-figures)

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The mountain dragon, *Rankinia (Tympanocryptis) diemensis* (Gray, 1841), is the only member of the Agamidae in Tasmania. It occurs in some of the coldest regions occupied by any dragon in Australia, and is found in a variety of habitats ranging from coastal heath to alpine scrub. This paper examines the reproductive ecology of *R. diemensis* in the most southerly range of its distribution, providing baseline data on timing of reproductive events, reproductive cycles, nesting behaviour and ovipositioning, clutch characteristics and incubation conditions. Winter torpor lasts approximately seven months with males emerging in early September and spermatogenesis occurring from September–November. Females emerge later, with vitellogenesis occurring from September–December. Gravid females may be found between October and January, but females are non-vitellogenic from late December until the following season. The first clutch is typically laid from October–December, with a variable clutch size (2–11 eggs). Females store sperm and a second clutch may be laid five weeks after the first. Eggs incubated in artificial enclosures at low altitude hatched after 72–106 days, after experiencing an average daily temperature of 19°–22°C, and a range of 5°–39°C.

Key Words: Agamidae, dragon lizard, reproductive ecology, *Rankinia*, Tasmania.

INTRODUCTION

Rankinia diemensis (Gray, 1841) is the only lizard species representative of the Family Agamidae, commonly known as dragon lizards, found in Tasmania; the remaining 17 species comprising Tasmania's lizard fauna are all skinks in the Family Scincidae (Hutchinson *et al.* 2001). It is distinctive among Australian dragons as it is the southernmost agamid in the world and occurs in arguably the coldest habitats occupied by any agamid in Australia (Kent 1987, Hutchinson *et al.* 2001). It is one of only three oviparous reptiles in the State — a strategy in itself that is atypical of cold-climate reptiles (Shine 1985).

Rankinia diemensis is a small cryptic species that exhibits strong female-biased size dimorphism (Cogger 1992). It is widespread throughout all of Tasmania east of Tyler's Line (a faunal divide defined by Shiel *et al.*1989) and occurs also in the Furneaux Group, Flinders Island and nearby islands in Bass Strait, as well as in Victoria and southern New South Wales. On the Australian mainland it is mostly restricted to higher altitudes, giving rise to its common name, the 'mountain dragon' (Kent 1987). This species has frequently been re-classified, but we use genus *Rankinia* because the most recent phylogenetic analyses by Melville *et al.* (2001) place the current status of this species in this monotypic group, rather than including it in the genus *Tympanocryptis.*

Agamids are typically distributed through hot, arid or tropical regions (Greer 1989, Witten 1993) and the cool-cold temperate climates found in Tasmania represent extreme conditions and result in a greatly reduced activity season compared to that of the island's skink fauna. Winter torpor in adult *R. diemensis* lasts for seven months (J.S-S. unpubl. data), significantly longer than that occurring in viviparous alpine skinks (e.g., *Niveoscincus microlepidotus* (O'Shaughnessy, 1874): 5–6 months). This paper provides preliminary data on the reproductive ecology of *R. diemensis.* Our aim is to provide baseline information on a species that has not been studied anywhere in its distribution and that represents an important element of the herpetological fauna of Tasmania.

MATERIALS AND METHODS

This study presents previously unpublished data collected over three breeding seasons (Welling 1999, Duraj 2002); animals were observed *in situ* or collected and held for study in individual outdoor enclosures at the University of Tasmania. The information presented relates predominantly to reproductive ecology but relevant data on morphology and behaviour are also provided.

Lizard collection

Gravid females were caught (while digging nesting burrows) by hand from areas of southeastern Tasmania in October/November 1998 and 2001 for investigation of reproductive output and strategy. Collections were made from similar habitat (coastal heathland and dry sclerophyll forest) in and around the Cape Deslacs Reserve, Clifton Beach, Kingston township and the University grounds. Individual enclosures were circular (made of sheet metal: diameter 1 m; walls 40 cm high), located on an easterly-facing slope and filled with brown road gravel to a depth ranging from 15–30 cm. Rocks and litter provided cover and vantage points, while a wire netting lid provided protection from predators. The entire set of enclosures was protected under bird netting. Water was provided *ad libitum* and food (ants or mealworms) was provided three times per week.

Nesting Behaviour and Egg Collection

Females preparing to oviposit undertake a period of test burrow-digging that lasts for several days. Once this behaviour was observed captive females were monitored twice daily. Date of test burrows was recorded, as were behaviours associated with actual nest-digging and laying. After oviposition, females were removed, weighed (± 0.1 g) and a range of morphometric characteristics (snout-vent and tail lengths; head width, depth, length; and interlimb and limb measurements) recorded using electronic calipers accurate to ±0.01 mm. Most eggs were carefully uncovered, transferred to the laboratory, weighed using a Sartorius electronic balance (±0.01 g) and used in a series of incubation experiments not reported here.

Natural Egg Incubation

A total of five nests (two in 1999, three in 2002) were randomly selected to remain *in situ* as outdoor enclosure nests. The nests were carefully uncovered so that a temperature logger could be placed adjacent to eggs to automatically record nest temperature every 15 minutes for the duration of the incubation period.

Reproductive Cycles

Gonad development and reproductive status were assessed by dissection of preserved material held in the collections of the Queen Victoria Museum, Launceston, and the Tasmanian Museum and Art Gallery, Hobart (n = 62: 14 adult males, 26 adult females and 22 juveniles). The animals had been collected from areas across Tasmania between 1936 and 1998, and were collected during all months of the activity season.

In males, the testes were measured using electronic digital calipers accurate to ±0.01 mm and testicular volume was calculated from the volume of an ovoid, and the epididymides were inspected for the presence of spermatozoa in the lumen. Subsequently, males were subjectively categorised as active (enlarged testes and milky epididymides), regressed (small testes and dark epididymides), or recrudescent (moderate enlargement of testes, but dark epididymides). Females were dissected (n=26) and classified based on the size and appearance of the follicles and the presence of oviductal eggs. The number of ovarian follicles and their diameter was recorded (using electronic calipers). Animals were categorised as: non-vitellogenic (follicle diameter <1mm), vitellogenic (follicle diameter 1–2 mm), gravid (oviductal eggs present) or recrudescent (vitellogenic follicles >1mm).

RESULTS AND DISCUSSION

Morphology

Rankinia diemensis is a relatively small, cryptic, dragon lizard exhibiting strong female-biased size dimorphism. In Tasmania the largest snout-vent length (SVL) we have recorded for females is 84 mm and for males is 66 mm. Table 1 allows comparison of mass and size of adults of both sexes (also see fig. 1). Sexual size dimorphism is common in Australian agamids; however, in most species males are the larger sex, a characteristic linked to the establishment and defence of territories (Brattstrom 1971). In most agamids, males are aggressive and conspicuous defenders of territories and this forms the basis of mate selection. The existence of female–biased sexual dimorphism and apparent lack of male territories in *R. diemensis* may have significant implications for sexual selection strategies in this species.

Colouration varies from pale beige, through to light and dark greys, bright orange or red-brown (J.S-S. unpubl. data, Hutchinson *et al.* 2001, fig. 1), with mixes of all colours seen in individuals. There does not appear to be sexual dichromatism in this species, which relies heavily on camouflage for avoidance of predators. The colouring reflects this — usually varying according to habitat; it also has modified epidermal scales characteristic of all agamids (Witten 1993), in the form of rough or spiny scales (Hutchinson *et al.* 2001). A distinctive line of dark diamond-shaped marks runs dorsally along the spine from head to tail base — with patches of lighter colour between the 'diamonds' (fig. 1). When the animal is cold, it becomes dark and patterning is obscured (Hutchinson *et al.* 2001). Colour changes also occur in the base colour of individuals (i.e., between the diamonds). These changes can occur relatively quickly (within minutes), and are common among agamids, probably pertaining to social interactions (Greer 2003).

Behaviour

Crypsis

Although *R. diemensis* relies heavily on camouflage to avoid predator detection, it also employs cryptic behaviour, spending most of its time motionless, even to the extent of appearing to regulate breathing. When approached it will typically run a short distance, before stopping abruptly (Hutchinson *et al.* 2001). The sudden stop is unexpected by the observer, and, even though it does not always occur when cover has been reached, it is still an effective form of predator escape because the observer's eye typically follows the direction of

TABLE 1
Comparison of snout-vent length, mass and tail length for adult male and female *Rankinia diemensis*

	Snout-vent length (mm)			Mass (g)			Tail length (mm)		
	Range	Mean	N	Range	Mean	N	Range	Mean	N
Male	49–66	57	24	2.8–6.8	4.6	24	82–113	97	24
Female	56–82	72	34	5.6–13.4	10.3	33	82-137	117	33

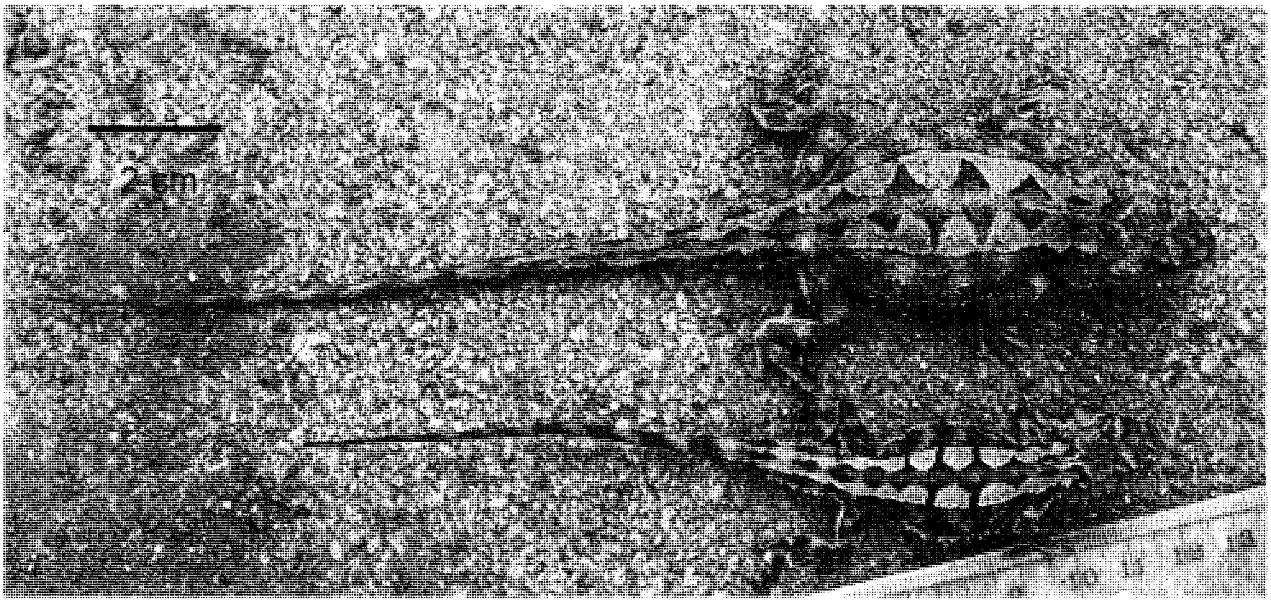

FIG. 1 — Dorsal patterning and sexual size dimorphism in Rankinia diemensis *(gravid female top, male below).*

movement beyond the lizard. The camouflage provided by the lizard's outline, colouration and patterning makes the motionless animal very difficult to detect.

Timing of events

Adults may undergo a torpor lasting up to seven months, but hatchlings appear to spend significantly less time in torpor — presumably since they do not have the ability to build sufficient reserves to support such an extended period without food. Field observations reveal that hatchlings remain active well into the autumn months (late April), while adults are rarely seen by late summer (mid-February). Adults have been maintained in laboratory torpor conditions for six months at 5°C — indicating that arousal from torpor to forage is not necessary, but during this time they have been observed drinking water occasionally.

Field observations reveal that males emerge in early spring (early September) at least two weeks before females. They spend considerable time perched on logs or rocks (at heights up to 1 m), which is atypical of their normal cryptic behaviour. It is unclear whether either sex maintains a territory, but there is certainly no obvious territorial behaviour. Females emerge later in spring, and are able to lay a clutch by early summer (November to mid-December). Females prefer relatively open sites to lay their eggs — disturbed soil is often favoured and the sides of quarries and edges of dirt roads are often used as nest sites.

Early in summer, and once the breeding season has finished, both males and females moult. Activity then undergoes one further peak of reduced intensity (late December to mid-January) when second clutching may occur. From this point on, adults are rarely seen. Immature lizards (including hatchlings from the previous year) are active throughout the season. Hatchlings emerge in March/April, and are active as long as the warmer weather lasts. Although hatchlings are commonly sighted, older juveniles are rarely seen at any time. This may be due to high mortality over the first winter season, consequent on the long incubation period and emergence close to the onset of winter, but it may also reflect the extremely cryptic behaviour typical of adults outside the breeding season.

Displays and communication

Communication is primarily visual among *R. diemensis*, as in agamids generally (Greer 1989, Witten 1993, Ord & Evans 2003), but hissing has been heard at capture (J.S-S. unpubl. data.). This behaviour is not unheard of in dragons, although it is rare (Greer 1989). Agamids typically produce discrete visual displays to mediate social behaviour (Watt & Joss 2003), and some of these are utilised by *R. diemensis*, including arm-waving, head-bobbing, and tail lashing. Typically these displays denote aggressive or submissive behaviour. The structure or function of these displays has not been determined for *R. diemensis* and they are the subject of a current study (J. S-S).

Reproduction

Reproductive cycles

Environmental conditions, particularly climatic, can have a strong influence on reproductive cycles. Oviparous lizards are not common in areas of cold, variable conditions because they do not have control over the conditions experienced during egg incubation (Heatwole & Taylor 1987). When seasonal temperatures are highly variable, as in Tasmania's climate, there is only a short summer period for reproduction, embryonic development and offspring dispersal to occur. Examination of museum specimens indicated that spermatogenesis occurs from early September to early November (n=15) with testes size reaching a maximum in late September. Testes have regressed to one quarter of their maximum volume by late October, and remained regressed thereafter until late February. Recrudescence begins in March (fig. 2). Late October to early November appears to be the main mating period, during which time males store sperm in their epididymides.

Females emerge from winter torpor later than males (late September), with vitellogenesis occurring from September–December, and gravid females recorded from late October to January. Females are non-vitellogenic from late December to March, when recrudescence begins (fig. 2).

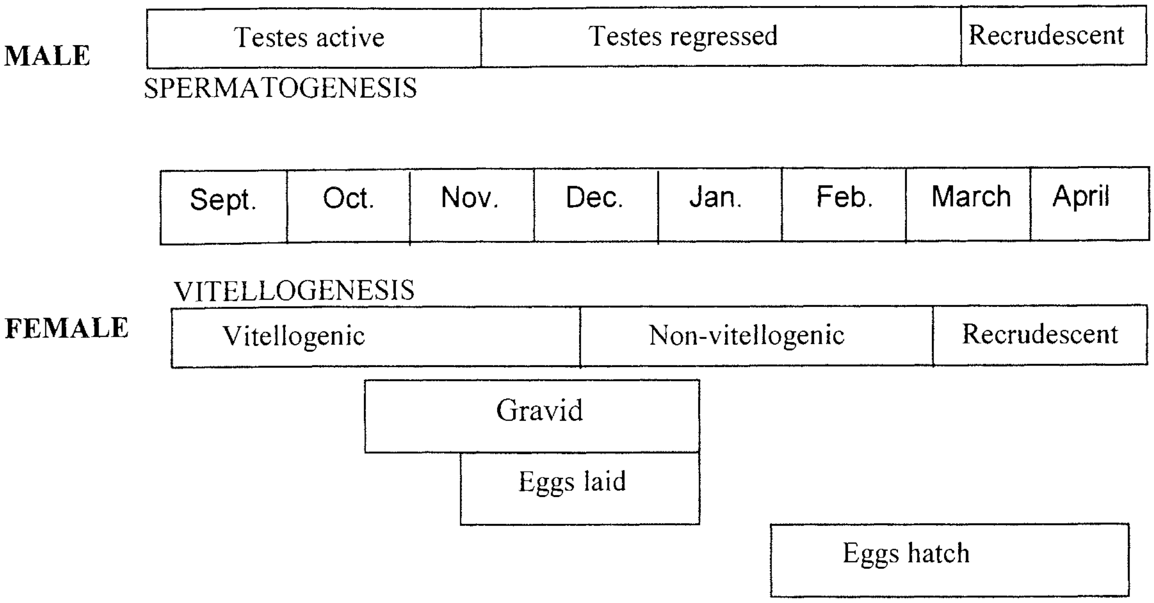

FIG. 2 — Calendar of major reproductive events in males (top) and females (below) of Rankinia diemensis.

Nesting behaviour and ovipositioning

Females produce first clutches between October and December in Tasmania. Gravid females usually excavate a series of 'test' burrows prior to digging the final nest; these are more shallow than the final nest, and remain uncovered. Females maintained in artificial outdoor enclosures (n=23) averaged two test burrows prior to oviposition, and the average time between the first test burrow and oviposition was five days. Test burrows surrounding natural nests (verified by uncovering nests) have also been observed in the wild, and on three occasions burrows have been filled in on a different day than that on which they were excavated. Test burrows are often quite close to the final nest site, and females have been observed digging burrows within 1.5 m of each other, at the same time, and in full view of each other. Observations of extensive 'tongue-flicking' (in enclosures) prior to oviposition suggest that chemical cues may be an important determinant in nest site selection. Nests are usually located in relatively open areas — with no direct shading, but still in close proximity to some form of cover.

Final burrow excavation and ovipositing takes most of a day and, if started late, may spill over to a second day. Before starting, females exhibit heightened alertness for as long as two hours, usually perched on a vantage point about 30 cm above ground at the edge of an open patch. Digging involves excavating soil with the forelimbs and flicking it backwards with the larger hind limbs. Digging takes place at an angle, creating a burrow 60–85 mm deep (n=23). During laying, the female reverses her position so that her head and forelimbs protrude from the nest, as does her tail (bent around to one side). When laying is finished she exits from the burrow, and may turn and move the eggs about with her snout before covering them. Digging and oviposition takes several hours. When finished the female covers the eggs by flicking soil back into the nest with her fore- and hind- limbs, with intermittent bouts of rapid fore-limb stamping and snout-pushing of the soil covering the eggs, presumably to compact it. She may spend as much as two hours on this activity; once completed it is impossible to locate the nest visually.

Clutch characteristics

Clutch size varies from 2–11 eggs, with female size being positively correlated with clutch size. Egg mass at oviposition is between 0.4 and 1.0 g (for eggs that hatch successfully), with dimensions averaging 110 x 70 mm (see table 2 for egg measurements). A second clutch can be produced five weeks after the first, but almost invariably this will contain fewer eggs than the first. Reduced clutch size later in the season is typical of lizards that produce multiple clutches in a single breeding season (Nussbaum 1981, Forsman 2001). James & Whitford (1994) concluded that progressively smaller clutches in the side-blotched iguanid *Uta stansburiana* (Baird & Girard, 1852) was an adaptive response to poor environmental conditions that occur late in the season; they argued that smaller clutches lower the risk of reproductive failure for the female. Similarly for *R. diemensis*, environmental conditions deteriorate later in the season, with cooler temperatures, reduced photoperiod, and often increases in rainfall. In *R. diemensis*, however, individual eggs in the second clutch are larger, indicating that, although fewer eggs are being produced, more energy is being allocated to each egg. Presumably this

TABLE 2
Reproductive investment and egg dimensions at oviposition

	Mean (± s.e.[1])	Range
Relative clutch mass[2] (%)	45 (2)	0.16–0.71
Clutch size	6.0	2–11
Clutch mass (g)	4.52 (0.23)	1.82–7.01
Egg mass (g)	0.69 (0.01)	0.43–1.01
Egg length (mm)	11.0 (0.07)	7.0–14.5
Egg width (mm)	7.0 (0.05)	5.0–8.0

[1] s.e. = standard error))

[2] Relative clutch mass = (mass of eggs/(mass of female – mass of eggs))*100

provides more energy for development if this is prolonged by poor incubation conditions and/or larger hatchlings with a greater chance of survival when emergence occurs very late in the season. Size at emergence has significant consequences for a hatchling's subsequent growth, survival (Sinervo 1993), and ability to forage effectively and escape predators (Phillips *et al.* 1990).

Females held in captivity from early spring, without access to males, are able to lay a second clutch, clearly demonstrating their ability to store sperm. Among Australian agamids this has only been demonstrated for one other species: the bearded dragon, *Pogona barbata* (Cuvier, 1829) (Amey & Whittier 2000), though it may be quite common. The advantages associated with sperm storage include improving opportunities for sperm competition between sperm from different males (Parker 1970) (assuming that females mate with more than one male). It may also reduce competition between the sexes for resources, thus facilitating production of a second clutch, and it also ensures that reproduction is still possible if the potential of encountering males is low (Kumari 1990) or if male activity decreases later in the season.

Incubation

Incubation duration ranged from 72–106 days in enclosure nests with a hatching success of ≥80%; duration strongly depended on the temperatures experienced during incubation. Warmer nest temperatures have strong implications for hatchling survival as they result in shorter incubation times, meaning longer foraging and basking times prior to the first winter torpor (Gutzke & Packard 1987, Packard & Packard 1988).

Data from temperature loggers in the five nests located in our outdoor enclosures revealed that eggs experienced average daily temperatures of between 19° and 22°C, although the range was from 5°–39.5°C. As expected, clutches that spent a greater amount of time at lower temperatures, had longer incubation durations. Since the period available to hatchlings for foraging prior to winter is limited, earlier emergence, from nests located in warmer incubation sites will provide more time for basking and foraging. Maternal nest site choice may therefore be a key determinant of a female's reproductive success. Unlike many other agamids, temperature-related sex determination does not occur in *R. diemensis* (J.S-S. unpubl. data).

CONCLUSIONS

Rankinia diemensis is a relatively small cryptic dragon lizard, although Tasmanian specimens reach a larger size than their mainland counterparts (Cogger 1992). In Tasmania, and probably elsewhere, its life history strategy is constrained by climate, which necessitates spending much of its time in torpor, severely reducing the time available for reproduction and growth. Egg incubation periods are long, due to cool nest temperatures, and hatchling survival is endangered by the short period of time prior to winter in which fat reserves are built. The species presents an ideal opportunity for examining the evolution and adaptation to cool climates of life history in oviparous lizards. Although we have provided the first extensive data on the reproductive ecology of the mountain dragon in Tasmania, many questions remain. Regarding reproduction, the existence of pronounced female-biased size dimorphism, very unusual for agamid lizards, raises intriguing questions about sexual selection strategies and their responses to climatic constraints. Likewise, an understanding of how conditions during and immediately following torpor influence survival and reproductive investment would yield valuable insight into how this unusual dragon maintains successful populations even on the exposed Central Plateau of Tasmania.

TABLE 3
Duration of incubation and nest temperatures in five nests located in artificial enclosures

Duration of incubation (days)	Nest temperature	
	Mean (±s.e.)	Range
72	19.7 (0.09)	5.6–38.1
78	20.3 (0.09)	8–39
99	21.1 (0.10)	10.3–38.1
106	17.3 (0.06)	8–37.5
106	17.7 (0.12)	6–39.5

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