

Reproductive ecology of the jacky dragon (*Amphibolurus muricatus*): an agamid lizard with temperature-dependent sex determination

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Abstract The jacky dragon, *Amphibolurus muricatus* (White, ex Shaw 1790) is a medium sized agamid lizard from the southeast of Australia. Laboratory incubation trials show that this species possesses temperature-dependent sex determination. Both high and low incubation temperatures produced all female offspring, while varying proportions of males hatched at intermediate temperatures. Females may lay several clutches containing from three to nine eggs during the spring and summer. We report the first field nest temperature recordings for a squamate reptile with temperature-dependent sex determination. Hatchling sex is determined by nest temperatures that are due to the combination of daily and seasonal weather conditions, together with maternal nest site selection. Over the prolonged egg-laying season, mean nest temperatures steadily increase. This suggests that hatchling sex is best predicted by the date of egg laying, and that sex ratios from field nests will vary over the course of the breeding season. Lizards hatching from eggs laid in the spring (October) experience a longer growing season and should reach a larger body size by the beginning of their first reproductive season, compared to lizards from eggs laid in late summer (February). Adult male *A. muricatus* attain a greater maximum body size and have relatively larger heads than females, possibly as a consequence of sexual selection due to male-male competition for territories and mates. If reproductive success in males increases with larger body size, then early hatching males may obtain a greater fitness benefit as adults, compared to males that hatch in late summer. We hypothesize that early season nests should produce male-biased sex ratios, and that this provides an adaptive explanation for temperature-dependent sex determination in *A. muricatus*.

Key words: Agamidae, incubation temperature, nest temperature, reproduction, sex ratio.

INTRODUCTION

The occurrence of genotypic and environmental mechanisms for sex determination in closely related reptile species has stimulated much scientific speculation and debate (e.g. Janzen & Paukstis 1991). Many plausible adaptive hypotheses have been proposed including several that suggest that differential effects of incubation temperature on hatchling physiology and morphology are associated with future reproductive success (Rhen & Lang 1995; Tousignant & Crews 1995; Roosenburg 1996; Reinhold 1998). However, there are few supporting data and there is no consensus among researchers for these various hypotheses.

Most Australian squamate reptiles, including some agamid lizards and all snakes, have genotypic sex determination. The family Agamidae is apparently unique among Australian squamates, in that it includes species

with genotypic and species with environmental sex determination. In some species of agamids, temperature-dependent sex determination (TSD) occurs, whereby egg incubation temperatures determine hatchling sex. Agamids occur in all Australian habitats from tropical rainforests to alpine woodlands, although the greatest species diversity occurs in the arid zone (Cogger & Heatwole 1981). There are over 70 species in 13 genera (Cogger 1992), displaying variation in sexual dimorphism and a range of life history strategies including annual and long-lived species (Greer 1989). This combination of features make agamid lizards an ideal group in which to test the competing hypotheses on the evolution of TSD.

However, before testing these hypotheses we need to identify the sex-determining mechanisms, life history traits and thermal environments of field nests for a wide range of agamids, information which is currently lacking. Although there are a variety of life history studies of Australian agamids (see Greer 1989), the sex-determining mechanism is only recorded in three species: one with genotypic sex determination (*Pogona*

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vitticeps: Viets *et al.* 1994), and two with temperature-dependent sex determination (*Physignathus lesueurii*: Harlow 1994; *Chlamydosaurus kingii*: Harlow & Shine 1999). There are no published temperature data for field nests of Australian agamids.

We investigated the sex-determining mechanism and reproductive ecology in an agamid, the jacky dragon (*Amphibolurus muricatus*). By incubating eggs over a wide range of temperatures, we identified the sex-determining mechanism and examined the effects of temperature on hatchling morphology. Further aspects of the reproductive ecology were examined in both wild-caught gravid females and preserved museum specimens. Important life history characteristics such as the occurrence of multiple clutching within a season, male reproductive cycles and sexual dimorphism in head and body size were obtained from preserved specimens. To validate the biological reality of the range of our laboratory incubation temperatures, we recorded temperatures in field nests. We then attempted to relate the seasonal temperature trends we observed in the field nests to the sex ratios that occurred in the laboratory incubations. In the light of this information, we discuss how the reproductive ecology of this species may be associated with the sex-determining mechanism observed, and propose a testable hypothesis to explain the adaptive significance of temperature-dependent sex determination in this species.

METHODS

Study species

The jacky dragon (*Amphibolurus muricatus* (White, ex Shaw 1790)) is one of the most common and conspicuous agamid lizards in the temperate southeast of Australia (Cogger 1992). It is a medium-sized agamid that occurs in natural rural and occasionally urban habitats. Despite its abundance and proximity to many large cities, most aspects of its basic ecology, including its reproductive ecology, remain unknown. Information available for this species includes reproductive data from museum specimens, data on captive reproduction and laboratory studies of thermal biology (Heatwole & Firth 1982; James 1983; Hawker 1996). Based on 14 lizards, James (1983) reported that clutch size was positively correlated with female body size, and that the minimum size at maturity for females was 78 mm snout-vent length.

Museum specimens

We obtained reproductive and morphological data from 283 preserved jacky dragons (281 from New South

Wales and two from southeastern Victoria) in the collection of the Australian Museum, Sydney. For each lizard we measured snout-vent length (SVL), total length and three head measurements: (i) jaw length from the posterior end of the lower jaw to the tip of the snout, (ii) head width at the corner of the mouth, and (iii) head depth measured from the lower jaw to the cranial platform immediately behind the eyes. The size and condition of the gonads were recorded, and the specimen weighed after any preserving fluid had been drained from the body cavity.

In males the maximum length and width of the left testis was measured, and the volume calculated using the standard formula for a prolate spheroid (Mayhew 1963):

$$\text{Testis volume} = 4\pi/3 \times \text{length}/2 \times (\text{width}/2)^2$$

An indication of the mating season can be obtained by examining the efferent duct where male lizards may store viable sperm after the testes have begun to seasonally regress. We scored the condition of the efferent duct depending on the presence or absence of sperm, from translucent and thin (0, non-reproductive) to opaque and thick (3, reproductive). Females were considered reproductive if they contained oviducal eggs, yolking follicles larger than 3 mm, or showed evidence that they had recently laid eggs. Post-partum females were distinguished by macroscopically visible *corpora lutea* and a thick and muscular oviduct. These characteristics regress after egg laying so that it is difficult to distinguish the reproductive females by the end of the reproductive season.

Female reproduction and egg incubation

In reptiles without heteromorphic sex chromosomes, such as the agamids (Witten 1983), no sex-specific genetic markers have been identified (Coriat *et al.* 1994). Consequently, the only way to establish the sex-determining mechanism in these reptiles is to sex hatchlings from eggs incubated over a wide range of temperatures (Viets *et al.* 1993). We obtained 32 clutches of eggs from wild-caught gravid females to investigate the mechanism of sex determination in jacky dragons. Seventeen females were from Myall Lakes National Park, New South Wales (32°35'S, 152°21'E), seven from Tomago Sandbeds, New South Wales (32°46'S, 151°48'E), and the rest were from other locations in southeastern New South Wales. The first two localities are approximately 50 km apart, and both consist of open woodland, coastal heath and open forest (Fox & Fox 1978; Fox *et al.* 1979, 1996). Gravid lizards were obtained in all months from late October through to early February.

Wild-caught lizards were kept in the laboratory in terraria containing deep soil and shelter sites. Water and

live food (crickets and cockroaches) were available *ad libitum*. An incandescent globe provided a basking site at one end of the terraria for 10 h per day. Each female was checked twice daily for oviposition and given a weekly intraperitoneal injection of synthetic oxytocin (60 IU/kg) to induce egg laying (Bedford *et al.* 1993). The mean time between capture and oviposition in the laboratory was 20 days, with a range of 3–50 days. Captive lizards were weighed at regular intervals, before injecting oxytocin, and again immediately after oviposition. We calculated relative clutch mass (RCM) by dividing the weight loss due to clutch mass by the postpartum mass of the female.

A total of 163 eggs from 32 clutches were incubated in the laboratory over six consecutive reproductive seasons: summer 1993–1994 to summer 1998–1999. Eggs were weighed to the nearest mg (usually within hours of being laid), and individually buried 3/4 deep in moist vermiculite (–200 kPa water potential or 120% water by dry mass of vermiculite) in a numbered 125 mL glass jar, then sealed with plastic wrap and secured with a rubber band. Eggs weighed more than 24 h after laying were not included in the egg mass analyses below. Eggs from 22 of the 32 clutches were divided between two incubation treatments, eight clutches were incubated at only one temperature and two clutches at three temperatures.

We used 10 incubation treatments: eight at constant temperatures (23, 25, 26, 28, 29, 30, 31 and 32°C) in temperature-controlled incubators, and two cycling-temperature incubators programmed for daily thermal fluctuations more typical of natural nests. These two cycling incubators were programmed to follow a 10-step daily sinusoidal curve (27 and $33 \pm 5.0^\circ\text{C}$; mean \pm SD). Their temperatures were measured every 30 min inside a jar of vermiculite by a calibrated temperature probe connected to a data logger. Over the incubation period these incubators maintained mean actual temperatures of $27.38^\circ\text{C} \pm 3.50^\circ\text{C}$ and $33.10^\circ\text{C} \pm 3.62^\circ\text{C}$, respectively. Jars were moved between and among shelves in the incubators twice each week to reduce effects of possible temperature gradients within the incubators (Harlow & Shine 1999).

Incubators were checked daily and the date of hatching recorded when the egg was pipped. After emergence from the egg, each hatchling was weighed (to the nearest 0.001 g) and measured (SVL and total length to the nearest 0.5 mm), then sexed by hemipene eversion (Harlow 1996) under a low-power microscope. Healthy eggs usually collapsed at pipping with release of egg fluids and the hatchling emerged within 24 h. If an egg collapsed, and the lizard had not emerged within two days, it was opened and the hatchling removed and processed as above. Hatchlings were released at the site of capture of the mother.

Field nests

During the summer of 1998/1999 we located five jacky dragon nests in Myall Lakes National Park. Apparently, Jacky dragons may excavate several short nesting burrows over several days, only one of which is eventually chosen for egg laying (personal observation, JET). After laying her eggs and refilling the nesting burrow, the female scatters sand, and sometimes leaves or lichen, over the area thus camouflaging the nest. By daily inspection of the sites where freshly prepared nesting burrows were observed, two newly laid nests were located in late spring and early summer, and a third was located when a gravid female was seen (but not disturbed) in the process of oviposition in mid summer. Two other nests were found, one in the process of hatching and one recently hatched. These nests were located by the distinctive holes left by hatching lizards emerging from the packed sand.

We recorded hourly nest temperatures in the three freshly laid field nests for 54–58 days, over a 125-day period. All nests were excavated with a teaspoon within two days of laying, and the tip of a data logger temperature probe (Hobo-Temp, Onset Computer Company, Pocasset, MA, USA) was inserted adjacent to, and touching the topmost egg. For nests 1 and 3 we also recorded nest temperatures at the level of the deepest egg. Only one temperature probe was used in nest 2 as all eggs were on the same horizontal plane. We measured the depth to each egg, then carefully refilled the nest to its original condition.

We returned 54–58 days later and excavated each nest. This time was prior to the estimated time of hatching, but after sex would have been determined in a TSD species (Bull 1987). Each egg was removed to an individual jar of damp vermiculite, and returned to the laboratory where incubation was completed in a constant 30°C incubator. All hatchlings were measured and sexed (as above), and released at the nest site.

We estimated the proportion of full sun directly over the egg chamber of nests 1 and 2 by measuring the photosynthetically active radiation (PAR) levels (Sunfleck Ceptometer: Model SF-80, Decagon Devices, Pullman, WA, USA). These measurements were made between 12.20 hours and 14.50 hours (Eastern Summer Time) on days with no cloud, and are a mean of 10 sequential readings taken at ground level and expressed as a proportion of maximum available PAR (i.e. full sun). Mean light levels for the general area were obtained by similar measurements at 100 randomly chosen coordinates over a 30 m \times 50 m area around these nests.

The five nests were within the boundaries of four 30 m \times 50 m trapping sites where the vegetation cover had been mapped in detail prior to finding the nests. All five nests were laid in areas categorized as 'bare sand with very sparse vegetation'. We did not measure light

directly at nests 3, 4 and 5, but calculated a mean light level based on two measurements (site with nest 3) and five measurements (site with nests 4 & 5) taken within the same vegetation category. This mean was compared with the mean available light over the site. In analyses we used one mean light value for nests 4 and 5 as they were on the same trapping site.

Statistical analysis

Analyses of variance (ANOVA) and simple linear regressions were used to test for seasonal differences in reproductive state; correlations between morphological and reproductive variables; effects of incubation treatments; and temperature differences among field nests. Analyses of covariance (ANCOVA) were used to test for incubation temperature effects on hatchling morphology, with initial egg mass as the covariate, and morphological differences between the sexes, with SVL as the covariate. In analyses where the slopes were not significantly different ($P > 0.05$), interaction terms were deleted and the analyses recalculated to investigate possible differences in intercepts (Sokal & Rohlf 1995). Prior to analyses, morphological data were log transformed to meet the assumptions of normality and homogeneity of variance. Partial correlation analysis was used to examine relationships among reproductive characteristics of wild-caught females. Contingency table analyses were used to compare sex ratios and hatchling mortality among incubation treatments. All tests were done using the SuperANOVA (Abacus Concepts 1991) or Statview 5.0 (SAS Institute 1998) statistical packages.

RESULTS

Museum specimens

Male reproduction

Male jacky dragons mature at a small body size in relation to the maximum size that can be achieved by some specimens. From 145 preserved males, the smallest reproductive male was 72 mm in SVL and 11.2 g in mass, while the largest was 117 mm in SVL and 67 g in mass (Table 1). Here 'adult male' refers to lizards ≥ 72 mm SVL. There was an annual cycle in testis size, with maximum testis volume in early spring (August–October), and minimum volume in mid to late summer (January–February). There was a highly significant difference in testis volume among the three seasons where lizards were available for comparison: spring (September–November), summer (December–February) and autumn (March–May) (ANOVA:

Table 1. Sexual dimorphism in adult jacky dragons (*Amphibolurus muricatus*) in the collection of the Australian Museum, Sydney

Trait	n	Males		n	Females		Unpaired t-test	d.f.	P	ANCOVA slopes		P	ANCOVA intercepts		P
		[mean \pm SE]	(range)]		[mean \pm SE]	(range)]	t			F			F		
Snout-vent length (mm)	87	91.7 \pm 1.2	(72–117)	69	90.5 \pm 1.0	(74–109)	-0.535	154	0.5396						
Tail length (mm)	87	202.2 \pm 3.9	(82–279)	69	189.2 \pm 4.5	(80–260)	-2.070	154	0.0401	0.246		0.6209	4.770		0.0305
Mass (g)	81	28.9 \pm 1.2	(11–67)	65	27.7 \pm 1.0	(12.5–44.5)	-0.145	144	0.8849	0.110		0.7408	0.163		0.6871
Jaw length (mm)	86	31.3 \pm 0.46	(22.2–40.5)	68	29.2 \pm 0.35	(21.9–35.0)	-3.100	152	0.0019	1.627		0.2041	42.628		0.0001
Head width (mm)	86	20.5 \pm 0.31	(16.0–28.0)	68	18.8 \pm 0.22	(14.0–22.8)	-4.166	152	0.0001	1.300		0.2560	52.589		0.0001
Head depth (mm)	83	14.6 \pm 0.22	(11.0–19.2)	67	13.4 \pm 0.16	(10.9–16.0)	-3.799	148	0.0002	3.465		0.0647	37.423		0.0001

Results are shown for unpaired t-tests, and for ANCOVA where sex is the factor and snout-vent length the covariate. Although mean lengths are shown in mm and mass in g, all statistical tests were performed on natural logarithm transformed data.

$F_{2,71} = 13.92$, $P = 0.0001$). Maximum testis volume for adult males was significantly correlated with body size; larger lizards having testes of greater maximum volumes compared with smaller lizards (SVL: $r^2 = 0.179$, $P < 0.0001$, $n = 92$) (Fig. 1a). Because of this correlation with SVL, we standardized the data to re-examine seasonal changes in testis volume, using the residuals from the regression of $\log_{10}(\text{SVL})$ versus $\log_{10}(\text{testis volume})$ (Fig. 1b). Similarly, scores for efferent duct condition were near maximum from August to November, then rapidly decreased to minimum scores by February, suggesting that the mating season may continue for perhaps one month after the testes have begun to regress.

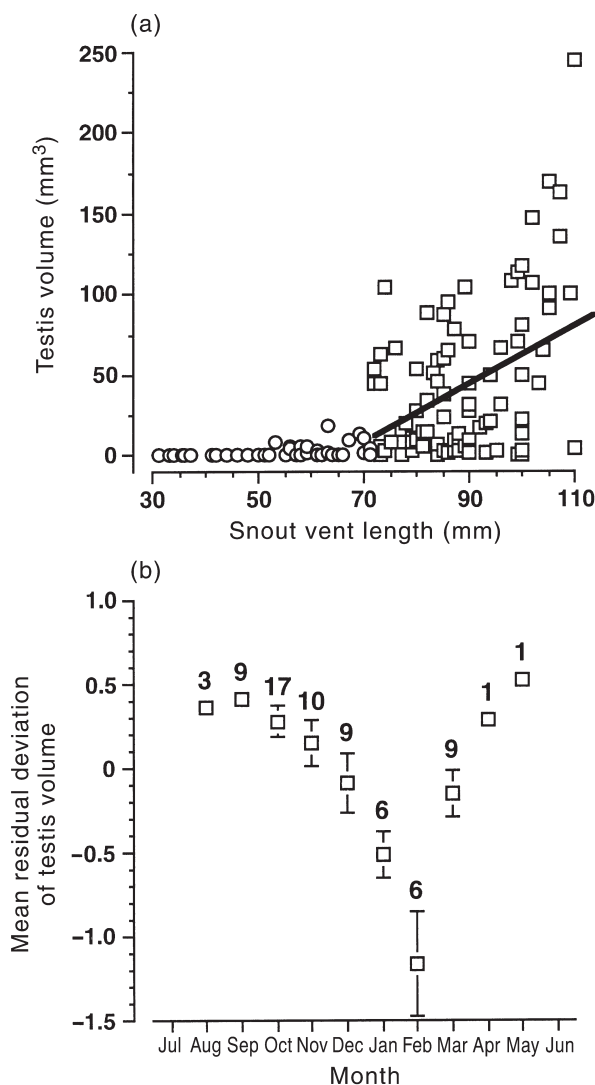


Fig. 1. Testis volume in jacky dragons (*Amphibolurus muricatus*). (a) Against snout-vent length (SVL), the regression line and formula is for (\square) males ≥ 72 mm SVL ($r^2 = 0.179$, $P = 0.0001$, $n = 92$, $y = 1.808x - 118.486$); (\circ) males < 72 mm SVL. (b) Seasonal variation in adults standardized for variation in body size, mean of the residuals (\pm SE) from the simple regression of $\log_{10}(\text{SVL})$ against $\log_{10}(\text{testis volume})$. Sample size for each month is shown.

Female reproduction

The minimum size at maturity for the 138 female museum specimens examined was 74 mm SVL (Table 1), while our smallest wild-caught gravid female was 72 mm. Thus 'adult female' refers to lizards ≥ 72 mm SVL. Clutch size was positively correlated with SVL ($r^2 = 0.337$, $P < 0.0001$, $n = 44$). Of 88 preserved adult females examined, 56 (64%) showed clear signs of recent reproductive activity (i.e. contained eggs, yolk-ing follicles or corpora lutea and thickened oviducts). Among these, seven (12.5%) also showed evidence of double clutching; six had both oviducal eggs and yolk-ing follicles, while one had yolk-ing follicles plus corpora lutea and thickened oviducts. Females were recorded with yolk-ing follicles from August to December, while oviducal eggs occurred in specimens captured from September to February (Fig. 2).

Of the non-reproductive females collected in late summer, many may have reproduced earlier in the season, so that corpora lutea had regressed and the previously thickened oviducts had reverted to the non-reproductive state by the time they were captured. Of the 44 preserved adult females captured from August to December (when reproduction is most apparent), 39 (89%) were reproductive. This implies almost all adult females breed every summer, and many individuals lay more than one clutch of eggs.

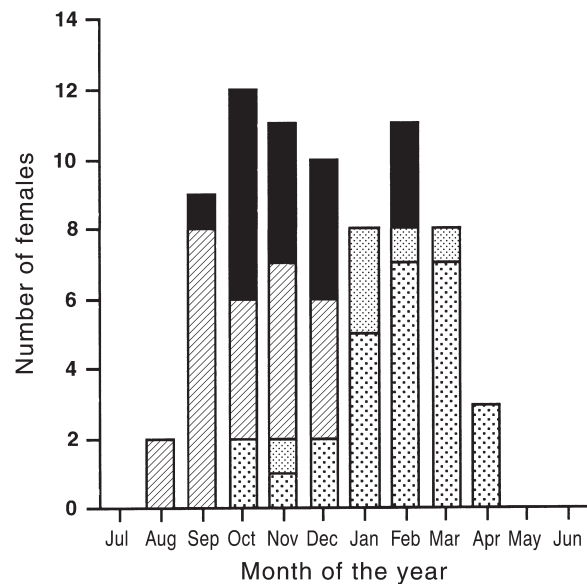


Fig. 2. Reproductive condition of 74 preserved female jacky dragons (*Amphibolurus muricatus*) with snout-vent lengths ≥ 72 mm by month of collection. Each female is only represented once, although five females with oviducal eggs also had yolk-ing follicles (Oct, Nov, Dec), and one female recorded with yolk-ing follicles was also post-partum (Dec). \blacksquare , Oviductal eggs; \square , yolk-ing follicles; \dots , post-partum; \square , non-reproductive.

Sexual size dimorphism

In adult jacky dragons the sexes were not significantly different in mean SVL or mass, although adult males averaged longer tails than females (unpaired t -test for tail length: $P = 0.04$). All three measurements of head size (jaw length, head width and head depth) were significantly larger in adult males than females (unpaired t -test for head dimensions: $P < 0.002$ in all cases) (Table 1). Adult mass covaried with SVL in a similar manner in both sexes, whereas tail length was significantly longer for males than for females, even when SVL was held constant (ANCOVA: $P = 0.03$). For analyses of jaw length, head width and head depth against SVL, a homogeneity of slopes test showed no significant differences between the sexes, although there were highly significant differences in the intercepts ($P = 0.0001$: Table 1). It appears that the relationship between body size and mass in adult male and female jacky dragons is similar, but that males have significantly larger heads than females from the earliest onset of maturity (72 mm) (Fig. 3).

Although mean adult SVL and mass were not significantly different between the sexes in these lizards, the largest individuals in a population are always male (Witten & Coventry 1984; PSH personal observation). For example, in this sample the largest female was 66% of the mass, and 93% of the SVL of the largest male. Thus we used the data for the largest 25% (SVL) of adults (22 males: 17 females) for further comparisons of maximum body size between sexes. We used unpaired t -tests and ANCOVA (with sex as the factor and

SVL as the covariate) to look for absolute and covarying differences in body proportions. The mean size for males is larger than for females in this subset of individuals (t -test $P = 0.004$ for all measurements; Table 2). Among these largest individuals, a homogeneity of slopes test showed no sex difference in the relationship between tail length or head dimensions with SVL (interaction term $P > 0.05$ in all cases), but there were highly significant differences in the intercepts for all these variables ($P = 0.003$ in all cases). Only mass covaried with SVL similarly in both sexes (Table 2). Apparently, occasional male lizards (with their relatively larger heads) can continue to grow beyond the maximum size that females can attain.

For the 83 preserved juvenile jacky dragons that we examined (40 male/43 female: SVL < 72 mm) t -tests showed no sex differences in any of the above morphological attributes ($P > 0.05$ in all cases), and for ANCOVA on tail length and all three head dimensions (with SVL the covariate) there were no significant sex differences in either slopes or intercepts in the analyses ($P > 0.05$ in all cases). The mass of juveniles however, differed between the sexes with males being slightly heavier than females (ANCOVA with SVL the covariate: slopes: $F_{1,79} = 2.783$, $P = 0.0992$; intercepts: $F_{1,80} = 5.223$, $P = 0.0249$).

Wild-caught gravid females

Wild-caught females laid between three and nine eggs and the number of eggs was positively correlated with

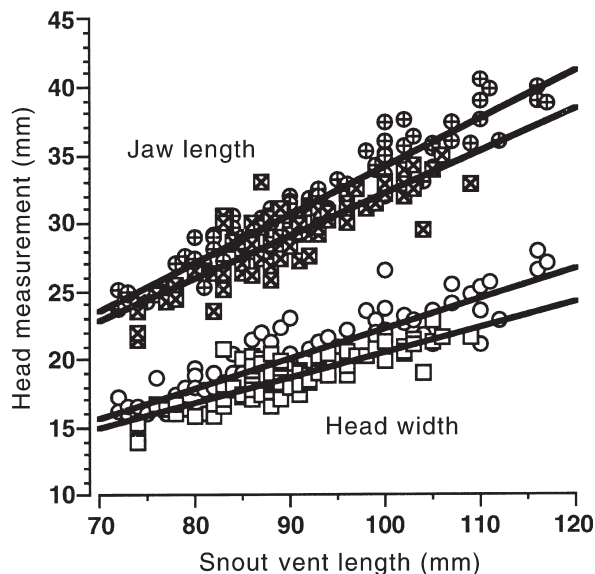


Fig. 3. Regression of SVL against jaw length (\oplus , male; \boxtimes , female) and head width (\circ , male; \square , female) in adult male and female jacky dragons (*Amphibolurus muricatus*). Males have longer jaws and wider heads than females at the same snout-vent length (see text for analyses).

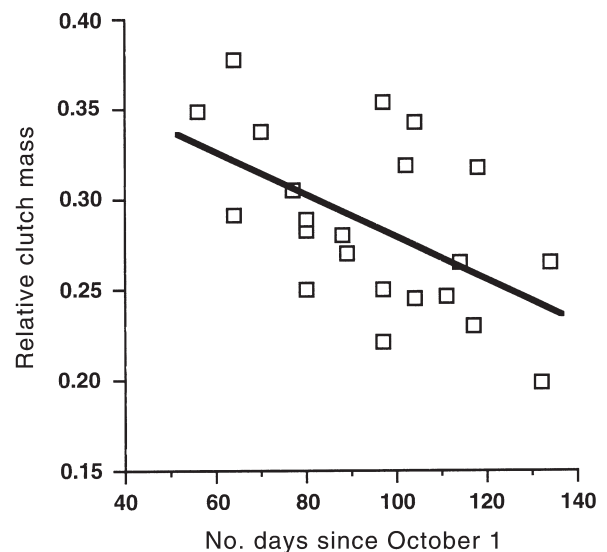


Fig. 4. Regression of female reproductive effort, the relative clutch mass (see text for methods), against the date of oviposition in wild-caught gravid jacky dragons (*Amphibolurus muricatus*) ($r^2 = 0.293$, $P = 0.0093$, $n = 22$, $y = -0.001x + 0.398$).

maternal SVL ($r^2 = 0.485$, $P < 0.0001$, $n = 35$). Females oviposited over a period of 109 days: from late October to early February, with a median laying date of December 20, and a mean laying date of December 30 (Table 3). Female investment in the clutch – the relative clutch mass (RCM) – was not correlated with female SVL or mean egg mass (partial correlation, Fisher's r to z transformation $P > 0.3$, $n = 18$). However, the RCM for females that laid their eggs early in the season was significantly larger than for females ovipositing later in the season (partial correlation of number of days since October 1 *vs* RCM: Fisher's r to z , $P = 0.003$, $n = 18$; Fig. 4). Relative clutch mass also increased significantly with clutch size (Fisher's r to z , $P = 0.022$). Female SVL, clutch size and mean egg mass were not correlated with laying date (Fisher's r to z , $P > 0.2$, $n = 18$). The correlations of both date of laying and clutch size with RCM imply that the number of eggs per clutch was greater earlier in the season,

an effect which we did not detect. Examination of RCM, clutch size and laying date in a larger number of lizards may clarify this.

Incubation period and mortality

Eggs required between 37 and 107 days to hatch, depending on the incubation temperature (ANOVA: $F_{9,130} = 421.4$, $P = 0.0001$). At increasingly higher constant incubation temperatures, the incubation period was shortened (Fig. 5). The incubation periods for the constant temperature of 28°C and the cycling $27 \pm 5^\circ\text{C}$ were not significantly different, and the constant 32°C and the cycling $33 \pm 5^\circ\text{C}$ also produced equivalent incubation periods (Scheffé's post hoc test: $P > 0.05$).

Neither hatching success nor the incidence of abnormalities were correlated with incubation

Table 2. Sexual dimorphism for the largest 25% (snout–vent length) of adult jacky dragons (*Amphibolurus muricatus*) in the collection of the Australian Museum, Sydney

Trait	Males		Females		Unpaired		ANCOVA		ANCOVA	
	[mean \pm SE (range)]		[mean \pm SE (range)]		<i>t</i> -test	<i>P</i>	slopes		intercepts	
					<i>t</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Snout–vent length (mm)	106.4 \pm 1.2	(100–117)	101.7 \pm 0.9	(96–109)	–3.067	0.0040				
Tail length (mm)	239 \pm 4.1	(195–279)	207.2 \pm 7.2	(142–260)	–3.929	0.0004	0.692	0.4112	10.058	0.0031
Mass (g)	42.7 \pm 1.7	(29.0–67.0)	35.8 \pm 1.2	(28.5–44.5)	–3.124	0.0035	0.797	0.3781	1.873	0.1873
Jaw length (mm)	36.6 \pm 0.45	(33.0–40.5)	32.6 \pm 0.33	(29.5–35.0)	–6.916	0.0001	0.456	0.5038	31.610	0.0001
Head width (mm)	24.0 \pm 0.43	(21.1–28.0)	20.7 \pm 0.24	(18.8–22.8)	–6.335	0.0001	0.379	0.5422	25.461	0.0001
Head depth (mm)	16.9 \pm 0.22	(14.7–19.2)	14.9 \pm 0.17	(13.2–16.0)	–6.976	0.0001	0.172	0.6810	30.525	0.0001

Results are shown for unpaired *t*-tests, and for ANCOVA where sex is the factor and snout–vent length the covariate. Sample sizes are 22 males and 17 females in all comparisons. Although mean lengths are shown in mm and mass in g, all statistical tests were performed on natural logarithm transformed data.

Table 3. Reproductive data for the jacky dragon (*Amphibolurus muricatus*)

Attribute	Mean \pm SE	<i>N</i> (<i>n</i>)	Range
Female snout–vent length (mm)	89.5 (0.93)	79	72–109
Female tail length (mm)	185.6 (3.7)	78	64–238
Clutch size	5.75 (0.17)	79	3–9
Female prepartum mass (g)	25.05 (1.21)	31	13.5–36.9
Female postpartum mass (g)	19.73 (0.86)	23	11.5–27.4
Female RCM	0.286 (0.010)	22	0.199–0.378
Date of laying	30 December (4.2 d)	36	24 October–12 February
Mean egg mass (g)	1.076 (0.039)	27 (171)	0.782–1.655
Mean hatchling mass (g)	1.104 (0.029)	30 (138)	0.789–1.401
Mean hatchling SVL (mm)	31.11 (0.270)	29 (139)	28.0–34.3
Mean hatchling tail length (mm)	54.7 (1.1)	29 (135)	38.5–67

For female snout–vent length, total length and clutch size, data from 44 museum specimens with oviducal eggs or yolking follicles greater than 3 mm are included with the data from 35 wild-caught gravid lizards. For clutch data: *N*, number of clutches; *n*, number of eggs or hatchlings.

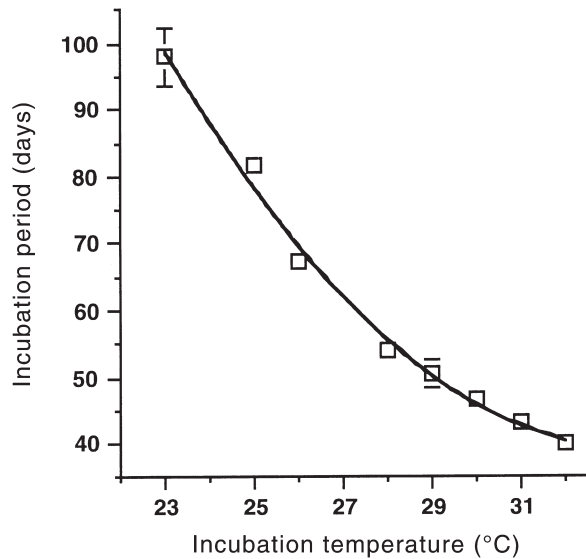


Fig. 5. Mean incubation period ($\pm 2\text{SE}$) at constant temperatures for eggs of the jacky dragon (*Amphibolurus muricatus*). The fitted curve is for a polynomial regression ($r^2 = 0.992$, $P = 0.0001$, $n = 8$, $y = 0.547x^2 - 36.575x + 650.676$).

temperature. Altogether 10 eggs died early during the incubation period or failed to develop, and thus the sex was not determined (Table 4). Another 14 eggs reached full term but embryos died before or during hatching or had serious deformities. A further 13 eggs produced hatchlings with 'nonlethal' deformities (very short or kinked tails, and one individual with 3 digits on one front foot). At the time of laying, all these eggs appeared similar to eggs that hatched normally, and were no different in mass (ANOVA: $F_{3,141} = 0.173$, $P = 0.9147$). For these 10, 14, and 13 eggs, the effects were not incubation temperature related and were seen across all treatments (three-way contingency table analysis: $\chi^2 = 26.54$, $P = 0.488$, d.f. = 27). Except for these 37 hatchlings, the hatchlings from all temperature regimes appeared completely normal.

Hatchling morphology

The random allocation of eggs to incubation treatments resulted in an initial difference in the mean egg mass in different treatments (ANOVA: $F_{8,136} = 4.210$, $P = 0.0002$). Because of this initial difference, we used ANCOVA to investigate possible effects of incubation treatment on hatchling morphology, using initial egg mass as the covariate. There were no significant effects of incubation treatment on hatchling mass (slopes: $F_{8,109} = 1.763$, $P = 0.0921$; intercepts: $F_{8,117} = 1.310$, $P = 0.2450$), SVL (slopes: $F_{8,109} = 1.651$, $P = 0.1187$; intercepts: $F_{8,117} = 1.821$, $P = 0.0780$), or tail length (slopes: $F_{8,109} = 0.754$, $P = 0.6435$; intercepts:

Table 4. Incubation temperatures and hatchling sex ratios for jacky dragon (*Amphibolurus muricatus*) eggs incubated in the laboratory at eight constant and two cycling temperatures

Incubation temperature (°C)	Number of eggs (females)	Males : females (unsexed)	P (d.f. = 1)
23	12 (5)	1 : 11 (0)	0.004
25	18 (4)	0 : 18 (0)	0.0001
26	21 (8)	4 : 14 (3)	0.0184
28	10 (5)	3 : 7 (0)	0.206
29	23 (8)	8 : 12 (3)	0.371
30	14 (7)	4 : 8 (2)	0.2482
31	3 (1)	2 : 1 (0)	
32	26 (8)	7 : 19 (0)	0.0186
27 ± 5	20 (8)	11 : 9 (0)	0.6547
33 ± 5	16 (7)	0 : 14 (2)	0.0002

The χ^2 P -values are for the sex ratio at each incubation temperature, against an expected outcome of 50 : 50 (male : female).

$F_{8,117} = 1.328$, $P = 0.3494$). Additionally, there was no significant effect of incubation temperature on hatchling tail length when we used SVL as the covariate (slopes: $F_{8,120} = 0.807$, $P = 0.5973$; intercepts: $F_{8,120} = 0.894$, $P = 0.5234$). The 31°C incubation treatment was excluded from all of these analyses as it contained only three eggs from one female.

To test for possible sex differences in these same hatchling traits, we used data from the four incubation temperatures where there was no significant difference in the number of males versus females hatched (28, 29, 30°C and $27.5 \pm 5^\circ\text{C}$: total $n = 24$ males and 28 females; Table 4). We found no significant effects of incubation temperature or sex on hatchling mass, SVL or tail length, and no significant interactions between these factors (two-factor ANCOVA, covariate egg mass, $P > 0.05$ in all cases).

Hatchling sex ratios

Overall, hatchling sex ratios were significantly female biased in incubation treatments where 10 or more hatchlings were sexed (contingency table analysis: χ^2 , $P = 0.0016$, d.f. = 8). At very low constant temperatures (23 & 25°C), and at very high constant (32°C) or high cycling temperatures ($33 \pm 5^\circ\text{C}$), sex ratios were significantly female biased (χ^2 , $P = 0.019$; Table 4). At medium incubation temperatures (constant 28, 29, 30°C and cycling $27 \pm 5^\circ\text{C}$), sex ratios were no different to the null hypothesis expectation of equal numbers of males and females. No incubation temperature produced significantly male biased sex ratios. Although the incubation periods for eggs at the two highest temperatures of constant 32 and cycling $33 \pm 5^\circ\text{C}$ were not significantly different, the sex ratios of hatchlings from these two treatments were significantly different (χ^2 , $P = 0.0326$, d.f. = 1) (Table 4).

Field nests

Nest site selection

Although a large range of thermally varied sites from full sun to full shade was available within metres of each nest position, females chose open areas that received significantly more sun than if nest positions were chosen at random (ANOVA, $P = 0.0001$: Table 5). Positions chosen for nests 1 and 2 received significantly more available light ($82.1 \pm 0.3\%$ SE) than the mean for randomly chosen points on the four trapping areas with nests ($53.25 \pm 1.8\%$ SE) (Scheffé's post hoc test $P = 0.0002$). The mean estimated light level for nests 3, 4 and 5 ($78.8 \pm 2.8\%$ SE) was also significantly higher than for these random points on the four sites with nests (Scheffé's $P = 0.0004$) but similar to light levels at Nest 1 and 2 (Scheffé's $P = 0.874$).

The five nest positions were in sites sand-mined approximately 25 years prior to the study and thus had very few large trees. Within 30 m of each of the five nests there were patches of dense vegetation 3–10 m tall (*Angophora costata*, *Leptospermum laevigatum* or *Banksia serrata*). However, all nests received sun for most of the day, as this dense vegetation was always further than 5 m from the southern side of a nest and at least 30 m from the nest in other directions. Thus, any nearby dense vegetation did not shade the nests. It is unlikely that we detected nests less easily in denser vegetation. We spent a similar amount of time working on sites

significantly less vegetated (mean light received $77.5 \pm 1.5\%$ SE: Scheffé's $P = 0.0006$) and significantly more vegetated ($42.0 \pm 2.0\%$ SE: Scheffé's $P = 0.0424$), but failed to locate any nests.

Eggs were buried in short, shallow burrows. For the five nests the mean depth from the soil surface to the top surface of the uppermost egg was 72 mm, and 83 mm to the top surface of the bottom egg (Table 5).

Nest temperatures

Egg temperatures in three viable nests varied over a 28°C range (13.4 – 41.1°C), in response to both daily and seasonal changes in weather conditions (Fig. 6;

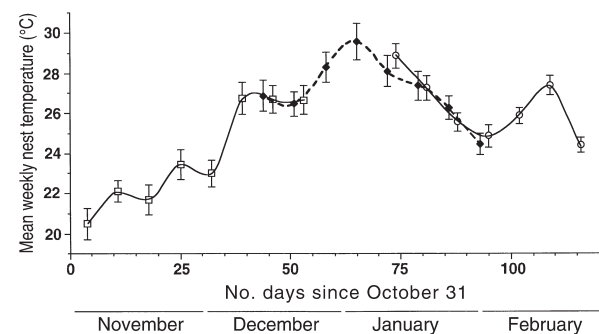


Fig. 6. Mean weekly temperatures ($\pm 2\text{SE}$) recorded in three jacky dragon (*Amphibolurus muricatus*) nests over one season (1998–1999). \square , nest 1; \blacklozenge , nest 2; \circ , nest 3.

Table 5. Field nest data for five jacky dragon (*Amphibolurus muricatus*) nests

	Nest 1	Nest 2	Nest 3	Nest 4	Nest 5
Number of eggs	7	6	4	6	5
Depth to top egg (mm)	52	55	80	85	90
Depth to bottom egg (mm)	52	76	85	97	105
Hatchling sex ratio, males : females	6 : 1	3 : 3	1 : 3	3 : 2 : 1*	*
Mean sun at nest (%)	81.7	82.5	81.5	76	76
Mean sun for trap site ($\% \pm \text{SE}$)	51 ± 3	58 ± 3	54 ± 3	50 ± 3	50 ± 3

Depth to egg, vertical distance from the soil surface to the uppermost surface of the egg; mean sun, percentage of full sun received at the nest. For nests 3, 4 and 5 'mean sun at nest' was not measured directly but was calculated as a mean light level for points of similar vegetation on the same sites. *Sex unknown.

Table 6. Field data for three jacky dragon (*Amphibolurus muricatus*) nests

Nest attribute	Nest 1	Nest 2	Nest 3
Date laid	31 Oct 1998	10 Dec 1998	8 Jan 1999
First date data collected	1 Nov 1998	12 Dec 1998	11 Jan 1999
Development in the nest (%)	66	100	91
Nest temperature ($^\circ\text{C}$, mean $\pm \text{SE}$)	23.7 (0.14)	27.3 (0.14)	26.1 (0.10)
Daily maximum temperature ($^\circ\text{C}$, mean $\pm \text{SE}$)	31.5 (0.66)	34.3 (0.65)	30.8 (0.52)
Daily minimum temperature ($^\circ\text{C}$, mean $\pm \text{SE}$)	19.3 (0.37)	22.4 (0.18)	22.9 (0.20)
Daily temperature range ($^\circ\text{C}$, mean $\pm \text{SE}$)	12.2 (0.57)	11.9 (0.62)	7.9 (0.47)
Maximum daily temperature range	18.3	18.4	13.9
Range of temperatures	13.4–38.7	19.4–41.1	20.1–38.2

Temperatures are based on hourly measurements at the top of the uppermost egg for 53 days.

Table 6). Mean daily temperature recorded by the top and bottom temperature probes in nest 1 showed no significant differences (paired t -test: $t = 0.174$, $P = 0.863$), while for the two probes in nest 3 there was a small but highly significant difference (paired t -test: $t = -13.81$, $P < 0.0001$), with the lower probe being 0.27°C warmer on average. The mean variance in daily temperatures between the upper and lower probes were significantly different in both nests (paired t -tests on daily standard error: $P < 0.0001$ for each nest). Shallow probes recorded a greater daily temperature variance than deeper probes. For subsequent temperature analyses we used the thermal data from the top probes only.

The hourly temperatures over the first 53 days were significantly different among nests in mean ($F_{2,3813} = 209.8$, $P < 0.0001$), mean daily maximum ($F_{2,156} = 9.347$, $P < 0.0001$), mean daily minimum ($F_{2,156} = 56.243$, $P < 0.0001$), and the mean daily range of temperatures recorded ($F_{2,156} = 19.153$, $P < 0.0001$: ANOVA with nest as factor, and days as replicates) (Table 6). However, nests 1 and 3 did not differ in mean daily maximum temperature (Fisher's Protected Least Significant Difference $P = 0.417$), nests 2 and 3 did not differ in minimum temperature (Fisher's PLSD $P = 0.1755$), and nests 1 and 2 did not differ in the mean daily range of temperatures (Fisher's PLSD $P = 0.695$).

For the 16 days when nest temperatures were recorded concurrently in nests 1 and 2, there were no significant differences in either the mean daily temperature recorded (paired t -test: $t = 0.197$, $P = 0.8462$), or in the variance in mean temperature (paired t -test on daily standard error: $t = 1.604$, $P = 0.1296$). In nests 2 and 3 there were 26 days when temperatures were recorded concurrently. Here, again the daily means were not significantly different between nests (paired t -test: $t = -0.259$, $P = 0.7975$), while the variances were significantly different (paired t -test on daily standard error: $t = 5.255$, $P < 0.0001$). Thus, it seems the dif-

ferences in mean temperatures recorded over the first 53 days in these three nests were due to the different dates of laying, and not to any differences in nest site selection. Although a gradual seasonal increase in mean nest temperatures is evident from a minimum in early November to a maximum in early January (Fig. 6), daily temperatures varied by up to 18.4°C , mostly in response to solar irradiation and rainfall (Fig. 7).

Five of the six eggs in nest 2 had pipped and began to emerge from the eggshell when we excavated this nest on day 57 in the field; these lizards hatched within two hours. The eggs in nests 1 and 3 were returned to the laboratory incubator where hatching occurred 16 and 4 days later, respectively. The sex ratios in the three nests appeared to vary, although numbers were too low for statistical comparisons (Table 5).

DISCUSSION

The hatchling sex ratio obtained from our laboratory incubations shows that the jacky dragon (*Amphibolurus muricatus*) possesses temperature-dependent sex determination (TSD). Females are produced at low and high incubation temperatures, and varying proportions of males are produced at intermediate temperatures. This is pattern II of Ewert and Nelson (1991), a similar pattern to that in other TSD lizards. None of the constant incubation temperatures we used produced a high percentage of males. Like the Australian freshwater crocodile (*Crocodylus johnstoni*), the jacky dragon is a shallow-nesting species, and the eggs experience fluctuating daily temperatures combined with a steady seasonal increase in mean temperatures (Webb & Smith 1984). In *C. johnstoni* the highest percentage of males produced at any constant incubation temperature in the laboratory is 39% (Webb *et al.* 1992). However, 100% male hatchlings are produced in some wild nests (Smith 1987), and can also be produced in the laboratory by steadily increasing the incubation temperature by a total of 5°C over the entire incubation period (Webb *et al.* 1992). Similar incubation conditions may increase the percentage of male jacky dragons produced in the laboratory.

If there is a similar effect of seasonally increasing mean temperature on jacky dragons, our field nest temperature data suggest that more males may be produced in spring nests, when environmental temperatures are low but steadily increasing towards summer maximums (Fig. 6). The early spring nest of seven eggs produced six males (Table 5), even though the mean nest temperature was a low 23.7°C . A similar constant incubation temperature would have produced all females (Table 4). Conversely, mid-summer nests experience higher means and may overproduce females, similar to the 100% females produced in our highest cycling laboratory incubation temperature of $33 \pm 5^\circ\text{C}$. The

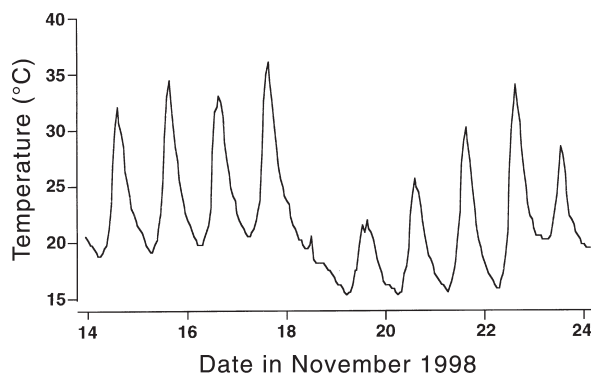


Fig. 7. Daily temperature variation in jacky dragon (*Amphibolurus muricatus*) nest 1 shown for 10 days in November 1998. Note the cooling effect of rain on 19 November 1998.

importance of both the mean and the variance in incubation temperature for explaining the sex ratios of natural nests has long been known (Bull 1985). Georges *et al.* (1994) demonstrated how, with increasing variance around a common mean, hatchling sex ratios could change from almost 100% male to 100% female in the TSD marine turtle *Caretta caretta*.

There are no data on nest temperatures and only anecdotal observations of nest-site selection (Harlow & Shine 1999) in other TSD lizards. Over the course of the egg laying season, the mean weekly nest temperatures that we recorded increased from 20.5 to 29.6°C during the period when sex is being determined (Bull 1987). Our data suggest that jacky dragon nests are not dug at random, but are consistently similar in aspect and in the amount of sun exposure. Two studies on captive lizards, including a gecko with TSD, found that females selected nest sites based on temperature (Bull *et al.* 1988; Castilla 1996). We have established that the prolonged egg laying season of jacky dragons encompasses somewhat predictable seasonal increases in nest temperatures (Fig. 6).

Over the wide range of both constant and cycling incubation temperatures used here, we could not identify any non-sex effects of temperature on any hatchling traits. Previous laboratory incubation studies on other species of agamids (Harlow & Shine 2000; Harlow *et al.* 2000) have shown incubation temperature effects on some of these same phenotypic attributes. Temperature-induced morphological effects have also been reported in a wide range of other reptile taxa; for example in the montane skink *Bassiana duperreyi*, body shape (SVL, mass, tail length) differences among hatchlings from different incubation regimes may last up to six weeks after hatching (Elphick & Shine 1998), but the ecological relevance of this is unknown.

The jacky dragon is in many respects representative of the 'typical' agamid lizard, exhibiting the general patterns of female fecundity increasing with body size, and adult males attaining a larger body size and relative head size than females, that are widespread in agamids (Greer 1989). Both male and female jacky dragons are morphologically similar until maturity (72 mm SVL), at which time relative head size begins to diverge between the sexes.

Male-larger sexual dimorphism is usually interpreted to reflect sexual selection pressures in mating systems where the reproductive consequences of body size are different in males and females (Anderson & Vitt 1990). Available data suggest that this may also be the case in jacky dragons. Spacing patterns of large adult males in the field suggest territoriality (PSH, personal observation), while captive male jacky dragons will quickly establish dominance hierarchies based on body size (Carpenter *et al.* 1970). Captive males will perform a ritualized display, occasionally escalating to an open-mouthed attack, when a new male is introduced into

the enclosure (M. Watt, pers. comm.). The large head of adult male jacky dragons, with the associated increase in jaw musculature, provides both a wider gape and more mechanical strength for biting than a small head. However, in the absence of supportive data on other life history variables, alternative explanations for head size differences may be just as valid (Cooper & Vitt 1989). For instance, they may have evolved from dietary differences that reduce competition for food between the sexes (e.g. Schoener 1967).

Although we have measured the relationship between body size and fecundity in female jacky dragons, data on how body size affects reproductive success in males are more difficult to obtain. If a male can defend a territory containing several females from other males, then his reproductive success would be greater than that of any single female (Stamps 1983; Olsson 1992). At the minimum size of maturity a female jacky dragon can produce 3 or 4 eggs; a mature male at this same size may have little opportunity to mate until the following summer, when he can make good use of his larger size and establish a territory. Thus, the variance in reproductive success may be greater for individual males than for females, and may be more directly influenced by body size.

Several authors have documented reproduction in captive jacky dragons (Groom 1973a,b; Lawton 1982; Hawker 1996), although no incubation temperatures or hatchling sex ratios have been recorded previously. In captivity this species can lay up to four clutches of eggs in a year, with a minimum of 38 days between successive clutches (Hawker 1996). A similarly prolonged reproductive season, with multiple clutches of eggs being laid, also occurs in the wild. At both Myall Lakes National Park and Tomago Sandbeds, females lay eggs from October through to February, and our examination of preserved jacky dragons showed that wild-caught females may also lay at least two clutches per season.

When viewed together, these phenomena (the prolonged female reproductive season, seasonally increasing field nest temperatures and male-larger sexual dimorphism) allow us to speculate on how these important life history attributes may relate to the sex-determining mechanism in this species. Within the range of possible incubation temperatures experienced by eggs, there may be a 'best' temperature or range of temperatures where developmental processes are optimized, and a superior hatchling is produced (Van Damme *et al.* 1992). Detrimental physiological effects at extreme hot or cold incubation temperatures are well known in a range of reptile species (Packard & Packard 1988). If one sex differentially increases its lifetime reproductive fitness by being produced at these optimal temperatures, perhaps through increased posthatching growth rates or larger maximum sizes at maturity, then TSD may offer an advantage over genotypic sex

determination. Support for this hypothesis comes from studies of a eublepharid gecko with TSD (Tousignant & Crews 1995), where the sex-determining pattern is similar to the jacky dragon. In this species the fastest growing and ultimately the largest female individuals hatch from the medium, mostly male-producing incubation temperatures.

Another hypothesis suggests that for species with an extended reproductive season in which there are predictable shifts in environmental temperatures, with TSD there will be a link between the date of egg laying and the sex of hatchlings. Support for this hypothesis comes from studies of the Atlantic silverside (*Menidia menidia*), a fish with TSD. In this species, eggs laid in the cooler waters of early summer produce mostly females, while late season eggs hatch mostly as males (Conover 1984). Early hatching fish have a longer growing season before reproduction the following year, and thus attain a larger body size at maturity than late season hatching fish. In this species a fecundity advantage to large body size has been shown in females, whereas male reproductive success does not covary with body size.

Seasonal trends in hatchling sex ratios are seen in several reptile taxa with TSD, including freshwater and marine turtles (Vogt & Bull 1984; Mrosovsky 1994), and a crocodilian (Webb & Smith 1984; Smith 1987). It is difficult to envisage how a few weeks difference in hatching date could impact on lifetime reproductive success in slow growing and long-lived taxa such as these. However, like the Atlantic silverside, jacky dragons grow quickly and early season hatchlings can mature in their first summer after hatching (JET, unpublished mark-recapture data). In contrast to the Atlantic silverside, male jacky dragons may disproportionately increase their reproductive success by early hatching. Although females reap a fecundity advantage from larger body size, males may disproportionately increase their reproductive fitness with larger body size by being better able to exclude rival males from their territories.

In the temperate region of Australia where jacky dragons occur, the winter dormancy or hibernation period extends from about April to August. During this time, activity is minimal and virtually no growth occurs. Lizards that hatch in summer (December) will have a four-month growth period before hibernation, compared with perhaps only a few weeks for late hatching (March) lizards. Differences in hatching date will therefore translate into significant differences in body size by the beginning of the next reproductive season in September. Late hatching individuals may have to postpone reproduction until their second summer, and in the face of high predation rates this will mean an increased risk of not reproducing.

Although there are no available data on hatchling sex ratios across the reproductive season for any TSD

lizard, our laboratory incubation and field nest temperature data together suggest that within-season sex ratio differences should occur in hatchling jacky dragons. At the lowest constant incubation temperatures used in the laboratory, only females hatched, whereas similar mean temperatures incorporating daily fluctuations such as occur in field nests produce males. This, combined with the polygynous mating system typical of male-larger sexually dimorphic agamids, allow us to speculate that TSD may provide an adaptive advantage over genetic sex determination in this species. However, this hypothesis is based on a series of assumptions that need to be investigated by detailed field studies.

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