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# Australian Journal of Zoology

Volume 45, 1997  
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## Intraspecific Variation in Reproductive Mode within the Scincid Lizard *Saiphos equalis*

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### Abstract

Although viviparity (live-bearing) has evolved from oviparity (egg-laying) more frequently in squamate reptiles than in any other vertebrate lineage, there are few well-documented cases of taxa that either (i) exhibit a 'transitional' reproductive state (i.e. with a reproductive mode intermediate between 'normal' oviparity and viviparity) or (ii) contain both oviparous and viviparous populations within the same species. Although rare, such taxa offer exceptional opportunities to test hypotheses concerning the evolution of viviparity in reptiles. Our data show that the scincid lizard *Saiphos equalis* displays both of the characteristics listed above. These small semi-fossorial skinks from south-eastern Australia exhibit geographic variation in reproductive mode, and some populations show an 'intermediate' mode. We examined the reproductive mode of *Saiphos equalis* over the geographic range of the species using preserved museum specimens, and we gathered detailed information on reproductive output of captive lizards collected from a high-elevation site (Riamukka, in the northern highlands of New South Wales) and from a coastal area (Sydney, southern New South Wales). Lizards from Riamukka were viviparous (i.e. they produced fully formed young enclosed in membranous sacs), whereas Sydney lizards produced incompletely developed embryos inside partially calcified eggshells. Incubation periods of the eggs from Sydney lizards were very brief ( $5.5 \pm 1.7$  days v.  $>35$  days in sympatric oviparous skinks), indicating that oviparous *S. equalis* represent a true evolutionary intermediate between 'normal' oviparity and viviparity.

### Introduction

Recent methodological advances have revolutionised the ways in which evolutionary biologists attempt to test adaptationist hypotheses. With the realisation that phylogenetic relationships should be incorporated into any such test ('the comparative method': e.g. Harvey and Pagel 1991) has come an increased understanding of the advantages of identifying actual evolutionary transitions rather than relying upon comparisons between species on either side of such transitions. Because any two species will differ in many aspects other than the one of direct concern, interspecific comparisons of this sort are inevitably confounded by numerous other factors. Thus, biologists interested in questions such as the selective pressures or physiological mechanisms involved in some evolutionary transition have increasingly searched for study systems in which such a transition has occurred within a single clade, ideally within a single species. In such a case, comparisons between taxa with ancestral and those with derived character states may be accomplished with minimal confounding. Similarly, species that show intermediate character states are of particular value for such a study, especially since the selective forces involved in transitions may be quite different from those that favour the subsequent success of the derived trait (e.g. Shine and Bull 1979).

These arguments apply to any evolutionary transition, but one of the clearest examples involves the evolutionary shift from oviparity (egg-laying) to viviparity (live-bearing). Definitions of these reproductive modes differ among authors (Blackburn 1993); we use the term 'oviparity' for the production of offspring at an early stage of embryonic development, enclosed in an opaque calcified eggshell; and the term 'viviparity' to refer to the production of fully formed offspring (including those enclosed in transparent membranes at birth). Although viviparity occurs in many taxa, viviparous species – and to an even greater degree, origins of viviparity –

are unevenly distributed throughout the animal kingdom. Of the 132 independent origins of viviparity in vertebrates identified by Blackburn (1992), 98 occur in squamate reptiles. Thus, viviparity has evolved far more often in reptiles than in any other lineage. Even in reptiles, however, most evolutionary origins of viviparity have been followed by or been associated with speciation and diversification. Thus, there are relatively few examples of intraspecific origins of viviparity (Blackburn 1982, 1985; Shine 1985), whereby a single species includes populations with different reproductive modes. Similarly, very few squamate reptile species are known to display reproductive modes that are intermediate between those of 'normal' oviparous and viviparous squamates (Shine 1983; Blackburn 1995). Hence, in order to facilitate rigorous tests of evolutionary hypotheses on the oviparity–viviparity transition in reptiles, we need to find species that are reproductively bimodal and/or that include transitional forms between oviparity and viviparity. In this paper, we describe the reproductive biology of such a species.

*Saiphos equalis* is a medium-sized (~180 mm total length) burrowing skink from moist habitats in south-eastern Australia. Earlier investigations of *S. equalis* suggested that this species may (almost uniquely) show both reproductive bimodality and transitional reproductive modes (Bustard 1964; Greer 1983, 1989; Shine 1985), but detailed data have not been available to confirm these statements. We set out to investigate these reports, using preserved museum specimens as well as live animals from two populations. Our studies on the taxonomy and phylogeny of this species, as well as the basis for our conclusion that viviparity in *S. equalis* has evolved from oviparity rather than *vice versa*, has been and will be presented elsewhere (Smith 1996; Smith, Austin and Shine, unpublished data).

## Methods

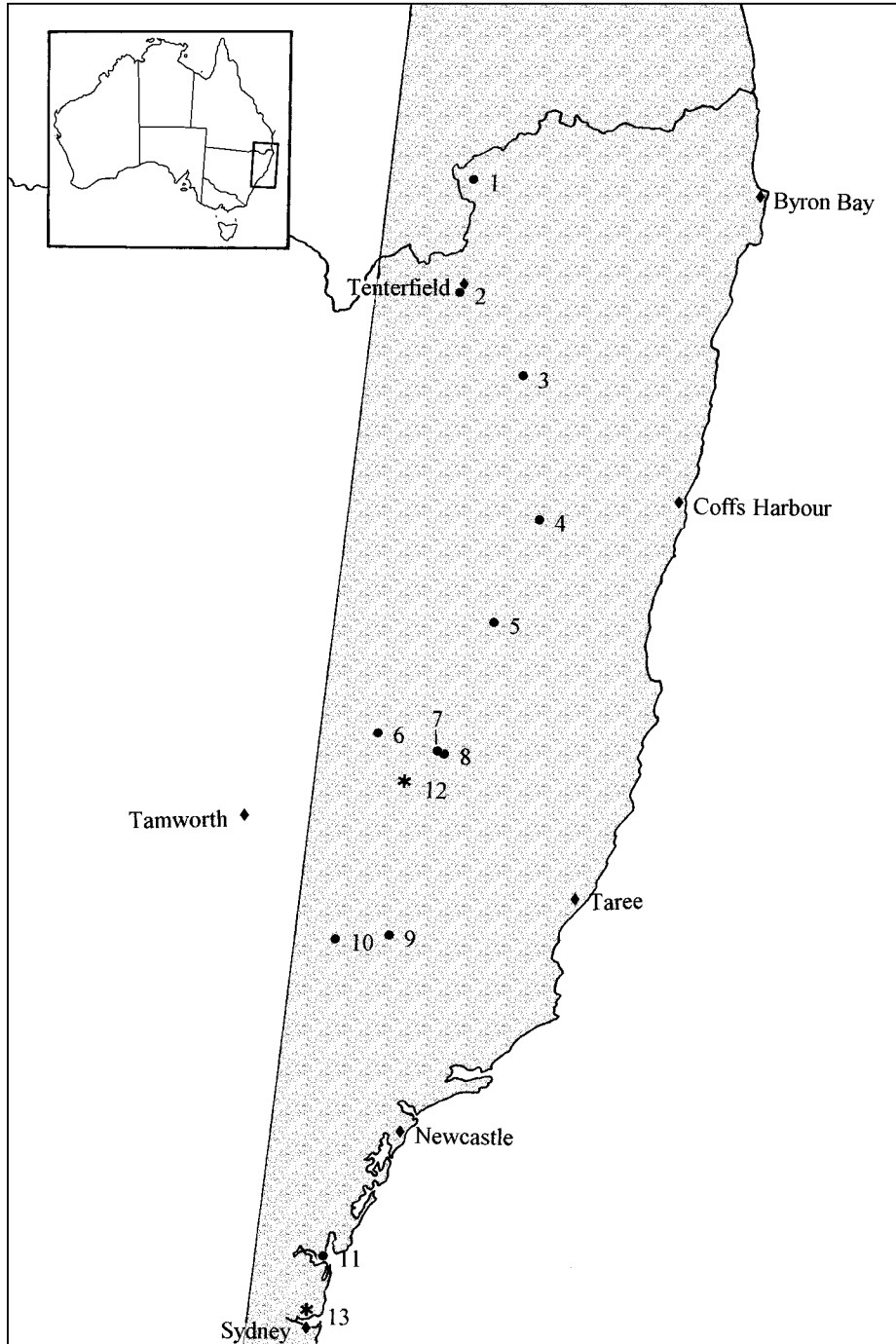
### Museum Specimens

To characterise reproductive modes, we examined gravid preserved specimens of *Saiphos equalis* from the collection of the Australian Museum (AM). We examined only specimens that contained relatively advanced embryos [at least Stage 28 of Dufaure and Hubert (1961)], because variability in the stage at which eggshells are deposited in oviparous species, and the presence of an eggshell-like covering during early embryonic development of viviparous species, make it difficult to infer reproductive mode from less-developed embryos (Blackburn 1993). For each such female, we recorded the location and date of collection, clutch size, pigmentation of the embryo, amount of yolk remaining external to the embryo (classed as small, medium or large), and the thickness and degree of opacity of the membrane or shell around the embryo.

### Live Specimens

During November and December 1995, we collected *S. equalis* by hand from two areas: Riamukka, in northern New South Wales (NSW) (31°20'S, 151°39'E), and Sydney, in southern NSW [Kurnell Peninsula (34°01'S, 151°09'E), North Sydney (33°48'S, 151°12'E) and Maroubra (33°57'S, 151°15'E)] (Fig. 1). We chose these sites on the basis of early reports of reproduction in *S. equalis* (see above) and because our examination of museum specimens suggested that animals from Sydney were oviparous and those from Riamukka were viviparous (see below). Riamukka State Forest is covered by open dry sclerophyll vegetation, at an elevation of 1250–1400 m; lizards were primarily found under rocks and logs. The animals collected from Sydney were found under rocks, logs and rubbish in areas of both introduced and native vegetation and backyard compost heaps, at elevations of less than 100 m.

All lizards were transported to the University of Sydney within 48 h of capture, and snout–vent length, inter-limb length, tail length (all  $\pm 1$  mm) and mass ( $\pm 0.001$  g) were recorded. We housed each animal in a separate plastic container (22  $\times$  13  $\times$  7 cm), the floor of which was lined with a damp sponge cloth and covered with moist potting soil to a depth of 5 cm. Each cage contained a 10  $\times$  10 cm wooden shelter. Cages were heated at one end to allow the animals to thermoregulate between approximately 23 and 38°C during the day, and room lighting was set to a 12 : 12 h photoperiod. Animals were provided with food (mealworms and earthworms) and water *ad libitum*. We checked each cage for eggs every morning. The following data were recorded upon discovery of eggs: post-partum mass of the female ( $\pm 0.001$  g); clutch size; the mass of each egg ( $\pm 0.001$  g); and the degree of opacity of each egg [subjectively estimated on a scale of 0 (= transparent) to 5 (= completely opaque)]. Before estimating opacity, we lightly brushed each egg with water to eliminate variation in eggshell colour due to different levels of hydration.



**Fig. 1.** Map of eastern New South Wales showing the locations of gravid specimens and populations of *Saiphos equalis* studied. Populations numbered 1–11 (●) are those from which gravid preserved specimens were available; see Table 1 for reproductive data on these animals. Populations 12 and 13 are those from which we collected live specimens (\*): Riamukka State Forest (12) and Sydney (13). The locations of various cities (◆) are shown for reference purposes.

We set aside one egg to be dissected from each clutch, and the remaining eggs were incubated in the laboratory at 23°C. Eggs were placed in individual 64-mL glass jars with moist vermiculite (~150 kPa, 130% water by dry mass of vermiculite) and covered with plastic food wrap to prevent moisture loss. We checked the incubators twice daily. Hatchling lizards were weighed ( $\pm 0.001$  g) and measured (snout–vent length, tail length and inter-limb length, all  $\pm 0.5$  mm). Hatchlings were maintained in conditions similar to those of adults, except that the potting-soil substratum in the containers was reduced to a depth of approximately 1 cm.

One ‘egg’ from each clutch was dissected to determine the developmental stage of embryos at oviposition. This involved carefully cutting away the eggshell to expose the embryo, which was immediately euthanased with 10% ‘Euthatal’ (pentobarbitone sodium). One drop of this solution was placed in the embryo’s mouth with a small needle. Following euthanasia, we separated and recorded the mass of the embryo and yolk. Embryos were fixed in 10% formalin for 24 h and stored in individual plastic vials in 75% ethanol.

Initially we scored development of the embryos using the Dufaure and Hubert (1961) (hereafter referred to as D & H) staging scheme. The stages that we observed in *S. equalis* embryos at oviposition fell between D & H Stages 39 and 40 but did not correspond exactly to either of these stages. Characteristics occurring in some embryos (e.g. everted hemipenes) corresponded to stages as early as D & H Stage 36. This discrepancy reflects the substantial morphological differences between *S. equalis* and *Lacerta vivipara* (the species on which the D & H system is based). To stage *S. equalis* embryos relative to each other, we recorded a number of additional characters for each embryo: pigmentation (scored subjectively as complete, partial or none); embryo and yolk mass (g); embryo length (mm); and degree of scale differentiation (complete, partial or minimal; scored ventrally and dorsally for both the head and body). We also took x-rays of each embryo, to determine the degree of development of tail vertebrae and phalanges (complete or incomplete). The length and mass of embryos at oviposition (in dissected eggs) were scored relative to the average values of these traits for their siblings at hatching.

Data were analysed with the Statview 4.5 and SuperAnova 1.11 statistical packages (Abacus Concepts 1991, 1995) on an Apple Power Macintosh Computer, Model 6100/66.

## Results

### *Museum Specimens*

Gravid specimens containing relatively advanced embryos were available from sites throughout the distribution of *Saiphos equalis* in NSW (Fig. 1). Of the 11 preserved females containing advanced embryos, only two (AM Specimen Nos R44766 and R96447) appeared to be oviparous (Table 1). These females contained large, fully pigmented embryos with small yolk masses enclosed by opaque shells. The remaining nine females contained embryos encased in transparent membranes (Table 1). The embryos of two of these specimens (R71084 and R137893) were inside the oviducts, but had broken partially free of their membranes; the embryo of another lizard (R71084) had also broken out of the oviduct. This situation may arise when a gravid animal is euthanased and embryos react by struggling (personal observations). It seems likely, then, that these embryos had developed almost to the stage of parturition when the females were collected, and had broken free of their membranes when the females were euthanased. Locality data revealed one area where both oviparous and viviparous specimens were collected in close proximity: within approximately 55 km of Tenterfield, NSW.

### *Live Specimens*

Adult lizards from the northern population (Riamukka) were significantly larger (greater snout–vent lengths and inter-limb lengths, and heavier) than same-sex animals from the southern population (Table 2). However, analyses of covariance showed that general body shape (i.e. mass and inter-limb length relative to snout–vent length) did not differ between the two populations. Hence, adults from the two populations differed in absolute size but not in body shape (Table 2).

The reproductive biology of the northern and southern populations of *S. equalis* showed many similarities, but also displayed significant differences. Clutch size and clutch mass did not differ between the two populations, either in absolute terms or relative to maternal snout–vent length (Table 3). However, the mass of the clutch relative to the female’s mass after oviposition/parturition (= relative clutch mass) was significantly lower in the northern females than in their southern counterparts (Table 3). Oviposition occurred earlier in the animals from the northern

**Table 1. Developmental characteristics of the embryos from gravid specimens of *Saiphos equalis* in the collection of the Australian museum**

The date of collection, location, clutch size, pigmentation of embryo, amount of yolk remaining (i.e. that not incorporated into the body of the embryo) and a description of the membrane or shell for the clutch of each gravid female are given. 'Map No.' refers to Fig. 1

Museum No.	Map No.	Date	Location	Clutch size	Pigmentation	Yolk	Membrane
R96447	1	12.xii.1980	50 km N Tenterfield	1	Complete	Small	Thick, opaque
R43810	2	18.ii.1972	3 mi SW Tenterfield	2	Moderate	Large	Thin, transparent
R139473	3	28.i.1992	Washpool National Park	4	Very faint	Large	Moderate, transparent
R13 262	4	7.ii.1992	Marengo State Forest	3	Light	Large	Thin, transparent
R71084	5	12.ii.1978	Styx River State Forest	1	Complete	Small	Thin, transparent
R43836	6	Unknown	1 mi W Walcha	3	Complete	Small	Thin, transparent
R112916	7	8.xii.1983	Walcha–Wauchope Rd	4	Moderate	Large	Thin, transparent
R43832	8	15.ii.1969	26 mi E Walcha	2	Light	Large	Thick, transparent
R137892	9	1992	Barrington Tops National Park	4	Complete	Medium	Thin, transparent
R137893	10	1992	Stewart's Brook State Forest	2	Complete	Small	Thin, transparent
R44766	11	1977	Ocean Beach	3	Complete	Small	Thin, opaque

**Table 2. Morphological differences between adult *Saiphos equalis* from Sydney and Riamukka**  
ANOVAs test for population differences in morphological traits. Analyses of covariance, with population as the factor, evaluate the effect of source population on body shape. Significant values ( $P < 0.05$ ) are shown in bold

Trait	Mean (s.d.)		ANOVA				
	Riamukka	Sydney	<i>F</i>	d.f.	<i>P</i>		
Comparisons of mean values of traits							
Snout–vent length of female (cm)	8.35 (0.73)	7.41 (0.64)	24.18	1,68	<b>&lt;0.0001</b>		
Snout–vent length of male (cm)	7.75 (0.40)	6.96 (0.89)	12.27	1,22	<b>0.0020</b>		
Inter-limb length of female (cm)	6.14 (0.48)	5.51 (0.54)	20.32	1,68	<b>&lt;0.0001</b>		
Inter-limb length of male (cm)	5.44 (0.26)	4.82 (0.74)	14.21	1,22	<b>0.0011</b>		
Mass of female (g)	5.20 (0.91)	3.74 (0.74)	15.08	1,58	<b>0.0003</b>		
Mass of male (g)	4.59 (0.67)	2.53 (1.12)	15.99	1,22	<b>0.0006</b>		
Trait	Covariate	Analysis of covariance					
		Homogeneity of slopes			Intercepts		
		<i>F</i>	d.f.	<i>P</i>	<i>F</i>	d.f.	<i>P</i>
Comparisons of relationships among traits							
Inter-limb length of female	Snout–vent length of female	0.84	1,29	0.37	0.18	1,30	0.68
Inter-limb length of male	Snout–vent length of male	2.06	1,17	0.20	14.19	1,18	0.05
Pre-partum mass of female	Snout–vent length of female	2.75	1,56	0.10	3.44	1,57	0.07
Mass of male	Snout–vent length of male	1.71	1,17	0.21	1.73	1,18	0.20

population than in those from southern NSW (Table 3). More importantly, the reproductive products of these two populations were also different. The northern females produced ‘neonates’ enclosed in transparent membranes, whereas southern females produced partially shelled eggs (Fig. 2). These eggs weighed less, were more opaque and incubated for longer periods prior to hatching than were the membrane-enclosed ‘neonates’ from the northern population (means of 5.5 v. 1.5 days; Fig. 3). The stage of development of the embryos/neonates at oviposition also varied markedly between the two populations (Table 3). The embryos from females collected in northern NSW were heavier and longer at oviposition (relative to final size at hatching), and had less unincorporated yolk, than were those from southern NSW. Contingency-table analyses on frequency data also showed that the northern-population offspring were more fully pigmented at parturition ( $\chi^2 = 29.82$ , 2 d.f.,  $P < 0.0001$ ), and displayed more fully developed scales ( $\chi^2 = 26.60$ , 2 d.f.,  $P < 0.0001$ ) and tail vertebrae ( $\chi^2 = 27.81$ , 1 d.f.,  $P < 0.0001$ ). The proportion of male offspring with everted hemipenes at the time of oviposition was also lower in the northern population ( $\chi^2 = 6.27$ , 1 d.f.,  $P < 0.013$ ). All of these data indicate that the Riamukka hatchlings were more completely developed at parturition than were their Sydney conspecifics.

## Discussion

Our data confirm and extend earlier reports of a very unusual (perhaps unique) diversity of reproductive modes among different populations of *Saiphos equalis*. *Saiphos equalis* from the northern highlands of NSW (Riamukka State Forest) are essentially viviparous, whereas those from the central coast of NSW (Sydney) display an unusual mode of reproduction that is intermediate between ‘normal’ oviparity and viviparity. In both cases, it is difficult to describe the reproductive mode in simple terms, because neither of the populations that we studied shows either ‘normal’ oviparity or ‘normal’ viviparity (i.e. as seen in other squamate reptiles). Females of the ‘viviparous’ (high-elevation) *S. equalis* population produce fully developed embryos/neonates that can emerge from their transparent birth membranes in less than 12 h, but sometimes remain inside those membranes for up to seven days. Similar conditions in other squamate

**Table 3. Differences in reproductive characteristics between *Saiphos equalis* from Sydney and from Riamukka State Forest**

ANOVAs test for differences in mean values between the two populations. Analyses of covariance, with population as the factor, test for differences between the two populations in the relationships of traits. Oviposition date was scored as the number of days after the date the first female laid her 'eggs'. 'Relative embryo mass' is the ratio of embryo mass at oviposition divided by the mean mass of siblings at hatching; similarly for 'relative embryo length' and 'relative yolk mass'. Egg colour was scored on a 6-point scale (see text and Fig. 3) and is treated here as a continuous variable for illustrative purposes only. 'Relative clutch mass' was calculated as clutch mass divided by maternal post-partum mass. Significant values ( $P < 0.05$ ) are shown in bold

Trait	Mean (s.d.)		F	ANOVA		P	
	Riamukka	Sydney		d.f.			
Comparisons of mean values of traits							
Oviposition date	15.5 (7.5)	26.9 (12.2)	18.23	1,45		<b>&lt;0.0001</b>	
Clutch size	3.28 (0.91)	3.33 (1.14)	0.04	1,45		0.85	
Clutch mass (g)	1.71 (0.575)	1.76 (0.507)	0.10	1,44		0.76	
Egg mass (g)	0.578 (0.075)	0.520 (0.049)	7.32	1,42		<b>0.0098</b>	
Embryo mass (g)	0.329 (0.037)	0.231 (0.027)	86.40	1,46		<b>&lt;0.0001</b>	
Relative embryo mass	1.005 (0.0246)	0.827 (0.109)	6.63	1,42		<b>0.0136</b>	
Relative embryo length	0.908 (0.077)	0.824 (0.036)	14.89	1,41		<b>0.0004</b>	
Yolk mass (g)	0.048 (0.033)	0.087 (0.025)	16.73	1,43		<b>&lt;0.0001</b>	
Relative yolk mass	0.152 (0.123)	0.389 (0.121)	37.34	1,43		<b>&lt;0.0001</b>	
Egg colour	1.14 (1.00)	4.06 (1.06)	244.91	1,139		<b>&lt;0.0001</b>	
Incubation period (days)	1.51 (1.52)	5.53 (1.69)	161.97	1,109		<b>&lt;0.0001</b>	
Relative clutch mass	0.407 (0.136)	0.588 (0.084)	22.28	1,44		<b>&lt;0.0001</b>	
Analysis of covariance							
Trait	Covariate	Homogeneity of slopes			Intercepts		
		F	d.f.	P	F	d.f.	P
Comparisons of relationships among traits							
Clutch mass	Post-partum mass	0.34	1,40	0.57	14.72	1,41	<b>0.0004</b>
Clutch mass	Snout-vent length	0.93	1,40	0.37	0.35	1,41	0.56
Clutch size	Snout-vent length	0.78	1,40	0.38	1.06	1,41	0.31
Post-partum mass	Pre-partum mass	0.09	1,34	0.77	7.18	1,35	<b>0.011</b>

species have been labelled as 'viviparous' (e.g. Shine 1985; Blackburn 1995), despite the existence of the brief 'egg' (membrane-bound) phase. The coastal (Sydney) animals are more difficult to classify. They produce relatively thick-shelled calcareous eggs that require up to nine days of incubation prior to hatching, although some eggs hatch in less than one day. These animals are clearly very close to viviparity, but nonetheless have an incubation period long enough that it is likely to be of biological importance both for hatchlings (which may be exposed to significant mortality prior to hatching) and for reproducing females (which must deposit their 'eggs' in microhabitats with suitable thermal and hydric conditions for incubation).

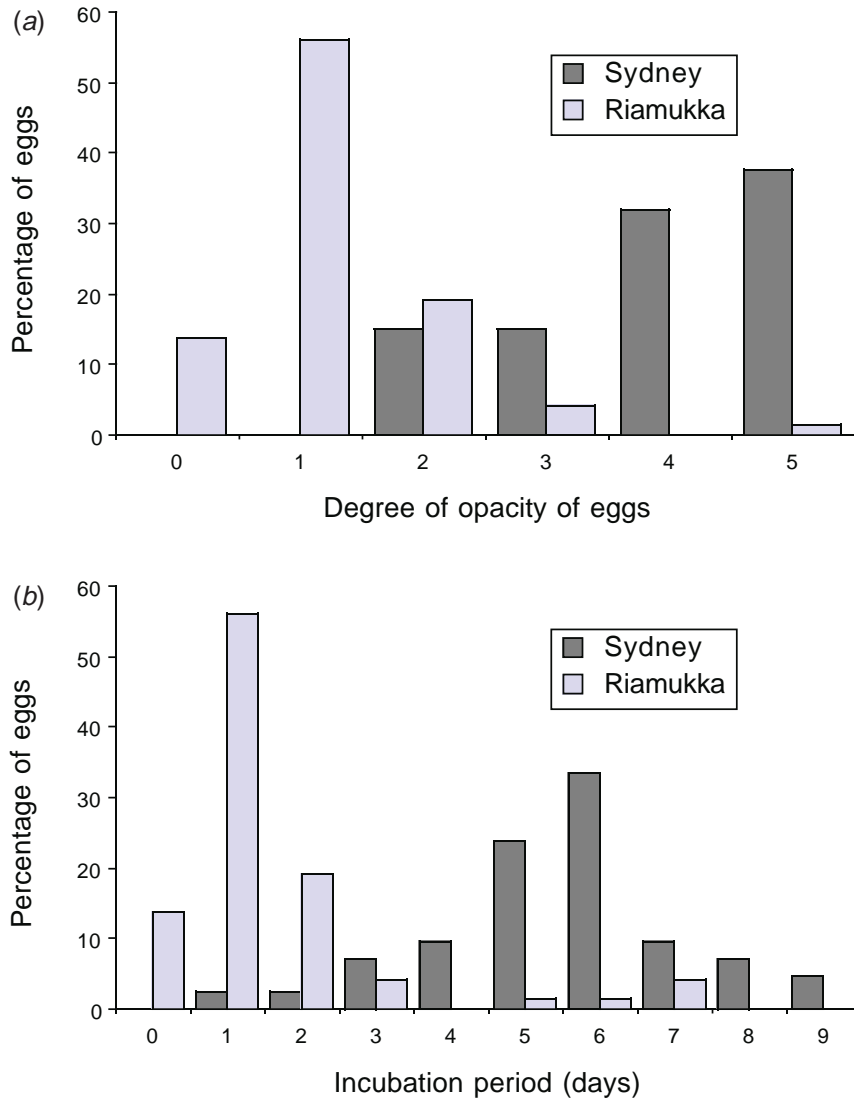
Squamate eggs are usually laid at around D & H Stage 30, with hatching occurring at D & H Stage 40 (e.g. Shine 1983; Blackburn 1995). In contrast, the eggs of Sydney *S. equalis* were laid at approximately D & H Stage 38–39. Similarly, all oviparous scincid species sympatric with *S. equalis* have incubation periods at 25°C that are longer than 35 days (see review by Qualls and Shine 1997), whereas the 'oviparous' *S. equalis* have incubation periods averaging less than six days at 23°C. Hence, we conclude that the reproductive mode of *S. equalis* from southern NSW is genuinely intermediate between 'oviparity' and 'viviparity', as these conditions are generally defined in reptiles.



**Fig. 2.** Reproductive products from the two *Saiphos equalis* populations. Females from the northern population (Riamukka) gave birth to fully formed offspring enclosed in transparent membranes (on right of photograph), whereas females from the Sydney area produced less-fully formed embryos in calcareous opaque eggshells (two eggs to left).

Bimodal reproduction has been reported in several reptile species, but many of these cases probably reflect errors in taxonomic assignment, or confusion between closely related species of different reproductive modes (see review by Shine 1985). This criticism cannot be applied to the case of *S. equalis*, because our taxonomic studies have confirmed that it is a single species [i.e. there are no fixed electrophoretic differences among populations, and there is very little geographic structuring of morphological variation within the taxon (Smith 1996)]. Errors in assigning reproductive mode may also occur if the animals display flexible responses to changes in local environmental conditions (Blackburn 1993). This explanation is worth examining in detail for *S. equalis*; given the relatively minor differences in reproductive mode between Riamukka and Sydney lizards, one could imagine that this variation reflects responses to local conditions rather than genetically coded differences. To test this idea, we maintained female *S. equalis* from both populations under a range of temperature and moisture conditions; neither of these variables affected the stage of development of their young at parturition (Smith 1996). Also, other work in our laboratory has confirmed that reproductive modes are consistent from year to year for females from each population (Shine, unpublished data).

Prior to our study, detailed data have been published on only two reproductively bimodal reptile species: a European lacertid (*Lacerta vivipara*) and an Australian skink (*Lerista bougainvillii*). *Lacerta vivipara* is viviparous throughout most of its range, but is oviparous in the extreme south-west of its distribution (including northern Spain, the Pyrenees and southern France) (e.g. Heulin *et al.* 1991). *Lerista bougainvillii* is oviparous throughout most of its range in south-eastern Australia but is viviparous on two offshore island groups (Kangaroo Island, South Australia; and Chappell and Flinders Islands and adjacent mainland Tasmania) (Qualls *et al.* 1995).



**Fig. 3.** Differences between Sydney and Riamukka *Saiphos equalis* in offspring traits. On our scale of egg opacity from 0 (transparent) to 5 (completely opaque), Sydney females produced more opaque eggs than did their Riamukka counterparts (a). The Sydney eggs took longer to develop through to hatching than did the Riamukka progeny (b).

In these two other intensively studied lizard species with reproductive bimodality, the viviparous form deposits its young at D & H Stage 40, whereas the oviparous animals have thick-shelled eggs that are deposited with embryos at a modal developmental stage of 31, in *Lacerta vivipara* (Brana *et al.* 1991; Heulin *et al.* 1991; Arrayago *et al.* 1996), or 32–33, in *Lerista bougainvillii* (Qualls 1996). That is, the oviparous forms are 'normal' egg-layers. However, a small population of *Lerista bougainvillii* in Gippsland (south-eastern Victoria) has an intermediate mode of reproduction, with the embryos being laid at D & H Stage 35–37 and incubating for approximately 19 days at 29°C (Qualls 1995, 1996, 1997; Qualls *et al.* 1995). The

reproductive mode of these 'intermediate' *Lerista bougainvillii* thus approaches that seen in the southern population of *S. equalis*, although the *Lerista bougainvillii* (because of their longer incubation period and lesser degree of embryogenesis at oviposition) are further towards the 'normal' oviparous condition than are either of the *S. equalis* populations. Other reptiles reported to show the 'almost-viviparous' condition of the southern *S. equalis* population include the iguanid lizard *Sceloporus scalaris* (Demarco 1992), the colubrid snake *Ophedrys vernalis* (Sexton and Claypool 1978) and artificially produced hybrids of oviparous and viviparous *Lacerta vivipara* populations (Arrayago *et al.* 1996).

Nonetheless, it seems clear that such 'intermediate' forms are very rare. Although there is a continuum of reproductive modes in squamates (Shine 1983), available data on the stage of development at parturition in squamate reptiles show that there is a clear bias towards the extremes of this spectrum. That is, most taxa are either fully viviparous, or they lay eggs with relatively minor embryonic development at the time of oviposition (Shine 1983; Blackburn 1995; Qualls and Shine 1996; Qualls *et al.* 1997). This dichotomy suggests that squamates have an evolutionary 'choice' between two stable reproductive options, and that the intermediate state (i.e. production of young at intermediate stages of development) is unstable over evolutionary time. Life-history models offer a possible explanation for this effect. A number of selective forces that favour either 'normal' oviparity or viviparity may not apply to intermediate stages (e.g. Shine and Bull 1979). If so, intermediate degrees of egg retention will incur the costs associated both with oviparity (e.g. nesting behaviour and the loss of calcium to the eggshell) and viviparity (e.g. physical burdening of the female and loss of the ability to have a second clutch) while gaining only part of the advantage associated with each mode (e.g. the ability to maintain egg temperature for some of the developmental period). These high 'costs' may explain why reproductively intermediate forms are rare in extant reptile taxa (e.g. Shine 1985; Qualls 1995, 1997). Adaptationist hypotheses such as this one are inevitably difficult to test rigorously, but our study shows that *Saiphos equalis* offers an ideal opportunity to study the costs and benefits involved in the evolutionary transition from oviparity to viviparity.

### Acknowledgments

We are especially grateful to Allen E. Greer, for his generous provision of advice, insight and unpublished data, and for many discussions. We also thank M. Elphick, M. Lee, R. Sadlier, G. Shea, W. Smart and G. Swan for assisting in the collection of animals. R. Sadlier kindly allowed us to examine specimens in the Australian Museum collection. Captive animals were held under Sydney University ACEC Protocol No. L04/11-94/3/1083. The work was funded by an Australian Research Council grant to R. Shine.

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