

A NOVEL PATTERN OF EMBRYONIC NUTRITION IN A VIVIPAROUS REPTILE

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Summary

Vitellogenesis and placental transfer both contribute substantially to embryonic nutrition in the viviparous scincid lizard *Pseudemoia entrecasteauxii*. Neonatal wet mass was 396% greater than egg wet mass and neonatal dry mass was 168% greater than egg dry mass. We estimate that 49% of the organic molecules for embryonic growth and metabolism were provided by placental nourishment. This pattern of embryonic nutrition, in which ovarian and uterine contributions are approximately equivalent, has not been reported previously for reptiles. Female *Bassiana duperreyi*, a closely related oviparous species, produced larger clutches of larger eggs. Although there was a great disparity in egg mass between these two species, differences in newborn composition were less pronounced. Mean dry mass, adjusted for female size, of *B. duperreyi* eggs was 135% greater than mean dry mass of *P. entrecasteauxii* eggs, yet mean dry mass of *B. duperreyi* offspring was only 21% greater than that of *P. entrecasteauxii* offspring. Embryonic gains in water and inorganic salts during gestation in *P. entrecasteauxii* were substantial and resulted in the production of neonates that contained greater quantities of these variables compared to offspring of *B. duperreyi*. These data confirm Weekes' hypothesis that *P. entrecasteauxii* is matrotrophic and support her hypothesis that this species has undergone evolutionary reduction in yolk quantity.

Introduction

The evolution of viviparity among vertebrates has involved two phenomena: shifts in the way in which young are produced and in the method of provisioning developing young with nourishment. The reproductive patterns of vertebrate taxa display a variety of combinations of these two distinct reproductive processes (Blackburn *et al.* 1985; Wourms *et al.* 1988; Wake, 1989; Blackburn, 1992; Wourms and Lombardi, 1992). With respect to the first of these, vertebrates either lay eggs (oviparity) or give birth to young (viviparity) (Wake, 1989; Blackburn, 1992; Wourms and Lombardi, 1992). Developing embryos may be nourished from yolk deposited in the ovary during vitellogenesis

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(lecithotrophy) or may be nourished by alternative pathways (matrotrophy) (Wourms, 1981; Blackburn *et al.* 1985).

Intrauterine gestation with parturition of independent neonates (viviparity) is a prominent reproductive mode among squamate reptiles (Blackburn, 1982, 1985; Shine, 1985). Sources of embryonic nutrition among these species include both yolk (lecithotrophy) and a form of matrotrophy, placental transfer (placentotrophy). Two primary patterns of nutrient provision are known (Blackburn, 1992; Stewart, 1992). Many species ovulate yolk-rich eggs that provide the primary nourishment to developing embryos, while the uterus also acts as an important source of nutrients. Functionally, these species are primarily lecithotrophic, although embryonic nutrition is supplemented by placentotrophy. In contrast, other species have a large neonate to egg mass ratio, indicating a second pattern of embryonic nourishment characterized by predominant or perhaps complete dependence on placental nutrition (Blackburn *et al.* 1984; Vitt and Blackburn, 1983; Ghiara *et al.* 1987; Blackburn and Vitt, 1992). These two recognized patterns are distinct yet might be described as ends of a continuum. Sources of embryonic nutrition for oviparous squamates are less well known and only two lizard species have been studied (Packard *et al.* 1985; Florian, 1990). No information about patterns of embryonic nutrition is available for closely related species with different reproductive modes and thus hypotheses for the evolution of patterns of fetal nutrition have not been based on historical relationships.

Australian scincid lizards historically placed within the genus *Leiopisma* (Mittleman, 1952; Greer, 1974) have long figured prominently in hypotheses concerning the evolution of viviparity and placentation among Squamata (Weekes, 1935). The significance of this group is based on the presence of both oviparous and viviparous species as well as the existence of variation in placental structure (Weekes, 1935). A recent revision of this genus has resulted in a phylogenetic hypothesis that distributes species among several genera (Hutchinson *et al.* 1990; Hutchinson and Donnellan, 1992) and thus differs from prior hypotheses (Greer, 1974, 1982).

Pseudemoia entrecasteauxii has a structurally elaborate chorioallantoic placenta (Harrison and Weekes, 1925; Weekes, 1930) and Weekes (1935) predicted that the species was matrotrophic on the basis of the small size of oviductal eggs. *Bassiana duperreyi* is an oviparous species and a close relative of *P. entrecasteauxii* in each of the competing phylogenetic hypotheses (Greer, 1974, 1982; Hutchinson *et al.* 1990).

Our primary goal was to test Weekes' (1935) hypothesis that *P. entrecasteauxii* is matrotrophic. Additionally, we provide the first comparison of the sources of embryonic nutrition in two closely related reptile species with different modes of reproduction. This comparison offers support for the hypothesis (Weekes, 1935) that the evolution of placentotrophy in Squamata was associated with a concomitant reduction in egg size.

Materials and methods

Pseudemoia entrecasteauxii (Duméril and Bibron) were collected from Kanangra Boyd National Park, New South Wales. Recently ovulated eggs were removed from the right oviduct of 19 females collected in October, 1990. Neonates were obtained following

parturition from a second series of 15 females collected from the same locality in January, 1991.

Twelve female *Bassiana duperreyi* (Gray) were collected in southeastern Tasmania in November, 1990, returned to the University of Sydney and maintained until oviposition. The shell and contents of one egg from each clutch were separated and frozen on the day of oviposition. Embryos in the oviposited eggs contained lightly pigmented eyes, an open choroid fissure and 'paddle-like' limbs; features corresponding to embryonic stages 30–31 of Dufaure and Hubert (1961). Additional eggs were incubated at temperatures that fluctuated between 23.8 and 26.8°C on a mixture of 2:1 (water:vermiculite), which corresponds to a water potential greater than -100kPa , determined for that batch of Terra Lite Grade 3 vermiculite by thermocouple psychrometry using a Wescor HR-33T dew-point microvoltmeter. Eighteen eggs, two in each of six clutches and one in each of the remaining six clutches, were incubated to hatching.

Eggs and neonates of *P. entrecasteauxii* and shell-free egg contents and hatchlings of *B. duperreyi* were treated in the same manner for analyses. Specimens were lyophilized, and ashed in a muffle furnace at 550°C for 24h prior to hot acid digestion (Kopp and McKee, 1979) in preparation for inorganic ion analysis. Quantitative estimates of calcium, magnesium and phosphorus were carried out on an ARL inductively coupled plasma spectrophotometer (model 3510). Potassium and sodium levels were estimated using atomic absorption spectrophotometry (Perkin-Elmer model 2380).

Differences between developmental stages within species were tested using either one-way analysis of variance (ANOVA) or two-way analysis of variance. Analysis of covariance (ANCOVA) was used for interspecific comparisons of fecundity and egg and offspring composition. Values are presented as mean \pm S.E.

Results

Mean snout–vent length for the total sample of female *P. entrecasteauxii* was $58.8\pm 0.8\text{mm}$ (range 48–68mm, $N=34$). Litter size, based on number of oviductal eggs and number of neonates (3.6 ± 0.2 , range 2–6, $N=34$) was positively correlated with female snout–vent length [$y=-2.3+0.1x$; $F(1,32)=8.6$, $P<0.01$]. Neither egg nor neonate size was correlated with female size. Neonates contained significantly greater quantities of water, ash and organic molecules, estimated as dry mass minus ash, than did eggs (Table 1). Because of their small mass, oviductal eggs taken from individual females were pooled for inorganic analyses. Mean values per egg or neonate per litter were used to test for differences between egg and neonate composition for inorganic ions. Quantities of calcium, phosphorus, magnesium, sodium and potassium were significantly greater in neonates (Table 2).

Mean snout–vent length for female *Bassiana duperreyi* was $66.8\pm 1.6\text{mm}$ (range 59–77 mm, $N=12$). Clutch size (5.8 ± 0.4 , range 4–9) was correlated significantly with female snout–vent length [$y=-7.9+0.2x$; $F(1,10)=11.0$, $P<0.01$]. Wet mass of shelled eggs sampled at oviposition ($318.3\pm 10.5\text{mg}$) did not differ [$F(1,22)=0.04$] from the initial wet mass of shelled eggs incubated to hatching ($315.5\pm 9.8\text{mg}$). The mean incubation time was $38\pm 0.4\text{days}$ (range 34–41days). Wet mass and water content of hatchlings were

significantly greater than wet mass and water content of shell-free eggs (Table 3). However, hatchlings contained significantly less dry mass and organic mass than oviposited shell-free eggs. In contrast, significantly higher quantities of ash and calcium

Table 1. *Composition (mean \pm S.E.) of oviductal eggs and neonates of Pseudemoia entrecasteauxii*

	Eggs (N=19) (mg)	Neonates (N=15) (mg)
Wet mass	72.4 \pm 1.6*	286.5 \pm 3.2*
Dry mass	32.5 \pm 0.8*	54.6 \pm 1.0*
Water	39.9 \pm 1.0*	231.9 \pm 2.8*
Organic mass	30.6 \pm 0.7*	49.3 \pm 0.9*
Ash mass	1.9 \pm 0.08*	5.3 \pm 0.08*

Asterisks indicate significant differences between columns; * P <0.001.
See Appendix 1 for analysis of variance.

Appendix 1

Analysis of variance tables for Table 1.

Wet mass	Source of variation	SS	d.f.	MS
	Stage (egg/neonate)	889659	1	889659
	Female	9407	32	294
	Litter (within female)	6000	43	140
	Total	905066	76	
Dry mass	Source of variation	SS	d.f.	MS
	Stage (egg/neonate)	9801	1	9801
	Female	1352	32	42
	Litter (within female)	496	43	12
	Total	11649	76	
Water mass	Source of variation	SS	d.f.	MS
	Stage (egg/neonate)	712705	1	712705
	Female	6117	32	191
	Litter (within female)	4394	43	102
	Total	723216	76	
Organic mass	Source of variation	SS	d.f.	MS
	Stage (egg/neonate)	7062	1	7062
	Female	1182	32	37
	Litter (within female)	444	43	10
	Total	8688	76	
Inorganic mass	Source of variation	SS	d.f.	MS
	Stage (egg/neonate)	224	1	224
	Female	13	32	0.41
	Litter (within female)	4	43	0.11
	Total	241	76	

in hatchlings compared to eggs indicates that the shell is an important source of inorganic nutrients for developing embryos. These data compare favorably with a similar analysis for the North American oviparous scincid lizard *Eumeces fasciatus* (Florian, 1990) and support prior work demonstrating that the shell of oviparous squamate reptiles is an important source of embryonic calcium (Packard and Packard, 1984, 1988; Packard *et al.* 1985).

Table 2. *Inorganic composition (mean per egg/neonate per litter \pm S.E.) of oviductal eggs and neonates of Pseudemoia entrecasteauxii*

	Eggs (N=19) (mg)	Neonates (N=15) (mg)
Calcium	0.30 \pm 0.02**	1.09 \pm 0.02**
Phosphorus	0.44 \pm 0.02**	0.75 \pm 0.02**
Magnesium	0.03 \pm 0.001*	0.04 \pm 0.001*
Sodium	0.09 \pm 0.009**	0.43 \pm 0.01**
Potassium	0.07 \pm 0.008**	0.40 \pm 0.01**

Asterisks indicate significant differences between columns; * P <0.005; ** P <0.001.

See Appendix 2 for analysis of variance.

Appendix 2

Analysis of variance tables for Table 2.

Calcium	Source of variation	SS	d.f.	MS
	Stage (egg/neonate)	5.26	1	5.26
	Residual	0.24	32	0.007
	Total	5.50	33	
Phosphorus	Source of variation	SS	d.f.	MS
	Stage (egg/neonate)	0.82	1	0.82
	Residual	0.20	32	0.006
	Total	1.02	33	
Magnesium	Source of variation	SS	d.f.	MS
	Stage (egg/neonate)	0.0003	1	0.0003
	Residual	0.0008	32	0.00003
	Total	0.0011	33	
Sodium	Source of variation	SS	d.f.	MS
	Stage (egg/neonate)	0.988	1	0.988
	Residual	0.046	32	0.001
	Total	1.034	33	
Potassium	Source of variation	SS	d.f.	MS
	Stage (egg/neonate)	0.882	1	0.882
	Residual	0.043	32	0.001
	Total	0.925	33	

Table 3. *Composition (mean per egg/neonate per litter \pm S.E.) and F values for the ANOVA for oviposited eggs and hatchlings of Bassiana duperreyi*

	Egg ^a (mg)	Hatchling ^a (mg)	Source of variation	
			Treatments ^b	Blocks ^c
Wet mass	245.5 \pm 9.2	270.2 \pm 8.9	5.8*	2.1 NS
Dry mass	79.8 \pm 2.6	68.0 \pm 2.0	66.2***	9.2***
Water	165.7 \pm 7.2	202.3 \pm 7.5	15.4**	1.5 NS
Organic mass	76.4 \pm 2.5	63.2 \pm 1.8	88.6***	8.8***
Ash mass	3.4 \pm 0.1	4.8 \pm 0.2	92.7***	3.7*
Calcium mass	0.44 \pm 0.02	1.01 \pm 0.04	305.4***	2.6 NS

^a $N=12$, except calcium mass, $N=11$.

^bDevelopmental stage.

^cClutch.

* $P<0.05$; ** $P<0.005$; *** $P<0.001$; NS, not significant.

See Appendix 3 for analysis of variance.

Appendix 3

Analysis of variance tables for Table 3.

Wet mass	Source of variation	SS	d.f.	MS
	Stage (egg/hatchling)	3 675	1	334
	Clutch	14698	11	1336
	Residual	6907	11	628
	Total	25280	23	
Dry mass	Source of variation	SS	d.f.	MS
	Stage (egg/hatchling)	846	1	77
	Clutch	1 296	11	118
	Residual	140	11	13
	Total	2 283	23	
Water	Source of variation	SS	d.f.	MS
	Stage (egg/hatchling)	8 048	1	732
	Clutch	8 606	11	782
	Residual	5 753	11	523
	Total	22407	23	
Organic mass	Source of variation	SS	d.f.	MS
	Stage (egg/hatchling)	1 054	1	96
	Clutch	1 152	11	105
	Residual	131	11	12
	Total	2 337	23	
Ash mass	Source of variation	SS	d.f.	MS
	Stage (egg/hatchling)	11.4	1	1.04
	Clutch	5.02	11	0.46
	Residual	1.35	11	0.12
	Total	17.8	23	

Calcium mass	Source of variation	SS	d.f.	MS
	Stage (egg/hatchling)	1.77	1	0.18
	Clutch	0.15	10	0.01
	Residual	0.06	10	0.006
	Total	1.98	21	

Female *B. duperreyi* were significantly larger than female *P. entrecasteauxii* [$F(1,44)=23.8$; $P<0.001$]. Clutch size, adjusted for female size by ANCOVA, of *B. duperreyi* was significantly higher than litter size of *P. entrecasteauxii* (Table 4). Shell-free eggs of *B. duperreyi* contained greater quantities of all variables measured compared to the yolk of recently ovulated eggs of *P. entrecasteauxii* (Table 4). Dry mass and organic mass of hatchling *B. duperreyi* were significantly greater than those of neonatal *P. entrecasteauxii*. However, neonatal *P. entrecasteauxii* contained greater quantities of ash and water and had significantly greater wet mass (Table 4).

Discussion

Embryonic nutrition in P. entrecasteauxii

In her comprehensive review of reptilian placentation, Weekes (1935) speculated that *Pseudemoia entrecasteauxii* (as *Lygosoma entrecasteauxii*) was matrotrophic. This hypothesis was based on the small size of oviductal eggs and the presence of a specialized chorioallantoic placenta in this species. Our estimates of net placental uptake confirm that *P. entrecasteauxii* is matrotrophic. Neonatal dry mass, as well as estimates of both organic and inorganic components of dry mass, exceeded that of recently ovulated eggs (Tables 1, 2).

Further, although the pattern of embryonic metabolism and thus the extent of placental transport of organic molecules, is unknown, the degree of matrotrophy in this species is

Table 4. Mean composition (mg) adjusted for female snout–vent length and F values for the ANCOVA for eggs and offspring of *Bassiana duperreyi* and *Pseudemoia entrecasteauxii*

	<i>B. duperreyi</i>	<i>P. entrecasteauxii</i>	F value
Clutch/litter size	5.0	3.9	6.8*
Egg wet mass	238.6	76.3	279.5***
Egg dry mass	78.3	33.3	201.1***
Egg water	160.3	43.0	255.0***
Egg organic mass	75.0	31.4	213.6***
Egg ash	3.4	2.0	31.1***
Offspring wet mass	266.1	292.0	4.8*
Offspring dry mass	67.2	55.4	17.5***
Offspring water	198.8	236.4	13.4**
Offspring organic mass	62.6	50.0	22.6***
Offspring ash	4.7	5.5	9.8**

* $P<0.05$; ** $P<0.005$; *** $P<0.001$.

substantial in comparison to that of many viviparous squamates (Stewart, 1992). Most viviparous species give birth to neonates with less dry mass than the large yolked eggs they ovulate (Thompson, 1977, 1981, 1982; Stewart and Castillo, 1984; Stewart, 1989; Stewart *et al.* 1990), although each of these species relies on some degree of placentotrophy, at least for inorganic molecules. The degree of matrotrophy in *P. entrecasteauxii* is impressive, yet embryonic gains in dry mass are much less than those recorded for two other scincid lizards. Dry mass of neonates of *Mabuya heathii* and *M. bistrinata* is 38000–48000% greater than egg dry mass (Blackburn *et al.* 1984; Vitt and Blackburn, 1991).

A comparison of egg and offspring dry mass among scincid lizards (Table 5) indicates that *P. entrecasteauxii* is intermediate in embryonic nutritional pattern in comparison to *Eulamprus quoyii* and the two species of *Mabuya*. For example, *E. quoyii* gives birth to neonates with less dry mass than its ovulated eggs, yet embryos do incorporate inorganic ions from placental sources in excess of yolk reserves (Thompson, 1977, 1982). The pattern of net placental transfer of ions for *E. quoyii* is similar to that of *P. entrecasteauxii*. However, the relative quantities provided by the placenta are greater in *P. entrecasteauxii*. Thus, 56% of calcium incorporated into *E. quoyii* neonates is provided from the placentae (Thompson, 1977), whereas placentotrophy in *P. entrecasteauxii* accounts for 72% of neonatal calcium (Table 2). The pattern of embryonic nourishment in *P. entrecasteauxii* differs from that of *E. quoyii* by placing less reliance on lecithotrophy and greater reliance on placentotrophy.

The mean dry mass of hatchling *B. duperreyi* was 85% and organic mass was 83% of shell-free egg values (Table 3). If the conversion ratio for *P. entrecasteauxii* development is comparable, i.e. the effects of scale due to egg size and source of energy are minimal, then yolk provides 51% (30.6mg; Table 1) of the organic material for growth and metabolism, with the remaining 49% (29.0mg) being transferred across the placenta. This estimate assumes that it takes 59.6mg of organic material to produce a neonate with an organic mass of 49.3mg (Table 1). In contrast, nearly all embryonic nutrients are transferred across the uterus in *M. heathii* and *M. bistrinata*.

Information on embryonic nutrition among viviparous squamates is scant, particularly in view of the great number of viviparous species. Nonetheless, the pattern that is emerging is that placentotrophy occurs in all viviparous squamate species, regardless of

Table 5. Egg dry mass and offspring dry mass for lizards of the family Scincidae

	Egg (mg)	Offspring (mg)	Offspring/ egg
<i>Eumeces fasciatus</i> ^a (O)	97.4	65.2	0.67
<i>Bassiana duperreyi</i> (O)	79.8	68.0	0.85
<i>Eulamprus quoyii</i> ^b (V)	286.0	240.0	0.84
<i>Pseudemoia entrecasteauxii</i> (V)	32.5	54.0	1.66
<i>Mabuya heathii</i> ^c (V)	0.40	154.0	385.00
<i>Mabuya bistrinata</i> ^d (V)	0.47	222.4	473.19

^aFlorian (1990); ^bThompson (1977); ^cBlackburn *et al.* (1984); ^dVitt and Blackburn (1991).
O, oviparous; V, viviparous.

the quantity of yolk present at ovulation (Blackburn, 1992; Stewart, 1992). The degree of placentotrophy in *P. entrecasteauxii* is unique among squamate species that have been studied in that yolk and placental nourishment are approximately equivalent.

Comparative embryonic nutrition in B. duperreyi and P. entrecasteauxii

Two hypotheses have been proposed for phylogenetic relationships among Australian lizard species assigned to the scincid genus *Leiopisma* (Greer, 1974, 1982; Hutchinson *et al.* 1990). Greer (1974) retained the generic designation *Leiopisma* and subdivided the included species into two groups. The Baudini group included *L. entrecasteauxii* and *L. duperreyi*. Hutchinson *et al.* (1990) assigned *L. entrecasteauxii* to the genus *Pseudemoia* and *L. duperreyi* to the genus *Bassiana*, yet hypothesized a common ancestor for these two taxa. Although there are substantive differences between these hypotheses, they are consistent in arguing for a close phylogenetic relationship between *P. entrecasteauxii* and *B. duperreyi*.

Variation in lizard life history patterns results from covariation among specific life history characteristics (Tinkle *et al.* 1970; Dunham *et al.* 1988). In general, viviparous species are late maturing, long lived and produce a single litter per reproductive season. Fecundity is higher in oviparous species that produce multiple clutches per season (Tinkle *et al.* 1970) and clutch size is larger in single-brooded oviparous species than in viviparous species (Dunham *et al.* 1988).

Compared to *B. duperreyi*, *P. entrecasteauxii* ovulates fewer, smaller eggs (Table 4). An average litter, adjusted for female size, for *P. entrecasteauxii* contains one less egg that has only 42% of the dry mass of an average *B. duperreyi* egg. Reduced clutch size in a viviparous species of lizard compared to a closely related oviparous species has also been demonstrated within the family Iguanidae (Guillette, 1982). Within these two lineages, the evolution of viviparity is associated with a reduction in clutch size.

Greater maternal commitment to individual young has been viewed as a characteristic of viviparity in comparison to oviparity (Shine, 1978; Guillette, 1982; Stewart, 1989). In support of this, both egg and neonate size were greater in *Sceloporus bicanthalis*, a viviparous species, compared to the oviparous *S. aeneus* (Guillette, 1981, 1982). In contrast, both eggs and hatchlings of *B. duperreyi* had greater dry mass, relative to female size, than eggs and neonates of *P. entrecasteauxii* (Table 4). However, two estimates of offspring content did indicate greater provision to individual embryos in *P. entrecasteauxii* as a result of uterine gestation. The total inorganic mass of *P. entrecasteauxii* neonates exceeded that of hatchling *B. duperreyi*. Additionally, embryos of the viviparous species were more efficient in the uptake, or at least the retention, of water, in spite of the substratum water potentials during incubation of *B. duperreyi* eggs being at levels considered high for squamate egg incubation (Packard *et al.* 1982; Packard and Packard, 1987).

Using calculations based on *B. duperreyi*, in the absence of placental nourishment, *P. entrecasteauxii* neonates would contain 25.3mg of organic mass and 27.7mg of dry mass. These neonates would be roughly half the size of those born into the population we sampled. Experimental reduction in yolk quantity, by up to 50%, in eggs of an oviparous iguanid lizard resulted in smaller, yet viable, hatchlings (Sinervo, 1990). Thus,

matrotrophy in *P. entrecasteauxii* may not be a physiological requirement for the production of viable neonates. An equally significant possibility is that lecithotrophy may not be necessary for the production of viable neonates. However, in the absence of matrotrophy, the production of smaller numbers of markedly smaller young would result in significant life history consequences.

Supplementation of yolk nourishment by placentotrophy is characteristic of viviparous squamate species that ovulate much larger ova than *P. entrecasteauxii* (Stewart, 1992). Thus, *P. entrecasteauxii* resembles other species in supplementing yolk nourishment by placentotrophy; it is the much greater degree of placentotrophy that is notable. Although the eggs of *P. entrecasteauxii* were much smaller than those of *B. duperreyi*, the size disparity at partition was greatly reduced as a result of uterine gestation (Table 4).

There are two possible historical sequences that could have resulted in the reproductive pattern of *P. entrecasteauxii*. Weekes' (1935) hypothesis was that egg content had undergone evolutionary reduction in quantity in association with an increased reliance on placental nourishment and, by implication, neonate size remained constant. Alternatively, egg content in the ancestors of *P. entrecasteauxii* did not differ from that in present populations, but neonates were much smaller. The advent of placentotrophy thus produced an evolutionary increase in neonatal size.

We propose that the most likely historical sequence is that offspring size has been conserved, that is, the ancestors of *P. entrecasteauxii* ovulated larger eggs, comparable to those of *B. duperreyi* and that the evolution of matrotrophy has been accompanied by a concomitant reduction in yolk quantity. The alternative hypothesis requires that the ancestor of both species had small eggs and that both lineages, representing two reproductive modes, converged on offspring size through two separate patterns of embryonic nutrition. That is, yolk content increased in the *B. duperreyi* lineage and a functional placenta evolved in *P. entrecasteauxii*.

The mode of embryonic nourishment in *P. entrecasteauxii* is unique among squamates in its balance between lecithotrophy and placentotrophy and contributes significantly to our understanding of variation in reptilian reproductive biology. The relationship between reproductive mode and embryonic nutrition is now known to occur in four patterns among Reptilia; (1) oviparous and lecithotrophic, (2) viviparous and predominantly lecithotrophic, (3) viviparous and equivalent contributions from lecithotrophy and placentotrophy and (4) viviparous and predominantly placentotrophic.

It is also important that the mode of embryonic nutrition shown by *P. entrecasteauxii* supports a gradualistic model for the evolution of placentotrophy among reptiles. The roughly equal contribution from ovarian and uterine sources is functionally intermediate between lecithotrophy and matrotrophy regardless of the yolk content of ancestral eggs.

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