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Source: *Functional Ecology*, August 2016, Vol. 30, No. 8 (August 2016), pp. 1373-1383

Published by: British Ecological Society

Stable URL: <https://www.jstor.org/stable/10.2307/48582233>

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One lump or two? Explaining a major latitudinal transition in reproductive allocation in a viviparous lizard

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Summary

1. In viviparous ectotherms, the interval between reproductive bouts is often extended by long gestation times, preventing multiple reproductive events per annum.
2. We assessed the potential roles of physiological adaptation and environmental constraints in driving an unusual case of geographic variation in life history, in the viviparous lizard (*Eulamprus quoyii*), which has either one or two reproductive bouts per annum, depending on the geographic location of the population.
3. Using dynamic energy budget theory, we developed an integrated model of the energetics of growth and reproduction in this lizard, and applied it in conjunction with biophysical calculations of body temperature and activity time across its geographic range to predict reproductive frequency.
4. Our model indicated that geographic variation in body temperature alone (i.e. environmental constraints) explained the observed pattern of litter frequency, suggesting that differences in energy allocation among populations were unlikely to be a major cause of differences in litter frequency in *E. quoyii*. It also suggested that natural selection should favour fixation of litter size in the transition zone.

Key-words: dynamic energy budget theory, *Eulamprus quoyii*, geographic variation, growth rate, life-history variation, litter size, reproductive frequency, reptile, skink, viviparity

Introduction

Constraints are a critical force shaping natural selection on life-history traits (Stearns 1992; Roff 2002). Such constraints may be extrinsic in nature, and for ectotherms, such as lizards, the thermal environment can be critically important (Adolph & Porter 1993, 1996). There may also be intrinsic constraints, including trade-offs in the allocation of nutrients and energy to maintenance, growth, development and reproduction (Levins 1968; Sibly & Calow 1986), constraints imposed by body volume (Shine 1992; Du, Ji & Shine 2005) and constraints associated with reproductive mode (Tinkle & Gibbons 1977; Ballinger 1983; Dunham, Miles & Reznick 1988; Shine 2005). The evolution of viviparity is a major life-history transition that, in squamate reptiles, has occurred independently in over 100 lineages (Shine 1999). Much has been written about the potential costs and benefits of this transition,

but one major cost that has received relatively little attention is the constraint it imposes on reproductive frequency; the interlitter frequency of viviparous species is necessarily extended by the gestation length (Ballinger 1983). For this reason, multiple litters per annum are extremely rare in viviparous reptiles, despite multiple clutches being quite common in oviparous species (Dunham, Miles & Reznick 1988).

World-wide, most viviparous lizards are constrained to reproduce once annually (Tinkle *et al.* 1970), or less (Schwarzkopf & Shine 1991; Van Wyk 1991; Cree & Guillelte 1995; Ibargüengoytia & Cussac 1996). Here, we investigate the potential causes of a very unusual pattern of geographic variation in litter frequency in a widespread viviparous lizard distributed along the eastern seaboard of Australia, the Eastern water skink (*Eulamprus quoyii*), in which females in some populations reproduce twice per year (L. Schwarzkopf, personal observation, and see below). One possible explanation for variation in reproductive frequency among populations of lizards is simply

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thermally induced variation in physiological rates, such as digestion and oogenesis (Adolph & Porter 1993, 1996). However, a common garden experiment using this species showed that populations from the latitudinal extremes of its range exhibit very different growth trajectories that are both locally adapted and depend on the thermal environment experienced during gestation (Caley & Schwarzkopf 2004). Thus, it appears possible that observed variation in litter frequency is caused not by simple variation in physiological rates driven by temperature in this species, but instead by local metabolic adaptations influencing energy allocation to reproduction.

To interpret this pattern, we developed a dynamic energy budget (DEB) model of growth and reproduction in *E. quoyii* and integrated it with a biophysical model of climatic constraints on body temperature and activity budget. This 'thermodynamic niche' modelling approach (Kearney *et al.* 2013) has been successfully applied to model climatic constraints on the energetics of lizards (Kearney 2012, 2013; Kearney, Matzelle & Helmuth 2012). In general, DEB theory provides a parameter-sparse approach to modelling the full life cycle energy and mass budget given different nutritional and thermal environments (Kooijman 2010). It differs from other energy budgeting approaches (van der Meer 2006; Kearney & White 2013) by considering the full elemental mass budget *via* the assumption of distinct pools of biomass of constant chemical composition, expressed in terms of elemental ratios (Kooijman 1995), and provides a powerful means to model the interaction between heat, water and nutritional constraints (Kearney *et al.* 2013).

Two qualitatively distinct biomass pools are considered in DEB theory: 'structure' and 'reserve', with the 'standard DEB model' (employed here) assuming just one structure and one reserve. The structure is the 'permanent' part of the biomass, which is empirically related to the cube of body length, and which requires energy expenditure for its growth, maintenance and development. The organism begins almost entirely as reserve (a freshly laid egg), and the reserve is mobilized for allocation to the growth, development and maintenance of the structure. The rate of reserve mobilization is proportional to the ratio of reserve to structure, which acts as a physical scaling constraint (Maino *et al.* 2013). From birth onward, the reserve pool is replenished through feeding. The density of reserve in the body fluctuates with nutritional state, rising to a maximum density at *ad libitum* food levels.

Prior to sexual maturity, a fixed proportion of the flux of mobilized reserve is used to maintain and increase the maturity state of the organism. Threshold levels of energy invested in maturation act as triggers for birth and puberty. Birth is defined as the point when feeding is initiated, whereas puberty occurs when resources are no longer used to increase maturity levels, but instead go to reproduction. Once the reproductive pool reaches the level required for a full litter, this biomass is then released as eggs in an oviparous species. In the present case, we are considering a

viviparous species with facultative placentotrophy (Stewart 1989; i.e. placental provision is not requisite to the production of viable offspring), and so in the model, eggs remain in the female for the duration of egg development (as described in Kearney 2013). Coupling a DEB model with a biophysical model of the impact of geographic variation in environmental conditions on body temperature and activity time enables us to assess the extent to which geographic variation in litter frequency in *E. quoyii* occurs because a short activity season constrains physiological time available for litter production more in the temperate zone, and less in the tropics (i.e. there is an environmental temperature constraint), or occurs because of variation in energy allocation strategies of different populations of *E. quoyii* (e.g. due to differences in energy allocation strategies to growth and reproduction, Caley & Schwarzkopf 2004).

Materials and methods

OBSERVATIONS OF GEOGRAPHIC VARIATION IN LITTER FREQUENCY

Eulamprus quoyii is distributed along the east coast of Australia from Cooktown, Queensland, in the north (approx. 15.5°S 145.3°E) to south of Sydney, New South Wales (approx. 34.4°S 150.9°E; Fig. 2). Across its geographic range, *E. quoyii* inhabits rocky and sandy, vegetated, riparian habitats ranging from cool temperate to warm tropical. To determine reproductive frequency, we collected gravid females from four high elevation and four low elevation locations along their range [high elevation populations included Paluma, Quart Pot Creek near Stanthorpe, Mimosa Creek on the Blackdown Tableland and Sharpe's Creek at Gloucester Tops in Barrington Tops National Park, whereas low elevation populations included Bluewater Creek, Alligator Creek and North Creek, all near Townsville (these were modelled as a single lowland location because of proximity), the Brisbane Cultural Centre, and Dawson Creek near Brisbane (were combined and called 'Brisbane' as the 2nd lowland location), Red Rock Creek near Yeppoon close to Rockhampton (the 3rd location), and Oxford Falls Creek and Frenchman's Creek in Sydney were combined to represent the 4th lowland location)]. Females were collected in the wild by noosing, hand capture or sticky traps, and transported to James Cook University, Townsville, Queensland, within 3 days of capture.

Females were housed individually in plastic boxes (550 L × 360 W × 305 H mm) in a constant temperature room maintained at 22 ± 1 °C. Ceiling fluorescent lights provided photoperiod (12L : 12D) and a 75-W incandescent light suspended at one end of each cage provided basking heat. Eight hours of available basking time was centred within the daylight hours of the photoperiod. When the incandescent lights were on, females could thermoregulate at temperatures from 27 to 45 °C. All females were fed commercial cat food (Purina Fancy Feast™, assorted non-fish flavours) three times weekly, and crickets (*Acheta domesticus*) and mealworms (*Tenebrio molitor*) once per week. Animals were fed to satiation at these times. Water was available *ad libitum*, in bowls large enough for females to become completely submerged. Newspaper and a small cardboard box were provided for shelter in each cage, and a tree branch was provided as a basking perch. The diet and thermal regimes were designed to be appropriate husbandry for these lizards until they gave birth (at most several weeks), and to keep them healthy after birth. They were not intended to be representative of any particular location in the range. Females were checked daily for the presence of offspring in the cages. The

date when offspring were first noted was recorded. Offspring were counted, measured and weighed at birth, and transferred to individual holding cages. After birth, females were maintained in captivity for up to 1–80 (average 36) days, depending on timing of collection and then sacrificed and dissected. Ovulated follicles, if present, were recorded.

A BIOPHYSICAL MODEL OF *E. QUOYII*

We used an R (R Development Core Team, 2012) implementation of the Niche Mapper biophysical modelling software ('NicheMapR', forthcoming) to model field body temperatures (operative temperatures) activity and energetics of *Eulamprus*, following the 'thermodynamic niche' modelling approach described in detail elsewhere (Kearney 2012, 2013; Kearney *et al.* 2013). This package consists of a microclimate model and an animal (ectotherm) model. We drove the microclimate model with daily interpolated gridded environmental data for Australia, as described in detail in Kearney *et al.* (2014). The animal model incorporates a behavioural/biophysical model for computing heat/activity budgets, and uses dynamic energy budget theory as the energy/mass budgeting model (see next section). Parameters for the biophysical model and their sources are described in Table 1.

ESTIMATING DEB PARAMETERS FOR *E. QUOYII*

We used the 'covariation method' (Lika *et al.* 2011; Kearney 2012; Kearney *et al.* 2013) to obtain estimates of DEB parameters, based on observations of growth from a previous study of *E. quoyii* (Caley & Schwarzkopf 2004). Caley & Schwarzkopf (2004) compared populations from the latitudinal extremes of *E. quoyii*'s range (Sydney and Townsville) and showed that trajectories of growth in hatchlings incubated in a crossed design and raised in a common garden, varied in a complex manner with maternal body temperature and source location (see Caley & Schwarzkopf 2004, for details of the experimental design and husbandry conditions in that experiment). We thus fitted DEB models based on data for each location (Sydney and Townsville) crossed with each maternal environment (cool vs. warm), and

explored the extent to which simple changes in DEB parameters could account for the observed differences.

The specific observations used to fit the DEB model included the following: ages (days) at birth and maturity, masses (g) and lengths (snout–vent length, SVL) at birth, maturity and ultimate size, annual reproductive output (number of offspring), longevity, together with length-at-age trajectories and length vs. mass relationships for individuals across ontogeny from birth to adult size. In estimating the parameters, one can assign different weightings to the observation data. We adopted the strategy of increasing the weights of observations that were statistically different between the populations and treatments (Caley & Schwarzkopf 2004).

An associated temperature is required for ages at birth and maturity, as well as reproductive rate, length-at-age and longevity, together with an Arrhenius thermal response curve [we used the 5-parameter model (Schoolfield, Sharpe & Magnuson 1981; Sharpe & DeMichele 1977)]. We estimated the Arrhenius temperature T_A from observations of temperature versus development time (Caley & Schwarzkopf 2004), and assumed that the lower threshold temperature for enzyme deactivation T_L corresponded with the critical thermal minimum (CT_{min}) and the upper threshold temperature T_H reduced the performance curve to zero at the critical thermal maximum (CT_{max}). All of the temperature-sensitive observations were made under diurnally fluctuating conditions. Thus, to obtain a 'constant temperature equivalent: CTE' (Orchard 1975), we estimated the mean Arrhenius temperature correction factor across all time intervals and then back-calculated the temperature required to produce this mean correction factor, which was then used as the CTE. For observations of reproduction rates and longevity, which were derived from field observations, we calculated the CTE based on biophysical simulations of an adult lizard thermoregulating across the years 1990–2009 in Sydney and Townsville.

LIFE-HISTORY SIMULATIONS

We simulated the life history of *E. quoyii* at the eight locations sampled for litter frequency, driving the simulations with environmental data from 1990 to 2009. We commenced the simulations at hatching on the 1st January in a given year. We explored the variation among simulations commenced in different years (i.e. the

Table 1. Heat/activity budget model parameters for *Eulamprus quoyii*

Parameter	Units	Value	Source
ϵ_{body} , skin longwave infrared emissivity	–	1.0	Default
α_{body} , skin solar absorptivity	–	0.857	Spellerberg (1972a,b)
ρ_{body} , flesh density	kg m ³	1000	Default
k_{body} , flesh thermal conductivity	W m ^{–1} °C ^{–1}	0.5	Default
C_{body} , flesh specific heat capacity	J kg ^{–1} °K ^{–1}	4185	Default
$F_{body,sky}$, configuration factor body to sky	–	0.4	Porter <i>et al.</i> (1973)
$F_{body,sub}$, configuration factor body to substrate	–	0.4	Porter <i>et al.</i> (1973)
A , lizard surface area	cm ²	10.4713 $W_w^{0.688}$ where W_w is wet weight in g	Porter <i>et al.</i> (1973)
A_{sil} , silhouette area normal to the sun	cm ²	3.798 $W_w^{0.683}$ where W_w is wet weight in g	Porter <i>et al.</i> (1973)
F_{sub} , fraction of surface area contacting the substrate	–	0.1	Assumed
F_{wet} , fraction of surface area that is wet	–	0.01	Assumed
T_{RB}^{min} , minimum temperature for leaving retreat	°C	17.4	Spellerberg (1972a,b)
T_B^{min} , minimum basking temperature	°C	17.4	Spellerberg (1972a,b)
T_F^{min} , minimum foraging temperature	°C	23.9	Spellerberg (1972a,b)
T_F^{max} , maximum foraging temperature	°C	34.2	Spellerberg (1972a,b)
T_{pref} , preferred temperature	°C	30.0	Spellerberg (1972a,b)
CT_{min} , critical thermal minimum	°C	6.0	Spellerberg (1972a,b)
CT_{max} , critical thermal maximum	°C	39.8	Spellerberg (1972a,b)

variation among cohorts), looping around to years prior to the start date of a given simulation to ensure a constant 20-year block (e.g. a simulation starting in year 2008 would then have used data for 2009 and then from 1990 to 2007).

Following Kearney (2012), we used the batch reproduction model (Pecquerie, Petitgas & Kooijman 2009) to simulate seasonal reproduction, whereby litter production was initiated by the winter solstice and terminated by the summer solstice, with a reproduction buffer building up in between. Feeding was assumed to continue through pregnancy, which is realistic (Huey *et al.* 2001; L. Schwarzkopf personal observation). Activity, and hence feeding, was only permitted during daylight hours when body temperature was within the thresholds for voluntary activity (Kearney *et al.* 2013). The lizard was permitted to select from between 0 and 90% shade for thermoregulation. We assumed that water did not constrain activity (i.e. that the lizard was living beside permanent water, which is realistic for these lizards, Law & Bradley, 1990) and that lizards experienced *ad libitum* food during activity periods. We also ran simulations for a set of 893 locations evenly sampled across eastern continental Australia (encompassing the geographic range of the species) to provide a broader picture of how temperature limits the life history across the species' potential geographic range.

Results

GEOGRAPHIC VARIATION IN LITTER FREQUENCY

Initially, visual observations of apparently gravid females present unusually late in the year (in April and May) were made in Paluma, around Townsville, and near Rockhampton. In addition, as part of a mark–recapture study conducted at Alligator Ck near Townsville, three females that had given birth in the laboratory in December were released into the field, and were recaptured, gravid, in April, verifying that it was indeed possible for individual females in some populations to give birth twice in 1 year (Schwarzkopf 2005; L. Schwarzkopf personal observation). We reasoned, therefore, that if individual gravid females could produce two litters of offspring, they must ovulate shortly after reproduction.

Over several years, we sampled 98 gravid females (7 from Paluma, 2 from Bluewater Creek and 27 from Alligator Creek and North Creek near Townsville, 3 from the Brisbane Cultural Centre, 2 from Dawson Creek near Brisbane, 7 from Quart Pot Creek near Stanthorpe, 20 from Red Rock Creek near Rockhampton, 10 from Mimosa Creek on the Blackdown Tableland, 5 from Sharpes Creek in Barrington Tops National Park [Gloucester Tops], 15 from Oxford Falls Creek and Frenchman's Creek in Sydney), and allowed them to give birth in the laboratory, then held them for up to 70 days (1–70, mean = 35), after which they were euthanized and dissected. Only females from Paluma, Townsville and Rockhampton had ovulated within 35 days of giving birth in late December or January [1/7 females from Paluma (14%), 4/29 from the Townsville areas (13%), 1/20 from the Rockhampton area (5%)]. One female collected in Brisbane in December 1997 that was not gravid at the time of collection had ovulated 4 follicles at the time of dissection on the 19 February 1998, suggesting

that there may, at least at times, be early and late reproductive females in that population. However, no females from Brisbane ovulated after giving birth.

Three females from Sydney that gave birth in the laboratory as part of other work were held in captivity for over 1 year, and provided with food and water *ad libitum*. These females ovulated more than 1 year after giving birth (average 420 days), and eventually ejected yolked ovulated follicles, indicating that *E. quoyii* females may not be able to resorb ovulated follicles and that dissection is a good method for assessing breeding status. In addition, we never observed gravid females after January in a 2-year mark–recapture study of *E. quoyii* conducted at Blackdown Tableland (Salkeld, Trivedi & Schwarzkopf 2008), and *E. quoyii* from around Sydney are not known to reproduce more than once (Borges-Landaez 1999; R. Shine, personal communication). Taken together, we used these data to indicate the likely reproductive frequency of different populations.

DEB PARAMETERS FOR *E. QUOYII*

The DEB parameter estimates and fits to the observed data for the Sydney-warm treatment are presented in Table 2 (see Tables S1–S3, Supporting information for parameters from fits to the data of the other three treatments). The associated MATLAB scripts used to estimate the parameters can be found at http://www.bio.vu.nl/thb/deb/deblab/add_my_pet/.

Attempts to capture the observed differences in growth trajectories by varying the core DEB parameters, one at a time, from the 'Sydney-warm model' failed to produce predictions qualitatively consistent with all of the life-history data (results not shown), with the exception of the thermal response curve. Specifically, the estimated DEB parameters for the Sydney-warm incubation treatment could also predict the more rapid growth of the Sydney-cool incubation treatment with a simple 3 °C downward offset of the entire temperature response curve (parameters T_L and T_H ; Fig. S1a). Moreover, the fastest empirical growth trajectories of the Townsville population under both the warm and cold treatment approached that of the Sydney-warm DEB model trajectory, although overall the growth trajectories at this site had a wider spread among individuals, especially for the cold treatment (Fig. S1b).

As we discuss further below, we conclude that the Townsville growth data from the cool gestation treatment may reflect poor acclimation abilities of a tropical populations, or low temperature-induced breakdown of normal growth processes, or both. We also conclude that the Sydney-cool treatment reflected an acclimation response. Thus, we focus on the Sydney-warm and Townsville-warm data sets as the most representative ones from which to estimate the DEB parameters, and used them for subsequent analyses of thermal constraints on life-history responses.

LIFE-HISTORY SIMULATIONS

The results of the population-specific simulations of growth and reproduction with the DEB model, when coupled with the biophysical model and run under the local weather conditions from 1990 to 2009, are summarized in Table 1 and Figure 1. The results of the landscape-scale simulations are depicted in Fig. 2b–g. Figures 1 and 2 show results only for the cohort starting in 1990, while the results in Table 2 are averages over the 20 different starting years.

The frequency of production of two litters increased with the body temperatures experienced at the site, with the highest frequencies at Townsville and the lowest at Gloucester Tops (Fig. 1, Table 1), and this was broadly

consistent with empirical observations of two litters. The intercohort variability in the frequency of production of two litters showed an inverse pattern, as indicated by the standard deviations (Table 1, expressed as a percentage of the mean). At the coldest site, Gloucester Tops, with the Sydney life history, half the cohorts produced two litters in their last year of life (Table 1). Under the Townsville life history, no double litters occurred at Gloucester Tops or Stanthorpe and the mean number of double litters at the other sites was lower. The mean intraannual litter frequency was positively correlated with the observed pattern of double litter production under both the Sydney and Townsville DEB models (Spearman rank correlation, Sydney $r = 0.79$, $S_6 = 17.8$, $P = 0.020$, Townsville $r = 0.79$, $S_6 = 17.84$, $P = 0.020$).

Table 2. Dynamic energy budget (DEB) model parameter estimation of *Eulamprus quoyii* estimated for the Sydney population under the warm maternal incubation treatment of Caley & Schwarzkopf (2004) (see Supporting Information for parameter estimates for other treatments). Part (a) shows the observed to the predicted data (fit of 9.6/10) and part (b) shows the core DEB parameter estimates (rates corrected to 20 °C), and additional DEB parameters either independently observed or assumed to have default values. The lengths relate to snout–vent length (SVL)

(a) Observed and predicted data				
Data	Obs.	Pred.	Units	Data source
a_b , age at birth	71.0	62.5	Days (25.8 °C)	Caley & Schwarzkopf (2004)
a_p , age at puberty	375.5	367.3	Days (25.8 °C)	Caley & Schwarzkopf (2004)
a_m , longevity	4380	4380	Days (17.7 °C)	L. Schwarzkopf unpublished
l_b , length at birth	3.8	3.8	cm	Caley & Schwarzkopf (2004)
l_p , length at puberty	9.0	8.6	cm	Caley & Schwarzkopf (2004)
l_∞ , maximum length	13.0	13.1	cm	L. Schwarzkopf unpublished
W_b , mass at birth	0.29	0.29	g, dry	Caley & Schwarzkopf (2004)
W_p , mass at puberty	3.3	3.4	g, dry	Caley & Schwarzkopf (2004)
W_∞ , maximum mass	12.5	13.2	g, dry	Schwarzkopf unpublished
R_∞ , max repro rate	5.0	5.2	# year ⁻¹ (17.7 °C)	Caley & Schwarzkopf (2004)
(b) DEB parameters				
Parameter	Value	Units	Source	
z , zoom factor (relative volumetric length)	2.825	–	Estimated	
δ_M , shape correction factor	0.2144	–	Estimated	
v , energy conductance	0.02795	Cm d ⁻¹	Estimated	
κ , allocation fraction to soma	0.8206	–	Estimated	
$[p_M]$, somatic maintenance	48.81	J cm ⁻³ day ⁻¹	Estimated	
$[E_G]$, cost of structure	7512	J cm ⁻³	Estimated	
E_H^b , maturity at birth	866.6	J	Estimated	
E_H^p , maturity at puberty	1.019×10^4	J	Estimated	
κ_X , digestion efficiency	0.85	–	Shine (1971)	
κ_R , reproduction efficiency	0.95	–	Default	
$[E_s^m]$, maximum specific stomach energy	350	J cm ⁻³	Kearney (2012)	
E_0 , energy content of ‘egg’	9220	J	Estimated	
$\{\dot{p}_{Xm}\}$, maximum specific food intake	12 420	J cm ⁻²	Assumed	
X_K , half-saturation constant	10	J ha ⁻¹	Assumed	
d_V , density of structure	0.3	g cm ⁻³	Assumed	
W_V , molecular weight of structure	23.9	g C-mol ⁻¹	Default	
μ_X , chemical potential of food	525 000	J C-mol ⁻¹	Default	
μ_E , chemical potential of reserve	585 000	J C-mol ⁻¹	Default	
μ_V , chemical potential of structure	500 000	J C-mol ⁻¹	Default	
μ_P , chemical potential of faeces	480 000	J C-mol ⁻¹	Default	
κ_{XP} , fraction of food energy into faeces	0.1	–	Default	
T_A , Arrhenius temperature	8817	K	Caley & Schwarzkopf (2004)	
T_L , lower bound for T_A	279	K	Matched to CT_{\min}	
T_H , upper bound for T_A	306	K	Matched to CT_{\max}	
T_{AL} , value of T_A below lower bound	50 000	K	Kearney (2012)	
T_{AH} , value of T_A above upper bound	90 000	K	Kearney (2012)	

Discussion

ENVIRONMENTAL CONSTRAINTS ON FREQUENCY OF REPRODUCTION

Empirical observations of populations of viviparous reptiles suggest that most are limited to a single reproductive episode per year (Ballinger 1983) and, indeed, many viviparous species reproduce biennially or less (Van Wyk 1991; Schwarzkopf 1993; Alison & Guillelte 1995; Ibargüengoytia & Cussac 1996; Olsson & Shine 1999; Cox, Skelly & John-Alder 2003; Pincheira-Donoso & Tregenza 2011). We observed that, in the tropical parts of their range, individual viviparous Eastern water skinks (*E. quoyii*) reproduce more than once per year, whereas in other locations females reproduce annually at most. A dynamic energy budget (DEB) model, combined with a biophysical model predicting body temperature and activity patterns, strongly suggests that much of the variation in reproductive frequency among populations of this species can be explained by constraints imposed by environmental temperatures, and the associated activity period available to the lizards. This occurs because, in our model, the animals have the same time window to breed (we assume they store up energy for reproduction between the summer and winter solstice, and yolk follicles between the winter and summer solstice, which is similar to what occurs in nature, L. Schwarzkopf personal observation), but as temperature changes along the transect, they have different amounts of physiological time available to bring their litter full term.

On average, the model predicted reproductive frequency correctly for each population (Table 3), which was remarkable given its limitations. Examination of Fig. 1, however, reveals that double litters were predicted, at least occasionally, for all modelled populations except Gloucester Tops. Unfortunately, we do not have records for reproductive frequency on multiple individuals, over many years with different weather conditions, in all these populations, to validate the model. However, our samples and observations from several mark-recapture studies suggest that water skinks, especially in Sydney and on the Blackdown Tableland, never reproduce twice in a year, whereas those from Townsville definitely are capable of two litters per year. Our samples from the other populations are broadly consistent with model predictions, and we observed double litters at Paluma and Yeppoon (near Rockhampton). Our observations from Brisbane suggested that the population may reproduce twice, but it is rare (or impossible) for individuals to do so. Our laboratory observations also suggested a relatively low frequency of production of two litters per annum generally (5–14% of individuals), and that the highest frequency of production of two litters per annum was in Townsville. These observations are consistent with the model.

The model's tendency to sometimes over-predict the production of two litters may occur because (i) individuals

in the model are never food restricted, whereas animals in real populations may be, reducing energy available for producing the second litter. Moreover, in the model, individuals could feed throughout pregnancy, whereas some water skinks stop feeding late in gestation (Schwarzkopf 1996), (ii) in the model, litter size is constrained to the mean size, whereas in the real world, litter size varies, linking the rate of production of two litters to the body size of females in the population, and allowing females flexibility in producing litters smaller or larger than the mean, (iii) in the model, there is no disadvantage to producing offspring very late in the year, essentially in winter, whereas in the real world, such a restriction is likely a very important selective force preventing the production of two litters in a single year. Reproduction increases the basking rate of females, which may be costly (Schwarzkopf & Shine 1991, 1992; Schwarzkopf 1993), and offspring may fare poorly if produced too late in the year (Wapstra *et al.* 2010). We think it likely that this last point is very important in determining actual reproductive frequency, because a mistake, that is producing a litter too late in the season, may be too costly to allow the evolution of multiple litters per annum in cooler populations. We suggest it is more advantageous for females to retain the energy, and allocate it to growth and potentially reap a size-dependent fecundity advantage the following year (Shine, Schwarzkopf & Caley 1996). Indeed, it seems that southern populations lack the physiological flexibility to produce a second litter, as southern (Sydney) females held in the laboratory at warm temperatures with *ad libitum* food failed to ovulate for over a year.

Litter frequencies produced by females at Blackdown Tableland and Brisbane (areas intermediate in physical conditions between populations producing one or two litters) are interesting with respect to the evolutionary influence of risks of a second reproductive event. Empirically, females at these locations produce a single litter; yet, the model suggests that the weather may allow two litters at times. High risks associated with a second litter, either due to predation on gravid females, low offspring success if produced late, low offspring quality (Qualls & Andrews 1999), or some combination of these, may cause obligate single litters to evolve in these transitional populations.

The relatively low frequency of double litters we observed across all the populations sampled also suggests that it would be instructive to measure the fitness and performance of offspring from second litters. It would also be useful to determine the influence of temperature on offspring fitness, to establish possible fitness costs if females are unable to maintain high body temperatures for much of the day, as may happen later in the season.

TEMPERATE VERSUS TROPICAL ENERGY BUDGETS

While the constraints of temperature and season length alone could explain much of the geographic variation in

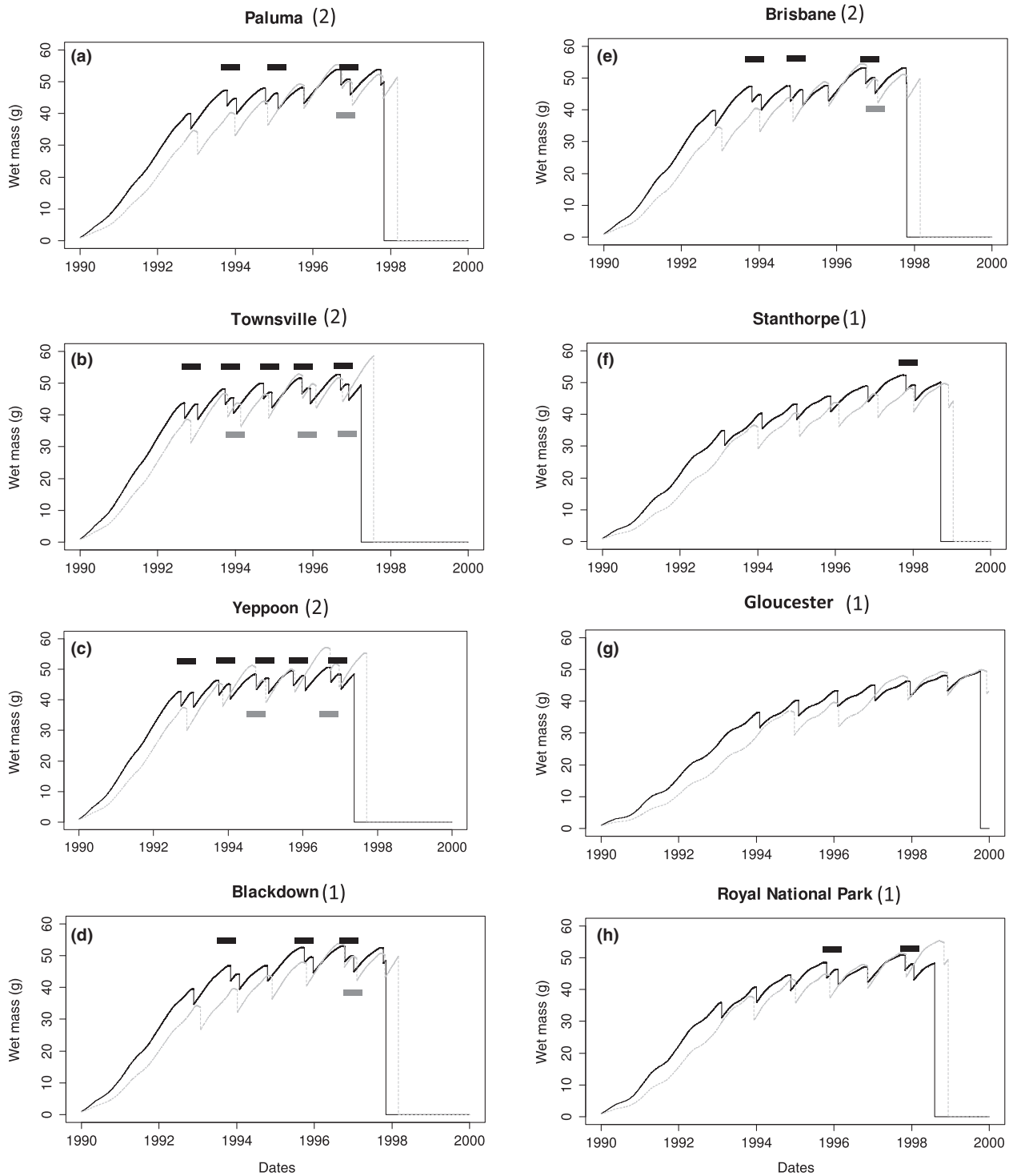


Fig. 1. Growth trajectories (wet mass) predicted for the Sydney-warm (black solid line) and Townsville-warm (grey dashed line) from dynamic energy Budget models for *Eulamprus quoyii* at eight sites across its range under the local weather conditions from 1990 to 2009 (all lizards had died from old age in the simulation by this time). The sudden drops in mass represent litters, with double litters appearing as two drops within a single year, indicated by the heavy horizontal bars. Observed annual frequency of reproduction is indicated after the site labels.

litter frequency that we observed in *E. quoyii*, it is also important to consider whether known geographic differences in growth trajectories (Caley & Schwarzkopf 2004) also play a role. Below, and in the context of the DEB

model we created for *E. quoyii*, we interpret the patterns in reproductive allocation strategies consistent with the growth trajectories reported in (Caley & Schwarzkopf 2004).

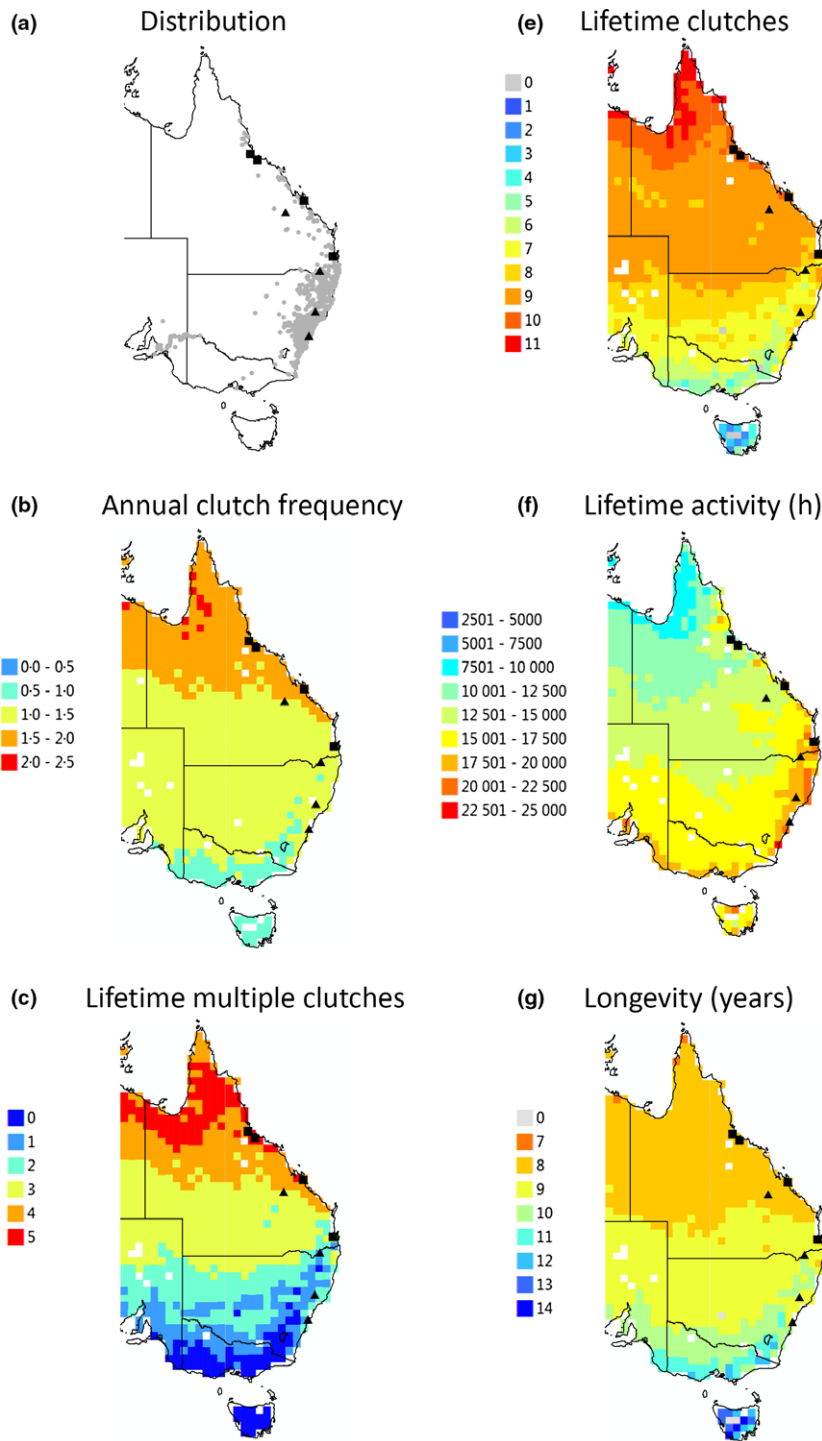


Fig. 2. The geographical distribution of *Eulamprus quoyii* (a) and results of landscape-scale simulations of its growth and reproduction assuming the Sydney-warm dynamic energy budget model (b–g). On all maps, the black squares are sites where *E. quoyii* produces two litters per annum (from north to south, these are Paluma, Townsville, Yeppoon, Brisbane) while the black triangles are sites where it produces one litter (from north to south, these are Blackdown Tableland, Stanthorpe, Gloucester Tops, Sydney [Royal NP]).

In the wild, there were no differences in asymptotic size or overall reproductive output among locations, and the length–mass relationships for all of four laboratory experimental treatments, cool (Sydney) origin individuals, cool and warm treatments, and warm (Townsville) origin individuals in cool and warm treatments (Caley & Schwarzkopf 2004; L. Schwarzkopf personal observation) were virtually indistinguishable (Fig. S2). The growth trajectories of offspring from the two temperature treatment groups from Sydney showed a striking convergence on

asymptotic size, despite the dramatic increase in growth rate imposed by the cooler gestation temperature treatment (Fig. S1a). This convergence suggests that there were no major changes in energy allocation strategies with gestational thermal environment. Instead, for the Sydney population, the cool gestation treatment may have imposed an acclimation response on the developing embryos such that their thermal optimum shifted to a cooler value. Thus, we conclude that Sydney animals had a wider thermal tolerance, and could acclimate to both the warm and cool

Table 3. Summary of life-history predictions of the integrated biophysical/dynamic energy budget model for *Eulamprus quoyii* at various sites across its geographic range, as well as observed litter frequencies, under (a) the Sydney dynamic energy budget (DEB) model parameters and (b) the Townsville DEB model parameters. These simulations used daily weather interpolations for the specified locations from 1990 to 2009 as input, assuming no food limitation when thermal conditions permitted activity. Results are means of 20 simulations covering all starting years, that is all possible cohorts of this time span. The values in parentheses represent the standard deviation of the inter-cohort variation expressed as a percentage of the mean

Site	Longitude	Latitude	Observed litter frequency	Predicted litter frequency	Lifetime double litters	Lifetime fecundity	Age at 1st reproduction (years)	Lifespan (years)	r_{\max}
(a) Sydney life history									
Paluma	146-21	-19-01	2	1.5 (0-0)	3-0 (0-0)	45-0 (0-0)	2-9 (0-3)	7-8 (0-3)	0-40 (0-5)
Townsville	146-78	-19-5	2	2-0 (0-0)	5-0 (0-0)	50-0 (0-0)	2-7 (0-4)	7-3 (0-3)	0-45 (0-2)
Yeppoon	150-65	-22-85	2	2-0 (4-2)	4-6 (14-8)	49-0 (4-2)	2-8 (0-6)	7-4 (0-6)	0-45 (2-9)
Blackdown	149-1	-23-82	1	1-5 (0-0)	3-0 (0-0)	43-3 (5-7)	2-9 (0-5)	7-8 (0-5)	0-40 (1-8)
Brisbane	153-02	-27-46	2	1-5 (0-0)	3-0 (0-0)	45-0 (0-0)	2-9 (0-3)	7-8 (0-2)	0-40 (1-4)
Stanthorpe	151-98	-28-69	1	1-2 (7-7)	1-4 (35-9)	35-8 (0-0)	3-8 (8-8)	8-7 (0-5)	0-34 (5-3)
Gloucester	151-61	-32-07	1	1-1 (7-5)	0-3 (156-7)	30-0 (7-8)	3-1 (7-0)	9-6 (1-3)	0-28 (1-2)
Royal NP	151-05	-34-07	1	1-3 (0-0)	2-0 (0-0)	40-0 (0-0)	4-1 (11-4)	8-5 (1-0)	0-36 (0-4)
(b) Townsville life history									
Paluma	146-21	-19-01	2	1-2 (0-0)	1-0 (0-0)	56-0 (0-0)	3-6 (8-4)	8-2 (0-3)	0-43 (0-1)
Townsville	146-78	-19-5	2	1-4 (2-4)	2-0 (0-0)	56-0 (0-0)	2-9 (0-4)	7-6 (0-3)	0-44 (1-9)
Yeppoon	150-65	-22-85	2	1-3 (0-0)	2-0 (0-0)	57-6 (5-7)	2-9 (0-6)	7-7 (0-6)	0-44 (0-3)
Blackdown	149-1	-23-82	1	1-2 (0-0)	1-0 (0-0)	56-0 (0-0)	3-0 (15-7)	8-1 (0-5)	0-43 (0-1)
Brisbane	153-02	-27-46	2	1-2 (0-0)	1-0 (0-0)	56-0 (0-0)	3-1 (0-3)	8-2 (0-2)	0-43 (0-1)
Stanthorpe	151-98	-28-69	1	1-0 (0-0)	0-0 (0-0)	48-0 (0-0)	3-9 (0-4)	9-1 (0-5)	0-34 (0-4)
Gloucester	151-61	-32-07	1	1-0 (0-0)	0-0 (0-0)	38-4 (8-5)	5-0 (6-0)	9-9 (1-3)	0-26 (5-5)
Royal NP	151-05	-34-07	1	1-1 (9-2)	0-5 (0-0)	47-2 (5-2)	3-8 (0-5)	8-8 (0-9)	0-33 (0-8)

thermal environments they were offered in the laboratory. The Townsville population lacked such a pattern but exhibited a wider spread in growth trajectories, especially for families exposed to the cool gestation treatment (Fig. 1b).

Caley & Schwarzkopf (2004) found that the Townsville population had larger litters but grew more slowly. Under the DEB framework, this was captured through changes in two main parameters: a lower value of kappa (the allocation term), which dictates the fraction of mobilized reserve that is directed to growth (rather than maturation or reproduction) at a given instant, and a higher value for somatic maintenance [p_m] (Table S1). Under the standard DEB model, as applied here, we assumed kappa remained constant for the whole life cycle. Thus, in the Townsville DEB model, growth happened more slowly at the expense of greater investment in reproduction. In DEB theory, however, decreasing kappa in isolation results in a smaller maximum size (ultimate length $L_\infty = \kappa \{p_{Am}\} / [p_M]$), which was not observed. Thus, fitting the DEB model to the Townsville population also necessitated a lower somatic maintenance term (Table S1). One interpretation of this is called ‘waste to hurry’ (Kooijman 2013) whereby animals exploiting short-term resources evolve high maintenance, allowing them to grow quickly to a small size with high reproductive output. According to this interpretation, the Sydney population, with a shorter growing season, would be ‘wasting to hurry’ compared with Townsville. The DEB parameters for the Townsville population, however, make double litters less likely compared to those for the Sydney population (Fig. 1). Thus, it does not seem that geographic

patterns in reproductive frequency can be explained by the differences in allocation to growth we observed; if anything, they should act in the opposite direction.

An alternative, non-adaptive interpretation of the disparity in growth responses between Townsville and Sydney families is that individuals from Townsville had narrower thermal tolerances, or less efficient acclimation responses, compared to those from Sydney. This interpretation is consistent with many recent papers suggesting that the thermal acclimation response of tropical species may be narrower than those of temperate species (Sunday, Bates & Dulvy 2011). In addition, the Townsville ‘warm’ environment provided to females for gestation in the Caley & Schwarzkopf (2004) experiment, although intended to represent a ‘Townsville gestation environment’, may have not been representative of the thermal environment females from Townsville usually experience. Our simulations of the likely gestation environment experienced in Townsville predicted considerably higher body temperatures, especially at night (Fig. S3b): the constant temperature equivalent (CTE) calculated from field temperature data was 28-0 °C compared to the 25-8 °C provided in the laboratory for the warm treatment. The CTE of the simulated gestation environment for Sydney was between those of the cool and warm gestation treatments (23-5 °C; Fig. S3a). Thus, it is possible that offspring from Townsville exposed to both the warm and cool treatments experienced thermal stress, thereby reducing growth rates. In any case, Townsville offspring responded with slow and variable growth to laboratory thermal treatments, compared to Sydney offspring.

Conclusion

There has long been a general appreciation that major transitions in the life histories of ectotherms are likely to be strongly influenced by temperature, and by the window of activity times available to different groups (Stevenson 1985; Adolph & Porter 1993, 1996). Here, we have combined empirical observations of life-history variation, including litter frequency, with a dynamic energy budget model and a bioenergetics model, to better understand a very unusual life-history transition for a viviparous Australian lizard from one to two litters per annum. Even given the simplifying assumptions of the model, the physiological activity window calculated by the model was an excellent predictor of the occurrence of this unusual life-history transition. Models, such as those developed here that integrate formal metabolic theory with biophysical ecological principles, have great potential to provide insights into constraints on life histories and how they vary through space and time (Kearney 2012, 2013).

Acknowledgements

The lizards in this study were collected under Queensland Parks and Wildlife Service, permit: WISPO2455904 and in accordance to the ethical guidelines of James Cook University, Permit # A939. We thank L. Valentine for help in the laboratory, feeding and caring for lizards.

Conflict of interests

We have no conflict of interests.

Author contributions

LS and MJC collected data and participated in the drafting the manuscript; MRK conducted the modelling and participated in the drafting the manuscript. All authors gave final approval for publication.

Data accessibility

Data can be accessed on the Tropical Data Hub at James Cook University, DOI: 10.4225/28/562DCC397ED57.

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Received 26 February 2015; accepted 3 November 2015

Handling Editor: Tony Williams

Supporting Information

Additional Supporting information may be found in the online version of this article:

Figure S1. Growth trajectories (snout vent length) of individual *Eulamprus quoyii* from (a) Sydney and (b) Townsville experiencing either a cool or warm maternal environment during gestation and reared in a common (warm) garden.

Figure S2. Fitted power functions for snout–vent length vs. wet mass in *Eulamprus quoyii* from Sydney or Townsville experiencing either a cool or warm maternal environment during gestation and reared in a common (warm) garden.

Figure S3. Cool (a) and warm (b) environmental exposures (from Caley & Schwarzkopf 2004).

Figure S4. Snout–vent length vs. wet mass for the Sydney population of *Eulamprus quoyii* experiencing either a cool or warm maternal environment during gestation.

Table S1. Dynamic energy budget (DEB) model parameter estimation of *Eulamprus quoyii* estimated for the Townsville population under the warm maternal incubation treatment of Caley & Schwarzkopf (2004).

Table S2. As above for the Sydney, cool maternal incubation treatment.

Table S3. As above for the Townsville, cool maternal incubation treatment.