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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.

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- 28 2. We assessed the potential roles of physiological adaptation and environmental
29 constraints in driving an unusual case of geographic variation in life history, in the
30 viviparous lizard (*Eulamprus quoyii*), which has either one or two reproductive bouts
31 per annum, depending on the geographic location of the population.
- 32 3. Using Dynamic Energy Budget theory we developed an integrated model of the
33 energetics of growth and reproduction in this lizard, and applied it in conjunction with
34 biophysical calculations of body temperature and activity time across its geographic
35 range to predict reproductive frequency.
- 36 4. Our model indicated that geographic variation in body temperature alone (i.e.,
37 environmental constraints) explained the observed pattern of litter frequency,
38 suggesting that differences in energy allocation among populations were unlikely to
39 be a major cause of differences in litter frequency in *E. quoyii*. It also suggested that
40 natural selection should favour fixation of litter size in the transition zone.

41

42 **Key-words:** viviparity, *Eulamprus quoyii*, skink, reptile, DEB theory, life history variation,
43 geographic variation, litter size, reproductive frequency, growth rate

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45

46

47 **Introduction**

48

49 Constraints are a critical force shaping natural selection on life-history traits (Roff, 2002;
50 Stearns, 1992). Such constraints may be extrinsic in nature and for ectotherms, such as
51 lizards, the thermal environment can be critically important (Adolph & Porter, 1993, 1996).
52 There may also be intrinsic constraints, including trade-offs in the allocation of nutrients and
53 energy to maintenance, growth, development and reproduction (Levins, 1968; Sibly &
54 Calow, 1986), constraints imposed by body volume (Du, Ji, & Shine, 2005; Shine, 1992) and
55 constraints associated with reproductive mode (Ballinger, 1983; Dunham, Miles, & Reznick,
56 1988; Shine, 2005; Tinkle & Gibbons, 1977). The evolution of viviparity is a major life-
57 history transition that, in squamate reptiles, has occurred independently in over 100 lineages
58 (Shine, 1999). Much has been written about the potential costs and benefits of this transition,
59 but one major cost that has received relatively little attention is the constraint it imposes on
60 reproductive frequency; the inter-litter frequency of viviparous species is necessarily
61 extended by the gestation length (e.g., Ballinger, 1983). For this reason, multiple litters per

62 annum are extremely rare in viviparous reptiles, despite multiple clutches being quite
63 common in oviparous species (e.g., Dunham et al., 1988).

64

65 Worldwide, most viviparous lizards are constrained to reproduce once annually (e.g., Tinkle,
66 1970), or less (e.g., Van Wyk 1991, Schwarzkopf & Shine, 1991, Cree & Guillette 1995,
67 Ibarquengoytia & Cussac 1996). Here we investigate the potential causes of a very unusual
68 pattern of geographic variation in litter frequency in a widespread viviparous lizard
69 distributed along the eastern seaboard of Australia, the Eastern water skink (*Eulamprus*
70 *quoyii*), in which females in some populations reproduce twice per year (L. Schwarzkopf,
71 pers. obs, and see below). One possible explanation for variation in reproductive frequency
72 among populations of lizards is simply thermally-induced variation in physiological rates,
73 such as digestion and oogenesis (Adolph & Porter, 1993, 1996). However, a common garden
74 experiment using this species showed that populations from the latitudinal extremes of its
75 range exhibit very different growth trajectories that are both locally adapted and depend on
76 the thermal environment experienced during gestation (Caley & Schwarzkopf, 2004). Thus, it
77 appears possible that observed variation in litter frequency is caused not by simple variation
78 in physiological rates driven by temperature in this species, but instead by local metabolic
79 adaptations influencing energy allocation to reproduction.

80

81 To interpret this pattern, we developed a Dynamic Energy Budget (DEB) model of growth
82 and reproduction in *Eulamprus quoyii* and integrated it with a biophysical model of climatic
83 constraints on body temperature and activity budget. This ‘thermodynamic niche’ modelling
84 approach (Kearney, Simpson, Raubenheimer, & Kooijman, 2013) has been successfully
85 applied to model climatic constraints on the energetics of lizards (Kearney, 2012; Kearney,
86 2013; Kearney, Matzelle, & Helmuth, 2012). In general, DEB theory provides a parameter-
87 sparse approach to modelling the full life-cycle energy and mass budget given different
88 nutritional and thermal environments (Kooijman, 2010). It differs from other energy
89 budgeting approaches (Kearney & White, 2013; van der Meer, 2006) by considering the full
90 elemental mass budget *via* the assumption of distinct pools of biomass of constant chemical
91 composition, expressed in terms of elemental ratios (Kooijman, 1995), and provides a
92 powerful means to model the interaction between heat, water and nutritional constraints
93 (Kearney et al., 2013).

94

95 Two qualitatively distinct biomass pools are considered in DEB theory: ‘structure’ and
96 ‘reserve’, with the ‘standard DEB model’ (employed here) assuming just one structure and
97 one reserve. The structure is the ‘permanent’ part of the biomass which is empirically related
98 to the cube of body length, and which requires energy expenditure for its growth,
99 maintenance and development. The organism begins almost entirely as reserve (a freshly laid
100 egg) and the reserve is mobilized for allocation to the growth, development and maintenance
101 of the structure. The rate of reserve mobilization is proportional to the ratio of reserve to
102 structure, which acts as a physical scaling constraint (Maino, Kearney, Nisbet, & Kooijman,
103 2013). From birth onward, the reserve pool is replenished through feeding. The density of
104 reserve in the body fluctuates with nutritional state, rising to a maximum density at *ad libitum*
105 food levels.

106

107 Prior to sexual maturity, a fixed proportion of the flux of mobilized reserve is used to
108 maintain and increase the maturity state of the organism. Threshold levels of energy invested
109 in maturation act as triggers for birth and puberty. Birth is defined as the point when feeding
110 is initiated, whereas puberty occurs when resources are no longer used to increase maturity
111 levels, but instead go to reproduction. Once the reproductive pool reaches the level required
112 for a full litter, this biomass is then released as eggs in an oviparous species. In the present
113 case we are considering a viviparous species with facultative placentotrophy (Stewart, 1989,
114 i.e., placental provision is not requisite to the production of viable offspring) and so in the
115 model, eggs remain in the female for the duration of egg development (as described in
116 Kearney (2013)). Coupling a DEB model with a biophysical model of the impact of
117 geographic variation in environmental conditions on body temperature and activity time
118 enables us to assess the extent to which geographic variation in litter frequency in *Eulamprus*
119 *quoyii* occurs because a short activity season constrains physiological time available for litter
120 production more in the temperate zone, and less in the tropics (i.e., there is an environmental
121 temperature constraint), or occurs because of variation in energy allocation strategies of
122 different populations of *Eulamprus quoyii* (e.g., due to differences in energy allocation
123 strategies to growth and reproduction, Caley & Schwarzkopf, 2004).

124

125

126 **Methods**

127

128 *Observations of geographic variation in litter frequency*

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

144 Females were housed individually in plastic boxes (550L x 360W x 305H mm) in a
145 constant temperature room maintained at 22°C ± 1°C. Ceiling fluorescent lights provided
146 photoperiod (12L:12D) and a 75-watt incandescent light suspended at one end of each cage
147 provided basking heat. Eight hours of available basking time was centred within the daylight
148 hours of the photoperiod. When the incandescent lights were on, females could
149 thermoregulate at temperatures from 27°C to 45°C. All females were fed commercial cat
150 food (Purina Fancy FeastTM, assorted non-fish flavours) three times weekly, and crickets
151 (*Acheta domesticus*) and mealworms (*Tenebrio molitor*) once per week. Animals were fed to
152 satiation at these times. Water was available *ad libitum*, in bowls large enough for females to
153 become completely submerged. Newspaper and a small cardboard box were provided for
154 shelter in each cage, and a tree branch was provided as a basking perch. The diet and thermal
155 regimes were designed to be appropriate husbandry for these lizards until they gave birth (at
156 most several weeks), and to keep them healthy after birth. They were not intended to be
157 representative of any particular location in the range. Females were checked daily for the
158 presence of offspring in the cages. The date when offspring were first noted was recorded.
159 Offspring were counted, measured and weighed at birth, and transferred to individual holding
160 cages. After birth, females were maintained in captivity for up to 1-80 (average 36) days,

161 depending on timing of collection and then sacrificed and dissected. Ovulated follicles, if
162 present, were recorded.

163

164 *A biophysical model of Eulamprus quoyii*

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

175

176 *Estimating DEB parameters for Eulamprus quoyii*

177 We used the 'covariation method' (see also Kearney, 2012; Kearney et al., 2013; Lika et al.,
178 2011) to obtain estimates of DEB parameters, based on observations of growth from a
179 previous study of *E. quoyii* (Caley & Schwarzkopf, 2004). Caley & Schwarzkopf (2004)
180 compared populations from the latitudinal extremes of *E. quoyii*'s range (Sydney and
181 Townsville) and showed that trajectories of growth in hatchlings incubated in a crossed
182 design and raised in a common garden, varied in a complex manner with maternal body
183 temperature and source location (see Caley & Schwarzkopf (2004) for details of the
184 experimental design and husbandry conditions in that experiment). We thus fitted DEB
185 models based on data for each location (Sydney and Townsville) crossed with each maternal
186 environment (cool vs. warm), and explored the extent to which simple changes in DEB
187 parameters could account for the observed differences.

188

189 The specific observations used to fit the DEB model included: ages (d) at birth and maturity,
190 masses (g) and lengths (snout-vent length, SVL) at birth, maturity and ultimate size, annual
191 reproductive output (number of offspring), longevity, together with length-at-age trajectories
192 and length vs. mass relationships for individuals across ontogeny from birth to adult size. In
193 estimating the parameters, one can assign different weightings to the observation data. We

194 adopted the strategy of increasing the weights of observations that were statistically different
195 between the populations and treatments (Caley & Schwarzkopf, 2004).

196

197 An associated temperature is required for ages at birth and maturity, as well as reproductive
198 rate, length-at-age and longevity, together with an Arrhenius thermal response curve (we
199 used the 5-parameter model (Schoolfield, Sharpe, & Magnuson, 1981; Sharpe & DeMichele,
200 1977)). We estimated the Arrhenius temperature T_A from observations of temperature versus
201 development time (Caley & Schwarzkopf, 2004), and assumed that the lower threshold
202 temperature for enzyme deactivation T_L corresponded with the critical thermal minimum
203 (CT_{min}) and the upper threshold temperature T_H reduced the performance curve to zero at the
204 critical thermal maximum (CT_{max}). All of the temperature-sensitive observations were made
205 under diurnally fluctuating conditions. Thus, to obtain a ‘constant temperature equivalent:
206 CTE’ (Orchard, 1975), we estimated the mean Arrhenius temperature correction factor across
207 all time intervals and then back-calculated the temperature required to produce this mean
208 correction factor, which was then used as the CTE. For observations of reproduction rates
209 and longevity, which were derived from field observations, we calculated the CTE based on
210 biophysical simulations of an adult lizard thermoregulating across the years 1990-2009 in
211 Sydney and Townsville.

212

213 *Life history simulations*

214 We simulated the life history of *E. quoyii* at the eight locations sampled for litter frequency,
215 driving the simulations with environmental data from 1990 to 2009. We commenced the
216 simulations at hatching on the 1st January in a given year. We explored the variation among
217 simulations commenced in different years (i.e., the variation among cohorts), looping around
218 to years prior to the start date of a given simulation to ensure a constant 20-year block (e.g. a
219 simulation starting in year 2008 would then have used data for 2009 and then from 1990-
220 2007).

221

222 Following Kearney (2012), we used the batch reproduction model (Pecquerie *et al.* (2009) to
223 simulate seasonal reproduction, whereby litter production was initiated by the winter solstice
224 and terminated by the summer solstice, with a reproduction buffer building up in between.
225 Feeding was assumed to continue through pregnancy, which is realistic (LS, pers. obs., Huey
226 *et al.*, 2001). Activity, and hence feeding, was only permitted during daylight hours when
227 body temperature was within the thresholds for voluntary activity (Kearney *et al.*, 2013). The

228 lizard was permitted to select from between 0 and 90% shade for thermoregulation. We
229 assumed that water did not constrain activity (i.e. that the lizard was living beside permanent
230 water, which is realistic for these lizards, Law & Bradley, 1990) and that lizards experienced
231 *ad libitum* food during activity periods. We also ran simulations for a set of 893 locations
232 evenly sampled across eastern continental Australia (encompassing the geographic range of
233 the species) to provide a broader picture of how temperature limits the life history across the
234 species' potential geographic range.

235

236

237 **Results**

238

239 *Geographic variation in litter frequency*

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

248

249 Over several years, we sampled 98 gravid females (7 from Paluma, 2 from Bluewater Creek
250 and 27 from Alligator Creek and North Creek near Townsville, 3 from the Brisbane Cultural
251 Centre, 2 from Dawson Creek near Brisbane, 7 from Quart Pot Creek near Stanthorpe, 20
252 from Red Rock Creek near Rockhampton, 10 from Mimosa Creek on the Blackdown
253 Tableland, 5 from Sharpes Creek in Barrington Tops National Park [Gloucester Tops], 15
254 from Oxford Falls Creek and Frenchman's Creek in Sydney), and allowed them to give birth
255 in the laboratory, then held them for up to 70 days (1-70, mean =35), after which they were
256 euthanized and dissected. Only females from Paluma, Townsville, and Rockhampton had
257 ovulated within 35 days of giving birth in late December or January (1/7 females from
258 Paluma (14%), 4/29 from the Townsville areas (13%), 1/20 from the Rockhampton area
259 (5%)). One female collected in Brisbane in December 1997 that was not gravid at the time of
260 collection had ovulated 4 follicles at the time of dissection on the 19 February 1998,

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

263

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

274

275

276 *DEB parameters for Eulamprus quoyii*

277 The DEB parameter estimates and fits to the observed data for the Sydney-warm treatment
278 are presented in Table 2 (see Tables S1-3 in Supporting Information for parameters from fits
279 to the data of the other three treatments). The associated Matlab scripts used to estimate the
280 parameters can be found at http://www.bio.vu.nl/thb/deb/deblab/add_my_pet/Species.xls.

281

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

293

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

301

302 *Life history simulations*

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

308

309 The frequency of production of two litters increased with the body temperatures experienced
310 at the site, with the highest frequencies at Townsville and the lowest at Gloucester Tops (Fig.
311 1, Table 1), and this was broadly consistent with empirical observations of two litters. The
312 inter-cohort variability in the frequency of production of two litters showed an inverse
313 pattern, as indicated by the standard deviations (Table 1, expressed as a percentage of the
314 mean). At the coldest site, Gloucester Tops, with the Sydney life history, half the cohorts
315 produced two litters in their last year of life (Table 1). Under the Townsville life history, no
316 double litters occurred at Gloucester Tops or Stanthorpe and the mean number of double
317 litters at the other sites was lower. The mean intra-annual litter frequency was positively
318 correlated with the observed pattern of double litter production under both the Sydney and
319 Townsville DEB models (Spearman rank correlation, Sydney $r = 0.79$, $S_6 = 17.8$, $P = 0.020$,
320 Townsville $r = 0.79$, $S_6 = 17.84$, $P = 0.020$).

321

322

323

324 **Discussion**

325 *Environmental constraints on frequency of reproduction*

326 Empirical observations of populations of viviparous reptiles suggest that most are limited to a
327 single reproductive episode per year (e.g. Ballinger, 1983) and, indeed, many viviparous

328 species reproduce biennially or less (e.g., (Alison & Guillette, 1995; Cox, Skelly, &
329 John- Alder, 2003; Ibarzüengoytía & Cussac, 1996; Olsson & Shine, 1999; Pincheira-
330 Donoso & Tregenza, 2011; Schwarzkopf, 1993; Van Wyk, 1991). We observed that, in the
331 tropical parts of their range, individual viviparous Eastern water skinks (*Eulamprus quoyii*)
332 reproduce more than once per year, whereas in other locations females reproduce annually at
333 most. A dynamic energy budget (DEB) model, combined with a biophysical model
334 predicting body temperature and activity patterns, strongly suggest that much of the variation
335 in reproductive frequency among populations of this species can be explained by constraints
336 imposed by environmental temperatures, and the associated activity period available to the
337 lizards. This occurs because, in our model, the animals have the same time window to breed
338 (we assume they store up energy for reproduction between the summer and winter solstice,
339 and yolk follicles between the winter and summer solstice, which is similar to what occurs in
340 nature, Schwarzkopf pers. obs.) but as temperature changes along the transect they have
341 different amounts of physiological time available to bring their litter full term.

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

357 The model's tendency to sometimes over-predict the production of two litters may
358 occur because (i) individuals in the model are never food restricted, whereas animals in real
359 populations may be, reducing energy available for producing the second litter. Moreover, in
360 the model, individuals could feed throughout pregnancy, whereas some water skinks stop
361 feeding late in gestation (Schwarzkopf, 1996), (ii) in the model, litter size is constrained to

362 the mean size, whereas in the real world, litter size varies, linking the rate of production of
363 two litters to the body size of females in the population, and allowing females flexibility in
364 producing litters smaller or larger than the mean, (iii) in the model, there is no disadvantage
365 to producing offspring very late in the year, essentially in winter, whereas in the real world,
366 such a restriction is likely a very important selective force preventing the production of two
367 litters in a single year. Reproduction increases the basking rate of females, which may be
368 costly (e.g., Schwarzkopf, 1993; Schwarzkopf & Shine, 1991; Schwarzkopf & Shine, 1992),
369 and offspring may fare poorly if produced too late in the year (Wapstra, Uller, While, Olsson,
370 & Shine, 2010). We think it likely that this last point is very important in determining actual
371 reproductive frequency, because a mistake, i.e., producing a litter too late in the season, may
372 be too costly to allow the evolution of multiple litters per annum in cooler populations. We
373 suggest it is more advantageous for females to retain the energy, and allocate it to growth and
374 potentially reap a size-dependent fecundity advantage the following year (e.g. Shine,
375 Schwarzkopf, & Caley, 1996) Indeed, it seems that southern populations lack the
376 physiological flexibility to produce a second litter, as southern (Sydney) females held in the
377 laboratory at warm temperatures with *ad libitum* food failed to ovulate for over a year.

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

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

392 *Temperate versus tropical energy budgets*

393 While the constraints of temperature and season length alone could explain much of the
394 geographic variation in litter frequency that we observed in *E. quoyii*, it is also important to
395 consider whether known geographic differences in growth trajectories (Caley &

396 Schwarzkopf, 2004) also play a role. Below, and in the context of the DEB model we created
397 for *E. quoyii*, we interpret the patterns in reproductive allocation strategies consistent with the
398 growth trajectories reported in (Caley & Schwarzkopf, 2004).

399 In the wild, there were no differences in asymptotic size or overall reproductive output
400 among locations, and the length-mass relationships for all of four laboratory experimental
401 treatments, cool (Sydney) origin individuals, cool and warm treatments, and warm
402 (Townsville) origin individuals in cool and warm treatments (Caley & Schwarzkopf, 2004
403 and Schwarzkopf pers. obs.) were virtually indistinguishable (Fig. S2). The growth
404 trajectories of offspring from the two temperature treatment groups from Sydney showed a
405 striking convergence on asymptotic size, despite the dramatic increase in growth rate
406 imposed by the cooler gestation temperature treatment (Fig. S1a). This convergence suggests
407 that there were no major changes in energy allocation strategies with gestational thermal
408 environment. Instead, for the Sydney population, the cool gestation treatment may have
409 imposed an acclimation response on the developing embryos such that their thermal optimum
410 shifted to a cooler value. Thus, we conclude that Sydney animals had a wider thermal
411 tolerance, and could acclimate to both the warm and cool thermal environments they were
412 offered in the laboratory. The Townsville population lacked such a pattern but exhibited a
413 wider spread in growth trajectories, especially for families exposed to the cool gestation
414 treatment (Fig. 1b).

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

429 to hurry' compared with Townsville. The DEB parameters for the Townsville population,
430 however, make double litters less likely compared to those for the Sydney population (Fig.
431 1). Thus, it does not seem that geographic patterns in reproductive frequency can be
432 explained by the differences in allocation to growth we observed; if anything, they should act
433 in the opposite direction.

434 An alternative, non-adaptive interpretation of the disparity in growth responses between
435 Townsville and Sydney families is that individuals from Townsville had narrower thermal
436 tolerances, or less efficient acclimation responses, compared to those from Sydney. This
437 interpretation is consistent with many recent papers suggesting that the thermal acclimation
438 response of tropical species may be narrower than those of temperate species (e.g. Sunday,
439 Bates, & Dulvy, 2011). In addition, the Townsville 'warm' environment provided to females
440 for gestation in the Caley and Schwarzkopf (2004) experiment, although intended to
441 represent a "Townsville gestation environment", may have not been representative of the
442 thermal environment females from Townsville usually experience. Our simulations of the
443 likely gestation environment experienced in Townsville predicted considerably higher body
444 temperatures, especially at night (Fig. S3b): the constant temperature equivalent (CTE)
445 calculated from field temperature data was 28.0 °C compared to the 25.8 °C provided in the
446 laboratory for the warm treatment. The CTE of the simulated gestation environment for
447 Sydney was between those of the cool and warm gestation treatments (23.5 °C) (Fig. S3a).
448 Thus, it is possible that offspring from Townsville exposed to both the warm and cool
449 treatments experienced thermal stress, thereby reducing growth rates. In any case,
450 Townsville offspring responded with slow and variable growth to laboratory thermal
451 treatments, compared to Sydney offspring.

452

453 *Conclusion*

454 There has long been a general appreciation that major transitions in the life histories of
455 ectotherms are likely to be strongly influenced by temperature, and by the window of activity
456 times available to different groups (e.g. Adolph & Porter, 1993, 1996; Stevenson, 1985).
457 Here we have combined empirical observations of life history variation, including litter
458 frequency, with a Dynamic Energy Budget model and a bioenergetics model, to better
459 understand a very unusual life history transition for a viviparous Australian lizard from one to
460 two litters per annum. Even given the simplifying assumptions of the model, the
461 physiological activity window calculated by the model was an excellent predictor of the

462 occurrence of this unusual life history transition. Models, such as those developed here that
463 integrate formal metabolic theory with biophysical ecological principles, have great potential
464 to provide insights into constraints on life histories and how they vary through space and time
465 (Kearney, 2012; Kearney, 2013).

466

467 Data Availability: Data can be accessed on the Tropical Data Hub at James Cook University,
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471 manuscript, MRK conducted the modeling and participated in the drafting the manuscript.

472 All authors gave final approval for publication.

473

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477 feeding and caring for lizards.

478

479 **Figure Captions**

480

481 **Figure 1.** Growth trajectories (wet mass) predicted for the Sydney-warm (black solid line)
482 and Townsville-warm (grey dashed line) from Dynamic Energy Budget models for
483 *Eulamprus quoyii* at eight sites across its range under the local weather conditions from
484 1990-2009 (all lizards had died from old age in the simulation by this time). The sudden
485 drops in mass represent litters, with double litters appearing as two drops within a single year,
486 indicated by the heavy horizontal bars. Observed annual frequency of reproduction is
487 indicated after the site labels.

488

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

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	(Ian F. Spellerberg, 1972)
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
$F_{\text{body,sky}}$, configuration factor body to sky	-	0.4	(Porter, Mitchell, Beckman, & DeWitt, 1973)
$F_{\text{body,sub}}$, configuration factor body to substrate	-	0.4	(Porter et al., 1973)
A , lizard surface area	cm ²	$10.4713W_w^{0.688}$ where W_w is wet weight in g	(Porter et al., 1973)
A_{sil} , silhouette area normal to the sun	cm ²	$3.798W_w^{0.683}$ where W_w is wet weight in g	(Porter et al., 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	(Ian F. Spellerberg, 1972)
T_B^{min} , minimum basking temperature	°C	17.4	(Ian F. Spellerberg, 1972)

T_F^{min} , minimum foraging temperature	°C	23.9	(Ian F. Spellerberg, 1972)
T_F^{max} , maximum foraging temperature	°C	34.2	(Ian F. Spellerberg, 1972)
T_{pref} , preferred temperature	°C	30.0	(Ian F. Spellerberg, 1972)
CT_{min} , critical thermal minimum	°C	6.0	(I. F. Spellerberg, 1972)
CT_{max} , critical thermal maximum	°C	39.8	(I. F. Spellerberg, 1972)

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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 and 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)	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	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
ν , 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 d ⁻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
$\{p_{Xm}\}$, maximum specific food intake	12420	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	525000	J C-mol ⁻¹	default
μ_E , chemical potential of reserve	585000	J C-mol ⁻¹	default
μ_V , chemical potential of structure	500000	J C-mol ⁻¹	default
μ_P , chemical potential of faeces	480000	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)

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 1990-2009 as input, assuming no food limitation when thermal conditions permitted activity. Results are means of 20 simulations covering all starting years, i.e. 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.

a) Sydney life history

Site	Longitude	Latitude	Observed Litter Frequency	Predicted Litter Frequency	Lifetime Double Litters	Lifetime Fecundity	Age at 1st reproduction (years)	Life Span (years)	r_{\max}
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

Site	Longitude	Latitude	Observed	Predicted	Lifetime	Lifetime	Age at 1st	Life Span	r_{\max}
			Litter	Litter	Double		reproduction		
			Frequency	Frequency	Litters	Fecundity	(years)	(years)	
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)

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Supporting Information:

Additional Supporting Information can be found in the online version of this article.

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 and Schwarzkopf (2004).

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

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

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.

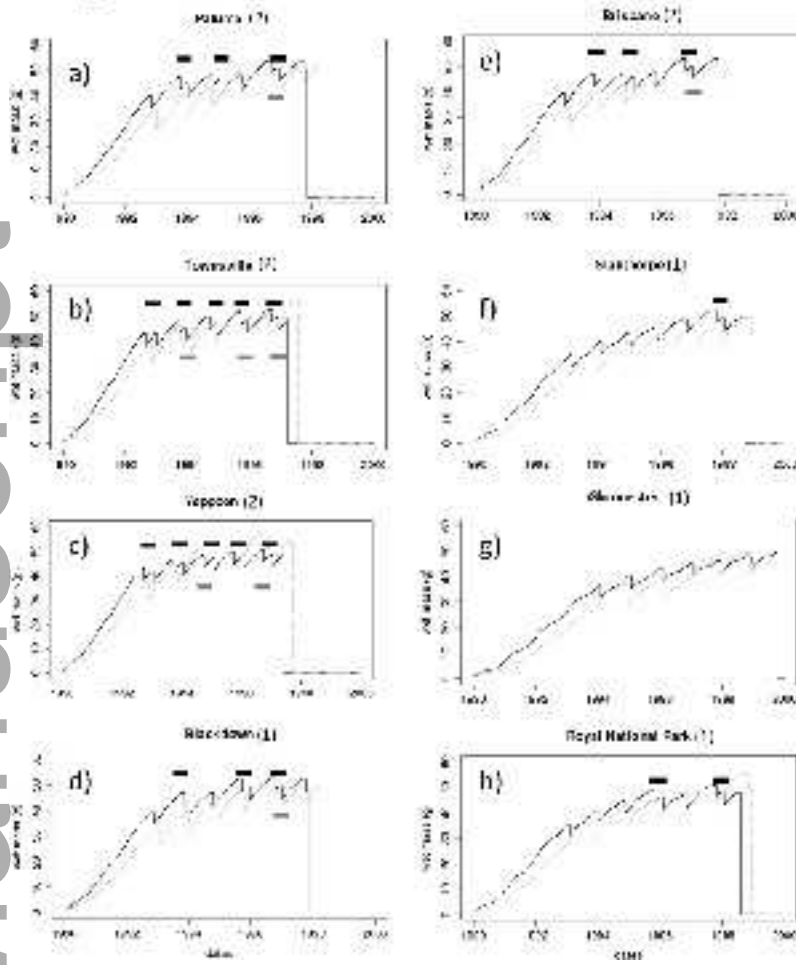
Figure S3 Cool (a) and warm (b) environmental exposures (from Caley and Schwarzkopf 2004).

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.

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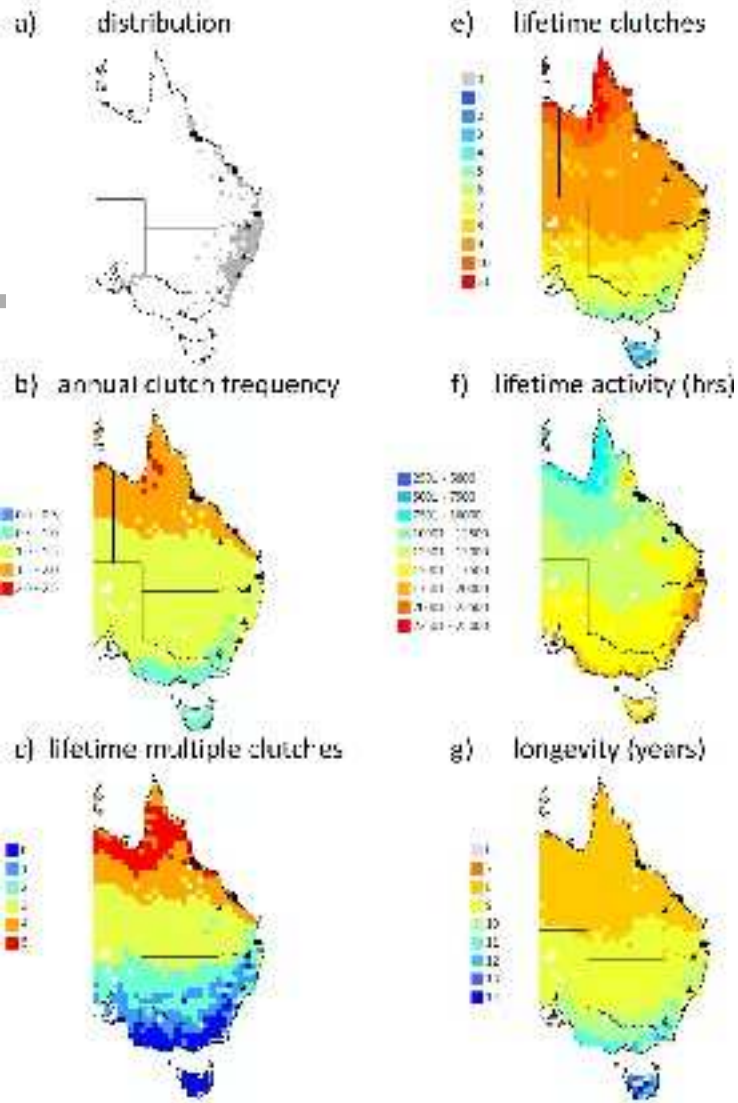
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Figure 1.



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Figure 2.



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