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1	Article Title	**Predicting the effects of climate change on reproductive fitness of an endangered montane lizard, *Eulamprus leuraensis* (Scincidae)**	
2	Article Sub- Title		
3	Article Copyright - Year	**Springer Science+Business Media B.V. 2010 (This will be the copyright line in the final PDF)**	
4	Journal Name	Climatic Change	
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21	Schedule	Received	27 May 2009
22		Revised	
23		Accepted	5 October 2010

24 Abstract

A shift in climatic conditions may directly modify critical organismal traits (such as reproductive output and offspring phenotypes), and experimental studies to document such direct effects thus may clarify the impacts of climate change on the species involved. The endangered Blue Mountains Water Skink (*Eulamprus leuraensis*) exhibits several traits predicted to imperil it under climate change: ectothermy, low reproductive output, specialisation to a restricted habitat type, montane endemicity, and a small geographic range. Congeneric species exhibit temperature-dependent sex determination, increasing potential sensitivity to climate change. We maintained wild-caught female lizards throughout pregnancy under thermal conditions simulating a shift in basking-time availability (3 vs 7 h/day) as might occur under climate change. Females with longer basking opportunities per day gave birth 2 weeks earlier, to slightly smaller offspring, that grew much faster in the first few weeks of life. Importantly, offspring sex ratios were not affected by maternal thermal regimes. Hence, some traits (e.g., offspring size, growth rates, dates of birth) are sensitive to ambient thermal conditions whereas other traits (e.g., offspring sex ratio and sprint speed) are not. On balance, the greatest threat to population persistence for *E. leuraensis* under climate change is likely to involve indirect effects

		mediated via habitat degradation (especially, drying-out of the hanging swamps) rather than direct thermal effects on lizard reproductive output or offspring phenotypes.
25	Keywords separated by ' - '	
26	Foot note information	

Climatic Change
DOI 10.1007/s10584-010-9963-x

Predicting the effects of climate change on reproductive fitness of an endangered montane lizard, *Eulamprus leuraensis* (Scincidae)

Sylvain Dubey · Richard Shine

Received: 27 May 2009 / Accepted: 5 October 2010

Abstract A shift in climatic conditions may directly modify critical organismal traits (such as reproductive output and offspring phenotypes), and experimental studies to document such direct effects thus may clarify the impacts of climate change on the species involved. The endangered Blue Mountains Water Skink (*Eulamprus leuraensis*) exhibits several traits predicted to imperil it under climate change: ectothermy, low reproductive output, specialisation to a restricted habitat type, montane endemicity, and a small geographic range. Congeneric species exhibit temperature-dependent sex determination, increasing potential sensitivity to climate change. We maintained wild-caught female lizards throughout pregnancy under thermal conditions simulating a shift in basking-time availability (3 vs 7 h/day) as might occur under climate change. Females with longer basking opportunities per day gave birth 2 weeks earlier, to slightly smaller offspring, that grew much faster in the first few weeks of life. Importantly, offspring sex ratios were not affected by maternal thermal regimes. Hence, some traits (e.g., offspring size, growth rates, dates of birth) are sensitive to ambient thermal conditions whereas other traits (e.g., offspring sex ratio and sprint speed) are not. On balance, the greatest threat to population persistence for *E. leuraensis* under climate change is likely to involve indirect effects mediated via habitat degradation (especially, drying-out of the hanging swamps) rather than direct thermal effects on lizard reproductive output or offspring phenotypes.

1 Introduction

There is broad scientific consensus that changes in global climate will imperil many species, and that the impacts will fall more heavily on some taxa than on others (e.g. Parmesan 1996; Hughes 2000, 2002; Deutsch et al. 2008; Gallagher et al. 2009). For

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example, Williams et al. (2008) predicted that the sensitivity of a species to climate change will be determined by a combination of intrinsic factors (such as physiological tolerance limits, ecological and behavioral traits, and genetic diversity), resilience (ability to survive and recover from a perturbation), and adaptive capacity (ability to exhibit plastic responses and/or adapt rapidly). Many authors have pointed out that dependence on a specific (and highly restricted) set of conditions may render some taxa especially vulnerable to changing climate (Jiguet et al. 2007; Forcada et al. 2008). However, the role of phenotypic plasticity in determining vulnerability to climate change has attracted less scientific attention (e.g., Aubret and Shine 2010). Most models designed to predict impacts of climate change on organismal distribution assume that the organism's biology will not be directly affected by a shift in climatic conditions, but that assumption in unrealistic for many traits in many species. For example, incubation and gestation temperatures directly modify the phenotypic traits of offspring in many reptile species (Deeming 2004; Shine 2004a). Incorporating information on such phenotypically plastic responses can strengthen our ability to predict the impacts of climate change.

More generally, many reptile species are likely to be at risk from climate change. As ectotherms, they are highly sensitive to local ambient thermal conditions (e.g. Huey and Tewksbury 2009; Kearney et al. 2009). Many reptile species exhibit low vagility (and hence, are unable to migrate in response to changing conditions: Jiguet et al. 2007) and low reproductive output (McKinney 1997; Williams et al. 2008). Many reptiles are habitat specialists, including a diverse array of taxa that are restricted to montane areas (such habitats may disappear entirely with rising ambient temperatures: e.g. Theurillat and Guisan 2001; Dirnbock et al. 2003). Lastly, as noted above, ambient thermal conditions affect fitness-relevant phenotypic traits of the offspring in many reptile species, and in some cases the traits affected by thermal regimes have clear implications for population persistence (e.g., species in which embryonic thermal conditions determine offspring sex: Telemeco et al. 2009; Wapstra et al. 2009). Rarity also may increase vulnerability to extinction: within any given taxonomic group, taxa that are already endangered may be at very high risk from climate change (because they have less chance of surviving any additional range reduction).

Clearly, a species that falls into more than one of these categories is even more vulnerable; and some species have the misfortune to fall into all of them. One such taxon is the Blue Mountains water Skink (*Eulamprus leuraensis*), a [medium-sized (to 20 cm total length) viviparous] scincid lizard that is restricted to less than forty swamps at 560 to 1,060 m elevation in the Blue Mountains and Newnes Plateau, west of the city of Sydney in south-eastern Australia. These small swamps (typically, <2 ha) are (1) valley swamps that form where deep deposits of sediment lie along gently-sloping creeks, often on the top of the plateau or (2) "hanging swamps" on steeper valley-sides where water seeping down through the ground is trapped and channelled to the surface by horizontal, water-impervious layers of mudstone and shale (see Fig. 1). In contrast to eucalypt-dominated woodland on surrounding drier areas, the swamps are characterized by accumulations of litter on moist soil, and support endemic sedges and shrubs (e.g. *Gymnoschoenus sphaerocephalus*, *Tetrarrhena turfosa*, *Baeckea linifolia*; LeBreton 1996).

This distinctive habitat type houses the only known populations of *E. leuraensis*. Congeneric *Eulamprus* species are distributed across southeastern Australia,

Fig. 1 The endangered Blue Mountain Water Skink, *E. leuraensis* (*lower*) is restricted to distinctive and widely separated "hanging swamps" in small valleys among eucalypt woodland (*upper*)

typically in riparian or cool damp montane habitats; most have wide geographic ranges (Cogger 2000). Morphological and genetic data suggest that *E. leuraensis* is most closely related to the alpine *E. kosciuskoi* (Shea and Peterson 1984; Dubey and Shine, unpubl. data). The ecology of *E. leuraensis* is poorly known, reflecting its restriction to these small montane swamps (LeBreton 1996; Shea and Peterson 1984). By analogy with other montane species, sexual maturation is likely to occur relatively late (at least 3 years of age in females), litter sizes are low (<6 offspring: this study; Dubey et al. 2010), and parturition may be less-than-annual (pers. obs. Doughty and Shine 1997). The species is classified as "endangered" under the Threatened Species Conservation Act (1995) and the Environmental Protection and Biodiversity Conservation Act (1999), on the basis that it is an ecological specialist, with severely reduced populations subject to substantial ongoing threats. Similarly, its restricted habitat (<2,000 km^2) is considered as threatened under the Threatened Species Conservation Act (1995) due to impacts associated with growing urbanisation, such as alteration of the hydrological system, invasion by weeds, increase of bushfires, longwall mining, and influx of pollutants. This lizard species thus may be under significant risk from global climate change. Models of climatic variation predict that

Table 1 A summary of the results of previous studies that have examined the effects of maternal thermal regimes during pregnancy (viviparous) or incubation regimes (oviparous) on the phenotypic traits of offspring, within Australian reptiles

Species and authority	Treatment	Phenotypic effects of warm treatment (or as mentioned within the table)
Scincid lizards		
Eulamprus heatwolei (viviparous)		
Shine and Harlow (1993)	2 vs 8 h basking per day (mean air temperature: 22–25°C)	Earlier birth, neonates larger, faster, more active
Langkilde and Shine (2005)	Maternal temperature monitored	Neonates smaller
Allsop and Shine (in prep.)	3 vs 10 h basking per day (air temperature when heating cable were switched off: 16°C)	Earlier birth, larger neonates with faster growth
Eulamprus quoyii (viviparous)		
Borges (1999)	3 vs 8 h basking per day (mean air temperature: 18°C)	Earlier birth, shorter tail, higher growth rate, higher survival rate
Caley and Schwarzkopf (2004)	6 h (mean air temperature: 17°C) vs 10 h (mean air temperature: 22°C) basking per day	Earlier birth, smaller neonate, larger litter
Eulamprus tympanum (viviparous)		
Robert and Thompson (2001)	Field vs constant 25, 30, and 32°C	Sex ratio shift towards male offspring
Allsop and Shine (in prep.)	3 vs 10 h basking per day (room temperature when heating cable were switched off: 16°C)	Earlier birth, larger neonates with faster growth
Eulamprus leuraensis (viviparous)		
This study	3 vs 7 h basking per day (mean air temperature: 18°C)	Earlier birth, smaller neonates with faster growth
Niveoscincus ocellatus (viviparous)		
Wapstra (2000)	4 h vs 10 h of basking per day for the gravid females	Earlier birth. Longer and heavier neonates with faster growth
Wapstra et al. (2004)	Field and 4 h (cold) vs 10 h (warm) basking per day for the gravid females	Litter sex ratio varied with birth date: male-biased litters were produced later in the season Warm treatment: female-biased, cold treatment: male-biased sex ratio
Wapstra et al. (2009)	7 years field study	Male-biased sex ratio when cold
Pseudemoia pagenstescheri (viviparous)		
Shine and Downes (1999)	6 h vs 12 h of basking per day for the gravid females	Earlier birth, larger neonates but slower

Egernia whitii (viviparous)		
While et al. (2009)	4 h (cold) and 10 h (warm) of basking per day for the gravid females	Earlier birth, neonates with faster sprint speed
		First born offspring within a clutch, faster than last born in the warm treatment; but last born faster than first born offspring in the cold treatment
Lampropholis guichenoti (oviparous)		
Qualls and Shine (1998)	Incubation at cold (up to 22°C) thermal regime for a highland site and warm thermal regime (up to 29°C) for a lowland site	Earlier birth, neonates lighter with longer tail, and slower
Bassiana duperreyi (oviparous)		
Shine and Harlow (1996)	1) Incubation at 22°C vs 30°C	Earlier birth, smaller neonates, faster, and basked more at one month of age
	2) Incubation at 23°C with no variance, moderate variance (±3.75°C), and high (±9.75)	High variance: earlier birth and neonates with longer tails
Shine et al. (1997a, b)	Incubation in natural nests	Earlier birth, neonates with longer tail
Elphick and Shine (1998a, b)	Incubation at 20 ± 4°C vs 27 ± 4°C	Earlier birth, heavier neonates, faster, with longer tails and higher survival rates
Q1 Elphick and Shine (1999)	Incubation 16–24°C vs 23–31°C	Earlier birth, neonates larger, heavier with faster growth and faster
Shine and Elphick (2001)	All incubation at 17°C ± 5°C, and then split into three categories for a two-week period either at 17°C ± 5°C (cool), 22°C ± 5°C (warm), or 27°C ± 5°C (hot) at different timing of the incubation, and then returned to 17°C ± 5°C	Earlier birth, higher hatching success
		Neonates heavier with shorter tails relative to SVL, and faster when exposed to a ‘hot treatment’ late in embryogenesis compared to sibling exposed earlier to a hot treatment
Flatt et al. (2001)	Incubation at 18°C ± 5°C vs 22 ± 5°C	Earlier birth, higher hatching rate, neonates with longer tails relative to SVL
Shine (2004b)	18 ± 5°C throughout incubation; others went gradually from cool (16 ± 5°C) to warm (20 ± 5°C); and others from warm (20 ± 5°C) to cool (16 ± 5°C)	These treatments significantly modified not only incubation periods (stable mean temperatures delayed hatching), but also neonatal traits: progressively decreasing temperatures yielded hatchlings with a higher incidence of deformities, smaller body size, relatively longer tails, and reduced locomotor performance than siblings compared to those from increasing temperatures

Table 1 (continued)

Species and authority	Treatment	Phenotypic effects of warm treatment (or as mentioned within the table)
Shine (2006)	Gravid females at 17 ± 5°C, 22 ± 5°C, or 27 ± 5°C for two weeks, then returned to a room with a range of 18 to 40°C during daylight hours. Then, eggs were incubated at either 17 ± 5°C or 18 ± 5°C	Earlier birth, shorter tail length relative to body size with faster running speed
Radder et al. (2008)	Incubation at 16°C ± 7.5°C vs 22°C ± 7.5°C	Warm treatment: 54% males; cold treatment: 70% males
Du et al. (2010)	Incubation at 16 ± 7.5°C vs 22 ± 7.5°C from three populations	Mean selected temperatures did not differ among neonates from three populations with differing thermal regimes in natural nests, nor were they affected by thermal conditions during incubation.
Telemeco et al. (2010)	Gravid females at cold or hot temperature, then dissection of one egg per clutch to check the embryonic staging. The remaining eggs were placed in incubators at 16 ± 7.5°C or 22 ± 7.5°C.	More advanced embryonic development, increased hatching success and neonate body size.
Nannoscincus maccoyi (oviparous)		
Shine (1999)	Cold (20°C ± 4°C) vs warm (27°C ± 4°C)	Earlier birth, smaller and slower neonates
Agamid lizards		
Amphibolurus muricatus (oviparous)		
Harlow and Taylor (2000)	23, 25, 27 ± 5, 28, 29, 30, 32, 33 ± 5°C	Females produced at low (23–25°C) and high (30–33°C) incubation temperatures, and both sexes produced at intermediate temperatures (25–30°C)
Warner and Shine (2005)	Cold (23°C), intermediate (27°C), warm (33°C)	Smaller with lower body condition
Warner and Shine (2008)	Incubation at cold (23–26°C), intermediate (27–30°C), and warm (30–33°C) temperatures	Earlier birth, strong positive effect on lizard body sizes before the onset of the reproductive seasons due to earlier birth.
Warner et al. (2010)	Cold (23°C), intermediate (27°C), warm (33°C)	Males produced under intermediate temperatures sired more offspring than those produced under extreme developmental temperatures.

Chlamydosaurus kingii (oviparous)		
Harlow and Shine (1999)	Incubation at 26, 29, 32, and 33 ± 5°C	Earlier hatching Effects of incubation conditions on svl, tail and body mass Females produced at thermal extremes and males at intermediate temperatures
Gekkonid lizards		
Heteronotia binoei (oviparous)		
Kearney and Shine (2004)	Incubation at 24, 27, and 30°C	Earlier birth, longer tail, lower labial scale counts, faster, and faster growth
Elapid snakes		
Acanthophis praelongus (viviparous)		
Webb et al. (2006)	Basking range of 25–31°C (naturally selected by gravid females) vs 23–33°C (selected by non gravid females) for the gravid females	Later birth, smaller neonates, lower survival rate for 23–33°C
Colubrid snakes		
Tropidonophis mairii (oviparous)		
Webb et al. (2001)	Variable (21.8–29.6°C) vs constant (25.2–26.5°C)	Constant temperature incubation yielded longer, thinner hatchlings
Brown and Shine (2006)	25.7±6°C vs 27.9±8.4°C	Smaller neonates
Pythonid snakes		
Liasis fuscus (oviparous)		
Shine et al. (1997a, b)	Warm and stable incubation (32°C), vs colder and more variable with maternal attendance (27.1–32.9°C), or not (24.3–32.9°C)	Earlier birth, faster growth rate

For studies on *Eulamprus* species, the table also shows details of experimental conditions, for comparison with the current study
SVL snout-vent length

the area inhabited by *E. leuraensis* will become both warmer (by up to 5°C) and drier (by up to 40%) within the next century (www.climatechangeinaustralia.gov.au). Such changes might affect both the skink's habitat (e.g., reduced rainfall and thus seepage might dry out the hanging swamps) and the lizard itself. Previous experimental studies have shown that thermal regimes during gestation can affect a wide variety of fitness-relevant biological traits of species within the genus *Eulamprus*, including offspring sex, body size, body shape, date of birth, locomotor performance, and growth rate (Shine and Harlow 1993; Borges 1999; Robert and Thompson 2001; Caley and Schwarzkopf 2004; Langkilde and Shine 2005; see Table 1). If *E. leuraensis* shows similar plasticity in response to ambient thermal conditions, climate change might severely disrupt significant features of the lizards' ecology. To evaluate this possibility, we exposed gravid female lizards to two basking regimes, designed to encompass the range of conditions that might be experienced by populations of this species under climate change. The main questions that we addressed were: (1) do experimentally-imposed differences in the availability of basking opportunities affect *E. leuraensis* reproductive output, the timing of parturition, the litter sex ratio, and/or the phenotypic traits of offspring (morphology, locomotor performance, growth rate)? (2) how might direct effects of climate change affect population viability, and thus conservation of this taxon? (3) will interspecific divergence in thermally-induced reaction norms within the genus *Eulamprus* influence the species' sensitivity to climate change? and (4) by what pathways is climate change most likely to affect these endangered lizards?

2 Materials and methods

We collected 36 gravid female lizards during November and early December. The lizards were caught using pitfalls and funnel traps and transported to Sydney, where they were measured and weighed. We then sorted the animals into two treatment groups ($N = 18$ in each group) such that mean values for all relevant traits (e.g. body sizes) were equivalent among the groups (no significant differences between treatment groups (cold versus warm) in mean values of any maternal traits at the beginning of the studies: one-factor MANOVA with treatment as the factor, $F_{7,28} = 0.72$, $P = 0.65$; ANOVAs on individual traits, all $P > 0.45$).

We housed lizards individually in plastic boxes (320 × 220 × 100 mm) in a room maintained at 18°C (daylight period 0700–1900 hours). Underfloor heating cables allowed each female to control her body temperature over the range 20–33°C for part of the day: either from 1100 to 1400 hours (total of 3 h/day; cold treatment) or from 0900 to 1600 hours (7 h/day; warm treatment). Outside that time the heating cables were switched off, so that cage temperature fell to air temperature overnight. Each female was fed five crickets twice weekly.

We selected these durations of basking opportunity based on field observations and meteorological data. In spring and summer, skinks are active from 0900 to 1600 hours under suitable weather conditions (sunny and a minimum of 18°C; Dubey and Shine, unpublished data), i.e. a maximum of 7 h/day. However, more than 40% of days are cloudy during this period, preventing basking (http://www.bom.gov.au/climate/averages/tables/cw_063039.shtml). Based on these observations, we estimated that the current mean basking time per day should be approximately 3 h. We chose 7 h basking availability per day for the warm treatment based on removal of that cloud-cover constraint. Given that climate change is predicted both to increase ambient temperature (enabling earlier emergence) and reduce cloud cover, we used the maximum number of hours available under current "good" days to represent warmer and drier conditions as expected under climate change. The accuracy of our assignment of "basking hours per day" can be evaluated by comparing gestation periods (and thus, dates of birth) in experimental treatments compared to those in the field in the same summer. We would expect parturition within the cold treatment to occur at the same time as observed in the field (based on the capture of neonates; Dubey and Shine, unpublished data), whereas females from the warm treatment should give birth earlier. This is exactly what happened, confirming that the "cold treatment" accurately mimics thermal conditions experienced by free-living females. Clearly, the extent of increase in basking availability due to climate change remains uncertain; our "warm treatment" animals thus simply show what might happen if conditions changed by this amount. A further advantage of the specific treatments we used is to facilitate comparisons with earlier studies on congeneric species.

Lizard boxes were checked at least once per day for the presence of neonates. The offspring were removed immediately, weighed and measured (as was the mother), and then all of the individually-marked progeny were transferred to large communal rearing enclosures (50 × 37 cm; 15 lizards per enclosure). Sex was determined by manual eversion of hemipenes (Harlow 1996). When the young lizards were 12 days old, we reweighed them and tested their locomotor speeds on a racetrack (1 m long, 4 cm wide) kept in a constant-temperature room held at 23 + 1°C. Lizards were allowed at least 60 min to reach this temperature before being tested. Each neonate was then introduced to the beginning of the track-way, and encouraged to run by gentle prodding with an artist's paintbrush. Speed was determined as the lizard crossed infrared beams (positioned at 25 cm intervals) connected to an electronic stopwatch. Our analyses are based on each animal's maximum speed over 25 cm.

Q1 Statistical analyses were conducted using JMP 7.0 (SAS Institute 2007). Nominal variables were analysed using contingency-table tests. Maternal traits were analysed using MANOVA and ANOVA with treatment group as the factor, or ANCOVA (with maternal size as the covariate) for traits plausibly linked to maternal body size (e.g., litter size). Analyses of offspring traits used nested MANOVA and nested ANOVA, with female identity (clutch identity) nested within treatment. To avoid treating siblings as statistically independent (thereby introducing pseudoreplication), we calculated mean values for sons and daughters from each litter, and included sex as a factor in the above analyses. Litter sex ratios were compared using ANCOVA with treatment as a factor, litter size as a covariate and number of sons as the dependent variable.

3 Results

3.1 Maternal reproductive output

The 36 females gave birth to a total of 93 offspring. Of these animals, two were stillborn, both from the cold treatment (incidence of still-birth vs treatment, $52 = 0.0$, $P = 0.95$). Litter sizes averaged 2.89 (range 1 to 5) in the cold treatment, and 2.82

(1 to 4) in the warm treatment (one-factor ANOVA, $F_{1,34} = 0.02$, $P = 0.87$; ANCOVA with maternal snout-vent length as covariate, treatment*SVL $F_{1,32} = 0.57$, $P = 0.45$; main effect of treatment $F_{1,33} = 0.10$, $P = 0.74$). Similarly, total litter mass relative to maternal mass did not differ significantly between females from the two treatments (same design as above, one-factor ANOVA, $F_{1,34} = 2.41$, $P = 0.41$; ANCOVA with maternal snout-vent length as covariate, treatment*SVL $F_{1,32} = 3.24$, $P = 0.08$; main effect of treatment $F_{1,33} = 1.13$, $P = 0.30$). In summary, reproductive output was not significantly affected by our experimental manipulation of basking opportunities.

3.2 Date of birth and litter sex ratios

Females from the warm treatment gave birth an average of 15 days earlier than did females from the cold treatment (Fig. 1; ANOVA $F_{1,34} = 28.40$, $P < 0.0001$). The timing of parturition within the cold treatment corresponded to the timing of birth in the field (based on the capture of neonates: Dubey and Shine, unpublished data), whereas birth in the warm treatment animals occurred before this period.

In total, 29 sons and 18 daughters were born from cool-treatment females (62% male), compared to 23 sons and 23 daughters from warm-treatment females (50% male). We compared litter sex ratios between treatments using ANCOVA with number of sons as the dependent variable, and total litter size as the covariate. No significant difference was apparent (heterogeneity of slopes test, $F_{1,32} = 0.48$, $P = 0.49$; ANCOVA, treatment $F_{1,33} = 1.70$, $P = 0.20$).

3.3 Offspring morphology

MANOVA with offspring sex, treatment, and maternal identity nested within treatment as factors, and offspring morphological traits as dependent variables, showed a significant effect of maternal thermal treatment on offspring phenotype ($F_{7,16} = 11.87$, $P < 0.0001$). A neonate's morphology also was affected by its sex ($F_{7,16} = 4.76$, $P < 0.005$) and differed among litters ($F_{238,122} = 3.12$, $P < 0.0001$). No interaction terms were significant (all $P > 0.05$).

Given the significant overall MANOVA, we conducted ANOVAs on individual traits using the same design. Treatment effects were significant for offspring snout-vent length ($F_{1,34} = 37.53$, $P < 0.0001$), head length ($F_{1,34} = 8.28$, $P < 0.01$) and interlimb distance ($F_{1,34} = 9.05$, $P < 0.007$), but not for mass ($F_{1,34} = 1.59$, $P = 0.22$), tail length ($F_{1,34} = 0.58$, $P = 0.45$), or limb lengths (front limbs—$F_{1,34} = 0.40$, $P = 0.53$; rear limbs—$F_{1,34} = 1.03$, $P = 0.32$). Offspring from the warm treatment averaged slightly smaller than those from the cool treatment for all of the variables measured.

3.4 Offspring locomotor performance and growth rates

Sprint speeds over a 25-cm distance were not significantly affected by maternal treatment (ANOVA $F_{1,28} = 1.40$, $P = 0.26$), nor by offspring body size (SVL effect $F_{1,27} = 0.89$, $P = 0.36$; interaction treatment*body size $F_{1,26} = 0.15$, $P = 0.70$). Although mean body masses at birth did not differ significantly between neonates from the two treatment groups (above), the offspring born to warm-treatment

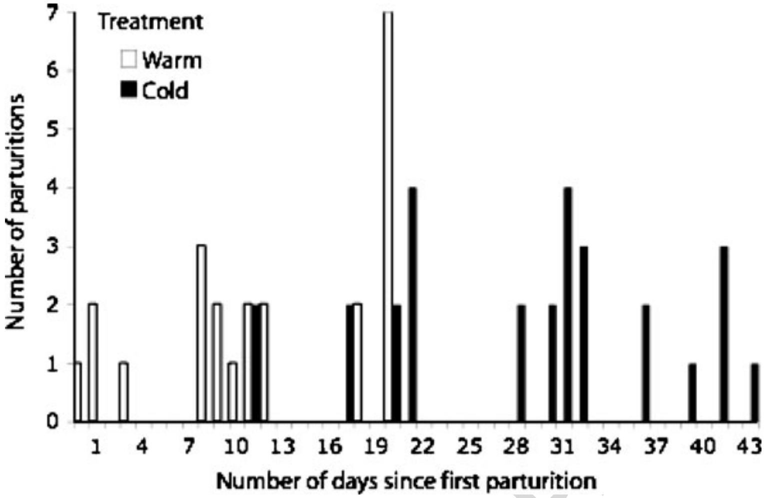


Fig. 2 Experimentally-imposed differences in the availability of basking opportunities ("warm" = 7 h/day; "cold" = 3 h/day) for female water skinks (*E. leuraensis*) substantially modified the seasonal timing of parturition. Females with less basking opportunities gave birth later than did conspecifics with greater basking opportunities

Q2

females grew much faster over the first 12 days of life (ANCOVA with mass at birth as the covariate, treatment effect $F_{1,28} = 23.69$, $P < 0.0001$; interaction treatment*initial mass $F_{1,27} = 0.33$, $P = 0.60$; see Fig. 2).

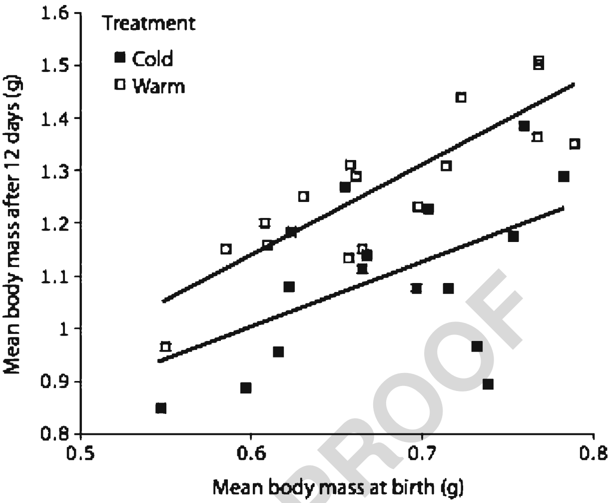
4 Discussion

Although the details of future climates are difficult to predict, there is broad consensus that many parts of the world will experience significant change over the next few decades (Hughes 2000; Kerr 2009). Most authorities predict that southeastern Australia will become warmer and drier, with an increase in fire frequency leading to a change in species composition (e.g. Steffen et al. 2009; www.climatechangeinaustralia.gov.au; www.ipcc.ch); the reduced cloud cover associated with lower precipitation also may substantially increase basking opportunities for heliothermic ectotherms (Kearney et al. 2009). Given the sensitivity of embryonic development in reptiles to minor thermal variation, even small shifts in maternal thermal regimes might significantly affect offspring phenotypes (e.g., *Vipera aspis*; Lourdais et al. 2004). Such thermally-driven developmental plasticity can affect organismal fitness (Shine et al. 2005). One trait of particular significance for population viability is litter sex ratio: marked plasticity in that trait might render a species vulnerable to highly-skewed sex ratios in response to climatic variation (Robert and Thompson 2001; Wapstra et al. 2004, 2009). Hence, a species' sensitivity to thermal shifts can determine the immediate impacts of a rapid increase in ambient temperatures (Fig. 3). Q3

Our experiments clarify the ways in which *E. leuraensis* might be affected by a major (more than twofold) increase in numbers of hours available for basking per

Q2

Fig. 3 Experimentally-imposed differences in the availability of basking opportunities ("warm" = 7 h/day; "cold" = 3 h/day) for female water skinks (*E. leuraensis*) had little effect on mean body sizes of their offspring at birth, but offspring from relatively warm gestation grew much more rapidly in the 2 weeks following parturition



day. Our data suggest that we could expect females to give birth much earlier than is currently the case, to neonates that are slightly smaller at birth but thereafter grow more quickly than do individuals in present-day populations exposed to present-day climatic conditions. Locomotor speeds of offspring seem unlikely to be affected, and—perhaps most importantly—the same is true for litter sex ratios. In this latter respect, *E. leuraensis* resembles the congeneric *E. quoyii* (no sex-ratio shift from mothers maintained at 3 vs 8 h/day basking: Borges 1999) but differs from its more closely related montane congeners *E. tympanum* (Robert and Thompson 2001) and *E. heatwolei* (Langkilde and Shine 2005; D. Allsop, pers. comm.). The diversity of sex-determining mechanisms is not reflected in other aspects of thermal biology: for example, field and laboratory research suggest that all *Eulamprus* species studied to date have very similar thermal preferenda (28.1°C to 30.2°C: Greer 1989).

A review of published studies on the effects of gestation and incubation temperatures on phenotypic traits of offspring in Australian snakes and lizards (Table 1) reveals wide divergences in reaction norms. For example, within scincid and agamid lizards, increased maternal basking (in viviparous species) or incubation temperature (in oviparous species) shifts offspring sex ratios in *Niveoscincus ocellatus* (Wapstra et al. 2004, 2009), *Bassiana duperreyi* (Radder et al. 2008), *Amphibolurus muricatus*, and *Chlamydosaurus kingii* (Harlow and Shine 1999), but not in *Pseudemoia pagenstescheri* (Shine and Downes 1999), *Egernia whitii* (While et al. 2009), or *Lampropholis guinchenoti* (Qualls and Shine 1998). Asian scincid species show similar diversity, with incubation temperature affecting offspring sex ratio in *Sphenomorphus indicus* (Ji et al. 2006a) but not in *Mabuya multifasciata* (Ji et al. 2006b). A recent field study on the oviparous *B. duperreyi* (Telemeco et al. 2009) showed that females of this species have adjusted both seasonal timing of oviposition and nest depth in response to rising ambient temperatures, but have been unable to compensate entirely for climate change. As a result, mean incubation temperatures in nests have increased over the last several years, affecting offspring sex ratios in the study population. Consequently, a shift in offspring sex ratio is already occurring in this species due to global warming.

Other offspring traits that are commonly influenced by incubation temperature (as shown by experimental manipulation of thermal regimes in the laboratory) include (a) development time (warmer conditions result in earlier birth, in all the tested species: Table 1), (b) morphology (observed in most of the studied species), (c) hatchling growth rates (e.g. Shine et al. 1997a, b; Elphick and Shine 1999; Wapstra 2000; Kearney and Shine 2004), (d) hatchling survival rates (e.g. Shine and Elphick 2001; Webb et al. 2006), and (e) hatchling locomotor performance (e.g. Shine and Harlow 1996; Shine 1999; Kearney and Shine 2004; Shine and Downes 1999; While et al. 2009). The fitness consequences of these thermally-induced effects are unclear, but are likely to be significant at least for some taxa. Importantly, reaction norms for embryonic development vary even among closely related species, prohibiting generalisations. The genus *Eulamprus* provides one of the best examples of this phenomenon (Table 1). Q1

Attempts to predict the effects of climate change on endangered species typically have focused on shifts in geographic range, and in particular how a species' "climate envelope" will shift in space as climates change (e.g., Beaumont et al. 2007). Nevertheless, this type of approaches is too simplistic to accurately estimate the probability of species persistence under climate change. Recent years have seen the development of more sophisticated mechanistic models, incorporating extensive information on animal biology (e.g., Phillips et al. 2008; Kearney et al. 2009). However, such models rarely address the possibility of phenotypically plastic responses, an important mechanism that allows animals to deal with novel challenges such as climate change (Waddington 1961; West-Eberhard 2003). In practice, both types of approach are essential to reliably predict impacts of climate change. We need to know both how the environment will change, and how the animal will respond to those shifts. Experimental studies simulating climate change (such as the present study) thus can play a significant role in documenting norms of reaction. When combined with classical "climate envelope" simulations, or mechanistically-based models of organismal responses, information on phenotypically plastic effects of climate modifications can help to predict biological consequences—and in some cases, such as within the genus *Eulamprus*, may identify cases where superficially similar (and closely related) taxa will respond differently because of interspecific variation in underlying norms of reaction.

4.1 Implication for the conservation of *E. leuraensis*

The lack of a thermally-induced shift in offspring sex ratios in *E. leuraensis*, and the generally small magnitude of incubation effects on offspring morphology, suggest that females of this species will be able to produce viable offspring over a wide range of thermal conditions. The most important fitness effect of increased temperatures likely will be in reducing age at sexual maturity: earlier birth and a more rapid juvenile growth rate in the first autumn of life may well translate into significantly earlier maturation. However, it is difficult to predict overall population-level effects. For example, the "positive" effects of an increased mean body temperature on parameters such as gestation period and age at maturity will potentially be opposed by increasing levels of intraspecific competition, if food resources do not increase as quickly as lizard body temperatures. Shifts in food availability could change life history traits (e.g. growth rate, sexual maturation, and reproductive allocation), inducing further changes in population structure (see e.g. Benton et al. 2005; Leips et al. 2008). The uncertainty about such effects is magnified by other effects of climate change, mediated through habitat degradation (drier conditions may imperil the existence of these distinctive montane swamps) and interspecific competition (any range extension of the larger *Eulamprus quoyii* from lowland areas into those swamps might be catastrophic for *E. leuraensis*). In the face of such complexities, and with uncertainty about the relative magnitude of complex effects, we need additional research before we can answer these questions. For example, we need to understand the reasons for this endangered species' strong habitat specificity. That is, why does *E. leuraensis* occur only in these distinctive montane swamps? Surveys could evaluate the importance of factors such as precipitation regimes, soil types, food supply, vegetation structure, and floristic variables. With a better understanding of the factors critical for persistence of lizard populations, we could then examine how climate change is likely to affect those critical variables.

On balance, direct thermal effects of climate change on offspring phenotypes seem likely to be less significant for *E. leuraensis* than are indirect effects mediated via habitat change. *E. leuraensis* currently occupies swamps over a wide range of elevations (560 to 1,060 m) in the Blue Mountains area, and thus clearly can tolerate a correspondingly wide range in thermal conditions. Additionally, the densely-vegetated swamps provide substantial thermal variation at small spatial scales: a fully sun-exposed patch of open ground may be 20°C hotter than the substrate in a nearby shaded site (unpubl. data). Thus, female *Eulamprus* may be able to behaviourally buffer the direct thermal effects of climate change (by shuttling between sun and shade), so long as their habitat persists.

If climate change occurs as predicted, the longterm viability of the hanging swamps may be precarious. These unusual systems are formed only under specific conditions of geology and climate. Reduction in rainfall, and thus in the rates of water seepage into the swamps, could rapidly dry out large areas of existing swamps. Given the sloping topography of the area, soil moisture levels (and thus vegetation characteristics) rely upon continuous hydric input. In turn, drying-out could modify vegetation cover in the swamps (and thus thermal conditions and antipredator refuges), as well as affecting the supply of invertebrate prey. Hence, although many uncertainties remain, the greatest vulnerabilities of *E. leuraensis* to climate change likely involve indirect habitat-mediated effects, rather than direct phenotypic modifications elicited by ambient thermal regimes during the reproductive season.

Acknowledgements We thank Michael Hensen and other staff of the Blue Mountains City Council for their support and encouragement, and Maya Chevalley for assistance during fieldwork. The study was funded by the Blue Mountains City Council and by the Australian Research Council.

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