RESEARCH PAPER

The geography of snake reproductive mode: a global analysis of the evolution of snake viviparity

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ABSTRACT

Aim Although most reptiles are oviparous, viviparity is a common mode of reproduction in squamates and has evolved multiple times in different lineages. We test two prevailing hypotheses regarding the biogeography of reptile reproductive modes to evaluate the selective forces driving the evolution of viviparity in snakes. The cold climate hypothesis posits that viviparity is selected for in cold climates, whereas the climatic predictability hypothesis predicts that viviparity is advantageous in seasonal climates.

Location Global.

Methods We collated detailed distribution maps and reproductive mode data for 2663 species of the world's terrestrial alethinophidian snakes. We studied the relationship between snake reproductive mode and environmental predictors. We applied both an ecological and an evolutionary approach to study snake reproductive mode by performing the analyses at the assemblage level and species level, respectively. We analysed our data at the global and continental scales to learn whether tendencies to viviparity are similar world-wide.

Results We found strong support for the cold climate hypothesis and the assumption that viviparity is an adaptation to cold environments. There was little support for the climatic predictability hypothesis. Nonetheless, viviparous species are not restricted to cold environments.

Main conclusions We conclude that viviparity is adaptive in cold climates, but not necessarily in unpredictable/seasonal climates. Current distributions may not reflect the climate at the time and place of speciation. We suspect many viviparous snakes inhabiting warm climates are members of lineages that originated in colder regions, and their occurrence in maladaptive environments is a result of phylogenetic conservatism.

Keywords
Cold climate hypothesis, maternal manipulation hypothesis, oviparity, predictability, reproductive mode, seasonality, Serpentes, temperature, viviparity.

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INTRODUCTION

Squamates reproduce either by laying eggs (oviparity) or by giving birth to live young (viviparity). Most squamate species are oviparous (*c.* 80–85%; Sites *et al.*, 2011), and reproductive mode is generally phylogenetically constrained [e.g. all homalopsids are considered to be viviparous (Murphy, 2007) and all anoles are oviparous (Vitt & Caldwell, 2009)]. Nonethe-

less, some families (e.g. Elapidae, Natricidae and Viperidae) and genera (e.g. *Eryx*, *Liolaemus* and *Pseudechis*) contain both viviparous and oviparous species (Blackburn & Stewart, 2011). Transitions between oviparity and viviparity are even present in different populations of the same species (e.g. *Zootoca vivipara*, *Saiphos equalis* and *Helicops angulatus*; Heulin *et al.*, 1997; Smith *et al.*, 2001; Scrocchi *et al.*, 2005), although such variability is rare (Smith *et al.*, 2001).

Oviparity is traditionally considered to be the ancestral mode of squamate reproduction (Shine & Bull, 1979; Shine, 2014); viviparity is thought to have evolved independently in at least 30 lineages of snakes (Shine, 1985) and in more than 100 lineages of squamates (Shine, 1985, 2005; Blackburn, 2006; Sites *et al.*, 2011; but see Pyron & Burbrink, 2014, who suggested an early origin of viviparity). This multitude of origins and the co-existence of oviparity and viviparity within the same clade raise questions regarding the selective forces behind the transition between reproductive modes.

The prevailing hypothesis is that viviparity in squamates has evolved as an adaptation to a cold climate (Packard, 1966; Tinkle & Gibbons, 1977; Shine, 1983; see a historical review in Shine, 2014). According to this 'cold climate hypothesis' (Shine, 1983), embryos kept inside a female's body benefit from warmer temperatures compared with exposed eggs, decreasing susceptibility to mortality due to low temperatures (Shine, 2005, 2014). Furthermore, suitable nesting sites are scarce in cold climates (Neill, 1964; Shine, 1985), rendering it beneficial to keep the eggs inside the female's body. Although viviparous species are distributed world-wide, they do constitute a larger proportion of the fauna at higher latitudes and elevations than at lower ones (Greene, 1970; Tinkle & Gibbons, 1977; Shine, 1985, 2005; Blackburn & Stewart, 2011). Moreover, viviparous species tend to occur in colder climates compared with their closest oviparous relatives (Shine & Bull, 1979; Shine, 1987). In Israel, for example, the mediterranean climate inhabitant *Daboia palaestinae* is oviparous whereas its close relative, *Montivipera bornmuelleri*, found only in cold climates at high elevations on Mount Hermon, is viviparous.

However, viviparous reptiles are not restricted to cold climates. Tinkle & Gibbons (1977) demonstrated that some warm regions, such as the tropics of South America, harbour more viviparous species than some cold regions. Thus, temperature per se (or latitude and elevation) cannot solely explain the evolution of viviparity in squamates. Tinkle & Gibbons (1977) suggested that egg retention enables the female to oviposit when environmental conditions are optimal. In line with this hypothesis, viviparity is most adaptive in regions of unpredictable climates (henceforth 'the climatic predictability hypothesis'), rather than in cold climates (Shine, 2014). This hypothesis, however, has rarely been tested (Shine, 2014; but see Shine, 2002). Shine (1995, 2004) suggested that the advantage of viviparity is concealed by the female's ability to provide constant, and not necessarily warmer, temperatures to the embryo. This, in turn, influences the offspring's phenotype, and is thus named 'the maternal manipulation hypothesis' (or the 'phenotypic plasticity hypothesis'; Shine, 1995; see Qualls & Andrews, 1999; Shine, 2004; Webb

et al., 2006; Li *et al.*, 2009). This is advantageous in both cold and warm environments, but most importantly, is probably more important in unstable environments. Because the female's ability to provide constant temperature can play a major role in unstable environments, the maternal manipulation hypothesis predicts the same outcome as the climatic predictability hypothesis, with regard to climatic variability.

Both pioneering works (e.g. Mell, 1929; Weekes, 1933; Neill, 1964; Tinkle & Gibbons, 1977; Shine & Bull, 1979; Shine, 1985) and more recent studies (e.g. Shine, 1987; Lambert & Wiens, 2013; Pincheira-Donoso *et al.*, 2013; Watson *et al.*, 2014) on the evolution of viviparity are either geographically constrained, sample few species or are taxonomically restricted. Recently, Pyron & Burbrink (2014) carried out a large-scale phylogenetic, species-based study of lizards and amphisbaenians. They found that viviparous species inhabit colder regions than closely-related oviparous species, supporting the cold climate hypothesis. However, no large-scale phylogenetic study has yet been carried out for snakes (Pyron & Burbrink, 2014) and reproductive modes in snakes are generally less studied than in lizards (Blackburn & Stewart, 2011).

To evaluate the selective forces driving viviparity in snakes, we studied the relationship between snake reproductive mode and climate. Our data include nearly all 'advanced' (i.e. Alethinophidia), non-marine snake species, making this the largest study of the evolution of viviparity in snakes (and in squamates). We performed the analyses at both the assemblage level and the species level. These analyses take into account both an ecological approach (studying which regions are inhabited by viviparous species) and an evolutionary approach (studying clade-level reproductive mode differences in relation to climate).

To test the cold climate and climatic predictability hypotheses, we studied how snake reproductive mode relates to mean spring environmental temperature, elevation and both temperature and precipitation seasonality. Following the cold climate hypothesis we expect to find a higher proportion of viviparity in cold environments. Furthermore, we predict that lower environmental temperatures characterize the distribution of viviparous species. Following the climatic predictability hypothesis, we expect to find a higher proportion of viviparity in more seasonal (less predictable) environments.

METHODS

Data collection

We mapped the distribution of all non-marine snake species belonging to the infra-order Alethinophidia (Feldman, 2015) in ArcGIS 10.0 (ESRI, 2011), following the taxonomy of Uetz (2015). Maps were derived from field guides, IUCN accounts, museum datasets, primary and grey literature and the Global Assessment Of Reptile Distributions Working Group (GARD; http://www.gardinitiative.org/index.html). We restricted our study area to continents and islands larger than 50,000 km^2 (Fig. 1), to avoid potential effects of insularity on snake life history (Boback & Guyer, 2003; Novosolov *et al.*, 2013).
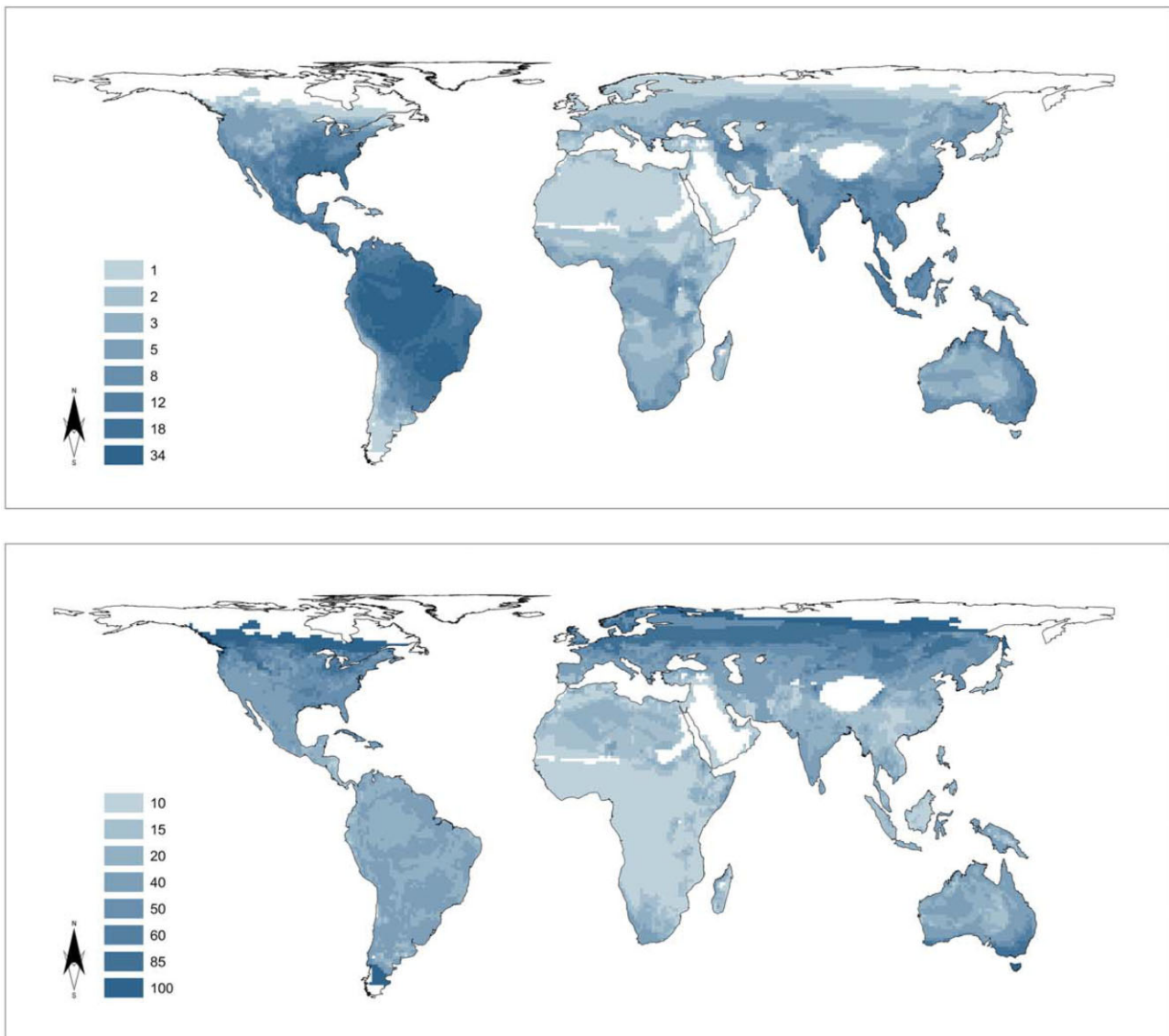
Figure 1 Top: richness of viviparous snake species in equal-area Behrmann projection grid cells (9309.5 km²) (light shading, low richness; dark shading, high richness). Bottom: the proportion of viviparous snake species in equal-area Behrmann projection grid cells (9309.5 km²) (light shading, low proportion; dark shading, high proportion). White areas in northern America and Eurasia, southern America and the Tibetan Plateau indicate grid cells with no snake species; other white areas are regions with oviparous but no viviparous species.

Scolecophidian snakes, the sister group to Alethinophidia, were excluded from the analysis because reproductive data are lacking for most species (though most are believed to be oviparous; Lillywhite, 2014). Furthermore, distribution data for scolecophidians are less complete than for alethinophidians, and in some cases are even very scarce (Feldman, 2015). Scolecophidians, however, are largely restricted to tropical and subtropical areas (Vitt & Caldwell, 2009), meaning that they have no truly cold climate representatives. Their exclusion, therefore, makes our analyses more conservative.

We scored the reproductive mode for 2663 snakes species as oviparous or viviparous (including ovoviviparous), using data from the literature (Appendix S1 in Supporting Information).

We treated ovoviviparous species as viviparous because the two modes are frequently not distinguished in the literature (Shine, 1985). More importantly, ovoviviparous females, like females of viviparous species, retain the eggs *in utero* almost until hatching and are thus effectively viviparous according to the predictions of both the cold climate hypothesis and the climatic predictability hypothesis. Our data include *c.* 98% of all non-marine alethinophidian species in mainland regions (Uetz, 2015).

Assemblage-level analyses

We used the distribution maps to create a gridded viviparous proportion map on an equal-area Behrmann projection

(9309.5 km²), by calculating total species richness and viviparous species richness for each grid cell. We excluded from the analysis all grid cells with less than 10% land area, leading to a total number of 13067 cells. We then calculated for each grid cell mean spring and early summer temperature (henceforth, 'temperature'; °C), seasonality in temperature (i.e. seasonal range in temperature; °C), seasonality in precipitation (i.e. seasonal coefficient of variation) and mean elevation (m; henceforth, 'elevation'). We used spring temperatures rather than annual temperatures because most snake species do not breed all year round, probably not even in the tropics (Shine, 2003). However, since the exact dates of the breeding period across a species' geographic range is seldom available for wide-ranging species, and data on the reproductive season are missing for many species, we considered 'spring' as the breeding period for all species. We calculated mean temperature (and seasonality) for the months of April–August in the Northern Hemisphere, and October–February in the Southern Hemisphere. We also analysed our data with mean annual values (temperatures and seasonality). Results are qualitatively the same, and we therefore report only the biologically more meaningful spring temperatures. All climatic variables were derived from WorldClim (Hijmans *et al.*, 2005) at a 0.16° × 0.16° grid cell resolution. Variables were log-transformed to meet the assumptions of normal distribution and were weakly collinear (all variance inflation factors < 4).

We analysed our data at both global and continental scales [North and Central America (henceforth, 'North America'), South America, Eurasia, Africa, and Australia], to learn whether tendencies to viviparity are similar world-wide. Since species-poor cells can bias the results, we conducted a sensitivity analysis, at the global scale, in which we excluded all cells with fewer than six species ($n = 2211$ cells). Results of this analysis were qualitatively similar to the full model (they had the same set of predictors retained and showed the same trends; see Appendix S2).

Species-level analyses

We used the distribution maps to calculate the mean value of the environmental variables across each species' range, and used those mean values as the predictors. As in the assemblage-level analysis, we defined the breeding season as the months of April–August in the Northern Hemisphere and October–February in the Southern Hemisphere. We conducted both global- and continental-scale analyses. Few species occur across North and South America (e.g. *Clelia clelia*) and, similarly, few species are distributed in both Eurasia and Africa (e.g. *Eryx jaculus*). For such cases we included the species in both continents. However, if a species is distributed mainly in one continent and only a small part of its distribution (< 20%) is in the other one, we included the species only in its prevalent continent. For example, *Atractaspis engaddensis* was included only in Eurasia because it is mainly an Asiatic species (ranging from Israel to Saudi Arabia), with a narrow distribution in the Sinai Peninsula.

Data analysis

Assemblage level

The proportion of viviparity in adjacent cells might be similar because of spatial autocorrelation (Dormann *et al.*, 2007). Hence, prior to analysis we calculated Moran's *I*, using the Moran I command in the R package 'ape' (Paradis *et al.*, 2004). Moran's *I* was significantly higher than zero ($P < 0.001$), indicating spatial autocorrelation. To control for this we used simultaneous autoregression of spatial errors (SAR; Dormann *et al.*, 2007; Bini *et al.*, 2009), using SAR model estimation in the 'spdep' package (Bivand *et al.*, 2006). Model selection was based on Akaike information criterion (AIC) scores. After finding the best model we calculated the standardized regression slope of each variable to scale predictors according to their relative importance.

Species level

We used multiple logistic regression and tested for a correlation between reproductive mode and each of the environmental predictors. For this we arbitrarily defined oviparity as ' 0' and viviparity as '1', so a negative correlation between reproductive mode and a variable indicates that the mean value across the range of a viviparous species is lower than that of an oviparous species. We selected the best model according to AIC scores. Snakes of different clades are ecologically diverse for reasons unrelated to parity mode. To compare closely related species, and because the reproductive mode in snakes is highly phylogenetically constrained, we conducted two more restricted analyses.

1. A phylogenetic analysis which included only species that are represented in the dated phylogenetic hypothesis of Pyron & Burbrink (2014; $n = 1048$). For that we used phylogenetic logistic regression (Ives & Garland, 2010), and tested the four variables simultaneously using the 'IG10' phylogenetic generalized linear model (PGLM) in the R package 'phyloglm' (Ho & Ané, 2013).

2. Logistic regression between reproductive mode and spring temperature only for species belonging to families with both modes of reproduction (Boidae, Colubridae, Dipsadidae, Elapidae, Lamprophiidae, Natricidae and Viperidae; $n = 2277$) while controlling for family.

All statistical tests were conducted using R 3.0.2. (R Development Core Team, 2013).

RESULTS

Assemblage level

We analysed 13067 grid cells containing between 1 and 124 snake species (0 to 34 viviparous species; Fig. 1). The proportion of viviparous species ranged from zero to 100% (Figs 1 & 2) and generally decreases from higher to lower latitudes in all continents. This trend is strong in the Northern Hemisphere and Australia, and less pronounced in Africa and South America
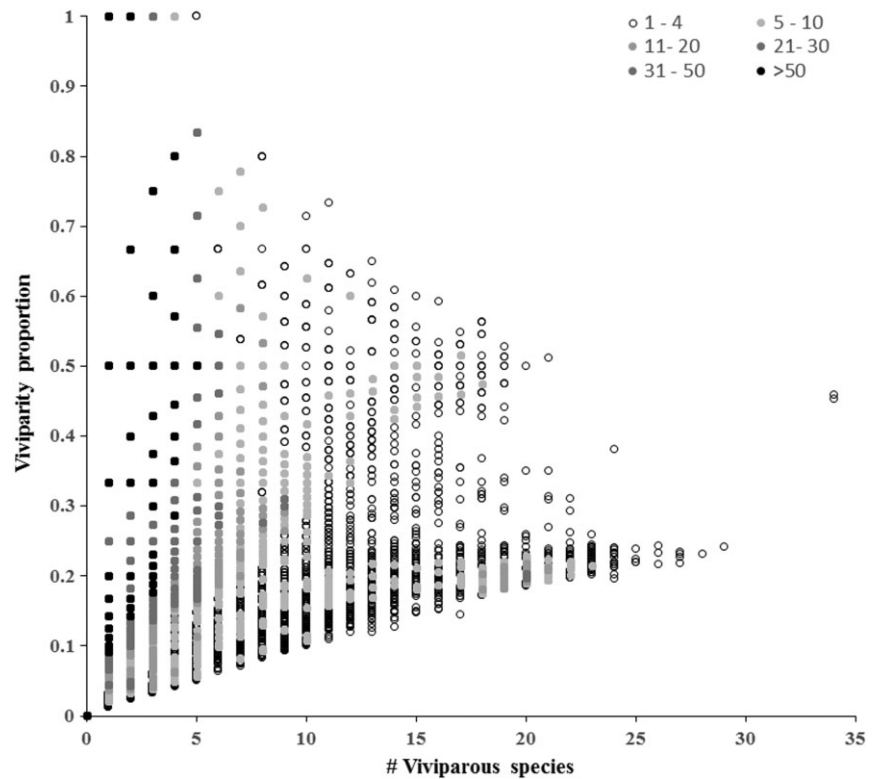
Figure 2 Relationship between the proportion of viviparity in a grid cell and the number of viviparous species in a grid cell (different shades represent different number of overlapping grid cells with the same properties, i.e. the number of species and proportion of viviparity).

Table 1 Descriptive statistics on the geography of snake viviparity.

Region	No. of cells	Temperature (°C, mean ± SE)	No. of viviparous species per grid cell (mean ± SE; range)	Proportion (%) of viviparity per grid cell (mean ± SE)	Percentage (%) of viviparity in richest cell
Africa	3347	26.3 ± 0.06	2.29 ± 0.02; 0–10	9.72 ± 0.10	13.5
Australia	894	25.8 ± 0.14	5.13 ± 0.08; 0–16	29.5 ± 0.56	59.2
Eurasia	4812	18.2 ± 0.11	3.64 ± 0.04; 0–34	38.7 ± 0.38	45.3
North America	1643	17.7 ± 0.15	6.80 ± 0.12; 0–22	51.1 ± 0.64	30.9
South America	1944	23.3 ± 0.11	14.35 ± 0.15; 0–29	22.2 ± 0.25	24.2
Global	13 067	21.7 ± 0.06	5.48 ± 0.05; 0–34	29.2 ± 0.22	45.3

The discrepancy between the global and regional number of grid cells is due to the omission of islands from the regional, but not the global, dataset.

(Fig. 1). The cells with the most viviparous species are not necessarily those with the highest proportion of viviparous species (Table 1, Figs 1 & 2). In fact, the proportion of viviparity is negatively correlated with the number of viviparous species in a grid cell (slope = − 0.0030 ± 0.0003), although this relationship only explains less than 1% of the variance of the proportion of viviparity.

The best global-scale model includes mean temperature, elevation and temperature seasonality, and explains 79.6% of the variance in the proportion of viviparity. The proportion of viviparity is negatively correlated with the three predictors, with mean temperature being the strongest predictor (Table 2). The mean temperature of cells containing ≥ 50% viviparous species ($n = 2706$) is 12.5 °C, compared with 24.1 °C in cells with < 50% viviparous species ($n = 10,361$).

The proportion of viviparity is also best explained by mean temperature (negative relationship) in four out of five conti-

nents (Table 2). Africa is the only region where the proportion of viviparity is not related to temperature. Continents differ with regard to the relationship between proportion of viviparity and seasonality, with either negative, positive or non-significant relationships (Table 2). Elevation emerged as a significant predictor only in Africa and North America (and marginally non-significant in Australia), negatively correlated to proportion of viviparity in both continents.

Species level

At the global scale, reproductive mode is negatively correlated to temperature and elevation both in the phylogenetic and non-phylogenetic models (Table 3). The relationship with temperature seasonality changes between the phylogenetic and non-phylogenetic analyses (negative and positive relationship, respectively; Table 3). Overall, viviparous species are distributed

Region	Predictor	Standardized slope	Standard error	*P*	*R*² model
Global	Temperature	−0.196	0.009	< 0.001	0.796
	Elevation	−0.070	0.006	< 0.001	
	Temperature seasonality	−0.040	0.013	< 0.001	
	Precipitation seasonality	*0.008*	*0.005*	*0.124*	
Africa	Elevation	−0.085	0.018	< 0.001	0.496
	Temperature seasonality	−0.076	0.027	0.005	
	Precipitation seasonality	−0.052	0.014	< 0.001	
	Temperature	*−0.032*	*0.022*	*0.137*	
Australia	Temperature	−0.884	0.030	< 0.001	0.833
	Temperature seasonality	−0.154	0.033	< 0.001	
	Precipitation seasonality	0.127	0.024	< 0.001	
	Elevation	*−0.029*	*0.015*	*0.058*	
Eurasia	Temperature	−0.141	0.021	< 0.001	0.847
	Temperature seasonality	−0.059	0.029	0.040	
	Precipitation seasonality	*−0.033*	*0.020*	*0.105*	
North America	Temperature	−0.589	0.028	< 0.001	0.807
	Precipitation seasonality	0.194	0.019	< 0.001	
	Temperature seasonality	0.152	0.051	0.003	
	Elevation	−0.102	0.017	< 0.001	
South America	Temperature	−0.141	0.021	< 0.001	0.554
	Temperature seasonality	−0.058	0.029	0.040	
	Precipitation seasonality	*−0.003*	*0.020*	*0.105*	

The *P*-value of all models is << 0.001. Parameter estimates are for predictors of the best model in each region. Predictors are ordered by their importance. Non-significant predictors are given in italics.

Table 3 Parameter estimates for the best logistic regression models of reproductive mode on environmental variables – species-level analyses.

Analysis	No. of species	No. viviparous	Mean temperature (°C) Viviparous	Mean temperature (°C) Oviparous	Predictor	Slope	SE	*P*
Global (phylogenetic)	1048	325	22.3	23.9	Temperature	−4.685	0.630	< 0.001
					Temperature seasonality	−0.270	0.066	< 0.001
					Elevation	−0.401	0.070	< 0.001
Global (non-phylogenetic)	2663	573	22.8	23.7	Temperature	−2.198	0.333	< 0.001
					Temperature seasonality	0.235	0.056	< 0.001
					Elevation	−0.285	0.054	< 0.001
					Precipitation seasonality	*−0.141*	*0.095*	*0.139*
Africa	491	58	22.8	24.3	Temperature	−7.646	1.584	< 0.001
					Elevation	−0.710	0.239	0.003
Australia	123	45	23.4	26.8	Temperature	−6.725	1.488	< 0.001
Eurasia	635	149	22.5	24.3	Temperature	−2.110	0.468	< 0.001
					Elevation	*−0.153*	*0.084*	*0.070*
North America	593	158	22.6	24.1	Temperature	−3.549	0.886	< 0.001
					Temperature seasonality	0.454	0.117	< 0.001
					Elevation	−0.244	0.109	0.025
South America	638	124	21.8	21.6	Temperature seasonality	0.367	0.152	0.015
					Elevation	*−0.173*	*0.108*	*0.110*

Continental analyses are all non-phylogenetic. Non-significant predictors are given in italics.

in colder environments than oviparous species (22.3 °C compared with 23.9 °C for the species included in the phylogenetic analysis, and 22.8 °C compared with 23.7 °C for all species). We also found a negative correlation between reproductive mode and temperature in the bi-modal families analysis (slope = −2.230 ± 0.377, *P* < 0.001).

Reproductive mode is negatively correlated to temperature in all continents, with the exception of South America where no

relationship is found. The probability of being viviparous is positively correlated with temperature seasonality only in North and South America. It is also negatively correlated with elevation in Africa and North America (Table 3). Reproductive mode is unrelated to precipitation seasonality at both the continental and the global scale.

DISCUSSION

We found a greater proportion of viviparous snakes in cold areas at the global and continental scale (except in Africa; Table 2, Fig. 1). Similar results were obtained in previous studies (Tinkle & Gibbons, 1977; Blackburn, 1982; Shine, 1983, 2014), indicating that viviparity is selected for in cold areas. Indeed, only few snake species inhabit very high latitudes, and they are all viviparous (e.g. *Thamnnophis sirtalis* in North America, *Vipera berus* in northern Eurasia and *Bothrops ammodytoides* in South America). Similarly, the snake species living at the highest elevation in the world is viviparous: the viper *Gloydius himalayanus* reaches elevations of 4876 m in the Himalayas (Schleich & Kästle, 2002). Although cold is a subjective term (Shine, 1985), these observations indicate that viviparous species tend to be predominant in the snake fauna in cold areas compared with warm areas, regardless of the regional climate. Interestingly, the amount of variance explained by the model was lower in Africa and South America (49.6 and 55.4, respectively, compared to > 80.0 in other continents and 79.6 globally), and Africa is the only region where the proportion of viviparity is not related to temperature. This perhaps indicates that the influence of temperature (and other climatic variables) on reproductive mode is more significant in cold areas than in warm areas, and further supports the cold climate hypothesis.

We also found support for the cold climate hypothesis at the species level. Both globally and at the continental scale (with the exception of South America; see below), we found that viviparous species live, on average, at lower mean temperatures across their distribution range compared with oviparous species (Table 3). Recently Watson *et al.* (2014) found that elevation was the single best predictor for lizard viviparity in North America. Interestingly, when included in a multiple predictor analysis we found that elevation was only significant in some models. Furthermore, contrary to expectations, it is negatively related to the proportion of viviparity or to reproductive mode (Tables 2 & 3). Thus we infer that studies that found a positive relationship between viviparity and elevation as a single predictor probably actually revealed the strong signal of temperature, but elevation per se (via its effects on reproductive physiology, for example oxygen pressure for the embryos) does not select for viviparity.

We found weak support for the climatic predictability hypothesis, and mainly at the species level. Globally (but only in the non-phylogenetic analysis) and in North and South America, viviparous species live, on average, in more temperature-seasonal environments than oviparous species. However, we found conflicting results between the species-level non-phylogenetic (which supported the hypothesis) and phylogenetic analysis (which showed the opposite pattern;

Table 3). Precipitation seasonality is seldom related to parity mode for either assemblage-level or species-level analyses (Tables 2 & 3). Thus, we conclude that overall our results do not support the climatic stability hypothesis.

Although our results strongly support the cold climate hypothesis, we should note that our analyses (and those of similar studies) are based on current species distributions and current climatic conditions. Thus, while we strongly demonstrate that viviparity is the preferred reproductive mode in cold areas, any conclusion about the selective forces for viviparity should be interpreted with caution (Blackburn, 1999a) because other factors can sustain viviparous species. Some interesting inter-regional variation in the relationship between parity mode and climate is potentially illuminating. South America, for example, has the most species-rich cells of viviparous snakes (with the exception of two cells in the Western Ghats of southern India), but the proportion of viviparity in these cells is relatively low (Table 1, Fig. 1). This theoretically supports the climatic predictability hypothesis (Tinkle & Gibbons, 1977). In South America, however, the Andes provide a ridge of cold habitats adjacent to very humid, warm lowlands. This may have helped dispersal of viviparous, cold-adapted lineages into many different warm portions of the continent, including Amazonia. One such lineage is the viviparous genus *Bothrops*, for which the tropical Andes represent a diversity hotspot (Fenker *et al.*, 2014). *Bothrops* is a member of the South American pitviper clade (Viperidae: Crotalinae) and all species are viviparous, with the exception of the oviparous genus *Lachesis* in Central and South America (Fenwick *et al.*, 2012), which presumably reversed to oviparity (King & Lee, 2015). Pitvipers are common in South America, but their origin is believed to be in Asia, with a single dispersal event into North America, and a later dispersal event to South America with radiation therein (Wüster *et al.*, 2002, 2008; Castoe *et al.*, 2009). Therefore, pitvipers have retained their ancestral, viviparous, reproductive mode regardless of local climates. Similarly, most species of Tachymenini (Dipsadidae) are viviparous (Appendix S1), and their range is concentrated in austral portions of South America. They probably originated in austral, colder areas and dispersed into warmer areas (Zaher *et al.*, 2009). Such a pattern (dispersal to warm regions after the development of viviparity) is seen also in three *Sceloporus* lizard species that are restricted to tropical, low-elevation environments of Central America (Lambert & Wiens, 2013). These examples suggest that our ability to infer the climate (and even geography) during speciation events from current distribution and climatic data alone is limited. Correspondingly the evolution of viviparity in many lineages probably occurred at different thermal and seasonal regimes than those associated with them currently. Nevertheless, we still obtained strong signals supporting the cold climate hypothesis in the phylogenetic analysis – and this is amply shown today in the distribution of viviparous species within grid cells.

If species dispersal masks possible drivers for the evolution of viviparity, then perhaps Australia is the best region to examine these patterns and drivers. Australia is the most isolated continent we examined, and its modern snake fauna probably evolved

after the separation from India *c.* 100 Ma (Johnson, 2009). Most speciation events leading to extant snake species occurred from the Eocene to the Miocene (Pyron & Burbrink, 2014). Australia's snakes could not have migrated to other regions if conditions within the continent had not matched their climatic adaptations, and may therefore offer the best test-case of the association between current climate and reproductive modes. The proportion of viviparous species in Australia is negatively correlated with temperature but, most importantly, temperature differences between oviparous species and viviparous species across their range is the largest (3.4 °C) of all the examined regions (Table 3) and environmental temperature is the only predictor for snake viviparity at a species-level analysis. This further strengthens the cold climate hypothesis.

Viviparity is beneficial in cold areas, but it is also energetically demanding and affects the female's ability to feed, move and escape from predators (Neill, 1964; Blackburn, 1999a; Gregory, 2009). While viviparity seems to be obligatory in cold areas, it can be potentially maladaptive in warm environments. Therefore, an interesting question is: why are there so many viviparous species inhabiting warm areas? One explanation, which we have already discussed, is phylogenetic constraint. While the transition from viviparity to oviparity is probably possible (Lee & Shine, 1998; Surget-Groba *et al.*, 2006; Lynch & Wagner, 2010; Fenwick *et al.*, 2012; Pyron & Burbrink, 2014), the process is generally thought to be less common, and more difficult to achieve, than a transition from oviparity to viviparity (Blackburn, 1999b; Shine & Lee, 1999; Lambert & Wiens, 2013; Pincheira-Donoso *et al.*, 2013; King & Lee, 2015). Thus, cold climate viviparous snakes that colonized warm regions may simply be 'stuck' in their ancestral reproductive mode. We suggest that this is a possibility in areas with abundant resources, such as the tropics of South America. In warm, less productive areas there may be a stronger selective pressure to re-evolve oviparity, as suggested by Pyron & Burbrink (2014). Alternatively, viviparous species may have gone extinct from such regions. Thus the proportion of viviparity to oviparity in snakes (and squamates in general) probably reflects a trade-off between the costs and benefits of viviparity.

CONCLUSIONS

Our study generally supports the cold climate hypothesis, which proposes that viviparity has evolved *in situ* in cold climates. On the other hand, support for the climate predictability hypothesis is weaker, with some of its assumptions contradicted by our results (e.g. more viviparous species in less seasonal environments).

It is important to note that inferring the climate in regions where speciation events occurred from modern-day distribution and climatic data has its limitations. This probably means that the results of the assemblage-level analyses, providing insights into the current ecological preferences of snakes, may be more reliable indicators of selection than the results of the phylogenetic analysis at the species level. The relatively large number, but small proportion, of viviparous species in South America is an example of substantial spatial non-stationarity in the distribution of different reproductive modes in snakes. Moreover, some cold areas have many oviparous species. The edges of the Tibetan Plateau are an example of a cold region with a large proportion of oviparous species (Fig. 1). In fact, some oviparous species are found in the coldest areas of the world (e.g. *Elaphe schrenckii* in northern China and Russia and *Natrix natrix* in Scandinavia and northern Russia). Thus, even the strong broad-scale pattern we identified has interesting regional exceptions, which require further research for a detailed mechanistic understanding.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's web-site.

Appendix S1 List of the 2663 snake species included in this study, their reproductive mode, climate and elevation across their range (as an excel file).

Appendix S2 Parameter estimates for the global relationship between the proportion of viviparity and environmental variables, with the exclusion of cells with fewer than six species.

BIOSKETCH

Anat Feldman is a post-doctoral fellow interested in the macroecology and biogeography of snakes.

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