

RESEARCH ARTICLE

Viviparity is associated with larger female size and higher sexual size dimorphism in a reproductively bimodal lizard

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Abstract

1. Squamate reptiles are central for studying phenotypic correlates of evolutionary transitions from oviparity to viviparity because these transitions are numerous, with many of them being recent. Several models of life-history theory predict that viviparity is associated with increased female size, and thus more female-biased sexual size dimorphism (SSD). Yet, the corresponding empirical evidence is overall weak and inconsistent. The lizard *Zootoca vivipara*, which occupies a major part of Northern Eurasia and includes four viviparous and two non-sister oviparous lineages, represents an excellent model for testing these predictions.
2. We analysed how sex-specific body size and SSD is associated with parity mode, using body length data for nearly 14,000 adult individuals from 97 geographically distinct populations, which cover almost the entire species' range and represent all six lineages. Our analyses controlled for lineage identity, climatic seasonality (the strongest predictor of geographic body size variation in previous studies of this species) and several aspects of data heterogeneity.
3. Parity mode, lineage and seasonality are significantly associated with female size and SSD; the first two predictors accounted for 14%–26% of the total variation each, while seasonality explained 5%–7%. Viviparous populations exhibited a larger female size than oviparous populations, with no concomitant differences in male size. The variation of male size was overall low and poorly explained by our predictors.

†Passed away on 8 October 2021.

4. Albeit fully expected from theory, the strong female bias of the body size differences between oviparous and viviparous populations found in *Z. vivipara* is not evident from available data on three other lizard systems of closely related lineages differing in parity mode. We confront this pattern with the data on female reproductive traits in the considered systems and the frequencies of evolutionary changes of parity mode in the corresponding lizard families and speculate why the life-history correlates of live-bearing in *Z. vivipara* are distinct.
5. Comparing conspecific populations, our study provides the most direct evidence for the predicted effect of parity mode on adult body size but also demonstrates that the revealed pattern may not be general. This might explain why across squamates, viviparity is only weakly associated with larger size.

KEYWORDSbody size, egg-laying, life history, live-bearing, reproductive mode, *Zootoca vivipara***1 | INTRODUCTION**

Body size, a fundamental phenotypic characteristic of the organism, continues to be an important research target in ecology and evolution (Blanckenhorn, 2000; Feldman et al., 2016; Meiri, 2008). This is because body size is strongly correlated with many physiological, life-history and behavioural characteristics which are tightly linked with both reproductive success and survival (Roff, 2002; Stearns, 1992). Due to inherent differences in reproductive (and often ecological) roles, males and females in the same population face both common and sex-specific selection pressures and constraints. As a result, in many species, males and females differ in body size. This sexual size dimorphism (SSD) exhibits pronounced variation at all taxonomical levels, and this variation is a prominent issue of evolutionary and ecological studies (reviewed by Fairbairn et al., 2007; see also Chelini et al., 2021; Horne et al., 2020; Roitberg et al., 2015, 2020).

Viviparity, the bearing of live young, is a striking example of a major evolutionary innovation that appears to be female-specific. It markedly increases overall costs associated with reproduction for females, with no obvious changes for males. A large number of independent origins of viviparity from oviparity (egg-laying) in diverse taxa (≥ 150 times in vertebrates and many times in invertebrates—Blackburn, 2015; Ostrovsky et al., 2016) favours exploration of putative causes and consequences of this evolutionary transition using comparative analyses.

Squamates (lizards, snakes and amphisbaenians) are of particular importance for such studies. Viviparity has evolved in this group ≥ 115 times, including numerous recent origins, so that 35 polymorphic genera and four reproductively bimodal species are known (Blackburn, 2015; Whittington et al., 2022). Oviparous reptiles lay macrolecithal (large, with many nutrients) eggs, and the vast majority of viviparous squamates possess primarily lecithotrophic fetal nutrition (Blackburn, 2015, 2018; Shine, 1985). These features, along with the absence of a larval stage, make

reproductive life histories of oviparous and viviparous squamates effectively comparable. In contrast, life-history comparisons between oviparous and viviparous taxa in fishes or amphibians are often confounded by varying degrees of matrotrophy, superfetation, patterns of larval development, etc. (Bassar et al., 2014; Bisazza, 1993; Blackburn, 2015, 2018; Kupfer et al., 2016; Velo-Antón et al., 2015; Wourms & Lombardi, 1992; see also Meiri et al., 2020). Therefore, ecological and phenotypic correlates of viviparity have been predominantly explored in snake and/or lizard models.

Life-history theory (Roff, 2002; Stearns, 1992) predicts that the transition from egg-laying to live-bearing is associated with evolutionary shifts in multiple life-history traits, including adult body size (Goodwin et al., 2002; Shine, 1985).

Several mutually non-exclusive hypotheses predict larger female size and more female-biased SSD in viviparous vs. oviparous organisms. First, due to longer gestation time and higher costs of pregnancy (see below), viviparity reduces reproductive frequency (Meiri et al., 2021). This should strengthen selection for per clutch fecundity, and thus for larger females (extension of Darwin's *fecundity-advantage hypothesis*—reviewed by Cox et al., 2003; Roitberg et al., 2015). Second, since the viviparous female carries her reproductive burden longer than the oviparous female, the survival and foraging costs due to impaired mobility (Bauwens & Thoen, 1981; Goodwin et al., 2002; Miles et al., 2000; Seigel et al., 1987; Shine, 1980; Sinervo et al., 1991; but see Cooper Jr. et al., 1990; Qualls & Shine, 1998a) are likely higher in live-bearers vs. egg-layers; this may also select for larger females, which are more efficient carriers and foragers (e.g. Angilletta et al., 2006). Third, viviparity may increase *physiological costs of pregnancy*, specifically metabolic expenditures (Bleu et al., 2012; Foucart et al., 2014; Guillette Jr, 1982; but see Van Dyke & Beaupre, 2011). These costs include a marked fecundity-independent component (Bull & Shine, 1979; Foucart et al., 2014), which may confer an additional advantage to larger, and thus more fecund, females

in terms of total energetic expenditures per unit offspring (cf. Madsen & Shine, 1994).

Although larger female size and more female-biased SSD in viviparous vs. oviparous organisms are predicted by several distinct mechanisms, the relevant empirical evidence, mostly coming from phylogenetic comparative analyses using multiple predictors, is overall modest. Fitch (1978, 1981) reported this pattern for the lizard genus *Sceloporus* and for squamates in general, but his pioneer research did not control for phylogeny. In later broad-scale studies on snakes (374 species, Shine, 1994) and lizards (302 species, Cox et al., 2003; 2295 species, Liang et al., 2022), where this control was applied, the expected effect of reproductive mode (=parity mode) was found, but it explained a relatively small part of the total variation in SSD. Recent studies on two speciose genera of iguanian lizards including both egg-laying and live-bearing species found no effect of parity mode on SSD (Jiménez-Arcos et al., 2017 on *Sceloporus*; Cabrera et al., 2013 and López Juri et al., 2018 on *Liolaemus*).

Horne et al. (2020) analysed SSD variation across 600 fish species; their data exhibit no SSD differences between oviparous and viviparous species, if oviparous species with brood care are excluded. Goodwin et al. (2002) made paired comparisons of viviparous and related oviparous clades and found the predicted effect of parity mode on adult size in elasmobranchs but not in teleosts. Phylogenetic comparative analyses by Meiri (2008) and Zimin et al. (2022), including almost 5000 species of lizards and 9000 species of squamates, respectively, found only a weak tendency to larger size in viviparous species. However, the three latter studies used maximum length as their size metric and did not differentiate between the sexes, preventing any direct conclusions on SSD differences between oviparous and viviparous taxa. Moreover, the metric (absolute) maximum size seems suboptimal for testing the parity mode effect, as in some fish and most lizard species the larger sex is males. Focusing on SSD only can also be insufficient, since more female-biased SSD in viviparous vs. oviparous forms can arise not only via increasing female size—as expected for the parity mode effect—but also via decreasing male size (as predicted for harder climates by the extended 'small male advantage hypothesis'—Chelini et al., 2021; Roitberg et al., 2020). Both SSD and sex-specific body size should be examined to detect which sex is the main driver of the observed SSD variation.

Almost all previous studies dealt with interspecific variation. However, the effect of parity mode can be more directly tested within species, where oviparous and viviparous counterparts are most comparable in terms of phenotypic architecture and phylogenetic history (Horreo et al., 2021; Qualls & Shine, 1998b; Recknagel & Elmer, 2019; Roitberg et al., 2020; Shine, 1985; Smith et al., 2001; Stewart, 2013; Whittington et al., 2022). Reproductively bimodal species with distinct viviparous and oviparous lineages (a few such species are known for vertebrates, and all are squamates) offer such ideal study systems (Whittington et al., 2022 and references therein). Generally, oviparous and viviparous conspecifics occur allopatrically, the viviparous populations tending to live in cooler climates with a shorter activity

season than the oviparous populations (Qualls & Shine, 1998b; see also Cornetti, Ficetola, et al., 2015; Horreo et al., 2021; Smith et al., 2001; Smith & Shine, 1997). The effect of parity mode should therefore be examined jointly with the effects of lineage and climate. While past research on the relationship between life-history traits and parity mode has often accounted for phylogeny, the climatic effects were rarely controlled for quantitatively (but see Horváthová et al., 2013; Meiri et al., 2020; Qualls, 1997; Roitberg et al., 2013, 2020). The latter control is important, as climate may strongly affect the SSD variation in squamates both within (Chelini et al., 2021; Roitberg, 2007; Roitberg et al., 2020) and among (Tarr et al., 2019) species.

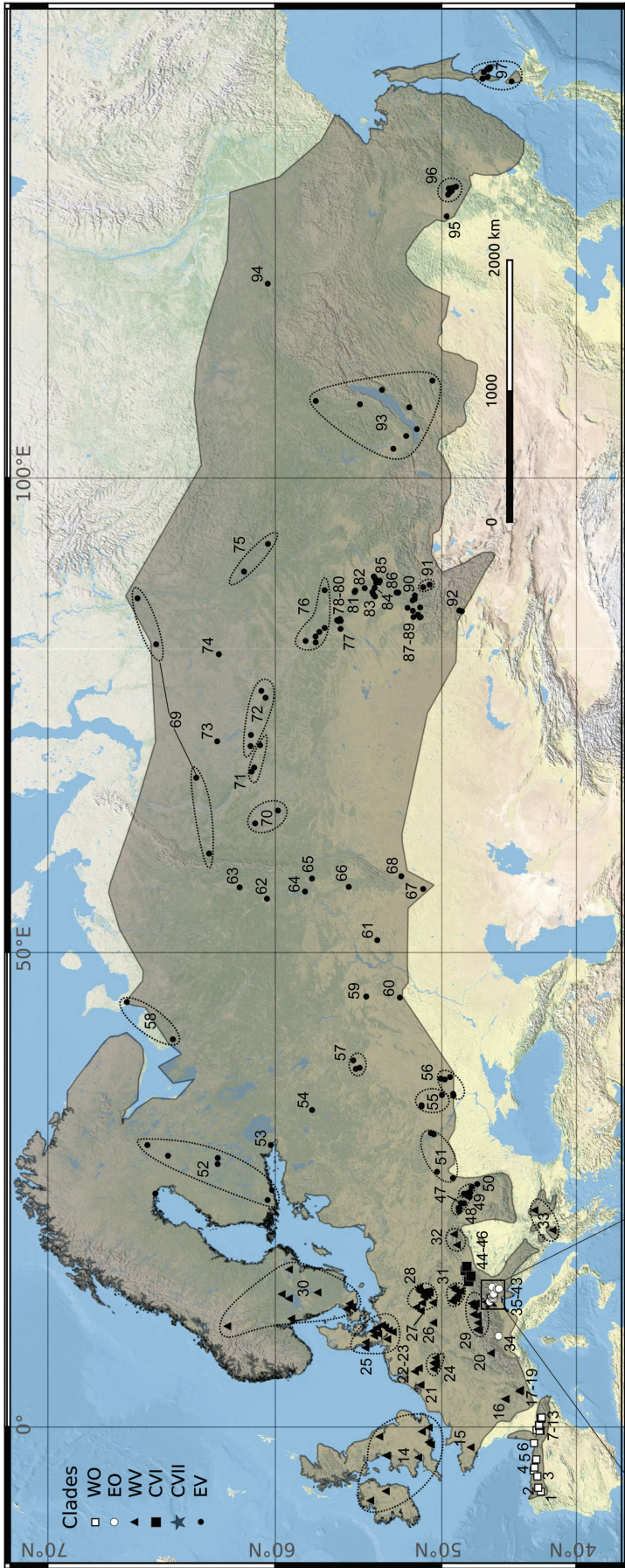
The lacertid lizard *Zootoca vivipara* is an excellent model for such studies. It occupies a major part of temperate Eurasia and includes four viviparous and two oviparous lineages (clades) (Figure 1). *Z. vivipara* is the most extensively explored reproductively bimodal vertebrate (Whittington et al., 2022), one of the best-studied European reptiles (Bauwens, 1999; Thiesmeier, 2013) and an important model for several topics in evolutionary ecology (e.g. see Roitberg et al., 2020; Thiesmeier, 2013 for references). For this species, there is a range-wide phylogeographic analysis (Surget-Groba et al., 2006, updated for particular regions by Horreo et al., 2018; Recknagel et al., 2018; Figure 1) and extensive data on body size and other life-history traits for multiple populations (Roitberg et al., 2020 and references therein).







Roitberg et al. (2020) studied intraspecific body size variation in *Z. vivipara*, but their study included only one oviparous and two sister viviparous clades, so the effects of parity mode and lineage identity remained confounded. Furthermore, the number and diversity of the studied oviparous populations were low in the previous analysis. The present study uses qualitatively enriched data that provide a rigorous test of the effect of parity mode on sex-specific body size and SSD in this species. It includes all six clades presently known for the species, neither oviparous, nor viviparous ones being a monophyletic group (Figure 1); furthermore, for five clades the study populations exhibit a wide climatic diversity. These conditions, together with the conspecificity of the studied oviparous and viviparous populations, allow us to examine life-history correlates of viviparity under more powerful control of confounding factors than in previous studies on squamates and vertebrates in general. We show that even when other factors are controlled for, viviparity is still associated with larger female size, with no corresponding shift in male size. We explore the generality of this pattern analysing published body size data for other reproductively bimodal lizard species.

2 | MATERIALS AND METHODS

2.1 | Study species

Zootoca vivipara is a small (adult snout–vent length [SVL] 40–80 mm), ground-dwelling, insectivorous, heliothermic lizard. It prefers humid



-  **WV** (Western Viviparous, samples 14–33)
-  **EV** (Eastern Viviparous, samples 47–97)
-  **WO** (Western Oviparous, samples 1–13)
-  **CVI** (Central Viviparous I, samples 44–46)
-  **CVII** (Central Viviparous II, samples 41–43)
-  **EO** (Eastern Oviparous, samples 34–40)

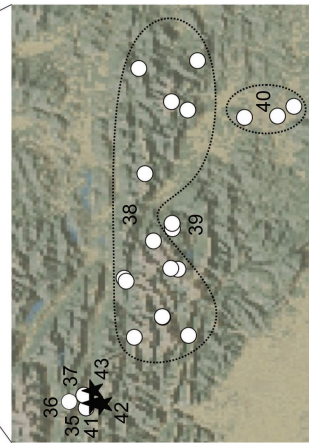


FIGURE 1 Geographic range of *Zootoca vivipara*, phylogenetic relationships of different clades (after Surget-Groba et al., 2006, with modifications from Recknagel et al., 2018) and our study sites. Details for study samples (1–97) are given in Table S1.

habitats, mostly in the forest vegetation zone (Thiesmeier, 2013). Phylogeographic studies based on mitochondrial DNA and genome-wide SNP data support six well-differentiated clades (Cornetti et al., 2014; Horreo et al., 2018; Recknagel et al., 2018; Surget-Groba et al., 2006). One clade (Western Oviparous, WO: northern Spain, south-western France) has an allopatric distribution relative to the rest of the species (Figure 1) and shows no signal of introgression with other clades (Recknagel et al., 2018). The remaining clades are: Eastern Oviparous (EO: northern and north-eastern Italy, southern Austria, Slovenia and north-western Croatia), Western Viviparous (WV: France to Eastern Europe), Eastern Viviparous (EV: Eastern Europe to Far East), Central Viviparous I (CV I: eastern Austria and most western Hungary) and Central Viviparous II (CV II: southern Austria and a few isolated locations in central Hungary) (Heulin et al., 2011; Horreo et al., 2018; Surget-Groba et al., 2006; see also Figure 1). These all come into contact with at least one other clade. However, only in the immediate contact zone between clades a low (if any) level of introgression may occur (Horreo et al., 2019). Introgression is lowest between sympatric oviparous and viviparous clades, and to date, only a single contact zone is known where hybridization in areas of direct contact does occur at a very low frequency (Lindtke et al., 2010; Recknagel et al., 2021; Recknagel & Elmer, 2019). Despite considerable research efforts, no clear signals of introgression have been found in other regions of overlapping oviparous and viviparous lineages (Cornetti, Belluardo, et al., 2015; Cornetti, Ficetola, et al., 2015; Horreo et al., 2019). Thus, while in immediate contact zones gene flow is possible, the six clades show clear and distinct evolutionary histories, with relatively old divergence times (Horreo et al., 2018; Surget-Groba et al., 2001).

2.2 | Body size data

We used SVL as a proxy for overall structural size (see Roitberg et al., 2011 for justifications). We summarized original and published SVL data for 22,059 common lizards from ca. 320 localities; these cover a major part of the species range (Figure 1; Table S1).

The original data come from museum samples or from previous studies performed for other purposes (e.g. Arribas, 2009; Bauwens & Verheyen, 1987; Recknagel & Elmer, 2019); therefore, no ethics approval was needed. Additional data were extracted from published histograms or individual values; in a few cases, we also used summary statistics for sex-specific adult SVL. In total, 5720 males and 7720 females were considered as adults and constituted our study populations (1–97; median sample sizes per population were 26 for males and 28 for females; Table S1). Further 881 adults, which could not be assigned to the above samples, were pooled in 'mixed samples' (101–107, Table S1). These mixed samples were only considered for estimating the upper range of body size variation in individual clades and in the whole species.

All study samples could be reliably assigned to a particular clade (Figure 1). Most samples are located within the known ranges of three widespread clades (WO, WV and EV) with parapatric or

allopatric distribution (Surget-Groba et al., 2006). The samples from the areas where two or more clades potentially occur were collected from the sites where the clade identity was determined by genetic analyses (Cornetti, Belluardo, et al., 2015; Giovine et al., 2016; Horreo et al., 2018, 2021; Recknagel et al., 2018; Surget-Groba et al., 2006; H. Recknagel & K. Elmer, unpublished data; W. Mayer, unpublished data). Samples from the only studied locality where two clades occur sympatrically (Straniger Alm in Southern Austria: populations 35 and 41, Figure 1; see Lindtke et al., 2010 and Recknagel & Elmer, 2019 for details) include genetically and/or reproductively studied individuals, as well as individuals whose clade identity could be reliably inferred from the spatial distribution of the two clades in this locality (Recknagel & Elmer, 2019: Figure 1).

In addition to the data on *Z. vivipara*, we analysed published data on sex-specific adult SVL for two other reproductively bimodal species (Australian skinks *Lerista bougainvillii* and *Saiphos equalis*) and a pair of closely related iguanian species, oviparous *Sceloporus aeneus* and viviparous *S. bicanthalis*; altogether, over 700 individuals from 13 oviparous and 6 viviparous populations (see Table S5 for data and references). These three systems are comparable to *Zootoca* in terms of overall phenotypic similarity and recency of divergence between oviparous and viviparous populations (Whittington et al., 2022; Zheng & Wiens, 2016 and references therein).

2.3 | Data analysis

When the geometric mean of male and female sample sizes exceeded 6.5 while the sample size of either sex exceeded 2, we used strictly local samples, both for original and published data. When local sample sizes were smaller, we pooled them into compound samples for larger geographic areas (Figure 1) and used in our analyses weighted means for the study traits and non-weighted means for climatic variables. By pooling samples, we accounted for (1) geographic distances, especially relative to the adjacent study samples; (2) homogeneity in terms of altitude, plant community zone and climate; (3) lack of pronounced differences between samples for the studied traits (Roitberg et al., 2013). Considering obvious differences in criteria for separating adults from non-adults between primary researchers (see below), we applied single inclusion criteria across samples: body length equal to or exceeding 45 mm for males and 48 mm for females (Table S1). These thresholds are close to typical minimum SVL of mature common lizards reported for most viviparous and some oviparous populations studied (see Roitberg et al., 2020 for references). Unless otherwise stated, our data points were sex-specific ln-transformed mean values for SVL in individual study samples. SSD was quantified with the index: $SDI = (\text{size of larger sex} / \text{size of smaller sex}) - 1$, conventionally expressed as positive if females are larger and negative if males are larger (Lovich & Gibbons, 1992). This index shows several favourable properties (Lovich & Gibbons, 1992; Smith, 1999) and is widely used in studies on sexual dimorphism (Fairbairn et al., 2007).

TABLE 1 Main models for geographic variation of sexual size dimorphism (SSD) and sex-specific body length in *Zootoca vivipara*.

	df1	df2	MS	F	p	Partial eta ² × 100	Adj. R ² (%)
Model: ln(male SVL) BY Repro Clade(Repro) WITH T1							3.6
Corrected model	6	89	0.002	1.59	0.160	97	
Intercept	1	89	545.759	4.71 × 10 ⁵	0.000	100.0	
Parity	1	89	5.54 × 10 ⁻⁶	0.01	0.945	0.0	
Clade(Parity)	4	89	0.002	1.41	0.238	6.0	
T1	1	89	0.000	0.11	0.740	0.1	
Model: ln(female SVL) BY Repro Clade(Repro) WITH T1							45.8
Corrected model	6	89	0.025	14.39	0.000	49.2	
Intercept	1	89	577.39	3.30 × 10 ⁵	0.000	100.0	
Parity	1	89	0.025	14.27	0.000	13.8	
Clade(Parity)	4	89	0.008	4.41	0.003	16.5	
T1	1	89	0.008	4.40	0.039	4.7	
Model: SSD BY Repro Clade(Repro) WITH T1							54.8
Corrected model	6	89	0.021	20.23	0.000	57.7	
Intercept	1	89	0.509	486.51	0.000	84.5	
Parity	1	89	0.033	31.46	0.000	26.1	
Clade(Parity)	4	89	0.006	5.52	0.001	19.9	
T1	1	89	0.007	6.97	0.010	7.3	

Note: See text for details.

Our main statistical tool was *general linear models* (GLMs) with Male size, Female size or SSD as the response variable; Parity mode (=Parity) and Clade (nested within Parity mode) as categorical predictors; and mean winter temperature (T1, Worldclim code BIO11) as a continuous predictor. T1 reflects variation in seasonality (Roitberg et al., 2020), which is a major predictor of body size variation in common lizards (Horváthová et al., 2013; Roitberg et al., 2013, 2020) and other perennial ectotherms living in temperate climates (Adolph & Porter, 1996; Hjernquist et al., 2012). Simpler models using the same response variables and Parity/Clade and T1 as predictors were employed in more special comparisons between individual clades differing in parity mode. One model compared sister clades WO and CVI (Figure 1); another model compared the clades EO and CVII sharing plesiomorphic states of karyotype and sex-determination system, which are absent in the other four clades (see Recknagel et al., 2018 for details and references).

Another group of GLMs jointly included population means for both males and females. In these 'both-sex models', the response variable was sex-specific SVL, and the predictors were Sex, Parity mode, Clade(Parity mode), T1, as well as first-order interactions of Sex with the other explanatory variables.

Simpler models of this kind (Size ~ Sex + Parity + Sex × Parity) were also used in our analyses of published body length data on other reproductively bimodal species. As the latter data sets (Table S2) include much smaller numbers of observation units (populations) than our study (Table S1), effect size (here the *partial eta squared*, i.e. the ratio of the variance explained by a given variable to the total variance remaining after accounting for variance explained

by other variables in the model; Cohen, 1973) should be more relevant for comparing the Sex × Parity interaction across study systems than statistical significance. The ratio of the partial Eta² of the Sex × Parity interaction to the partial Eta² of the main effect of Parity, henceforth referred to as *PER*, was used as a measure of sex bias of association of adult body length with viviparity. *PER* is much less sensitive to the model structure (e.g. presence/absence of additional predictors) than the absolute value of partial Eta² for the Sex × Parity interaction.

To test whether the results of our main GLMs (Table 1) are biased by spatial autocorrelation, for model residuals, we computed spline correlograms based on Moran's I statistic; for this, we used the 'ncf' package (Bjornstad, 2013) in R (R Core Team, 2017). No significant autocorrelation was detected (Figure S1), suggesting that spatial autocorrelation did not bias our models (Dormann et al., 2007).

The extraction and processing of climate data were performed as described in Appendix 1 to Roitberg et al. (2020), but for this study, we used the more recent Worldclim data version (v2.1) that averages yearly values over 1970–2000, rather than 1950–1990 (v1.4).

Virtually all study samples could be reliably assigned to a particular clade (Figure 1), as they either located within the known ranges of a particular clade (WO, WV and EV), or they were collected at sites where the clade identity was determined by genetic analyses (Cornetti, Ficotola, et al., 2015; Giovine et al., 2016; Horreo et al., 2018; Recknagel et al., 2018; Surget-Groba et al., 2006; H. Recknagel and K. R. Elmer, unpublished data; W. Mayer, unpublished data). As the six major clades have been thoroughly identified in *Zootoca vivipara* (Horreo et al., 2018;

Recknagel et al., 2018; Surget-Groba et al., 2006) and can be inferred with high confidence in our study populations (see above), while finer-level phylogenetic resolution is not available for most populations, we used clade identity to control for ancestry, following Díaz et al. (2012), Roitberg et al. (2013, 2015, 2020) and Ficetola et al. (2016).

2.4 | Methodological caveats

In species with continuing growth after maturity, numerous factors unrelated to true population differentiation, such as local and temporal fluctuations in the abiotic and/or biotic environment, can affect body size distribution in a particular study sample (see Roitberg et al., 2020 for details and references). Further biases can arise from compiling data collected by several independent researchers. They may differ in measuring routine, type of material (living vs. freshly euthanized vs. preserved specimens) and in their criteria of separating adults from immature animals, that is inclusion criteria (these can be based on body size and/or colour pattern vs. the state of gonads—e.g. Dunham et al., 1988). The biases from the first two factors are expected to be within a few per cents (Fitch, 1978; see Roitberg et al., 2020 for further references), and this is much lower than the observed variation within and among our study samples. Indeed, the type of material was never significant when included in our main models as an additional predictor (see Results). We also examined potential bias from temporal trends in adult body size (e.g. Chamailié-Jammes et al., 2006; Green & Middleton, 2013) by adding the factor Time (1950–1990 vs. 1991–2000 vs. 2001–2022); this addition did not improve our main models (see Results).

3 | RESULTS

Geographic variation in male SVL was weak (range of sample means 9 mm, min-max 48–57 mm; Table S1; Figure 2a) and poorly explained with our predictors. The adjusted R^2 amounts to 4% only (Table 1).

Compared with males, body size variation in females is markedly higher (range of sample means is circa 20 mm, min-max 51–70 mm, Table S1; Figure 2b), with a much larger part of this variation being explained by our predictors (46%, Table 1). The effects of Parity mode and Clade are of similar size (14% and 17%) and are both highly significant (Table 1).

SSD was consistently female-biased: SSD index varied from 0.01 to 0.25 (Table S1; Figure 2c), that is females were on average 1%–25% larger in SVL than males. Variation in SSD is even more predictable than the absolute female size: our model explains 55% of the total variation. For SSD, the effect of Parity mode is slightly higher than that of Clade (26% vs. 20%, Table 1). For female size and SSD, the effect of mean winter temperature (T1) was lower than those of Parity mode and Clade (5–7%) but still significant for both (Table 1).

Two comparisons between individual clades differing in parity mode fully conformed to our main analyses: They show a significant effect of Parity mode/Clade for SSD (WO vs. CVI, $F_{1,13} = 11.41$, $p = 0.005$; EO vs. CVII, $F_{1,7} = 17.77$, $p = 0.004$) and female size (WO vs. CVI, $F_{1,13} = 10.06$, $p = 0.007$; EO vs. CVII, $F_{1,7} = 10.06$, $p = 0.016$) in the predicted direction, with no differences in male size (WO vs. CVI, $F_{1,13} = 2.67$, $p = 0.127$; EO vs. CVII, $F_{1,7} = 3.49$, $p = 0.104$). This pattern is especially pronounced when comparing the syntopic populations of EO and CVII clades from Straniger Alm (Table S1, Samples 35 and 41): mean SVL in viviparous vs. oviparous adults is 4.5 ± 0.34 mm longer in females while 0.4 ± 0.33 mm shorter in males.

To test whether our main results are robust to potential biases in our data structure we did some additional analyses. Considering that one clade (EV) has a much wider range of experienced seasonality than the rest of the species (Figure 2), all main models were rerun using a data set truncated to the total climatic range of the other five clades, that is $T1 \geq -5.6^\circ\text{C}$ (Table S3). This truncation reduced the effect of T1, while the effects of Parity and Clade(Parity) did increase, their relative impacts remaining roughly the same as in the main analyses. Further, all models were rerun using two additional predictors considered as potential confounding factors: type of material (living vs. freshly euthanized vs. preserved specimens) and sampling time (before 1991 vs. 1991–2000 vs. 2001–2022). Both additional predictors were non-significant (Table S4).

Different 'both-sex models' tested for *Zootoca* consistently show a significant Sex \times Parity mode interaction; its rate of explained variance is comparable to that of the main effect of Parity mode, their ratio (PER) amounting 0.7–1.2 (Table S5). In *Lerista bougainvillii*, PER is much lower than in *Zootoca* (0.09–0.14, Table S6). In the *Sceloporus aeneus/bicanthalis* system, PER is only moderately lower than in *Zootoca* (0.54, Table S6), indicating a potentially appreciable sex bias of the Parity effect. However, opposite to *Zootoca*, body size differences between oviparous and viviparous populations in this system are male-biased (Figures 3d and 4). For *Lerista bougainvillii* and the *Sceloporus aeneus/bicanthalis* group, both-sex models were also run on surrogate individual-based data (Table S7). These analyses, which account for the numbers of studied individuals, confirm the pattern revealed by the both-sex models presented above: The sex bias of differences in adult SVL between oviparous and viviparous populations is weak in the former, while moderate (but male-biased, see above) in the latter system.

Data on *Saiphos equalis* (Smith & Shine, 1997) include only one oviparous and one viviparous population and could not be examined with GLMs as above. To compare the pattern of interest in all four study systems, we compiled shifts in adult SVL in viviparous vs. closely related oviparous populations using sex-specific averages of population means (Figure 4). The differences in male size between egg-laying and live-bearing *Z. vivipara* are clearly smaller than those in female conspecifics and than the male size differences between oviparous and viviparous populations in the other systems (Figure 4).

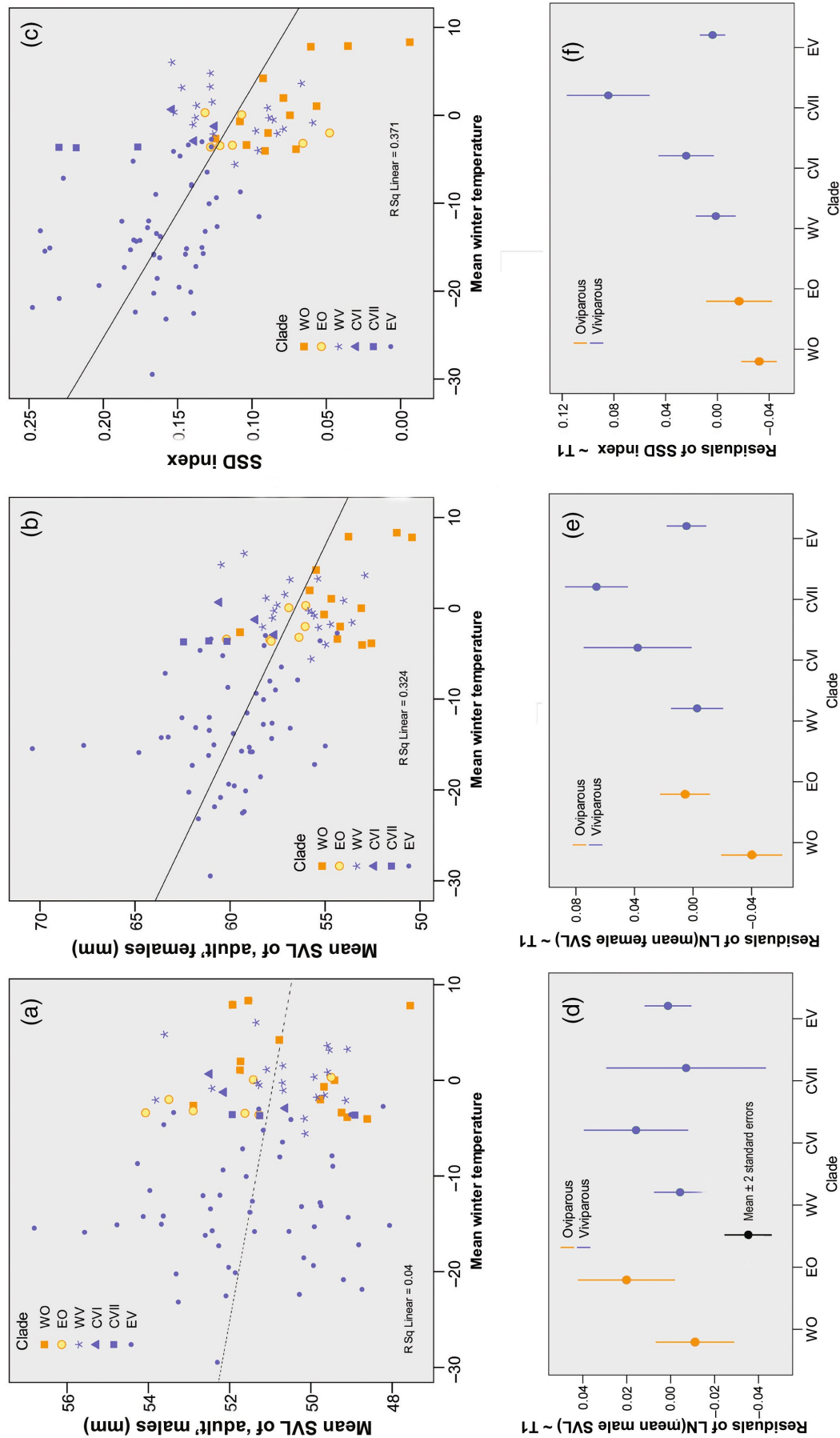


FIGURE 2 Male body size, female body size and sexual size dimorphism (SSD) in *Zootoca vivipara*. (a–c) Trait values of individual populations plotted against mean winter temperature (T1, our proxy for seasonality). (d–f) Variation among clades based on residuals of Trait ~ T1 models, where Trait is LN(male size), LN(female size) or SSD. Regression lines are shown whenever the slopes differ from zero at $p < 0.05$ (broken line indicates $p = 0.05$). See Figure 1 for full designations of the clades and their phylogenetic and geographic relationships.

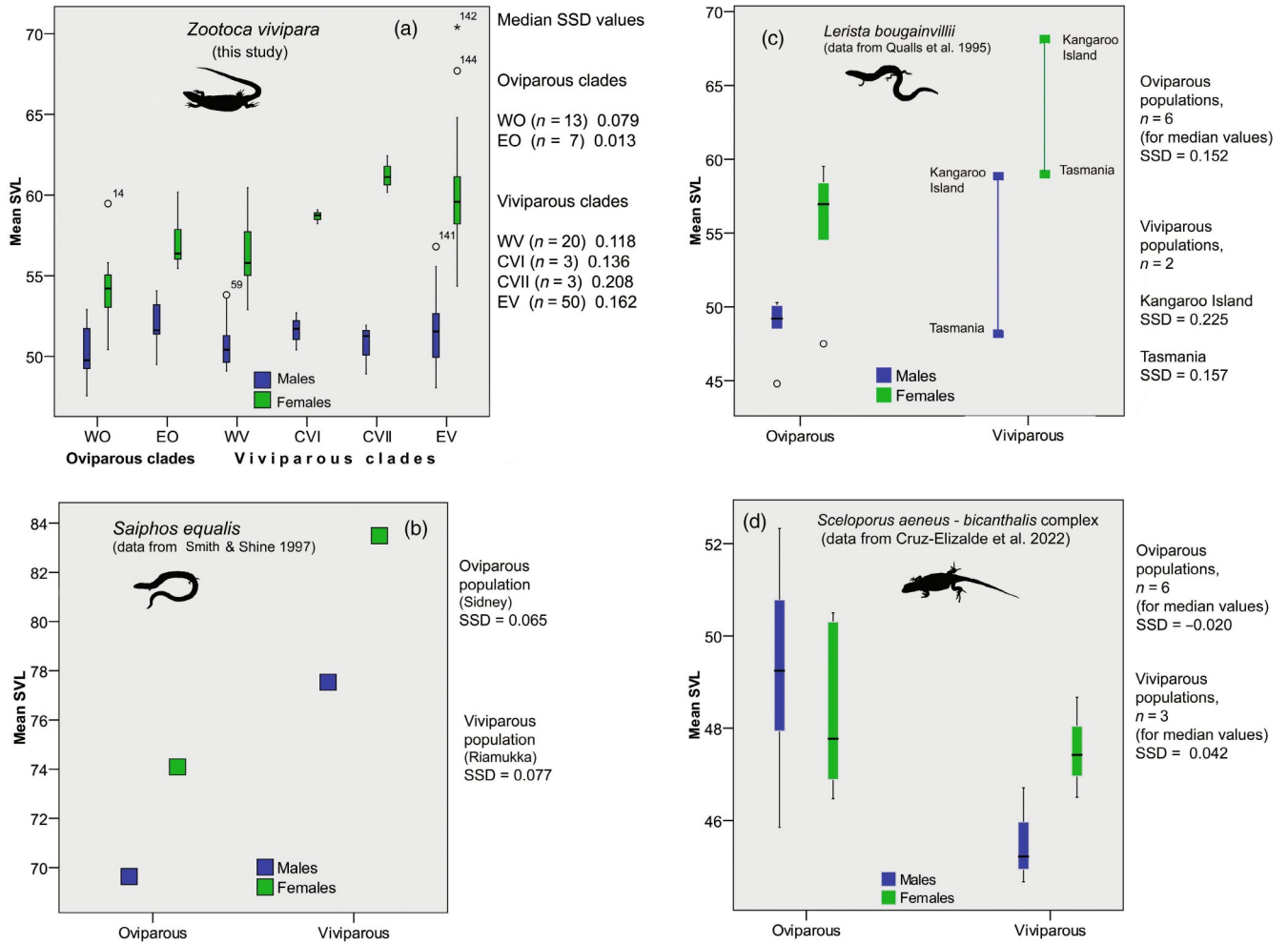


FIGURE 3 Sex-specific body length (snout-vent length [SVL]) and sexual size dimorphism (SSD) in four systems of closely related lineages of lizards differing in parity mode.

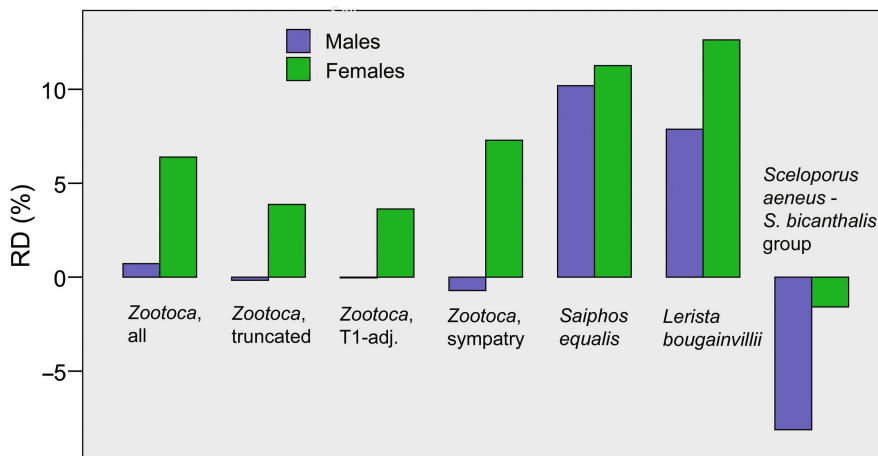


FIGURE 4 Relative differences in sex-specific body length of viviparous vs. closely related oviparous populations [$RD (\%) = 100 \times (SVL_{viv} - SVL_{ov}) / SVL_{ov}$] in four reproductively bimodal lizard taxa. For *Zootoca vivipara*, four different data sets (all data; data truncated to $T1 \geq -5.6^\circ\text{C}$; data adjusted for $T1$ using ANCOVA; sympatrically occurring oviparous and viviparous populations) were used to demonstrate that a distinctly strong female bias in RD is robust to climatic effects, which were not available for the other bimodal taxa. See text for details and Figure 3 for data sources. SVL, snout-vent length.

4 | DISCUSSION

Our study tested the effect of parity mode (=reproductive mode) on adult body size and SSD under powerful control for confounding factors. We compared oviparous and viviparous populations within a species, thus maximizing their similarity in the traits unrelated to parity mode. Each parity mode was represented by at least two non-sister clades (Figure 1), allowing us to effectively separate the effect of parity mode from that of ancestry. For most individual clades, and for the whole species, we used a highly representative set of populations living in diverse climates (Figure 2a–c). Thereby, we could control for both phylogeny (lineage identity) and current environment (climatic seasonality), whereas most previous comparative studies on life-history correlates of viviparity accounted for phylogeny only (see Section 1). We show that the effect of parity mode was consistently absent for male size, while highly significant for female size and especially SSD. These patterns (Table 1) were robust to the inclusion of additional predictors related to data heterogeneity (Table S4) or the exclusion of populations from regions with high climatic seasonality (these large regions are occupied by the EV clade only; Figure 2) (Table S3). In more specific comparisons within pairs of clades with differing parity modes (sister clades WO and CVI; clades EO and CVII which share two plesiomorphic traits absent in the rest of *Zootoca*), the viviparous clade also exhibited larger female size and more female-biased SSD than the oviparous clade. This pattern was clearly seen between the oviparous (EO) and the viviparous (CVII) population syntopically occurring in Straniger Alm (Samples 35 and 41, Figure 1; Table S1).

Within *Z. vivipara*, the effect size of parity mode (14%–26% of the total variation) was similar to that of clade identity (17%–20%), the latter factor being slightly more influential for female size, while less influential for SSD (Table 1). The effect of climatic seasonality, as estimated by mean winter temperature, was significant but less influential than the first two factors (5%–8%, Table 1). Across different lizard species, parity mode explained less than 5% of the total SSD variation in analyses using all data, this proportion increasing to nearly 20% when the analysed variation was trimmed to divergences between sister clades which differ in parity mode (Cox et al., 2003). A related study on snakes (Shine, 1994) reported similar values. Although our study differs from the above ones in the set of tested predictors and statistical procedures, a rough comparison of effect sizes among these studies is possible. Thus, the effect size of parity mode on SSD in our study (26%) can be considered as quite high.

Our study shows that the increase in adult body size in viviparous vs. oviparous populations of *Zootoca vivipara* is strongly female-biased or even female-specific. Such a pattern is fully expected, since the transition to viviparity involves primarily the female phenotype, as do all theoretical predictions for the shift in body size (see Section 1). Surprisingly, this pattern is not evident from available data on other systems of closely related oviparous and viviparous populations. Our analyses of published body length data for two reproductively bimodal skinks (*Lerista bougainvillii* and *Saiphos equalis*) and a pair of closely related oviparous (*Sceloporus aeneus*)

and viviparous (*S. bicanthalis*) iguanian species revealed either no substantive sex bias in the predicted increase in adult body size in viviparous vs. oviparous populations (*L. bougainvillii* and *S. equalis*) or the differences between oviparous and viviparous lineages were male-biased (the *Sceloporus aeneus*–*S. bicanthalis* group) (Figures 3 and 4). In the latter case, the predicted shift to more female-biased SSD in the viviparous relative to the oviparous lineage occurs via decreasing male size, rather than increasing female size (Figures 3d and 4); this pattern argues for the *small male advantage hypothesis* (Chelini et al., 2021; Ghiselin, 1974; Roitberg et al., 2020; see Section 1) rather than for an effect of parity mode.

The presented differences between *Zootoca* and the three other systems of closely related oviparous and viviparous lineages are unlikely to be mostly caused by sampling bias. While only two populations were studied in *Saiphos equalis*, each of the other systems includes six oviparous and two to three viviparous populations (Table S2), covering a large part of their geographic areas. Moreover, the strong female bias in body size differentiation between oviparous and viviparous clades in *Zootoca* persists, when data for this system are truncated to populations inhabiting less seasonal climates (Figure 4; Table S5).

Why does *Zootoca* exhibit the predicted, strongly female-biased pattern of increasing adult body size in viviparous vs. oviparous populations, whereas the other studied systems of closely related oviparous and viviparous lineages do not? Below, we present a hypothesis that might explain this distinction. Even though live-bearing in *Z. vivipara* may have evolved less recently than in the two reproductively bimodal Australian skinks (see Whittington et al., 2022 for references), the evolution of viviparity in this species may have encountered stronger phylogenetic constraints than in the other three systems in this comparison. As a result, viviparous reproduction in *Z. vivipara* may function less efficiently and be more costly for the female organism (especially in relation to oviparous conspecifics) than in *Lerista bougainvillii*, *Saiphos equalis* and the *Sceloporus aeneus*–*S. bicanthalis* complex. Note that for the latter three systems, multiple independent origins of viviparity are known within the same family, subfamily or tribe. Within the last 50–70 million years of evolution, there have been at least eight transitions in parity mode within Phrynosomatidae (including *Sceloporus*) and eight transitions within Lygosominae (a clade of the family Scincidae which includes both *Saiphos equalis* and *Lerista bougainvillii*) (Table S8). In contrast, only a single transition (in *Zootoca*) occurred within the tribe Lacertini (Table S8). Moreover, there has been only one other transition to viviparity in the entire family Lacertidae (Table S8) represented by the *Eremias multiocellata*–*E. przewalskii* complex, a monophyletic group of closely related species (Orlova et al., 2022) belonging to a different tribe, Eremiadini (Arnold et al., 2007). Estimations of the most recent common ancestors with closest viviparous relatives and the minimum time interval of continuous oviparity (Table S9) also exhibited much higher values for *Zootoca vivipara* compared with *Lerista bougainvillii*, *Saiphos equalis* and *Sceloporus bicanthalis*.

The rarity of transitions to viviparity in lacertid lizards is hardly due to the absence of appropriate selective forces. Multiple Lacertini species occur in colder climates; some of them resemble oviparous *Zootoca* by evolving prolonged egg retention (Arribas & Galán, 2005;

Braña et al., 1991; Ljubisavljević et al., 2007), yet not live-bearing. Remarkably, the live-bearing in *Zootoca* is not only 'phylogenetically isolated', but also evolutionarily unstable. In one lineage, the WO clade (subspecies *Z. v. louislantzii*, Arribas, 2009), viviparity has apparently reversed to oviparity (Recknagel et al., 2018; Surget-Groba et al., 2006)—an exceptionally rare case in the squamate evolution (see Whittington et al., 2022 for references).

Taken together, the above patterns suggest that genetic, developmental or physiological constraints 'against' viviparity (Blackburn, 2015, 2018) may indeed have been stronger in *Zootoca* than in the other vertebrate systems of closely related oviparous and viviparous populations studied to date. As a result, viviparity in *Zootoca* may be associated with higher overall costs of reproduction, and thus stronger *female-specific* selection for larger body size, including fecundity selection (see Section 1), than in taxa with frequent transitions to live-bearing. Notably, in *Zootoca*, viviparous clades exhibit markedly smaller offspring size than oviparous clades (Recknagel & Elmer, 2019; Roitberg et al., 2013; see also Lindtke et al., 2010). This pattern is not seen in the other three systems of closely related oviparous and viviparous populations (Qualls & Shine, 1995; Rodríguez-Romero et al., 2002; Smith & Shine, 1997). The small offspring size in viviparous *Zootoca* associated with high clutch mass (Roitberg et al., 2013 and references therein; Recknagel & Elmer, 2019) likely reflects increased selection for female fecundity (cf. Roitberg et al., 2015). Further data on sex-specific adult body size, female reproductive traits and particularly the costs of female reproduction in systems of closely related viviparous and oviparous clades other than *Zootoca* could reveal the extent to which the strongly female-biased shift in adult body size associated with viviparity is distinct for our study species and whether the increase in total costs of female reproduction in live-bearing relative to egg-laying conspecifics is especially high in *Zootoca*, as we hypothesize. Whatever the underlying reasons, if our finding that body size correlates of viviparity differ between reproductively bimodal species is supported with additional data, it may help to understand why the effect of parity mode on the broad-scale SSD variation across squamate species is overall weak (Cox et al., 2003; Shine, 1994; see above).

The strong predicted effect of parity mode on SSD found in *Z. vivipara* is substantially impacted by the fact that the differences between oviparous and viviparous lineages for *male* size are virtually lacking. These differences are distinctly small not only relative to those in female conspecifics but also relative to the male size differences between egg-laying and life-bearing populations in the other comparable systems (Figure 4). The inter-population variation in male size is overall low in *Z. vivipara* (Roitberg et al., 2020; this study). Such a pattern where the driver of intraspecific divergence in body size is the female sex is unusual in amniotes (see Roitberg et al., 2020 for references). For instance, in three other lizard species studied range-wide, geographic body size variation was considerably stronger in males than in females (Aglar & López-Darías, 2016; Chelini et al., 2021; Roitberg, 2007). Noteworthy, in two iguanian lizard genera (*Sceloporus* and *Liolaemus*), including numerous egg-laying and live-bearing species, male size varied stronger than

female size among species (Jiménez-Arcos et al., 2017; Pincheira-Donoso & Tregenza, 2011); right in these systems, no effect of parity mode on SSD was found once phylogenetic relationships were controlled for (Cabrera et al., 2013; Jiménez-Arcos et al., 2017; López Juri et al., 2018). In congruence, two sister *Sceloporus* species with contrasting parity modes differ in male rather than female size (Figure 3d; see above). Apparently, in *Sceloporus* and *Liolaemus*, sexual selection (Jiménez-Arcos et al., 2017; Pincheira-Donoso & Tregenza, 2011) or other factors unrelated to parity mode are more important determinants of body size than in *Zootoca*. The causes of the low male size variation in *Z. vivipara* present an interesting avenue for future research.

Our study focused on overall structural size (SVL), to get more data and more comparability to other related studies. However, exploring interspecific, interpopulational and sexual differences in body *shape* (Braña, 1996; Scharf & Meiri, 2013) could provide additional insights into phenotypic correlates of viviparity.

5 | CONCLUSIONS

Using an exceptionally extensive data set on the reproductively bimodal lizard *Zootoca vivipara*, we showed that viviparous populations exhibited a larger female size than oviparous populations, with no corresponding differences for male size. Comprehensive studies on other systems of closely related viviparous and oviparous populations, particularly within species, will demonstrate whether this strongly female-biased effect of parity mode is consistent across such systems. If in some systems, the expected increase in body size in viviparous populations exhibits no or only a slight female bias—as seems likely from our analysis of limited published data—then additional hypotheses, other than the reproduction-related models presented here, should be considered. Albeit closely related viviparous and oviparous lineages with otherwise similar life histories (e.g. as regards the fetal nutrition) are unknown in non-squamate vertebrates (Blackburn, 2015), comparisons between viviparous species and their closest oviparous relatives (e.g. in poeciliid fishes, Bisazza, 1993 or cat sharks, Blackburn & Hughes, 2024) could also be of interest.

AUTHOR CONTRIBUTIONS

Evgeny S. Roitberg conceived and designed the study. All authors provided morphometric and other data from their fieldwork or museum samples. Anamarija Žagar provided climatic data. Evgeny S. Roitberg conducted statistical analyses and wrote the manuscript, to which all co-authors contributed and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data are available from the Dryad Digital Repository <https://doi.org/10.5061/dryad.66t1g1k97> (Roitberg et al., 2024).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Figure S1: Spline correlograms for the residuals of our main models for geographic variation of male size, female size and SSD (Table 1) in *Zootoca vivipara*.

Table S1: Summary statistics for snout–vent length (SVL) in male and female samples of *Zootoca vivipara*, geographic and climatic characteristics of these populations, and some other data.

Table S2: Summary statistics for snout–vent length (SVL) in geographically distinct populations of *Lerista bougainvillii*, *Saiphos equalis*, *Sceloporus aeneus* and *S. bicanthalis*.

Table S3: Models for geographic variation of SSD and sex-specific body length in *Zootoca vivipara* run on a data set truncated to $T1 \geq -5.6^\circ\text{C}$.

Table S4: Models for geographic variation of SSD and sex-specific body length in *Zootoca vivipara* extended for two additional predictors (Mat, type of material; Time, time interval).

Table S5: Models for geographic variation in sex-specific body length in *Zootoca vivipara* which jointly include both sexes.

Table S6: ‘Both-sex models’ for geographic variation in sex-specific body length in *Lerista bougainvillii* and the *Sceloporus aeneus/bicanthalis* group. Data points are population means.

Table S7: ‘Both-sex models’ run on surrogate individual-based data on body length variation in *Lerista bougainvillii* and the *Sceloporus aeneus/bicanthalis* group.

Table S8: Evolutionary age (in mya), number of oviparous and viviparous species, and number of independent transitions to viviparity in three lizard families (and subordinate taxa) which include three reproductively bimodal species (*Zootoca vivipara*, Lacertidae/Lacertinae/Lacertini; *Saiphos equalis* and *Lerista bougainvillii*, Scincidae/Lygosomatinae) and the pair of sister species (*Sceloporus aeneus* and *S. bicanthalis*, Phrynosomatidae/Sceloporinae) differing in parity mode.

Table S9: Reproductively bimodal species and their evolutionary history of viviparous reproduction within their larger phylogenetic clades.

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