# Parity-specific differences in spatial genetics and dispersal in the common lizard

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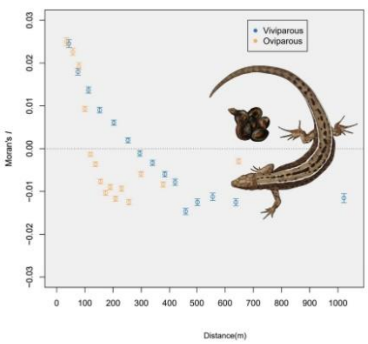
# Abstract

Dispersal is a key demographic parameter that plays an important role in determining spatial population dynamic and genetic structure. Linking differences in dispersal patterns to key life-history traits is often confounded by inconsistent environmental pressures experienced by different populations. To explore the link between dispersal and life history, we focus on a site where oviparous and viviparous lineages of the common lizard (*Zootoca vivipara*) are found adjacent to each other. We take advantage of this shared environment to investigate parity-specific dispersal patterns using high resolution, individual-level spatial genetic autocorrelation and population genomic approaches (11,726 SNPs; 293 oviparous and 310 viviparous individuals). We found isolation-by-distance patterns to be present in both the oviparous and viviparous populations. Density was 2.5 times higher in the viviparous population than the oviparous one, though heterozygosity and genetic diversity measures were similar in the two populations. We found marked differences in the extent of genetic neighbourhoods between the lineages, with the viviparous population showing both dispersal ($\sigma$) and spatial genetic autocorrelation (Moran's *I*) at two-fold greater geographic distances than the oviparous population. We found clear evidence of male-biased dispersal from genetic estimates in the viviparous population. In the oviparous population, evidence of male-biased dispersal is weak or absent. These differences are likely to be closely linked to specific requirements of the alternative reproductive strategies and may be the demographic consequences of mother-offspring interactions. Fine-scale geographic and individual-level measures are key to understanding parity mode differences at microevolutionary scales and to better identifying their ecological and evolutionary impacts.

Keywords: spatial-genetic autocorrelation, landscape genomics, squamate, sex-biased dispersal, oviparous, viviparous, isolation-by-distance

# Graphical abstract



## Introduction

Successful reproduction is a fundamental component of evolutionary theory, and differing reproductive strategies represent a crucial phenotype on which natural selection can act. Egg-laying (oviparous) and live-bearing (viviparous) species are extreme examples of alternative reproductive strategies that are directly linked to key demographic and life history parameters, such as fecundity (Domínguez-Guerrero *et al.*, 2022). In squamates there have been over 115 transitions to viviparity from oviparity (Blackburn, 2015) and the abundance of oviparous and viviparous taxa enables investigation into drivers of reproductive mode evolution and its consequences at the macroevolutionary scale. Multiple analyses have demonstrated a link between the evolution of viviparity and increased diversification, generally attributed to expansion into novel ranges (Lynch, 2009; Lambert & Wiens, 2013, but see (Li & Wiens, 2022)). Viviparous lineages tend to inhabit more variable environments (Pincheira-Donoso et al., 2013), which likely leads to the increased speciation and higher rates of extinction that have been observed (Pyron & Burbrink, 2014). In turn, this is expected to have consequences regarding parity-related population persistence under climate change (Sinervo *et al.*, 2010; Pio Caetano Machado *et al.*, 2023). Underlying these macroevolutionary patterns are a wide range of fundamental microevolutionary differences that to date have rarely been quantified (Rolland *et al.*, 2023). Studying extant populations that differ in the trait of interest, but are similar in most other aspects, is a powerful context to identify factors associated with the evolution of that trait. However, suitable study populations for such comparisons are rare, especially in cases where ecological and environmental differences themselves may drive transitions in the trait of interest (Shine, 2005).

Dispersal is a key component of population dynamics in relation to landscape use and can have a major impact on the demography, diversity, and genetic structure of populations (Clobert *et al.*, 2001; Elmer et al. 2007). Individuals are expected to disperse when it results in an increase in fitness large enough to compensate for the cost of relocating (Bowler & Benton, 2005), but many environmental and demographic factors interact to determine the outcome of this cost-benefit trade-off. Propensity to disperse can be broadly categorised into the environmental drivers, often acting through changes in population structure, and the underlying genetic component that determines the response to these drivers (Clobert *et al.*, 2001). Differences in the probability of dispersal within species are attributed to behavioural differences between individuals (Cote & Clobert, 2006; Michelangeli *et al.*, 2017), differences in body condition (Olsson *et al.*, 1997; Massot & Clobert, 2000; Meylan *et al.*, 2002; Le Galliard *et al.*, 2003; Cote *et al.*, 2007; Cote & Clobert, 2010; Rugiero *et al.*, 2012), can be heritable and have genetic associations (Massot *et al.*, 2003; San-Jose *et al.*, 2023) and be influenced by maternal effects and environment (San-Jose *et al.*, 2023). At the population level, differences are likely to be driven through age and sex structuring, which may in turn lead to age (Marvá & San Segundo, 2018) and sex biased dispersal (Perrin & Mazalov, 2000). These between-individual and between-population differences are likely to vary between evolutionarily distinct lineages, making it challenging to determine the association between traits of interest while controlling for confounding factors.

Sex-specific factors are particularly likely to be important determinates of dispersal through mechanisms such as mate competition, resource competition, and the likelihood of inbreeding (Greenwood, 1980). Analysis across phylogenetic scales supported this link between mating system and sex-biased dispersal but found that parental care and sexual dimorphism showed stronger associations (Trochet *et al.* 2016). The range of factors associated with dispersal are unlikely to alter the direction of the sex-bias, although they may affect its magnitude (Greenwood 1980). Within squamates, male-biased dispersal has been reported within oviparous (Dubey *et al.*, 2008; Johansson *et al.*, 2008; Jessop *et al.*, 2022) and viviparous (Massot *et al.*, 2003; Pernetta *et al.*, 2011; Keogh *et al.*, 2007) species, as has female-biased dispersal (Olsson & Shine, 2003; Myers *et al.*, 2013). Other studies have found no sex-bias (Luiselli *et al.*, 2011; Blouin-Demers & Weatherhead, 2021), populations with alternative sex-biases (Lane & Shine, 2011) or sex biases in only some populations (Berry *et al.*, 2005; Zwahlen *et al.*, 2021). Together these studies suggest that in squamates ecological factors are greater determinants of the patterns of sex-biased dispersal than life history, but comparisons across parity modes are usually confounded with a large range of evolutionary and ecological differences.

*Zootoca vivipara* is one of only a handful of taxa in which both viviparous and oviparous lineages can be found in close geographic proximity and represents one of the most recent evolutionary transitions between parity modes (Recknagel *et al.*, 2021b; Whittington *et al.*, 2022). The drivers of dispersal in this species have been relatively extensively studied, although almost exclusively in viviparous populations, and include density, relatedness, sex-ratio, food availability, habitat quality, and predators (e.g Boudjemadi *et al.*, 1999; Bestion *et al.*, 2014; Cote & Clobert, 2007; Cote & Clobert, 2010; De Fraipont *et al.*, 2000; Massot & Clobert, 1995; Meylan *et al.*, 2007; Massot *et al.*, 2008; Vercken *et al.*, 2012; Zajitschek *et al.*, 2012; Massot & Aragón, 2013; Pellerin *et al.*, 2022). Genetic analyses have identified candidate genes associated with dispersal phenotypes and demonstrated that it is a heritable trait, at least in a semi-natural viviparous population (San-Jose *et al*., 2023). Research has however lacked the comparative context between lineages that is needed to identify parity-specific dispersal differences. These comparisons are challenging because the extreme complexity of the dispersal process, which involves interactions among biotic factors, abiotic environment, and phenotype (Clobert et al. 2001).

Based on theoretical and empirical expectations, several currently untested predictions exist for similarity and differences in dispersal and population structure in oviparous and viviparous common lizards. First, dispersal is expected to be influenced by the levels of relatedness (Gandon, 1999). In common lizards, kin competition, between the juveniles and their mother, has been demonstrated as a driver of individual dispersal (Léna *et al.*, 1998; Ronce *et al.*, 1998; Le Galliard *et al.*, 2003; Cote *et al.*, 2007; Cote & Clobert, 2010). Viviparous common lizard clutches have on average one offspring fewer than oviparous clutches (Recknagel & Elmer, 2019). This suggests that smaller clutches, through reduced kin-competition with siblings, could lead to reduced dispersal in the viviparous population relative to the oviparous one. Further, there is likely to be differences in mother-offspring kin competition between the two lineages. Offspring of viviparous females directly experience their mother; this may result in higher levels of mother-offspring competition, and consequentially higher juvenile dispersal. There is some evidence that this type of kin-competition is present in viviparous common lizard populations (Léna *et al.*, 1998; Ronce *et al.*, 1998; Le Galliard *et al.*, 2003; Meylan *et al.*, 2004; Vercken *et al.*, 2007; Cote *et al.*, 2007).

Third, resource availability is a key determinant of population dynamics (Nurmi & Parvinen, 2011; Reyes *et al.*, 2023); for nesting species the presence of suitable nest sites is an important resource that differs between oviparous and viviparous taxa. Consequently, we predict lower dispersal in the oviparous population under the assumption that nest sites are sufficiently abundant at the habitat of origin and that dispersal for nests is risky, selecting against dispersing phenotypes. Empirical studies demonstrating this to be the case in squamates are scarce, but artificially increasing burrows resulted in increased population density in the skink *Tiliqua adelaidensis* (Souter *et al.*, 2004) and similarly has also been demonstrated in some bird species (Winkler *et al.*, 2005; Swift *et al.*, 2021). Dispersal for nests is risky, and Bonnet *et al.* (1999) demonstrated a higher level of mortality in females of oviparous snake species during the period when they search for laying sites. Travelling large distances to find suitable nest sites has also been demonstrated in the lizard species *Sceloporus undulatus* (Angilletta Jr. *et al.*, 2009), highlighting how this aspect of the reproductive strategy can drive individual movement patterns.

Finally, lineage-specific dispersal patterns and life-histories are likely to result in differences in sex-biased dispersal between oviparous and viviparous lineages. The extent to which these patterns vary between lineages is not known but may be high due to the differences in sex-specific resource requirements between the viviparous and oviparous lineages (Greenwood, 1980; Trochet et al., 2016), particularly nest site availability. Other potential factors increasing the probability of female dispersal include maternal care, which broadly includes viviparity (Clutton-Brock, 1991), and proximity to the mother, which is likely to be more extreme in viviparous individuals (Le Galliard *et al.*, 2003, Trochet et al., 2016). Genetic studies of sex-bias in squamates have identified dispersal that is male biased, female-biased, or varies across populations, and can be additionally driven by intrasexual competition in males (e.g. Massot *et al.*, 2003; Olsson & Shine, 2003). Quantifying dispersal measures informed by sex is key to informing demographic and evolutionary predictions (Trochet et al. 2016).

Here we quantitatively and explicitly compare dispersal, via spatial genetic measures, of oviparous and viviparous *Z. vivipara* populations that share an overlapping environment. This close geographic proximity intrinsically controls for environmental and ecological factors whose effects would otherwise confound comparisons between the parity modes, as they are usually geographically separated.  Using a high-resolution genomic dataset, we investigate the relationship between dispersal, parity mode, and sex-bias through spatial-genetic analyses that reflect how genetic relatedness between individuals changes with geographic distance (Malécot, 1950; Wright, 1943, 1946). Using these approaches, we show evidence that there is more dispersal in the viviparous population than in the oviparous one. The viviparous population also displays a male-biased dispersal pattern, while there is less evidence of sex-biased dispersal in the oviparous population. Together these results support expectations based on the potential role of competition between mother and offspring motivating dispersal. Our results suggest that other parity-specific factors, such as laying-site requirements particular to oviparous populations, may also influence dispersal and warrant further investigation.

## Methods

### Biological system:

This study is based on previously collected coordinate and genomic data from adult lizards that were sampled at a study site in southern Austria (Supplementary Figure 1) over a period of three years (2014 – 2016; see Recknagel *et al.*, 2021a). At this location, the Eastern Oviparous (oviparous) and Central Viviparous II (viviparous) lineages are adjacent and narrowly overlap (Recknagel *et al.*, 2021a). Oviparous individuals are primarily found in the lower altitudes (sites 1-3) and viviparous individuals at the higher altitudes (sites 4-6; sites defined per Lindtke *et al.*, 2010) (Figure 1A, Table 1). All habitat sampled from is alpine meadow, subject to summer grazing by cows and goats, and both lineages have similar microhabitats available to them (Recknagel et al., 2023). Equal collection effort with regard to oviparous and viviparous individuals was aimed for, but females were preferentially targeted. Therefore, our capture data should effectively represent abundance differences in the oviparous and viviparous populations but cannot inform on population sex-ratios.

### Population density:

To estimate relative population sizes relative to geographic area, we calculated a density metric using cumulative capture data across all three years. Site areas were calculated using coordinates (WSG84 coordinate system) of the site boundaries based on the tree line and other barriers, such as small rivers and the road, reflecting the areas where sampling takes place. These were converted to polygons and stored as sf objects using the sf package v1.0.14 (Pebesma, 2018; Bivand, 2023). The area of each polygon was calculated in $m^2$ using the st_area function. Any individual whose capture coordinates were outside these areas were assigned to their nearest area using the nearest_site function, having first converted both the capture coordinates and areas to the NAD83 coordinate reference system. Our density metric at each site was calculated as the number of individuals assigned to the site divided by its area. The estimate of the population density experienced by each parity was found by taking the mean of this value across the sites that are primarily inhabited by the oviparous (1 – 3) or viviparous population (sites 4 – 6). Additionally, population size estimates ($\widehat{N}$) for these two groups were calculated as $\sum_t (C_t \times M_t) / \sum_t R_t$ following the Schnabel method (Schnabel, 1938) and using each year as a sampling set. Where $C_t$ is the number caught at time $(t)$, $M_t$ is the number of previously caught individuals in the population and $R_t$ is the number of individuals caught that have been caught in previous years. For the purposes of this calculation when an individual moved between parity sites it was counted once in each, rather than as a recapture.

### Genomic data:

Raw double-digest RADseq data (150bp read lengths) of ~5M reads per individual were retrieved from NCBI (PRJNA657575). Stacks v1.44 (Catchen *et al.*, 2011) was used to demultiplex the data following methods of (Recknagel *et al.*, 2021a). Assignment of individuals to oviparous/viviparous lineages were based on previously established q-values (Recknagel *et al.*, 2021a). Individuals with q-values of 0.9 or above were classified as viviparous and individuals with a q-values of 0.1 or below were classified as oviparous. Hybrid individuals (q-value < 0.9 and > 0.1) are found at this site but were excluded.

Stacks v2.60 (Rochette *et al.*, 2019) was used to call SNPs using the components of the de novo pipeline. Previously identified putative recaptures of the same individual on multiple occasions were confirmed using photograph comparisons of ventral pattern and merged prior to SNP calling. Prior to running the pipeline optimal values, shown in brackets, of the m (3) and M (5) parameters for the ustacks component and the n (6) value of the cstacks component were identified following recommendations in Paris *et al.* (2017). This optimisation used 20 individuals: 5 female and 5 male oviparous individuals and 5 female and 5 male viviparous individuals. When running the cstacks component a reduced population map was used consisting of 200 individuals, again evenly divided between sex and lineage. All other parameters were kept as default. Following the de novo pipeline, Bwa-mem2 v2.1 (Vasimuddin *et al.*, 2019) was used to map the loci catalog to an in-house genome assembly of the Eastern Oviparous lineage (*Eovi.ref.V1.19Chr*), using the default parameters. These mapped loci were sorted using Samtools v1.11 (Danecek *et al.*, 2021) and then the stacks-integrate-alignments script, from Stacks, was used to assign mapped genomic coordinates. Finally, the populations component was used to generate a vcf file. This approach of starting with de novo SNP calling was chosen over the reference map-based Stacks pipeline to maximise SNP retention across the two lineages. The males and females for each lineage were extracted from the vcf separately resulting in four sets of individuals. Using BCFtools v1.16 (Danecek *et al.*, 2021) each of the vcf files were sorted, indexed and filtered individually. Sex chromosomes were excluded from the dataset and only biallelic sites were retained. SNP calls with a depth less than 8 or a genotype quality annotation less than 30 were marked as missing. Next, any SNPs that were fixed or missing in more than 50% of samples were removed. SNPs were also filtered to remove extreme linkage disequilibrium ($r^2 > 0.7$). Finally, BCFtools isec was used to identify SNPs shared across all the groups and they were merged together including only these SNPs, resulting in a final dataset with good representation across lineages and sexes. The final vcf file was converted to binary format using Plink v1.90b6.24 (Purcell *et al.*, 2007).

### Population genetic metrics:

Using this filtered dataset, the hierfstat package v0.5.11 (Goudet & Jombart, 2022) was used in R v4.0.4 (R Core Team, 2021) to calculate relative values of observed heterozygosity ($Ho$), within population gene diversity ($Hs$) and Wright's inbreeding coefficient ($F_{IS}$) to allow comparisons between lineage. The fixation index ($F_{ST}$) (Nei, 1987) between the two populations was also calculated.

### Spatial-genetic relationships:

Dispersal patterns within the populations were estimated from spatial-genetic structuring using pairwise measures of geographic and genetic relatedness (Legendre, 1993; Epperson, 2005). Absence of spatial-genetic autocorrelation implies that individuals at a given geographic distance are no more similar than any other pair, while positive autocorrelation indicates geographically closer individuals are more similar than expected by chance. The distance at which spatial-genetic autocorrelation is zero reflects `patch size` by

Sokal & Wartenberg (1983) and relates to migration distance. This is conceptual similar to Wright's 'neighbourhood size', which is the area in which most matings occur (Wright, 1946). An alternative but related metric is that of dispersal distance ($\sigma$), which uses regression to link pairwise genetic and geographic distances for populations (Rousset, 1997).

Correlograms of spatial autocorrelation for each lineage were plotted using Moran's *I* (Moran, 1950). This analysis was carried out in R using packages, detailed below, and custom script (see Data Availability) to mirror the implementation in SPAGeDi (Hardy & Vekemans, 2002). The BEDMatix package v2.03 (Grueneberg & De Los Campos, 2019) was used to read Plink format files into R and convert them to a genotype matrix. These were then recoded from the standard 0,1,2 Plink genotype format to 0,0.5,1 allowing calculation of Moran's *I* between each pair of individuals. The spatial distance, in m, between each pair of individuals was calculated from the longitude and latitude coordinates using the spherical law of cosines. The number of distance classes was set at 15 and the distance covered in each class, for each lineage, was chosen to allow an equal number of pairwise comparisons within each class. Bootstrapping, with 15,000 replicates, was implemented using the boot package v1.3.28.1 (Davison & Hinkley, 1997; Canty & Ripley, 2022) and 95% bCa bootstrap confidence intervals were estimated.

Parity and sex-specific dispersal distances ($\sigma$) were calculated as:

$$\sigma = \sqrt{1/(b * 4D\pi)}, \tag{1}$$

where $b$ is the regression slope between the pairwise genetic distances and the natural log of corresponding geographic distances. These geographic distances are the same spatial distances described previously. The measure of genetic distance used is Rousset's $\hat{a}$ (Rousset, 1997), again these were calculated in R following the methods utilised in SPAGeDi. Population density ($D$) is the number of individuals in a $m^2$, which was estimated i) using the previously calculated density metric for adults of each parity mode and ii) assuming our sampling collected 1/5th of the extant population (i.e. $D$*5). A reasonable approximation of density is sufficient and appropriate, as our focus is on the differences between lineages and sexes and a demographic estimate of effective density is not available. Bootstrapping of the genomic data was performed, as described previously, with 15,000 replicates to allow 95% bCa bootstrap confidence intervals to be calculated for the regression slopes, and therefore the dispersal distances.

Additionally, the hierfstat R package was used to calculate the corrected assignment index (AIc) as described in Goudet *et al.* (2002), which estimates the probability that each individual is an immigrant at its location. The mean corrected assignment index ($mAIc$) compared between sexes is a measure for sex-biased dispersal (Goudet *et al.*, 2002). After recoding the genotypes into the required format, the sexbias.test function using the mean corrected assignment index (mAIc) test, a two-sided test statistic and 20000 permutations was used to test for sex biased dispersal in each parity mode.

## Results

### Spatial distribution

The final dataset consisted of 11,726 SNPs for 310 oviparous (111 male, 199 female) and 293 viviparous individuals (72 male, 221 female) sampled at high spatial resolution (Figure 1A). The mean distance between a pair of oviparous individuals was 178 m. The maximum spatial distance between a pair of oviparous individuals was 648 m. The mean distance between viviparous individuals was 326m and the maximum spatial distance between a pair of viviparous individuals was 1021 m (Figure 1B,C). The combined area of the oviparous sites (72,670 $\mathrm{m}^2$) is smaller than that of the viviparous sites (171, 552 $\mathrm{m}^2$) while our density metric for the collected individuals in the oviparous population (0.464 ind/100m$^2$) was 2.5-fold higher than in the viviparous population (0.189 ind/100m$^2$) (Table 1). At the oviparous sites, 28 individuals were caught more than once and four individuals were caught in all 3 years. In the viviparous sites, 21 individuals were caught more than once. This resulted in population sizes estimates, using the Schnabel method, of 1.708 ind/100m$^2$ (1241 individuals for the oviparous sites and 0.751 ind/100m$^2$ (1289 individuals) for the viviparous sites (Supplementary Table 1). Two individuals moved from an oviparous site to a viviparous site between years, no other individuals moved between sites.

### Diversity and differentiation

The levels of population genetic diversity were similar for the oviparous and viviparous populations. Observed heterozygosity was 0.225 for the oviparous population and 0.215 for the viviparous one. Within population gene diversity was 0.276 for the oviparous population and 0.266 for the viviparous population. The inbreeding coefficient was 0.185 for the oviparous population and 0.192 for the viviparous population. Population differentiation ($F_{ST}$ ) was substantial between the two populations, at 0.25.

### Inter-individual spatial genetic distance

As inferred from Moran's *I* correlograms, the autocorrelation between genetic and spatial distance decreases faster in the oviparous population than in the viviparous population (Figure 2, Supplementary Table 2), indicating that the genetic relatedness between oviparous individuals is more spatially restricted. The correlation in the oviparous population approximately crosses zero at 117 m and in the viviparous one it crosses zero at 280 m; distances beyond those values mean that any two individuals are no more related than any pair at random in the population. The x-intercept approximately represents patch size (roughly akin to neighbourhood area; Sokal & Wartenberg (1983)). Correlograms using kinship metrics (Loiselle et al., 1995; Ritland, 1996) provide additional support for these results and are consistent in their pattern (Supplementary Figure 2).

### Sex-specific spatial genetic patterns

Using Rousset's $\hat{a}$ estimations (Supplementary Figure 3) we inferred greater gene dispersal distances ($\sigma$) in the viviparous population (31.4 $m$ 95% CI 30.2 - 32.7) than in the oviparous population (14.8 m, 95% CI: 14.4 - 15.2) and greater dispersal distances in males compared to females (Figure 3, Supplementary Figure 4). In the viviparous population, the estimate for males was 41.8 m (95% CI, 38.3 - 46.8) and approximately 1.5x higher than that for females at 28.9 m (95% CI, 27.9 - 30.1). In the oviparous population, males were estimated at 18.9 m (95% CI: 17.9 - 19.9) and females at 13.7 m (95% CI: 13.3 - 14.2).

For the oviparous population, the mean corrected assignment index (mAIc) did not differ between the sexes: 3.333 ± 37.108 (standard error) for oviparous males and -1.859 ± 28.916 for oviparous females (statistic = -0.110, p=0.912) (Figure 4A). In the viviparous population, we found that the mAIc estimates of males (-101.920 ± 53.893) and females (33.205 ± 29.628) differed (statistic = 2.197, p = 0.033) (Figure 4B). The lower mAIc value in viviparous males compared with females indicates male-biased dispersal.

## Discussion

We identified important and marked population genetic and dispersal differences between oviparous and viviparous lizards. The two *Z. vivipara* lineages with differing life histories and reproductive strategies are adjacent and even overlap, so they therefore experience similar environments. We found the viviparous individuals have larger genetic patch size or neighbourhood area, as reflected in the Moran's $I$ correlogram. This biological pattern is also supported in the dispersal distances (Rousset's $\sigma$). While exact geographic distances need to be interpreted cautiously, here the direct comparison of genetic matrix and the same environment robustly shows that there are differences between lineages, with more spatial restriction, smaller genetic neighbourhood, and more limited individual dispersal in oviparous common lizards than in viviparous ones. Oviparous and viviparous populations had very similar population level diversity statistics, indicating no major underlying asymmetry. Our findings will provide a platform to enable direct comparisons to other amniotes with differing life histories as well as lizards in other species and environments.

Higher dispersal in the viviparous population compared to the oviparous one contradicts some of the previously discussed predictions regarding the potential drivers of parity-specific differences. For example, it does not support the prediction that the smaller clutches of viviparous females have reduced dispersal because of relatively less kin-competition among sibs and inbreeding avoidance. Similar population-wide inbreeding coefficients ($F_{IS}$) also suggest that inbreeding avoidance, more generally, may not be a driver of movement differences between the populations. This agrees with studies that have found little evidence that sibship relatedness (Léna *et al.*, 1998; Laloi *et al.*, 2009) and specifically its action through clutch size (Massot & Clobert, 2000; Cote *et al.*, 2007) play a role in determining dispersal in this species. Furthermore, the cost of inbreeding was demonstrated to be weak in a semi-captive population (Richard et al., 2009). It is unclear whether size plays a role in dispersal, though it is known that in some cases larger adult *Z. vivipara* are more likely to disperse (Le Galliard *et al.*, 2005a). Most dispersal happens in juvenile stage and viviparous neonates are smaller than oviparous hatchlings (Recknagel & Elmer, 2019), while adult viviparous females are larger than oviparous females (Recknagel & Elmer 2019). Viviparous and oviparous males do not differ in size (Roitberg et al., 2020; Elmer unpubl). Additionally, there are often complex relationships between size, dispersal and the environment (Clobert et al., 2009; Cote and Clobert, 2007; Stevens et al., 2014). Establishing any relationship between individual lizard body size and propensity to disperse at these sites is unfortunately not possible with current data. However, if size is a motivator it may result in dispersal differences between the juvenile and the adult stage, given that which parity mode is large changes between those tomes. The life stage at which dispersal is happening at this site warrants further investigation.

Our finding of greater dispersal distance in viviparous *Z. vivipara* is consistent with an influence of mother-offspring interactions. Viviparous offspring are more likely to directly experience the mother. This provides additional cues, absent in oviparous clutches, about the quality of the habitat or the degree of mother-offspring kin-competition (Léna *et al.*, 1998; Le Galliard *et al.*, 2003). This life-history difference may explain the increased dispersal in the viviparous population; as a mechanism of avoiding strong kin competition from the mother (Vercken *et al.*, 2007; Li & Kokko, 2019) or the ability to make more informed decisions about dispersal regarding the quality of the current habitat (Vercken *et al.*, 2012). These factors could, in turn, have led to the evolution of more frequent dispersal through increased reproductive success of dispersers. Furthermore, research has demonstrated that pre-natal stress plays an important role in determining if offspring will disperse (Meylan *et al.*, 2004; Vercken *et al.*, 2007). These cues are likely to be stronger for viviparous offspring as they are received at a later development stage and closer to parturition than in the case of oviparous clutches. Alternatively, there is an argument that due to their longer period out of the mother (i.e. external incubation), oviparous clutches are more sensitive to environmental signals that could inform dispersal decisions. However, information is likely to be localised to the nest site and evidence for an effect of incubation environment on dispersal is equivocal (Gifford et al 2017). The role of environmental effects and maternal cues during development and in relation to dispersal require further study, as do the mechanisms through which they operate.

Our finding is also compatible with our predictions based on resource availability in the form of nest sites. Nest site abundance within and outside the current habitat is likely - in oviparous lineages only - to inflict a selective pressure against dispersal from a site with suitable habitat. While specifics about nest sites requirements are unknown, it is likely that both humidity (Recknagel *et al.,* 2019, 2023; Rodríguez-Díaz and Braña, 2011) and temperature play important roles (Rodríguez-Díaz *et al.*, 2010). That we identified notably lower dispersal in the oviparous population (approximately half that found in the viviparous population) suggests that nest site availability at the study site is not limiting and this resource may influence of dispersal differences between parity modes. This may further be influenced by the oviparous species being limited by suitable nest incubation temperature rather than nest sites, given the high-elevation location of these populations (Figure 1A) relative to the overall distribution of the lineage. Previous research has shown that, even with the same habitat available to the oviparous and viviparous lizards at this site, the use of microhabitat differs by sexes and parity modes (Recknagel *et al.,* 2023). Females are found less often in open ground than males are, and oviparous individuals more often in wetter areas than are viviparous individuals (Recknagel *et al.,* 2023).

Abundant nest-site availability might explain the reduced evidence of male-biased dispersal in the oviparous population relative to the viviparous one. The observation that polygyny leads to male-biased dispersal is often attributed to males being the resource limited sex; this contrasts with the situation in most oviparous species where it is female reproduction that is directly limited by local resources (Li & Kokko, 2019). In this situation the major limiting resource for males is likely to be mate availability, leading to a positive relationship between male and female dispersal. There is some previous evidence of male biased-dispersal in *Z. vivipara* in two viviparous populations in Southern France (Sorci *et al.*, 1994; Le Galliard *et al.*, 2003, 2005a) but at one of these locations different studies found no evidence of sex bias (Massot & Clobert, 2000; Léna *et al.*, 1998; Lecomte *et al.*, 2004; Laloi *et al.*, 2009), and it has also been found to be absent in other locations (Strijbosch, 1995; Hofmann *et al.*, 2005). Genetic methods such as assignment index require that relatively strong sex-bias exists in the population for it to be detected (Goudet *et al.,* 2002). In our study, we have equivalent high-density spatial sampling and high numbers of individuals for both parity modes, so our comparisons have relatively high power to confidently draw comparisons. It is likely that sex-biased dispersal varies both spatially and temporally throughout the lizard active period, and these patterns and their consequences for demography need further investigation.

Viviparous squamates tend to have a more diverse range of habitats that they are able to occupy (Whittington *et al.*, 2022). Consequently, the risks of dispersal for viviparous individuals are likely reduced, which is predicted to facilitate the evolution of higher levels of dispersal (Kisdi, 2002; Nurmi & Parvinen, 2011). This is particularly true at our study site, where the oviparous population is at the top edge of its altitudinal range (Horreo *et al.*, 2018; Recknagel *et al*. 2021). More informed decisions about when to disperse through signals from, and kin-competition with, the mother (Léna *et al.*, 1998; Le Galliard *et al.*, 2003; Meylan *et al.*, 2004; Vercken *et al.*, 2007), along with increased chance of successful dispersal, provides more opportunities to colonise new habitats in the viviparous individuals (Clobert *et al.*, 2009). From an evolutionary point of view, along with higher dispersal, this may explain the prevalence of the viviparous lineages across Eurasia compared to much more restricted distribution of the oviparous lineages (Horreo *et al.*, 2018). Levels of dispersal directly relate to the amount of gene flow between neighbouring populations; this is likely to have a major impact on genetic differentiation over geographical space, and ultimately the likelihood of diversification events over evolutionary time-scales (Slatkin, 1973; Kisel & Barraclough, 2010).

The differing selection pressures experienced by the alternate parity modes may lead to changes in a wide range of genetic mechanisms through which parity-specific dispersal patterns arise. Some major-effect candidate genes relating to dispersal have been identified across diverse amniotes; several studies have found links to circadian clock genes (Chakarov et al., 2013; San-Jose et al., 2023; Saatoglu et al., 2024) and those involved in nervous system function (Delmore et al., 2016; San-Jose et al.2023) while other identified genes are more likely system specific (Caillaud et al., 2002; Niitepõld and Saastamoinen, 2017). The nature of a behavioural phenotype such as dispersal is complex, and may operate through various related traits, for example mobility, navigational ability, cognitive performance, or body size. An increased propensity to disperse may also be part of a wider behavioural syndrome including other traits, such as activity and boldness (Fraser et al., 2001; Dingemanse et al., 2003; Duckworth and Badyaev, 2007). Relationships of this nature have been identified in *Z. vivipara* (Cote and Clobert, 2006; Cote et al., 2010) and a genetic component to dispersal has been demonstrated (San-Jose et al., 2023). Therefore, further research will provide a powerful system to explore these potential mechanisms in a parity-specific context and continue to elucidate the evolutionary drivers of population structure. In combination with explicit landscape modelling, this would enable linking environmental variables to the genotypes present (Joost et al., 2007). The presence of hybrid individuals at this site (Recknagel et al. 2021a), which were not included in the current study, further increases our ability to identify whether landscape use is related to particular genotype combinations and how this alters dispersal.

Future research would benefit from increased sampling effort over a longer timescale, allowing estimates of fundamental demographic parameters such as survival and fecundity. The link between individual variation and parity-specific dispersal patterns could provide a more complete understanding of the population dynamics within each lineage. Other important components of demography may require the use of mark-recapture studies, or tracking devices, to directly measure dispersal in a way that cannot be achieved through genetic data alone (Cayuela *et al.*, 2018). Finally, multigenerational datasets, and associated pedigree information, allow more detailed investigation into the processes that generate isolation-by-distance patterns (Aguillon *et al.*, 2017). This type of data would allow questions to be answered regarding the variables (intra-individual, inter-individual and environmental) that determine the probability that any individual, of a given parity, sex, or stage will disperse and over what distances this is likely to happen. Such measures will be key to linking microevolutionary parity mode differences to their macroevolutionary impacts.

## Conclusion

Through population genomic and spatial data across the landscape, we have demonstrated clear differences in dispersal between two different reproductive strategies of *Z. vivipara*. The viviparous population has approximately two-fold more dispersal and extent of spatial genetic autocorrelation than the adjacent oviparous population, reflective of greater dispersal distances for viviparous individuals and larger patch sizes or neighbourhood areas. We found population genetic evidence of male-biased dispersal in the viviparous population. In the oviparous population, evidence for male-biased dispersal was weak or absent. We therefore infer that the females of both parity modes are the more philopatric sex. A reasonable explanation for these parity-specific differences is that at our study site nest sites are abundant and act as a limiting resource for females in the oviparous population; a pressure which is absent in the viviparous population. We speculate that these differences arose due to the different evolutionary histories of the two species and their specific habitat requirements. These findings enhance understanding of parity mode differences at microevolutionary scales and will enable comparisons to other taxa.

**Data Availability:**

This study uses previously published genomic data (NCBI: PRJNA657575). The genotype vcf file and scripts used in analysis are permanently archived on the University of Glasgow Enlighten repository, https://doi.org/10.5525/gla.researchdata.1703.

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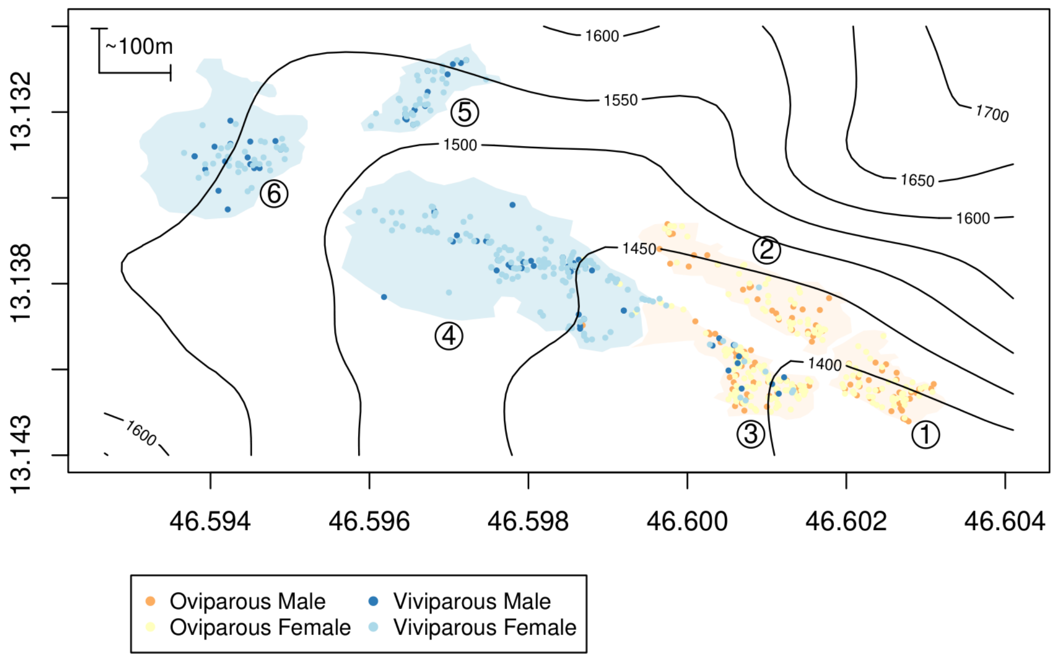
Table 1: Density information calculated for each of the six sampling sites combined across years.

| Site | Oviparous Individuals($n_o$) | Viviparous Individuals($n_v$) | Area ($100m^2$) | Density metric (($n_o + n_v$)/$100m^2$) |
|---|---|---|---|---|
| 1 | 79 | 0 | 177 | 0.447 |
| 2 | 79 | 1 | 309 | 0.259 |
| 3 | 143 | 22 | 241 | 0.685 |
| 4 | 9 | 164 | 1035 | 0.167 |
| 5 | 0 | 49 | 171 | 0.287 |
| 6 | 0 | 57 | 510 | 0.112 |

(A)



(B) Oviparous

(C) Viviparous

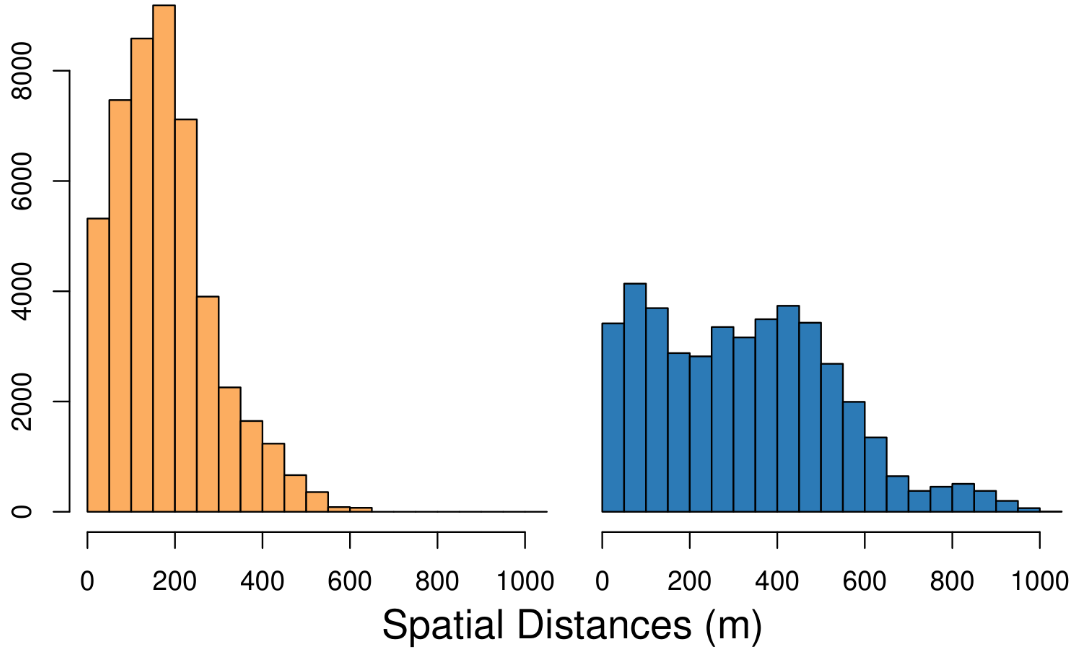


Figure 1: Maps showing sample sites and locations (A) of the oviparous population (orange) and viviparous population (blue). The number assigned to each site is shown in a circle. Latitude (N) and longitude (E) are presented on the y and x axes. Histograms showing the distribution of pairwise spatial distances between individuals from the oviparous lineage (B) and the viviparous lineage (C).

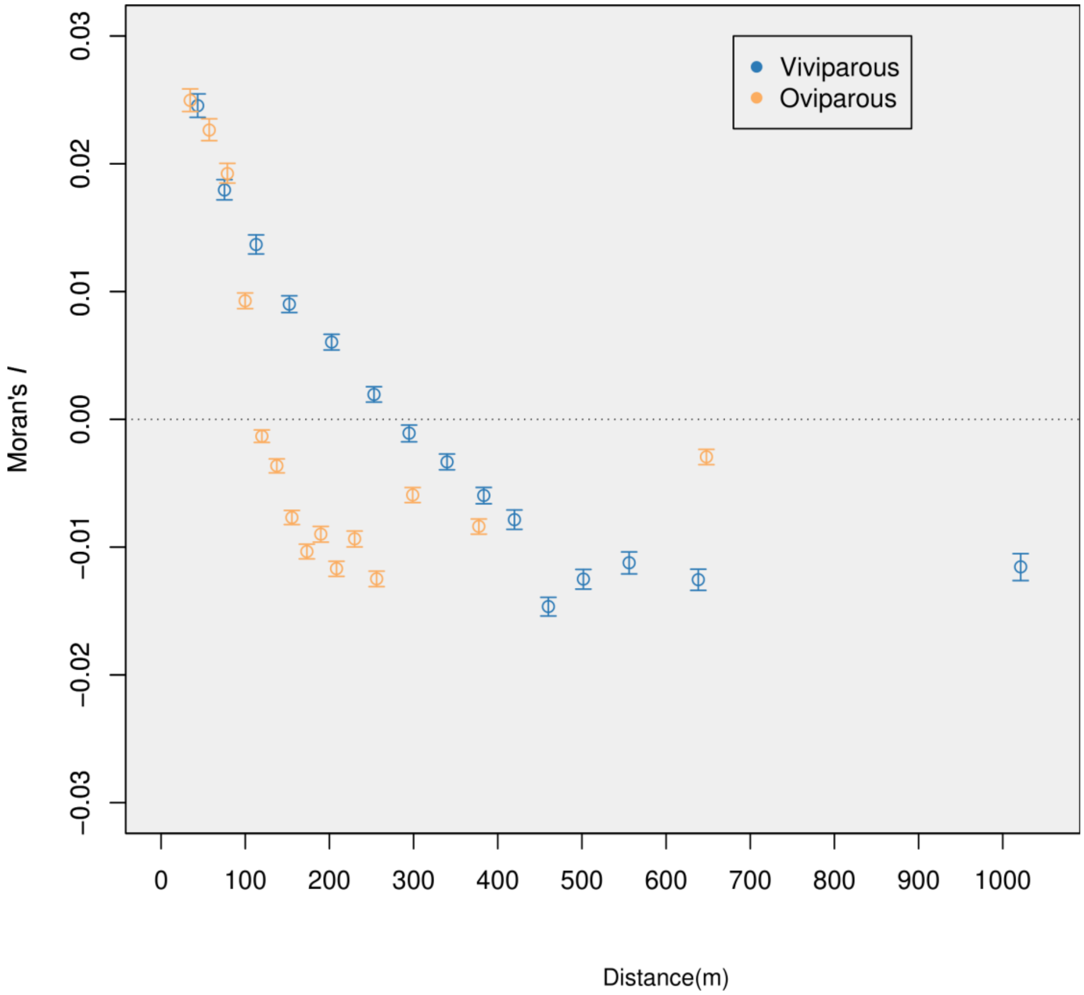


Figure 2: Moran's *I* correlograms for the viviparous lineage (blue) and the oviparous lineage (orange). Error bars indicate the 95% BCa bootstrap confidence intervals. The plotted values and distance classes are provided in Supplementary Table 2

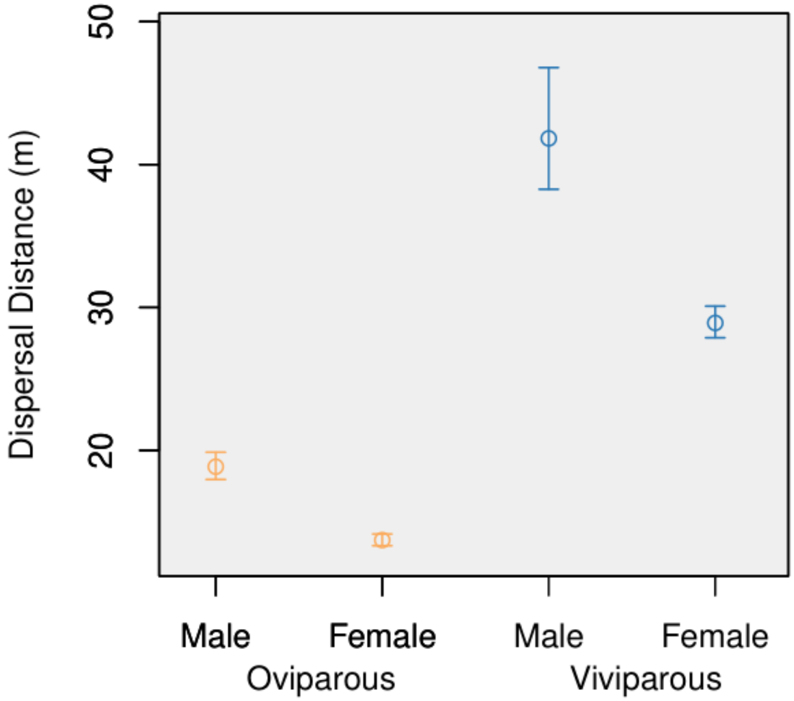


Figure 3: Estimated dispersal distances ($\sigma$) for each sex, based on Rousset's $\hat{a}$ (Rousset, 1997) for the oviparous lineage (orange) and the viviparous lineage (blue). Error bars indicate the 95% BCa bootstrap confidence intervals.

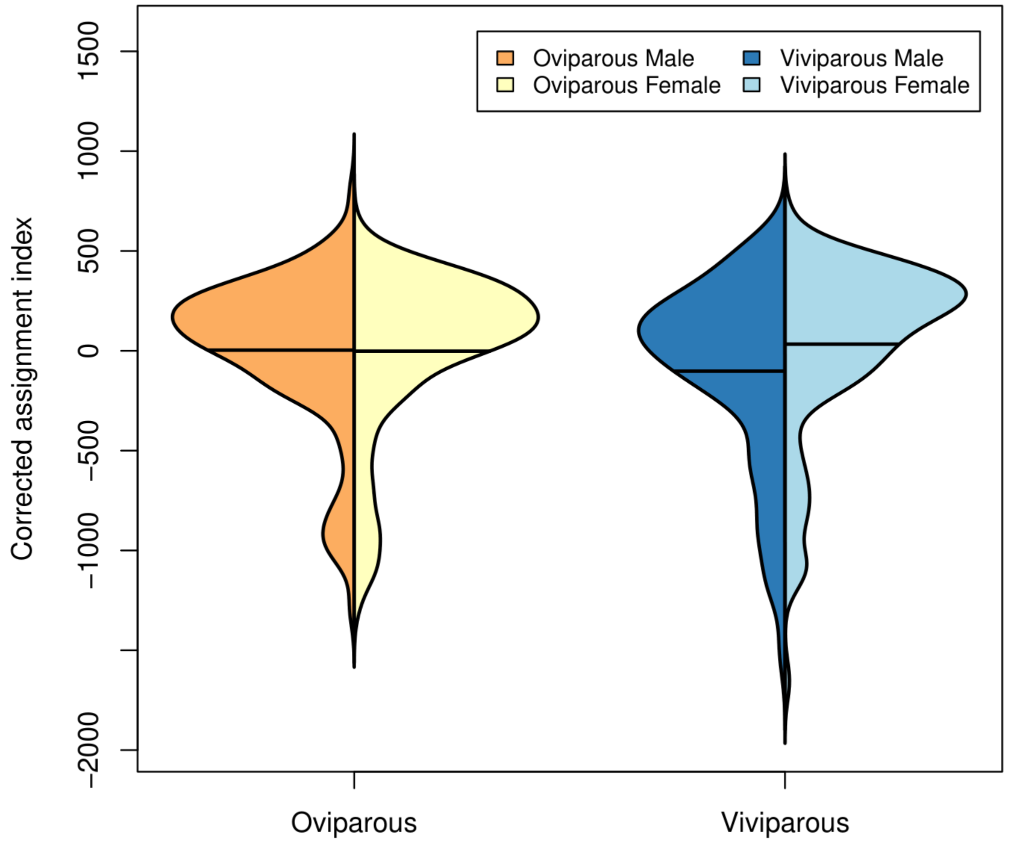


Figure 4: Density plots showing the corrected assignment index per sex for the oviparous lineage (orange) and the viviparous lineage (blue). Horizontal lines indicate the mean AIc.