RESEARCH PAPER

Environmental drivers of sexual dimorphism in a lizard with alternative mating strategies

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Abstract

Understanding the relative importance of sexual and natural selection in shaping morphological traits is a long-standing goal of evolutionary ecology. Male-biased sexual size dimorphism (SSD) is typically associated with male–male competition. Similarly, male polymorphisms are considered a consequence of competitive social interactions. This classic paradigm overlooks the fact that environmental factors mediate social interactions and can lead to ecological adaptations. Common side-blotched lizards, *Uta stansburiana,* are a model system for this paradigm due to well-known rock-paper-scissors social dynamics between male morphs. SSD in this species has been considered primarily a consequence of social interactions, with male size resulting from the number of morphs in each population and female size being constrained through fecundity benefits. We test if the environment explains intraspecific variation in SSD and number of male morphs in *U. stansburiana.* By compiling data from 49 populations, we show that environmental variables are stronger predictors of SSD than the number of male morphs. Similarly, we show that the environment mediates SSD and potentially contributes to morph loss in colder environments. We propose that the environment favours smaller males in areas of high seasonality. Our results demonstrate the importance of the environment as a mediator of SSD.

KEYWORDS
polymorphism, reverse Bergmann cline, side-blotched lizard, SSD, temperature-size rule, *Uta stansburiana*

1 | INTRODUCTION

Evolution often gives rise to multiple optimal phenotypes within a single species (Ford, 1945; Gross, 1996; Huxley et al., 1955; Rueffler et al., 2006). Sometimes, this results in females and males presenting distinct morphologies and/or behaviours, which is known as sexual dimorphism (Lande, 1980). The evolutionary origin of SSD is typically attributed to sexual and natural selection creating different optimal phenotypes in males and females (Blanckenhorn, 2005; Fairbairn et al., 2007; Hedrick & Temeles, 1989). In this traditional view, male

fitness depends greatly on male–male competition, and female fitness depends mostly on her fecundity (Lande & Arnold, 1985).

Sexual selection by male–male competition is one of the main drivers of large male body size in nature (Kingsolver & Pfennig, 2004). For example, larger males have been shown to have an advantage in acquiring mates relative to smaller males in lions, beetles, primates, pinnipeds, cichlids and birds, among other taxa (see reviews in Andersson, 1994; Blanckenhorn, 2000; Kingsolver et al., 2001). Fecundity advantages associated with large female size have also been well-documented using wide phylogenetic comparisons in

spiders (Head, 1995), experimental evolution in *Drosophila melano-gaster* (Reeve & Fairbairn, 1999) and with the weevil *Callosobruchus chinensis* (Kyogoku & Sota, 2020), common-garden experiments with water striders (Preziosi et al., 1996), and in studies of growth patterns of mole-rats (Thorley et al., 2018), among other groups (Blanckenhorn, 2005; Shine, 1988).

A less common form of intraspecific variation occurs in the form of intrasexual polymorphisms, that is, morphological and behavioural differences between individuals of the same sex (Brockmann & Taborsky, 2008; Engqvist & Taboorsky, 2016; Gadgil, 1972; Svensson, 2017). As with the evolution of SSD, the evolution of intrasexual polymorphisms is often thought to be strongly influenced by social interactions between individuals with morph-specific alternative reproductive tactics (Shuster & Wade, 2003), where the costs and benefits associated with each particular phenotype depend on conspecific social interactions (Alonzo & Sinervo, 2001; Gross, 1996; Svensson et al., 2005).

Yet, social interactions like male–male competition happen in a complex landscape. Abiotic and biotic variables such as temperature, precipitation, seasonality, vegetation profile, and the presence/absence of predators and competitors can vary across a species geographic distribution. Such landscape variation may greatly alter the balance between natural and sexual selection (Chenoweth et al., 2008; Machado et al., 2016; Rotenberry & Zuk, 2016). Moreover, environmental variables are known to influence social interactions (Lancaster et al., 2017), and modulate the intensity of sexual conflict (García-Roa et al., 2019; Svensson et al., 2020). As such, sexual and intrasexual polymorphisms are unlikely to remain constant across an entire species range (Barbosa et al., 2018; Blanckenhorn et al., 2006; Cooper, 2010; Cox & Calsbeek, 2010; Cox et al., 2003; Littleford-Colquhoun et al., 2019; Stillwell et al., 2007). Indeed, SSD varies geographically and along environmental gradients in lizards (Cox et al., 2003; Tarr et al., 2019), bobcats (Dobson & Wigginton, 1996), bats (Storz et al., 2001), beetles (Stillwell et al., 2007), and multiple other vertebrate and invertebrate taxa (Blanckenhorn et al., 2006). Yet, whether the environment actually drives the evolution of SSD and intrasexual polymorphisms is poorly understood (Slatkin, 1984; Shine, 1989, but see Temeles et al., 2000; Laiolo et al., 2013; Tarr et al., 2019, Lancaster et al., 2017). Not taking into consideration the role played by both biotic and abiotic variables in generating intraspecific phenotypic variation may therefore lead to erroneous conclusions regarding trait evolution and diversification (Hendry et al., 2014).

In lizards, SSD has been attributed to intrasexual selection favouring large males (intrasexual selection hypothesis), and fecundity selection favouring large females (fecundity selection hypothesis, Cox et al., 2007). In this scenario, populations under different environmental pressures, such as longer or shorter winters, may be under stronger or weaker selection, leading to variation in the resulting female and male sizes and, consequently, in the degree of SSD found across the species range. Support for either of these hypotheses is far from ubiquitous, though. A study encompassing almost 500 lizard populations from 302 different species found only

weak support for both the fecundity hypothesis and the intrasexual selection hypothesis (Cox et al., 2003). Additionally, ecological differences between the sexes have been shown to play a greater role in the evolution of sexual dimorphism than sexual selection in *Anolis* lizards (Butler et al., 2000, 2007), while a meta-analysis of 446 lizard species from across Central and North America also failed to support the fecundity hypothesis as a driver of SSD evolution, rather finding an effect of seasonality on male size (Tarr et al., 2019). Male size has been shown to be more variable than female size in horned lizards and in anoles, driving most of the intraspecific variation in SSD observed in these species (Bonneaud et al., 2016; Zamudio, 1998). Together, these results suggest that the fecundity hypothesis and the intrasexual selection hypothesis are unlikely to be the sole drivers of SSD variation in lizards.

One of the best-studied model species for polymorphism evolution is the side-blotched lizard, *U. stansburiana* (Baird & Girard, 1852). *Uta stansburiana* exhibits both male and female colour polymorphisms which are associated with alternative reproductive tactics (Sinervo & Lively, 1996; Sinervo & Zamudio, 2001). *Uta stansburiana's* degree of SSD has been shown to vary along a north–south gradient (Corl et al., 2010; Parker & Pianka, 1975). The number of morphs found in a population of *U. stansburiana* is strongly correlated with its degree of sexual size dimorphism, with populations containing all three morphs presenting male-biased SSD, populations with two morphs presenting small degrees of male-biased SSD, and populations where only one morph persists lacking SSD or exhibiting slightly female-biased SSD (Corl, Davis, Kuchta, Comendant, et al., 2010). The prevailing hypothesis explaining this correlation states that morph loss relaxes sexual selection, and therefore reduces the benefits associated with large male size, while female size is maintained by fecundity benefits (Corl, Davis, Kuchta, Comendant, et al., 2010). Varying degrees of SSD would therefore be the result of varying intensities of sexual selection acting on males, lower survivorship of large males in colder environments, and increased selection for female fecundity in seasonal areas (Corl, Davis, Kuchta, Comendant, et al., 2010).

Uta stansburiana is distributed across the Western United States, Northwestern and Northern Mexico, where it can be found in rocky outcrops, crevices and dry washes, from low elevation deserts to mountain slopes (McKinney, 1971). Given its vast geographic range, populations of this species are exposed to a wide range of environments, from low elevation deserts to mountain slopes. Such environmental differences are likely to play an important role in the intraspecific phenotypic variation observed across *U. stansburiana's* range. Moreover, as male morphs and females of this species differ in their territoriality and use of habitat (Calsbeek & Sinervo, 2002a; Sinervo & Zamudio, 2001), both sexes, and morphs within each sex, are likely to interact differently with the environment surrounding them.

Here, we address how an environmental gradient may influence both the degree of SSD and male polymorphisms in *U. stansburiana*. We operationally define "environment" as the set of abiotic and biotic variables (other than intraspecific interactions) to which

any given population is exposed. We seek to: (I) determine how population-level variation in morph number and SSD is distributed in a phylogeny of *U. stansburiana*. We predict that SSD is more male-biased in populations presenting all three male morphs (i.e. Corl, Davis, Kuchta, Comendant, et al., 2010). Then, (II) we test if geographic variation, characterized here as the combination of latitude and elevation, explains intraspecific variation in SSD and number of male morphs in *U. stansburiana*. More specifically, we predict that the environment influences growth patterns in *U. stansburiana*, affecting the resulting degrees of SSD independently of a population's number of morphs. Finally, (III) we take a closer look at SSD and the number of morphs individually and test the relationship between four abiotic and two biotic environmental variables on the intraspecific variation in SSD and number of morphs. We predict that male-biased SSD and polymorphism are driven by a similar set of environmental variables, which would explain their frequent co-occurrence.

2 | METHODS

2.1 | Study system

Male *U. stansburiana* belong to one of three colour morphs (orange, yellow and blue). Orange males are aggressive and defend large territories, yellow males sneak copulations from orange males' territories, and blue males cooperatively guard small groups of females. Although the three male morphs differ in mass (Sinervo et al., 2000), they do not differ in snout–vent length (Corl, Davis, Kuchta, Comendant, et al., 2010), the metric of body size typically used in calculations of SSD in lizards (Cox et al., 2007). The male morphs have a rock-paper-scissors mating system, where orange wins over blue but loses to yellow, and blue wins over yellow (Sinervo & Lively, 1996; Sinervo & Zamudio, 2001). Female *U. stansburiana* are dimorphic: orange females lay large clutches of small offspring, and yellow females lay small clutches of large offspring (Sinervo et al., 2000). Orange and yellow females do not differ in snout–vent length (Corl, Davis, Kuchta, Comendant, et al., 2010).

Male and female morphs have been shown to have a heritable genetic basis, with orange and yellow males being either homozygous or heterozygous (with orange being dominant over yellow) and blue males being always homozygous and recessive to both orange and yellow (Corl et al., 2010; Sinervo & Lively, 1996; Sinervo & Zamudio, 2001; Zamudio & Sinervo, 2000). Males presenting orange markings, either in a solid colour (presumed homozygotes—*oo*) or in mixed patches with yellow or blue (presumed heterozygotes—*oy* or *ob*), exhibit an aggressive orange male strategy. Similarly, males presenting yellow markings, either in a solid patch (presumed homozygotes—*yy*) or mixed with blue (presumed heterozygotes—*yb*), exhibit a sneaker yellow male strategy (Corl, Davis, Kuchta, & Sinervo, 2010; Sinervo & Lively, 1996; Sinervo & Zamudio, 2001; Zamudio & Sinervo, 2000). *Uta stansburiana* also presents sexual

dimorphism in size (SSD) and colour, where females are generally smaller than males (some populations excepted) with much subtler coloration than males (Corl, Davis, Kuchta, Comendant, et al., 2010; Ferguson, 1966).

2.2 | Data collection

2.2.1 | Field data collection

We sampled 15 populations of *Uta stansburiana* (Table S1) from the Southwestern United States in April-June 2016, 2017. Five of these populations were sampled in the vicinity of localities from Corl, Davis, Kuchta, Comendant, et al. (2010) and Corl, Davis, Kuchta, and Sinervo (2010). In each population, adults were captured by lassoing, sexed, measured (snout-to-vent length, SVL) to the closest 0.1 mm with calipers, weighed and photographed. We only included sexually mature animals, determined by the smallest size at which males exhibited breeding coloration and females exhibited evidence of gestation. Prior to releasing them, we clipped 1 cm of tail and preserved it in RNA-preserving tissue storage solution (following protocol by https://sfg.stanford.edu/RNAbuffer). Samples were maintained refrigerated at 4°C throughout transportation until long-term storage at −80°C.

We categorized male and female colour morphs based on independent inspection by two experienced observers following Corl, Davis, Kuchta, Comendant, et al. (2010). Populations were scored as trimorphic based on the presence of at least one male of each morph (orange, yellow or blue), dimorphic when at least one male of two different morphs was found, and monomorphic when all individuals captured belonged to the same colour morph. For yellow and orange males, we treated homozygotes and heterozygotes as belonging to the same morph (yellow or orange), since heterozygotes and homozygotes exhibit the same behavioural strategy (Sinervo & Zamudio, 2001). We aimed at sampling 15 males and 15 females at each locality; however, in some regions with small populations all individuals encountered were opportunistically captured. Only populations where at least five individuals of each sex had been sampled were included in our analyses. To ensure that in monomorphic populations males had not been under sampled, we conducted a Poisson regression with the number of males found in each population as the predictor variable and the population's number of morphs as the response variable. We calculated the degree of SSD of each population using a two-step process, following previously established methodologies for studies of SSD in *U. stansburiana* (Corl, Davis, Kuchta, Comendant, et al., 2010): if males are larger than females, SSD = average male size/average female size. If females are larger than males, SSD = 2 − female size/male size. This method has the advantage of resulting in SSD indexes that vary linearly and continuously, and are centred around 1 rather than 0, with indexes > 1 indicating male-biased populations and indexes < 1 indicating female-biased populations (Corl, Davis, Kuchta, Comendant, et al., 2010; Smith, 1999).

2.2.2 | Molecular analyses

We extracted DNA from the tissue samples of all individuals collected using a Qiagen DNEasy Blood and Tissue Kit®. Once extracted, we randomly selected up to 10 males and 10 females from all populations and amplified the mitochondrial genes Cytochrome b (*CytB*) and ATPase 6 (*ATP6*). We amplified both genes following the methods outlined in Corl, Davis, Kuchta, Comendant, et al. (2010) and Corl, Davis, Kuchta, and Sinervo (2010), but with increased annealing temperatures (55°C). Individual polymerase chain reactions (PCR) for both genes were 25 µl in total volume and contained 1 µl of genomic DNA, 0.5 µl of each primer (in a 10 µM solution), 10.5 µl of molecular grade water and 12.5 µl of GoTaq® G2 Hot Start Green Master Mix (Promega). PCR products were purified with SeraSpeed Beads, following Reich's (2012) protocol modified by Faircloth and Glenn (2016), and sequenced by the University of California, Berkeley DNA Sequencing Facility. We then aligned, manually edited and assembled the obtained sequences into a single consensus sequence for each individual using Geneious© Biological (Biomatters). Sequences are available on GenBank (ATP Synthetase accession numbers: MZ332537–MZ332728. Cytochrome b accession numbers: MZ332729–MZ332919).

2.2.3 | Literature data

We compiled data from 34 populations originally sampled by Corl, Davis, Kuchta, Comendant, et al. (2010) focusing solely on those from the mainland USA, as that is the area for which we obtained the most environmental variables (see *Assessing environmental drivers of SSD and number of morphs*, below). We gathered the average female and male size of each population from the literature, as well as the number of male morphs present at the time of collection. We obtained genetic sequences for these populations from GenBank (accession numbers GQ272687–GQ272944).

Phylogenetic patterns of population-level variation in morph number and SSD

We are primarily interested in the phylogenetic relationships among populations; therefore, we constructed a mitochondrial time-tree phylogeny including all populations for which we had data, compiling our sequence data with data from Corl, Davis, Kuchta, Comendant, et al. (2010) and Corl, Davis, Kuchta, and Sinervo (2010) (Figure S1). We jointly estimated the phylogeny and time tree using a multicoalescent species-tree approach with *BEAST2 (Bouckaert et al., 2014). We undertook multiple sequence alignments for each gene in Geneious© R11 Biological (Biomatters) using the MUSCLE algorithm. We checked alignments by eye to ensure cohesive reading frames and that there were no stop codons within coding regions. We then ran each gene partition in jModelTest v2.1 (Darriba et al., 2012) to determine the appropriate model of molecular substitution. We found that a GTR + I + G model best fit the data for both the *ATP6* and *CytB* partitions. We coded populations as tips in the

species-tree analysis. To be conservative, samples from locations in the vicinity of those in Corl, Davis, Kuchta, Comendant, et al. (2010) and Corl, Davis, Kuchta, and Sinervo (2010) were coded as separate populations since the exact locations reported in the literature could not be determined.

Because there are no internal fossil calibrations, we used a fixed rate of substitution for the *CytB* locus at 1.3% per million years, while allowing the substitution rate of ATP to be estimated. This rate for *CytB* is in line with many reported estimates for substitution rate in lizards (Brown et al., 2008; Macey et al., 1998). Using the BEAST2 v2.4 package (Bouckaert et al., 2014), we used a Yule model with a strict clock and standard settings set up in BEAUti for *BEAST2 analyses. We ran the analyses for 100 million generations, sampling every 5,000 generations with a 10% burn-in. We used Tracer v1.7.1 (Rambaut et al., 2018) to monitor plots of marginal posterior probabilities for convergence (Effective Sample Sizes > 150). At the completion of the run, we processed log and tree files using LogCombiner v2.4.7. We processed the posterior probability density of trees using TreeAnnotator v2.4.7 outputting a maximum clade credibility tree for use in downstream analyses. We also kept the posterior distribution of trees, minus burn-in, for downstream analyses. Analysis runs sampling from the prior confirmed that our results were not driven entirely by our priors. We retained 1,000 trees randomly sampled from the posterior distribution of trees to investigate the effects of phylogenetic uncertainty on our results.

Once we obtained the phylogeny, we trimmed it to the 49 populations for which we had high enough sample sizes, and mapped the calculated SSD indexes and numbers of male morphs onto it using the function *contMap*, from the package *phytools* (Figure 2). This function recreates the evolutionary trajectory of each character using a Brownian Motion correlation structure (Revell, 2012).

Geography as a driver of intraspecific variation in SSD and number of male morphs

To test our hypothesis (variance in SSD and number of morphs are both driven by environmental factors), we first ran a phylogenetically corrected ANOVA to test for differences in SSD between populations with one, two or all three male morphs. We ran this test using the function *phylANOVA* from the package *phytools* (Revell, 2012). Analyses were iterated over 1,000 trees to assess the effects of phylogenetic uncertainty.

Next, to determine what is the cause or consequence relationship between environment, SSD and number of morphs, we conducted a phylogenetic confirmatory path analysis. Path analysis is based on prespecified candidate path models (Figure 1), employing the *d* separation method (Gonzalez-Voyer & von Hardenberg, 2014).

To keep our models as simple as possible and to avoid collinearity issues, which may severely hinder the fit of path analysis models (Gonzalez-Voyer & von Hardenberg, 2014), we selected two variables to represent the environment in this analysis: elevation and latitude. Elevation and latitude are ideal environmental proxies for studies of wide geographic patterns (such as ours).
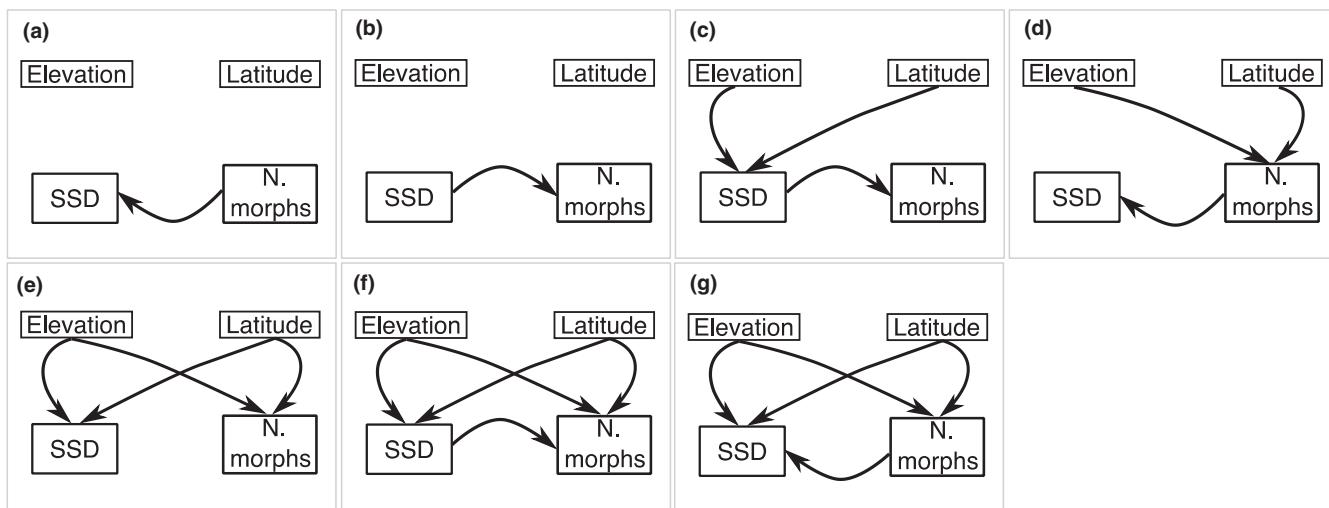
FIGURE 1 Set of candidate models for confirmatory phylogenetic path analyses determining the cause-and-effect relationship between environment, number of morphs and degree of SSD in populations of *Uta stansburiana*

Climatic variables such as temperature, precipitation and seasonality are known to vary in a predictable way along latitude and elevation gradients (Roff, 2002). Unlike climatic variables, however, elevation and latitude exhibit no correlation to one another. Animals and plants are known to exhibit many life-history shifts along elevation and latitude gradients, including changes in size and reproductive strategy (Cardillo, 2002; Jump et al., 2009; Tieleman, 2009), both factors central to our hypothesis. Indeed, the correlation between elevation, latitude and size is so well-known that they form the basis for a very general biological rule: Bergmann's rule, which states that organisms from higher latitudes/elevations will exhibit larger body sizes (Blackburn et al., 1999; Blanckenhorn, 2004; Mousseau, 1997).

To assess model support in our phylogenetic path analysis, we compared our full set of models (Figure 1) based on their degrees of separation and CIC values. Models with Fisher's C test smaller than 0.05 were discarded as poorly fit. Models with Fisher's C test higher than 0.05 were compared based on their CIC values, and those falling within a ΔCIC of 2.5 were averaged to provide the best-fit model (Gonzalez-Voyer & von Hardenberg, 2014). We ran these analyses using the R package *phylopath* (van der Bijl, 2018). We iterated our analyses over 1,000 trees chosen at random to assess how our results are affected by phylogenetic uncertainty.

Assessing environmental drivers of SSD and number of morphs
To better understand how the biotic and abiotic environments influence the intraspecific variation observed in degrees of SSD and number of morphs in *U. stansburiana*, we tested for evolutionary correlations between our variables of interest and the environment using phylogenetic-general-least-square models (PGLS—Grafen & Hamilton, 1989; Martins & Hansen, 1997; Pagel, 1999). Phylogenetic uncertainty in these analyses was assessed by iterating over 1,000 trees from the posterior distribution. To describe the environment in a precise manner, we used a multivariate approach. We compiled six publicly available GIS layers

comprising climatic descriptors and phenological indicators based on NDVI (Normalized Difference Vegetation Index, a measure of the "greenness" of an environment seen from above, which is an indicator of photosynthetic activity) (see references in Table 1).

Temperature, precipitation and their seasonality (climatic descriptors) provide us a precise indication of the year-round climate in any given region and are fundamental abiotic attributes of any ecosystem (Peel et al., 2007). Phenological indicators, such as amplitude of NDVI and duration of growth season, provide a precise estimate of how climatic variables influence the vegetation (a crucial biotic attribute in any given environment) at each of our population sites (Pettorelli et al., 2005). This particular set of variables also has the advantage of presenting relatively low levels of collinearity, as estimated by their variance inflation factors ($1.21 < $ VIF < 3.67).

Each layer was converted to a WGS84 latitude/longitude geographic projection, resampled at a 1 km^2 resolution and clipped to the general area around our 49 focal localities using the packages *raster* (Hijmans & van Etten, 2012) and *rgdal* (Bivand et al., 2019) in R. We then checked variables for normality and log-transformed those that were not normally distributed.

For each response variable (SSD, number of male morphs, and female and male size), we compared a set of PGLS models taking into account phylogenetic signal in the residuals of the linear regression, using correlation structures based on Brownian motion (BM) models (Revell, 2010). Each set of models originated from the full additive model including all environmental variables described in Table 1, on which we performed backward and forward stepwise regressions based on each model's AICc value. Since our backward and forward model selection procedure did not include a null model, we calculated the likelihood ratio of the best-fit model by comparing it to a null PGLS model, to eliminate the possibility that a null model would explain our results better than our best-fit model. We performed the PGLS analyses with the function *gls*, from the R package *nlme*

Environmental variable	Source
Average annual temperature (°C)	WorldClim 2.0 (http://worldclim.org/version2)
Annual precipitation (mm—log)	
Temperature seasonality (log)	
Precipitation seasonality (log)	
Duration of growing season (days)	2015 Aqua eMODIS Phenology Metrics (http://phenology.cr.usgs.gov)
Amplitude of photosynthetic activity (log)	

TABLE 1 Variables compiled to describe the environment in which focal populations of *Uta stansburiana* are found

(Pinheiro et al., 2019), and the backward and forward model selection with the function *stepAIC*, from the package *MASS* (Venables & Ripley, 2002).

3 | RESULTS

3.1 | Phylogenetic patterns of population-level variation in morph number and SSD

Sexual size dimorphism varied across our target populations between 0.973 (slightly female-biased) and 1.138 (male-biased), with a mean of 1.053. Only three populations had female-biased SSD: population 16, in Arizona, population 22, in Nevada, and population 30, in Utah. All three female-biased populations were found at high elevations (>1,300 m—Figure 2). In 20 populations, males were less than 5% larger than females (monomorphic for size). In the remaining 26 populations, males were between 5.1% and 13% larger than females (male-biased SSD). Female size (SVL) ranged from 42 mm to 53 mm, with a mean of 46.66 ($SE = 0.36$), and male size ranged from 44.6 to 57.6 mm, with a mean of 49.1 ($SE = 0.42$). With regard to number of morphs, 13 of our populations were monomorphic, 10 had two colour morphs, and 26 exhibited all three-colour morphs. Male sample size had no effect on the likelihood of finding one, two or all three male morphs (Estimate < 0.01, $df = 47$, $SE = 0.01$, $z = 0.61$, $p = .54$).

Our population-level phylogeny of *U. stansburiana* is broadly congruent with published data regarding relationships among clades (Corl, Davis, Kuchta, & Sinervo, 2010; Figure 2, see Figure S1 for posterior probabilities). Female-biased size dimorphism appears independently three times in our phylogenetic tree. Morph loss appears four times independently with three later re-acquisitions of the lost yellow morph, or eight times if morphs are never recovered once lost (Figure 2, see Corl, Davis, Kuchta, & Sinervo, 2010).

3.2 | Geography as a driver of intraspecific variation in SSD and number of male morphs

Our phylogenetically corrected ANOVA confirmed that populations with three male morphs have higher degrees of male-biased SSD than populations where morphs have been lost ($F = 12.25$, $df = 49$, residual $df = 47$, $p = .023$). This result held up when iterated over 1,000 trees from the posterior distribution (Mean $F = 12.25$, Standard Deviation (SD) $F = 0$; Mean $p = .021$, SD $p = .009$) where 100% of trees confirmed this result. Populations with one or two male morphs do not differ significantly in their degree of SSD whereas differences approach significance between one morph and three morph populations (pairwise comparisons—one morph versus two morphs: $t = 1.20$, $p = .261$; one morph versus three morphs: $t = 4.75$, $p = .057$; two morphs versus three morphs: $t = 2.75$, $p = .176$). Results with phylogenetic uncertainty iterated across 1,000 posterior trees showed no variance in t for these post hoc comparisons, but some variation in p values (pairwise comparisons—one morph versus two morphs: $t = 1.20 \pm 0$, $p = .25 \pm .013$; one morph versus three morphs: $t = 4.75 \pm 0$, $p = .051 \pm .012$; two morphs versus three morphs: $t = 2.75 \pm 0$, $p = .175 \pm .018$) where 47.3% of trees support significant differences between populations with one and three morphs.

The confirmatory path analysis showed that both SSD and number of morphs are more strongly influenced by the latitude and elevation than by each other (Figure 3). Of the seven models we compared, only three passed the threshold of fit determined by the Fisher's C test and were averaged to produce to final model (Table 2). These results were robust to phylogenetic uncertainty, with these 3 models ranked the same across all 1,000 posterior trees. The standard errors of the coefficients of the averaged best model show that, of the four variables used in our models, only the relationship between environment and SSD and environment and number of morphs is consistently positive (Figure 4). Indeed, note that the standard errors of the relationships between SSD and number of morphs are larger than the effect sizes themselves and encompass zero. These results are also reflected across all 1,000 posterior trees (Table 2).

3.3 | Environmental drivers of SSD and number of morphs

The model that best predicted variation observed in the degree of SSD across our populations using the median tree consisted of the additive effect of average precipitation, temperature seasonality (log), precipitation seasonality (log) and duration of growth season (Residual $SE = 0.17$, $df = 49$, Likelihood ratio = 20.95, $p < .0001$ for model on median tree, Residual $SE = 0.19 \pm 0.04$, $df = 49$, Likelihood ratio = 28.43 ± 27.08, $p = .02 \pm .07$ across 1,000 trees with 89.9% of
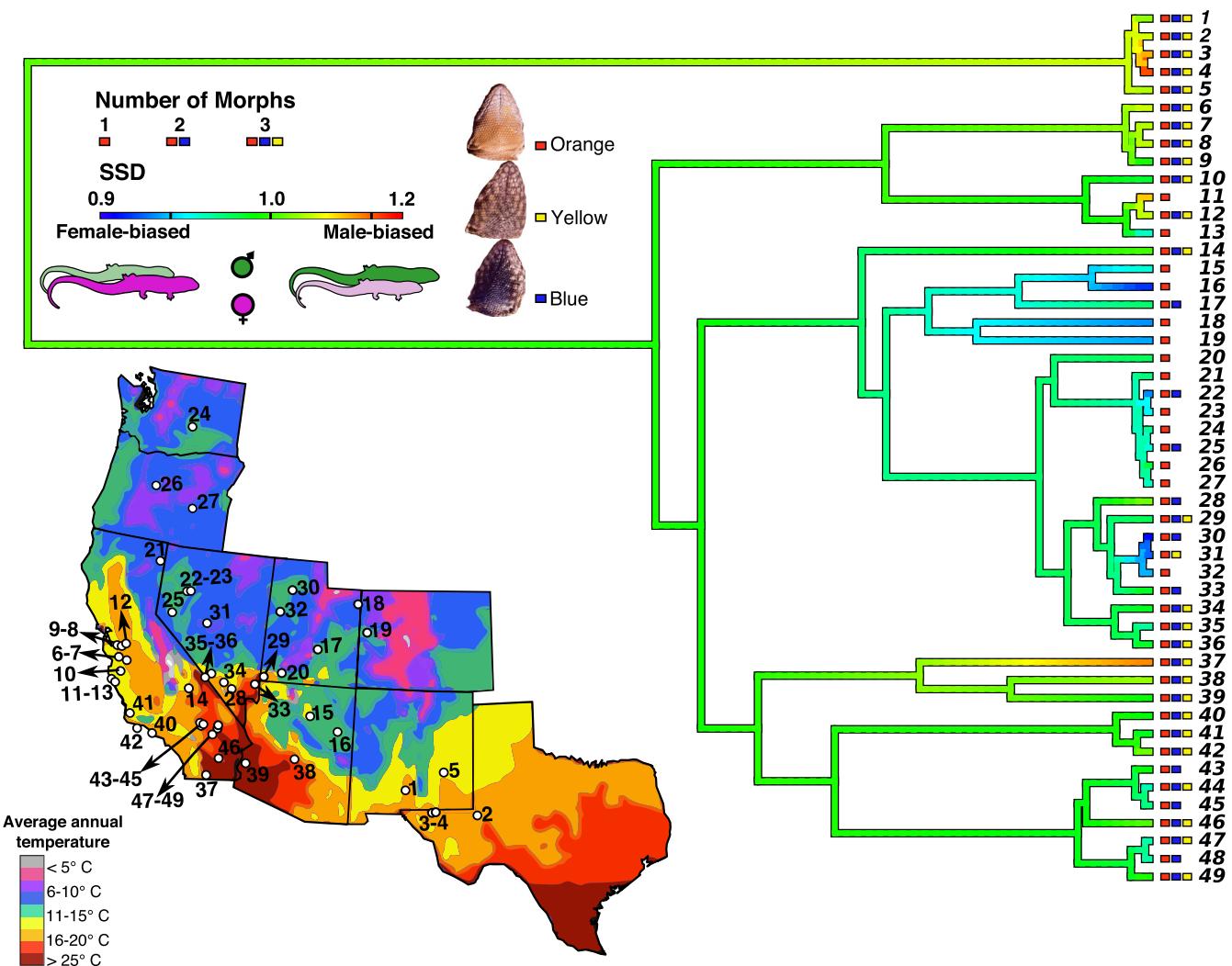
FIGURE 2 Phylogenetic distribution of the number of morphs and degree of sexual size dimorphism (SSD) across populations of *Uta stansburiana*. Colour at tips indicates the degree of SSD found in each population, with colder colours representing female-biased SSD and warmer colours representing male-biased SSD. The number and colour of the squares next to each tip represent the number and type of male morphs found in each population (with orange corresponding to orange males, blue to blue males and yellow to yellow males). The map indicates the site of origin of each population across the southwestern United States. Colours on the map indicate the average annual temperature to which each population is exposed

trees with $p < .05$). See Table 3 for full model estimates and associated p values from the median tree analysis. Assessments of the effect of phylogenetic uncertainty show that the set of four variables retained in our analyses for the median tree were retained in the full model 100% of the time when tested across a posterior distribution of 1,000 trees with average precipitation (46.9%; $t = −2.04 \pm 1.01$; $p = .13 \pm .19$; 46.9% significant contribution), temperature seasonality (39.4%; $t = −1.83 \pm 1.07$; $p = .18 \pm .22$; 39.4% significant contribution), precipitation seasonality (51.1%; $t = 2.23 \pm 1.05$; $p = .09 \pm .15$, 56.8% significant contribution) and duration of growth season (45.4%; $t = 2.10 \pm 3.13$; $p = .19 \pm .25$; 45.5% significant contribution) each contributing to a significant proportion of variation in models in many of the posterior distribution tree models. Average temperature was only retained 32% of the time and was never significant contributor to variation in the model in the posterior trees ($t = −0.13 \pm 0.79$; $p = .59 \pm .27$). Amplitude of photosynthetic activity was also retained

in 78% of cases, but only was a significant contributor in 5.4% of cases ($t = −0.69 \pm 0.93$; $p = .44 \pm .27$).

The number of morphs in a population was best predicted by the addition of average precipitation (log) and precipitation seasonality (log) (Residual $SE = 4.12$, $df = 49$, Likelihood ratio = 26.87, $p < .001$, Table 3 for the median tree, Residual $SE = 5.0 \pm 1.81$, $df = 49$, Likelihood ratio = 32.05 ± 28.11, $p = .01 \pm .04$ for the posterior trees). Our results show that the variables retained in the median tree analysis were retained 100% of the time across a distribution of posterior trees (average precipitation: $t = −2.41 \pm 1.31$, $p = .09 \pm .15$, 60.3% significant contributions; precipitation seasonality [$t = −1.65 \pm 1.32$; $p = .24 \pm .25$, 28.4% significant contributions], along with many posterior trees retaining temperature seasonality: 94.4%, $t = 0.57 \pm 0.77$, $p = .53 \pm .26$, 4% significant contributions). Other variables were not retained with such high frequencies, including average temperature (56.6%; $t = 0.01 \pm 0.52$; $p = .71 \pm .21$,
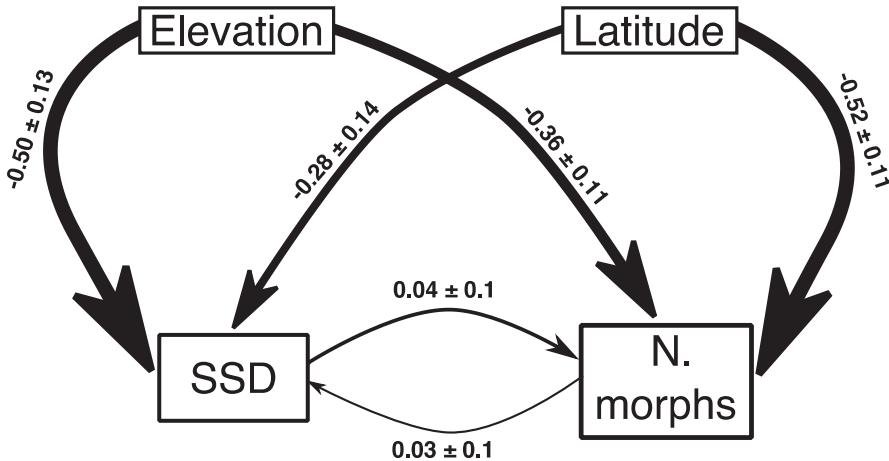
FIGURE 3 Averaged best model illustrating the phylogenetically corrected relationship between SSD, number of morphs, and elevation and latitude as descriptors of the environment. Values correspond to coefficients ± *SE*. Arrow thickness represents the strength of the relationship

0.1% significant contributions), duration of growth season (57%; $t = −0.54 \pm 3.77$; $p = .23 \pm .28$; 21.9% significant contribution) and amplitude of photosynthetic activity (33.7%; $t = −0.28 \pm 0.79$; $p = .59 \pm .26$; 1.2% significant contribution).

Female size was best predicted by the combination of average annual temperature, annual precipitation (log) and amplitude of photosynthetic activity (Residual *SE* = 12.82, *df* = 49, Likelihood ratio = 55.35, $p < .0001$, see Table 3 for median tree model, for posterior trees Residual *SE* = 14.42 ± 2.46, df = 49, Likelihood ratio = 47.96 ± 33.91, $p = .002 \pm .02$ with 99.2% $p > .05$). Variables retained in 100% of posterior trees were average annual temperature ($t = 2.09 \pm 1.26$; $p = .11 \pm .18$; 56.7% significant contribution), annual precipitation ($t = −3.49 \pm 2.07$; $p = .04 \pm .11$; 87.5% significant contribution) and amplitude of photosynthetic activity ($t = 5.65 \pm 4.05$; $p = .005 \pm .04$; 97.9% significant contribution) with most trees retaining precipitation seasonality (87%; $t = −0.29 \pm 1.12$; $p = .53 \pm .29$; 6.1% significant contribution). Other variables were not retained with such high frequencies, including temperature seasonality (22.5%; $t = −0.05 \pm 0.55$; $p = .72 \pm .21$, 0.1% significant contributions) and duration of growth season (27%; $t = −1.02 \pm 1.44$; $p = .37 \pm .31$; 6% significant contribution).

Finally, the model that best predicted variation in male size consisted of average annual temperature, annual precipitation (log), temperature seasonality (log) and amplitude of photosynthetic activity (log) (Residual *SE* = 12.05, *df* = 49, Likelihood ratio = 48.20, $p < .0001$ for the median tree see Table 3, for the posterior distribution of trees, Residual *SE* = 13.67 ± 2.35, df = 49, Likelihood ratio = 42.26 ± 30.79, $p = .002 \pm .027$ where 99.2% of trees are significant). Average annual temperature ($t = 1.95 \pm 0.80$; $p = .12 \pm .18$; 48.1% significant contribution), annual precipitation (log) ($t = 2.77 \pm 1.61$; $p = .07 \pm .16$; 72.8% significant contribution) and amplitude of photosynthetic activity (log) ($t = 5.52 \pm 3.41$; $p = .006 \pm .04$; 98% significant contribution) were all retained in the model across posterior trees, with temperature seasonality (log) retained most of the time (83.2%; $t = −1.10 \pm 0.74$; $p = .35 \pm .25$; 8.9% significant contribution). Duration of growth season (24%; $t = 0.57 \pm 1.57$; $p = .41 \pm .31$; 3.3% significant contribution) and precipitation seasonality were not retained as frequently (52.7%; $t = 1.00 \pm 0.99$; $p = .36 \pm .27$; 6% significant contribution).

Figure 4 illustrates the relationship between our response variables and elevation, latitude, average annual temperature and precipitation seasonality.

4 | DISCUSSION

In times of rapidly changing climate, addressing how environmental conditions influence the evolution of sexually dimorphic traits is paramount to hone our understanding of the factors that determine phenotypic evolution. Our results show that both SSD and number of morphs covary along an environmental gradient across populations of *U. stansburiana*, as well as across the phylogeny for the species (Figures 2–4). All of our results were robust to tests across 1,000 random trees from the posterior distribution. To explain this covariance between SSD and number of morphs, previous studies hypothesized that morph loss leads to weaker sexual selection within populations, which in turn leads to a smaller degree of SSD (Corl, Davis, Kuchta, Comendant, et al., 2010). However, our results imply that rather than influencing each other directly, SSD and number of morphs are co-determined by biotic and abiotic environmental variables (Figures 3 and 4), thus suggesting a strong effect of natural selection on traits long thought to be solely under sexual selection.

4.1 | Environment and sexual size dimorphism

Both male and female *U. stansburiana* exhibit smaller body sizes in colder and more seasonal environments, in line with results found in hundreds of other lizard species (Tarr et al., 2019). Interestingly, this pattern is the opposite of what is predicted by the temperature-size rule (Angilletta & Dunham, 2003; Atkinson, 1994; Pincheira-Donoso et al., 2008), challenging the pervasive assumption that climate change will lead to a reduction in species' sizes (Gardner et al., 2011; Root et al., 2003; Sheridan & Bickford, 2011). Parker and Pianka (1975) had previously described a body size cline in populations of *U. stansburiana* distributed along a North–South gradient. By looking not only at geography but also at temperature and

TABLE 2 Confirmatory phylogenetic path analyses showing results for alternate models, including the models being compared, the number of independence claims made by the model (k), the number of parameters (q), the C-statistic and the accompanying p value (a p value < .05 indicates that the available evidence rejects the model), the C-statistic information criterion corrected for small sample sizes (CICc), the difference in CICc with the top model (ΔCICc), the associated relative likelihoods (I) and CICc weights (w)

Model	k	q	C	p	CICc	ΔCICc	I	Weight
E—SSD ~Env; N. morphs ~Env (100%)	2	8	**1.96 (2.02 ± 2.28)**	**.74 (.74 ±.03)**	**21.6 (21.62 ± 2.28)**	**0 (0 ± 0)**	**1.00 (1 ± 0)**	**0.46 (0.48 ± 0.06)**
F—SSD ~Env; N. morphs ~SSD + Env (100%)	1	9	**0.002 (0.22 ± 2.28)**	**.99 (.93 ±.06)**	**22.6 (22.84 ± 2.28)**	**1.06 (1.21 ± 0.05)**	**0.59 (0.55 ± 0.01)**	**0.27 (0.26 ± 0.003)**
G—SSD ~ N. morph +Env; N. morphs ~Env (100%)	1	9	**0.002 (0.22 ± 2.28)**	**.99 (.93 ±.06)**	**22.6 (22.84 ± 2.28)**	**1.06 (1.21 ± 0.05)**	**0.59 (0.55 ± 0.01)**	**0.27 (0.26 ± 0.003)**
D—SSD ~ N. morphs; N. morphs ~Env (100%)	3	7	14.59 (16.19 ± 2.48)	.02 (.01 ±.005)	31.3 (32.92 ± 2.48)	9.76 (11.30 ± 1.03)	0.008 (0.004 ± 0.002)	0.003 (0.002 ± <0*)
C—N. morphs ~SSD; SSD ~Env (100%)	3	7	21.53 (21.24 ± 2.33)	.001 (.002 ± 0*)	38.3 (37.96 ± 2.33)	16.7 (16.34 ± 0.43)	<0.001 (0* ± 0*)	<0.001 (0* ± 0*)
A—SSD ~ N. morphs (69.3% 6th best model)	5	5	38.27 (44.75 ± 7.63)	<.001 (0* ± 0*)	49.7 (56.14 ± 7.63)	28.10 (34.52 ± 7.29)	<0.001 (0* ± 0*)	<0.001 (0* ± 0*)
B—N. morphs ~SSD (30.7% 6th best model)	5	5	47.37 (48.42 ± 2.51)	<.001 (0* ± 0*)	58.8 (59.82 ± 2.51)	37.21 (38.19 ± 1.01)	<0.001 (0* ± 0*)	<0.001 (0* ± 0*)
Null	6	4	63.12 (69.87 ± 7.77)	<.001 (0* ± 0*)	72.0 (78.78 ± 7.77)	50.46 (57.16 ± 7.43)	<0.001 (0* ± 0*)	<0.001 (0* ± 0*)

Note: The three models in bold are those that passed the p > .05 threshold and fell within a D CICc of 2. Our final results (see Figure 3, below) consist of the average between these three models. In brackets, the average across 1,000 posterior trees is shown along with the standard deviation of values across trees.

*<.001.

seasonality, our results confirm that *U. stansburiana* belongs to the list of species that exhibits a reverse Bergmann cline, alongside other ectotherms like other squamates, arthropods, amphibians and some birds (Bidau & Martí, 2007; Blanckenhorn, 2004; Cruz et al., 2005; Mousseau, 1997; Muñoz et al., 2014; Olalla-Tarraga et al., 2006; Pincheira-Donoso et al., 2008). These reverse Bergmann clines are often explained by the interactive effect of season length at a given latitude (or elevation) and the physiological time available for growth and development (Abrams et al., 1996; Mousseau, 1997; Roff, 1980).

Although season length and development time provide reasonable explanations for our observed smaller body sizes in colder environments, they do not by themselves explain the differences between female and male size, resulting in a gradient of SSD. A similar switch from female-biased SSD in cold environments to male-biased SSD in warm ones has been described in multiple studies of lizard species, including previous studies of *U. stansburiana* (e.g. Cox et al., 2003; Parker & Pianka, 1975; Schoener et al., 1982; Tarr et al., 2019). A previous study hypothesized that these shifts could be due to lower survivorship of large males in colder environments, reduced sexual selection and increased selection for female fecundity in seasonal areas (Corl, Davis, Kuchta, Comendant, et al., 2010). Increased fecundity selection may explain why females and clutch sizes of some species, such as the lizard *Sceloporus undulatus*, are larger in colder environment (Angilletta et al., 2006), but those do not seem to be the rule. Indeed, a large meta-analysis with hundreds of lizard species showed little support for the fecundity and niche divergence hypotheses (Tarr et al., 2019), leading the authors to suggest that weaker sexual selection on males should be the main driver of this reversal in SSD direction, from male-biased to female-biased, in colder environments. Our results reveal that that female size is far less variable than male size, thus suggesting that the fecundity hypothesis does not explain SSD variation in *U. stansburiana*, as variation in male size is the main determinant of variation in SSD (Figure 4, Figure S2).

In ectotherms as a whole, the relationship between temperature seasonality and SSD has previously been assumed to be a consequence of weaker sexual selection on male size due to shorter breeding seasons and fewer mating opportunities found in highly seasonal environments, combined with fecundity selection on female size due to the benefits associated with larger female size (Machado et al., 2016). Although we cannot fully dismiss this hypothesis, our results suggest that seasonal environments with short reproductive seasons alter the direction of sexual selection, from favouring large males able to defend large territories to favouring small males who mature earlier in the season, but not necessarily its strength. In species that have a long developmental period prior to reaching sexual maturation, like *U. stansburiana*, short reproductive seasons, as seen in highly seasonal environments, favour small males that reach sexual maturation earlier (Blanckenhorn, 2000). Indeed, large males, who reach maturation later, may be outcompeted if females mate early in the season. Moreover, smaller *U. stansburiana* are known to exhibit a faster growth rate than larger individuals, adding to the benefits of small size when fast maturation is an important element of fitness (Hazard et al., 2019).
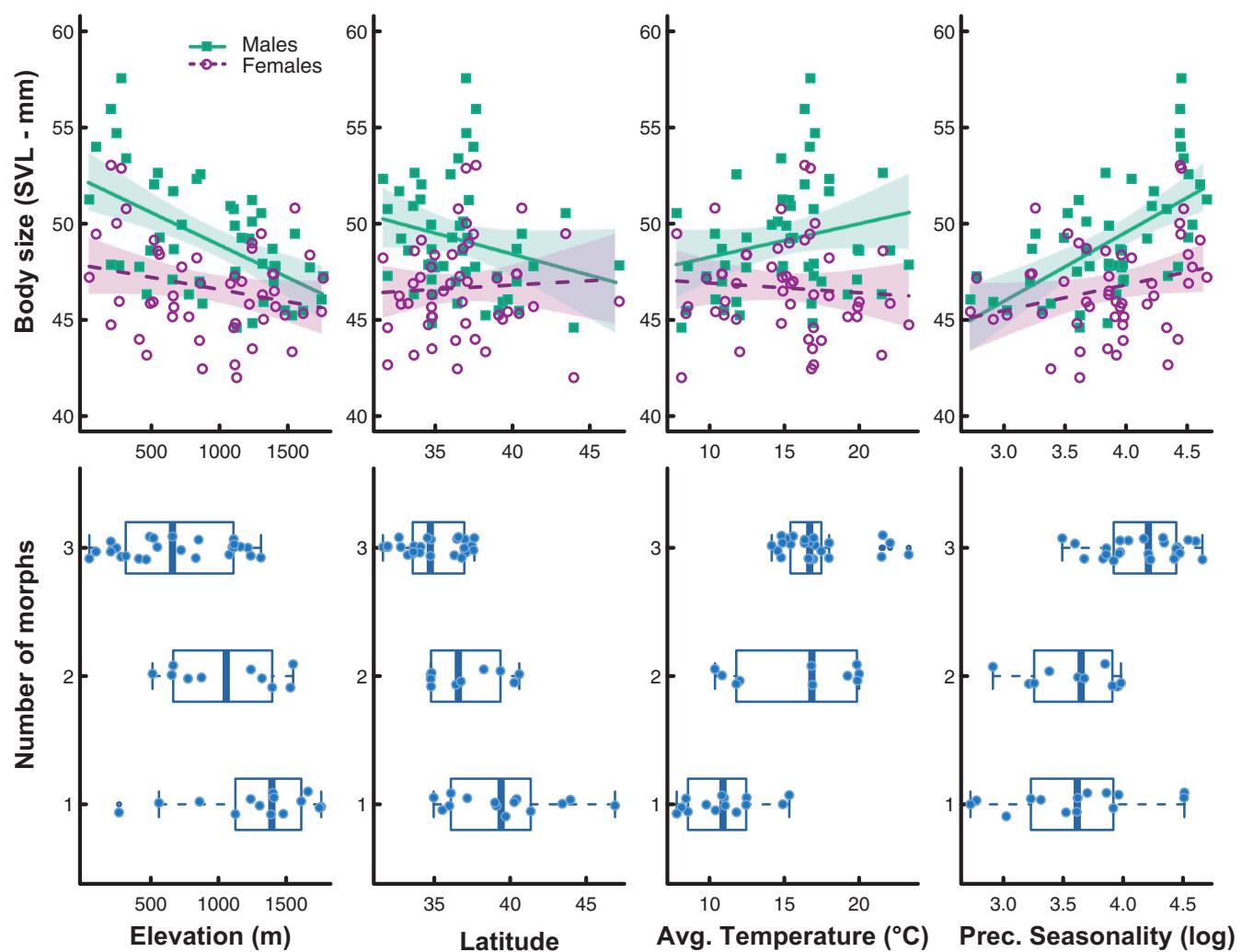
FIGURE 4 Environment versus female size and male size (and consequently, sexual size dimorphism—top row), as well as number of morphs of *Uta stansburiana* (bottom row). In the top row, lines correspond to the values predicted by a linear model between size and the environmental variable, and light purple and light green areas surrounding the lines represent the 95% confidence intervals. In the boxplots, the boxes represent the data contained between the 25th and 75th percentile, the band represents the median (50th percentile) and the whiskers represent the maximum and minimum values

As such, the direction of sexual selection acting on males switches in seasonal environments, resulting in smaller degrees of SSD.

Smaller sizes at higher latitudes may also be related to food abundance: in mild climates, arthropods are abundant year-round, while in seasonal environments food becomes scarce around wintertime (Payne & Wilson, 1999). Males have been shown to exhibit greater developmental plasticity than females in *Anolis* lizards, growing to larger sizes and leading to greater degrees of SSD when food is abundant (Bonneaud et al., 2016). Such a pattern in body size between the sexes coincides with our results, as female size remained more constant across all populations than male size.

4.2 | Environment and number of morphs

Uta stansburiana's number of morphs seem to be less influenced by the environment than their degree of SSD. Nonetheless, seasonality

may affect number of morphs due to a shorter reproductive season, potentially reducing the benefits associated with sneaker morphs, such as *U. stansburiana's* yellow males. The yellow morph seems to be the first to be lost in our populations, with the exception of population 31 (Figure 2), which is consistent with the results of Corl, Davis, Kuchta, Comendant, et al. (2010). The fitness benefits of sneaker morphs are tied to sperm competition and cryptic female choice, which in turn rely on delayed oviposition and sperm retention (Birkhead, 1998). Territorial morphs such as *U. stansburiana's* orange males, on the other hand, may be favoured by a short reproductive season, as they specialize in gaining paternity early in the season (as observed by Zamudio & Sinervo, 2000 and Calsbeek & Sinervo, 2002 in a trimorphic population).

Microhabitat variation has been shown theoretically to modulate sexual selection and influence the maintenance of male polymorphisms (Chunco et al., 2007). Environmental variables such as temperature may also alter the frequency-dependence relationship between morphs (Lancaster et al., 2017) or alter the way in which

TABLE 3 Summaries of best-fit phylogenetic-generalized-least-square (PGLS) models looking at the relationship between the environment, SSD, number of morphs, female and male size in *Uta stansburiana*

Response variable	Predictor variable	Coefficient ± SE	t value	p value
SSD	Intercept	1.60 ± 0.21	7.69	<.001***
	Annual precipitation	−0.03 ± 0.01	−2.86	.006**
	Temp. seasonality	−0.07 ± 0.02	−3.24	.002**
	Precip. seasonality	0.03 ± 0.01	2.78	.008**
	Duration gr. season	<0.001 ± <0.001	2.23	.03*
Number of morphs	Intercept	−10.8 ± 3.0	−3.59	<.001***
	Annual precipitation	−0.99 ± 0.26	−3.8	<.001***
	Precip. Seasonality	−0.62 ± 0.25	−2.39	.02*
Female size	Intercept	8.50 ± 11.38	0.75	.46
	Avg. temperature	0.53 ± 0.19	2.76	.008**
	Annual precipitation	4.49 ± 0.95	4.71	<.001***
	Amplitude photos.	1.89 ± 0.23	8.34	<.001***
Male size	(Intercept)	36.4 ± 15.09	2.41	.02*
	Avg. temperature	0.57 ± 0.20	2.81	.007**
	Annual precipitation	3.63 ± 0.91	3.99	<.001***
	Temp. seasonality	−3.00 ± 1.89	−1.59	.12
	Amplitude photos.	1.71 ± 0.23	7.47	<.001***

Note: Also shown for each model are the model coefficient (± *SE*), the *t* value and significance level (*p* value; *p* ≥ .05—not labelled; *p* ≤ .05—*; *p* ≤ .10—**; *p* ≤ .001—***).

one sex affects the other, particularly in species where sexual conflict is a strong source of selection, such as in the damselfly genus *Ischnura* (Svensson et al., 2020). In insects, variation in morph frequency along an elevation gradient is common (see review in Hodkinson, 2005), and has been most often associated with thermoregulation or resistance to desiccation [e.g. *Drosophila jambulina* (Parkash et al., 2009) and grasshoppers (Forsman, 2000; Köhler & Schielzeth, 2020)]. Finally, the environment may influence the frequency of each morph through background contrast and predation avoidance (Hoekstra et al., 2004; Palma & Steneck, 2001). The relationship between environment and *U. stansburiana's* number of morphs could be influenced by all of these factors, but testing these hypotheses falls beyond the scope of our study.

4.3 | Social interactions or ecological adaptation?

Seasonal environments seem to lead to life-history shifts in *U. stansburiana* (Payne & Wilson, 1999; Stearns, 1989). In mild climates, males develop slowly, live longer and are likely not nutrition limited. Females can afford to delay oviposition and males benefit from a larger size and from sperm competition—favouring the sneaker yellow morph. In harsh seasonal climates, males are fast-developing, smaller and possibly nutritionally deprived, and female fitness depends greatly on timing of oviposition, likely favouring small males who reproduce early in the season. As such, social interactions by themselves are unlikely to be the underlying cause of SSD and male polymorphism in this classic study system.

It is important to take into account that, while our results are likely broadly applicable to many species of ectotherms, our methods also have their limitations. Since our climatic variables are intrinsically correlated to elevation and latitude, the results from our PGLSs are not fully independent from the results of our phylogenetic path analysis. Moreover, while we can hypothesize that the environment directly impacts the direction of sexual selection, we did not measure sexual selection per se, but rather the intraspecific variation in traits long assumed to be sexually selected. Similarly, our data only allow us to hypothesize on the underlying effect of the environment on the number of morphs found in each population. Finally, we focused our study on the relationship between male–male competition and the environment. Other mechanisms of sexual selection, such as male–female interactions (Lancaster et al., 2014), mate choice (Calsbeek & Sinervo, 2003) and sexual conflict (Svensson et al., 2009), may also interact with the environment and play a role in the degree of variation in SSD and number of morphs observed in *U. stansburiana*.

What our results reveal, however, is that environmental conditions can mediate SSD and intrasexual polymorphisms independently. Moreover, they indicate how environmental conditions may determine phenotypic variability across a species range. These results suggest that rapid changes in environmental conditions may influence the prevalence of polymorphisms and SSD in populations of ectotherms. As a consequence, we predict a gain in intraspecific variability as temperatures rise worldwide, a result already observed in longitudinal studies with spiders (Hoye et al., 2009).

Intrasexual polymorphisms are typically studied in the light of their association with alternative reproductive tactics in lizards (Galeotti et al., 2013; Noble et al., 2013; Thompson et al., 1993), birds (Roulin, 2004), insects (Willink et al., 2019) and fish (Oliveira et al., 2001). We show here that environmental factors may play a role in the evolution of intrasexual polymorphisms, possibly mediating the balance between alternative reproductive strategies. The fact that climatic variables influence both SSD and polymorphisms independently shows that our results are applicable not only to species presenting a combination of SSD and alternative reproductive strategies, but potentially also to species where males and females grow to different sizes and/or present different morphologies.

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CONFLICT OF INTEREST

The authors have no conflict of interest to declare.

AUTHOR CONTRIBUTIONS

MCC, KB, JY and DLE conceived the idea. KB, JY and DLE conducted fieldwork. MCC conducted laboratory work. MCC gathered literature data. MCC and DLE ran statistical analyses. MCC wrote manuscript. KB, JY and DLE revised subsequent versions of manuscript.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

A data table is available as a supplementary material. Genetic sequences are deposited on GenBank (accession numbers MZ332537-MZ332919). Code for the statistical analyses is available upon request.

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SUPPORTING INFORMATION

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