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ALTERNATIVE MATING STRATEGIES AND THE EVOLUTION OF SEXUAL SIZE DIMORPHISM IN THE SIDE-BLOTCHED LIZARD, *UTA STANSBURIANA*: A POPULATION-LEVEL COMPARATIVE ANALYSIS

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Population-level comparative analyses can link microevolutionary processes within populations to macroevolutionary patterns of diversification. We used the comparative method to study the evolution of sexual size dimorphism (SSD) among populations of side-blotched lizards (*Uta stansburiana*). *Uta stansburiana* is polymorphic for different male mating and female life-history strategies in some populations, but monomorphic in others. We tested whether intrasexual selection among males, fecundity selection on females, and the presence of polymorphic strategies affected levels of SSD. We first resolved a phylogeny for 41 populations across the range of the species and documented a substantial regional structure. Our intraspecific data had significant phylogenetic signal, and correcting for phylogeny using independent contrasts had large effects on our results. Polymorphic populations had male-biased SSD and changes in male body size, levels of tail breaks, and SSD consistent with the intrasexual selection hypothesis. Monomorphic populations had changes in female size, clutch size, and SSD consistent with the fecundity selection hypothesis. Fecundity selection is a likely cause of some monomorphic populations having no SSD or female-biased SSD. Our results suggest that changes in mating strategies are associated with phenotypic diversification and multiple evolutionary forces can shape SSD.

KEY WORDS: **Fecundity selection, independent contrasts, intrasexual selection, phenotypic diversification, phylogeny, polymorphism.**

Sexual selection arises from competition for mates and can lead to phenotypic diversification within and among species (Darwin 1871; West-Eberhard 1983; Andersson 1994). Most studies of sexual selection have focused either on selection within populations (Sinervo and Lively 1996; Krakauer 2005; Clutton-Brock et al. 2006; Chaine and Lyon 2008) or have compared sexually selected traits across species (Owens et al. 1999; Cox et al. 2003; Stuart-Fox and Owens 2003; Emlen et al. 2005). Fewer studies have investigated how sexual selection may vary among populations. However, such intraspecific comparative studies have been important for documenting the rapid phenotypic diversification of sexually selected traits (Wikelski and Trillmich 1997; Uy and Borgia 2000; Masta and Maddison 2002; Svensson et al. 2004; Boul et al. 2007). Comparative analyses among populations are important because they link microevolutionary processes within

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populations to patterns of macroevolutionary divergence across species, including species formation and the evolution of phenotypic diversity.

We considered the effects of sexual selection on phenotypic diversification by studying alternative mating strategies, which are characterized by genetic polymorphisms for distinct mating phenotypes, such as morphs with different sizes or coloration adapted for a particular mating behavior (Gross 1996). Alternative mating strategies have been found in many taxonomic groups including isopods (Shuster and Wade 1991), damselflies (Gosden and Svensson 2007), fish (Taborsky 1994), birds (Lank et al. 1995; Tuttle 2003), and lizards (Carpenter 1995; Sinervo and Lively 1996; Sinervo et al. 2007). Alternative mating strategies illustrate how strong multivariate disruptive sexual selection can result in phenotypic diversification within populations (Sinervo and Svensson 2002). In this study, we investigated how alternative mating types could contribute to phenotypic diversification among populations.

Below we present three hypotheses of how sexual selection, life history, and alternative mating strategies can affect the evolution of sexual size dimorphism (SSD) among populations of the side-blotched lizard *Uta stansburiana.*

INTRASEXUAL SELECTION HYPOTHESIS

Sexual selection resulting from male–male competition is thought to be a major driver of male-biased SSD. Male–male competition can result in male-biased SSD if larger males are able to obtain more mates (Darwin 1871; Wikelski and Trillmich 1997; Cox et al. 2003). Larger males often gain access to more females, because they are more dominant and control better territories (Wikelski and Trillmich 1997; Panhuis and Wilkinson 1999). The intrasexual selection hypothesis thus predicts that changes to SSD across populations will be positively correlated with changes to male size (Fig. 1).

Intrasexual selection is likely to affect the evolution of SSD in *U. stansburiana* based on detailed studies conducted at a population near Los Banos, CA. This population has male-biased SSD, which is likely a result of strong male–male competition between three genetically determined male mating strategies (Sinervo and Lively 1996; Sinervo et al. 2001). Male–male competition takes the form of a rock–paper–scissors game in which each male mating strategy beats and is beaten by one other strategy (Sinervo and Lively 1996). Males with orange throats can usurp territory from blue-throated males because they are more massive, have higher plasma testosterone, and have greater endurance (Sinervo et al. 2000a). As a result, orange males are able to control large territories of high thermal quality containing many females (Sinervo and Lively 1996; Calsbeek and Sinervo 2002a). Blue-throated males closely guard females, cooperatively defend territories, and are able to beat the sneaking strategy of yellow-throated males (Sinervo and Lively 1996; Zamudio and Sinervo 2000; Sinervo and Clobert 2003). Yellow-throated males are not territorial, but rather mimic female behavior and coloration to sneak onto the large territories of orange males to copulate with females (Sinervo and Lively 1996; Zamudio and Sinervo 2000). Thus, intrasexual selection affects many aspects of the male phenotype in this population of *U. stansburiana* and is therefore likely to affect male size and SSD in populations with multiple male mating strategies.

The evolution of SSD by intrasexual selection requires that males are aggressive toward one another and that larger males have an advantage in male–male combat (Cox et al. 2003). Therefore, the intrasexual selection hypothesis predicts that levels of male–male aggressive behavior will be positively correlated with male size and SSD (Fig. 1). Direct measures of male aggression are difficult to obtain, but one potential indirect measure is the frequency of tail breaks. While fighting, *U. stansburiana* males may bite and hold onto each others tails, which has been observed to result in tail injury and loss in the field (Tinkle 1967b; Sinervo, pers. obs.) and the laboratory (A. Corl, pers. obs.). Tail loss results in reduced social dominance in *U. stansburiana* (Fox and Rostker 1982) and thereby impacts male–male competition. Therefore, we predict that levels of male tail breaks will be positively correlated with traits shaped by intrasexual selection such as male size and SSD. We also consider an alternative hypothesis that longevity differences potentially cause interpopulational variation in tail break frequency (see the Methods section).

FECUNDITY ADVANTAGE HYPOTHESIS

Sexual size dimorphism may result from other forms of selection than intrasexual selection or may represent a balance between

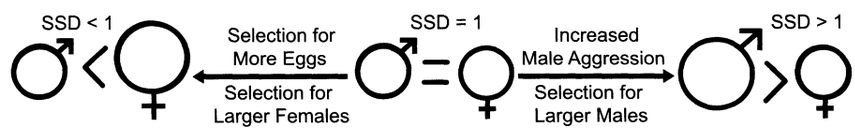

Figure 1. Outline of hypotheses for SSD evolution. If intrasexual selection predominates, increases in male size and aggression will be associated with increases in male-biased SSD. If fecundity selection predominates, increases in female size and numbers of eggs will be associated with decreases in levels of male-biased SSD, or increases in female-biased SSD. Observed levels of SSD represent a balance between these two opposing, but not mutually exclusive, selection pressures. Values of SSD greater than 1 are male-biased, values below 1 are female-biased, and a value equal to 1 means that the sexes are the same size.

multiple types of selection (e.g., Preziosi and Fairbairn 2000). The fecundity advantage hypothesis predicts that selection on female life-history traits mediates the evolution of SSD (Darwin 1871; Prenter et al. 1999; Cox et al. 2003). Darwin proposed that natural selection should favor large female body size if female size is related to fecundity (Darwin 1871). Larger females could have higher fecundity if they have higher feeding rates, larger energetic stores, or larger body cavities for storing eggs (Angilletta et al. 2006). The fecundity advantage hypothesis has typically been used to explain the evolution of female-biased SSD (Darwin 1871; Prenter et al. 1999; Cox et al. 2003), but the degree of male-biased SSD could also be affected by changes in female size. The fecundity advantage hypothesis predicts a negative correlation between female size and male-biased SSD (Fig. 1). In order for fecundity selection to affect female body size, fecundity (e.g., clutch size) must be positively correlated with female body size (Zamudio 1998), which could then lead to a negative correlation between fecundity and SSD.

Female *U. stansburiana* at Los Banos have different life-history strategies relating to fecundity. Orange-throated females (*r* strategists) produce large numbers of small progeny and are favored at low densities (Sinervo et al. 2000b). Yellow-throated females (K strategists) produce fewer, but higher quality offspring and are favored at high density (Sinervo et al. 2000b). Although the two female morphs do not differ in body size, they demonstrate that selection on egg characteristics and female life history is found within a population of *U. stansburiana.* In addition, female size is positively correlated to clutch size within many populations of *U. stansburiana* (Tinkle et al. 1970; Parker and Pianka 1975). We therefore predict that female size and clutch size should be correlated among populations.

ALTERNATIVE MATING STRATEGIES AND DIVERSIFICATION HYPOTHESIS

Populations may lose particular mating strategy morphs due to genetic drift or natural selection (West-Eberhard 1986; Eckert and Barrett 1992). Loss of polymorphic strategies may be associated with phenotypic diversification for multiple reasons (West-Eberhard 1986; West-Eberhard 2003). First, selection in a new ecological environment may drive the loss or fixation of a morph and this new environment may also favor novel phenotypes. Second, morph fitness can depend on the frequency of other types in a population and many morph traits (e.g., sneaking) arise because they are advantageous for competition with other morphs. Loss or fixation of a morph could thus generate a new competitive and selective environment among the remaining morph(s), in turn favoring different phenotypes. Third, genetic evolution may be constrained in polymorphic populations because new alleles may be unable to spread if they increase the fitness of one morph, but decrease the fitness of other morphs (West-Eberhard 1986). These alleles can invade when morphs are lost or fixed, which can result in rapid phenotypic evolution in the direction of specialization on the remaining morph phenotypes, a process called "character release" (West-Eberhard 1986).

The evolution of the male and female morphs across populations of *U. stansburiana* was studied by Corl (2007). Geographic variation in the presence and absence of morphs was assessed by observing throat colors of lizards in 41 populations across the range of *U. stansburiana* (Corl 2007). Male and female strategies and their throat colors are genetically determined by the OBY locus (for orange, blue, and yellow), which is likely a single gene with three alleles, or two tightly linked genes, as determined by field pedigree data (Sinervo et al. 2000b), laboratory breeding experiments (Sinervo et al. 2001), gene mapping studies (Sinervo et al. 2006), and theoretical models (Sinervo 2001). Reconstructed transitions in throat color on a phylogeny showed that there have been at least eight independent losses of OBY alleles across the range of the species. In both males and females, the mating strategy polymorphism has gone from trimorphic to dimorphic in four locations and from trimorphic to monomorphic in four locations (Corl 2007). All eight changes to the polymorphism involve the loss of the yellow allele that codes for sneaker males and K-strategy female morphs (Corl 2007). Monomorphism has been achieved in two different ways, either by fixation on orange or by fixation on a phenotype of blue throats bordered by orange (Corl 2007).

Our goal is to better understand why changes in morphs may be associated with phenotypic diversification between populations, which could occur by any of the three general mechanisms described above. We test whether monomorphic and polymorphic populations have faced differing levels of intrasexual and fecundity selection. We also assess whether monomorphic populations have different levels of SSD than polymorphic populations. Note that the loss of a particular morph would not automatically lead to a change in SSD because although male morphs differ in mass (Sinervo et al. 2000a), they do not differ in body length, the metric we used to calculate SSD. Therefore, we have general predictions that polymorphic and monomorphic population could differ in SSD, but not specific predictions that they should differ in a particular direction.

OVERVIEW OF METHODOLOGY

We use phylogenetically based comparative methods for our analyses. There has been widespread recognition that comparative studies among species need to account for phylogeny because data for species are not independent due to shared ancestry (Felsenstein 1985; Garland et al. 2005). There are few intraspecific studies that have corrected for phylogenetic history (but see Edwards and Kot (1995), Zamudio (1998), Richmond and Reeder (2002), Angilletta et al. (2006)), despite the fact that phylogeographic studies often

reveal phylogenetic structure among populations (Avise 2000). In this study, we resolve a phylogeny for *U. stansburiana* and use it to account for shared ancestry among populations when comparing morphological and life history characteristics. Additionally, we employ standard statistical analyses that do not correct for phylogeny and compare these results with our analyses of independent contrasts to assess the utility of using phylogenetic comparative methods within a species.

Materials and Methods

FIELD MEASUREMENTS

Lizards were individually caught by noose in 41 populations (Fig. 2, Table S1), measured, and released. The snout-vent length (SVL) of each lizard was measured to the nearest half millimeter to provide a measure of body size. The presence/absence of broken or regenerated tails was noted. Regenerated tails were scored as a tail break and are visibly distinguishable because they are uniform brown/gray while regrowing, and when fully regrown they have smaller scales than nonregenerated tails. Populations with a total sample size of less than 25 individuals were excluded from analyses of tail breaks because accurate estimates of tail break frequencies are unlikely with a low sample size.

Tail breaks may result from fighting between males in *U. stansburiana* (Tinkle 1967). However, some broken tails are due to predation because tail autonomy is an antipredator escape tactic. We are primarily interested in tail breaks due to male–male competition so we calculated a measure of "sex-biased" tail breaks, which is the frequency of male tail breaks (= broken or regenerated tails) minus the frequency of female tail breaks (Table S2). If males and females have similar tail break frequencies due to predation, then greater values of sex-biased tail breaks reflect greater male–male aggression. The assumption of no sex bias in predation may be justified for *U. stansburiana,* because a study of mortality patterns across seven populations (four of which are included in this study) concluded that differences in mortality

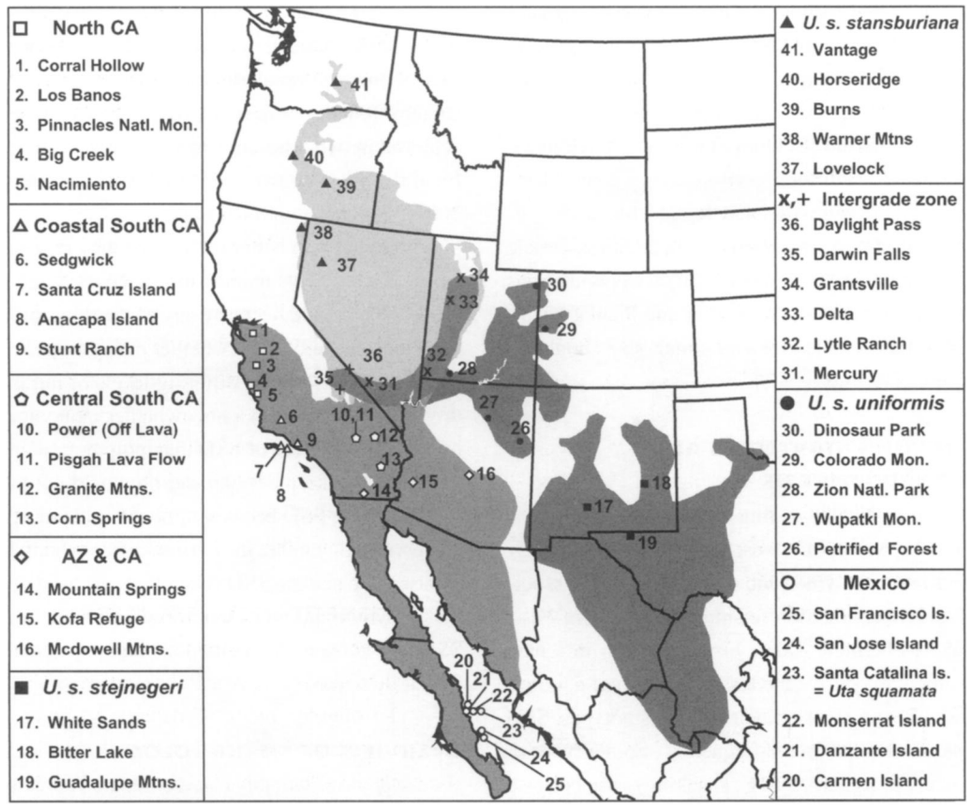

Figure 2. Locations sampled across the geographic range of *U. stansburiana.* Different shades of gray denote previously proposed subspecies and an intergrade zone (Pack and Tanner 1970; Ballinger and Tinkle 1972). For *U. s. stejnegeri, U. s. stansburiana, U. s. uniformis,* and the intergrade zone, the populations sampled are listed below the subspecies name. All other populations are considered part of *U. s. elegans* and the geographic location of the separate clades within that subspecies (see Fig. 3) are given above the sampled populations. Populations in different clades within *U. s. elegans* are depicted on the map as different open shapes, filled shapes denote the other three subspecies, and + and × symbols denote two clades within the intergrade zone. One of the six islands (Santa Catalina Island) sampled off of Baja California in Mexico is home to a different species, *Uta squamata* (Grismer 2002).

by sex were weak or nonexistent (Wilson 1991). We predict that male size and SSD will be positively correlated with levels of sex-biased tail breaks because of differences in male–male aggression among populations. We also test an alternative hypothesis that longevity differences between populations could give rise to a correlation between size and tail breaks. Longer lived populations could have both larger individuals and a greater cumulative probability of having a tail break. Evidence consistent with this hypothesis would be a positive correlation of tail breaks with body size for both males and females. If only male tail breaks are correlated with male size, then there is not a general longevity effect and some populations must have greater male–male aggression and/or greater male longevity.

SEXUAL SIZE DIMORPHISM

Sexual size dimorphism was calculated using the two-step ratio method (Smith 1999). Designating M as male size and F as female size, if $M \geq F$, then $SSD = M/F$ and if $F \geq M$, then $SSD = 2 - F/M$. With $M > F$, SSD increases in a linear fashion from 1, and with $F > M$, SSD decreases from 1 in a symmetrical and linear fashion. This method was recommended in an extensive review of methods for calculating SSD because it has the desired statistical properties of being linear, symmetrical, and continuous (Smith 1999). Although only the results of the two-step ratio method are presented (Table S3), our results are robust across other methods of calculating SSD, such as M/F and ln (M/F).

After an initial survey to discover sites, many populations were resampled to gather larger sample sizes and data on the presence/absence of mating strategies. We restricted our population estimates of mean male SVL, mean female SVL, and SSD to the sampling trip with the largest sample size to avoid problems of averaging body size across different time points of growth in the different samples. For one population (Guadalupe mountains), data from the sampling trip with a smaller sample size were used because these data were collected in a time of year more comparable with the other populations. We also included only animals above the minimum size for reproduction as determined by the smallest size at which breeding coloration or evidence of developing ovarian follicles was exhibited.

CLUTCH SIZE DATA

Clutch size data for 16 populations were gathered from the literature (Table S4). Clutch size was either estimated by the number of eggs laid in a single oviposition bout (Sinervo and Licht 1991; Zani 2005) or by dissecting lizards and counting the number of yolked ovarian follicles or oviductal eggs (Tinkle et al. 1970; Parker and Pianka 1975; Case et al. 2002). Our sampled populations exactly matched most locations for the published data, but in a few instances we used data gathered from geographically close populations (see Table S4). An average value of clutch size was used when multiple estimates were given for a single population. Clutch size data of oviposited eggs are newly reported for 10 populations in this study (Table S4) and was collected as described in the Supporting Information.

PCR AND SEQUENCING CONDITIONS

Tail tips were taken from lizards in the field. From 1 to 3 cm of tail tip was cut into small pieces and digested overnight with 125 μg of proteinase K. DNA was extracted from tail tissue using the protocols detailed in Pogson et al. (1995).

The mitochondrial genes cytochrome b (cyt b) and ATPase 6 were amplified using polymerase chain reaction (PCR) conditions given in the Supporting Information. We obtained a 1174 base pair (bp) fragment for cyt b and a 666 bp fragment of ATPase 6. PCR fragments were gel purified using a Zymoclean Gel DNA Recovery Kit following the manufacturer's instructions. Sequencing reactions were performed using a Big Dye Kit version 3.1 (Applied Biosystems, Foster City, CA) following the manufacturer's instructions, but scaled to 1/5th reactions. Sequencing products were cleaned using ethanol precipitation and run on an ABI 3100 sequencer. For cyt b, internal sequencing primers were used as detailed in the Supporting Information. The PCR product for cyt b ended with noncoding sequence and part of tRNA-Thr. This ending sequence proved difficult to align so only base pairs 1–1150 of the coding region of cyt b were used in further analyses. Sequences obtained from the primers for each gene were aligned, manually edited, and assembled into a single consensus sequence for each individual using Sequencher 3.3.1 (GeneCodes, Ann Arbor, MI). All sequences have been deposited in GenBank (accession numbers GQ272687–GQ272944).

The most closely related outgroup taxa are lizards in the genera *Urosaurus, Sceloporus,* and *Petrosaurus* (Schulte et al. 2003). Two outgroup species (*Urosaurus ornatus* and *Petrosaurus mearnsi*) were sequenced using the procedures described above. The sequence for the other outgroup species (*Sceloporus occidentalis*) was obtained from GenBank (accession no. AB079242).

PHYLOGENETIC RECONSTRUCTION

Phylogenies were reconstructed using maximum likelihood and Bayesian methods on two separate datasets. The phylogeny given below is from our "reduced" dataset, which contained sequence from only a single individual from each population. However, we also analyzed a "complete" dataset, which included sequences for multiple individuals from each population. The complete dataset was used to assess whether retention of sequence polymorphism within populations affected inferences of phylogenetic relationships among populations. The complete dataset suggested three possible minor rearrangements of the tip branches of the tree generated from the reduced dataset. Given the close concordance between the phylogenies from the two datasets, we only give details

on the construction and topology of the tree from the complete dataset in the Supporting Information. However, our comparative analyses included the optimal phylogenetic reconstructions resulting from both datasets (TreeBase study accession no. S2442).

Maximum likelihood analyses were conducted using PAUP* version 4.0b10 (Swofford 2002) and used stepwise addition of taxa, TBR branch swapping, and the TIM + I + G model selected by Modeltest 3.7 (Posada and Crandall 1998). Branch support was assessed by 1000 bootstrap replicates with a neighbor joining starting tree and TBR branch swapping. Bayesian phylogenetic analyses were performed using MrBayes version 3.1.2 (Huelsenbeck and Ronquist 2001; Ronquist and Huelsenbeck 2003) with the concatenated dataset partitioned by gene and by codon position within each gene. Models of evolution for the six partitions were selected using MrModeltest 2.2 (Nylander 2004) and were: Cyt b position 1, Atp position 1, Atp position 3: nst = 6, rates = gamma; Cyt b position 2: nst = 6, rates = propinv; Cyt b position 3: nst = 6, rates = invgamma; and Atp position 2: nst = 2, rates = propinv. Five independent searches, each with four heated chains and a temperature of 0.2, were run for 5 million generations. Stationary log-likelihoods of all the runs were observed after a burnin of 100,000 generations. We conservatively used a burnin of 500,000 generations and constructed a 50% majority rule consensus tree from the remaining trees. To verify convergence, we used the online program Are We There Yet (Nylander et al. 2008) to plot the posterior probabilities of the splits for all pairs of runs and to assess that the runs were highly correlated, with no obvious outliers. We also constructed consensus trees for each run in PAUP* and verified that the topologies of each run were congruent. The maximum difference in posterior probabilities observed for a node was 62–76% support. The posterior probabilities for well-supported nodes differed very little among runs and the topologies of each run were identical, which indicated convergence.

PHYLOGENETIC SIGNAL

Tests for phylogenetic signal were conducted using the program PHYSIG (Blomberg et al. 2003) and methods detailed in Blomberg et al. (2003). If phylogenetic signal is present, then relatives should have a significant tendency to resemble one another. To test this, 1000 datasets with no phylogenetic signal were generated by randomly permuting the data across the tips of the tree. Then, the variance of independent contrasts calculated from the random datasets was compared with the variance from the real dataset. If the phylogenetic signal is present, the real dataset should have a significantly lower variance due to relatives having similar trait values. We quantified the amount of phylogenetic signal using the K-statistic (Blomberg et al. 2003). If $K < 1$, then relatives are less similar than expected from Brownian motion along the tree, and if $K > 1$ relatives resemble each other more than expected. We also calculated the d-statistic, which provides an explicit test of whether phylogenetic versus conventional statistical methods should be used (Blomberg et al. 2003). If the best estimate of d is zero, then a star phylogeny better fits the data than the candidate tree or transformations of it and if $d = 1$ the original candidate tree adequately fits the data (Blomberg et al. 2003). Analyses that do not correct for phylogeny assume a star phylogeny, so if $d = 0$ these analyses may be justified. However, if the hypothesis of $d = 0$ is rejected, then phylogenetic corrections would be appropriate. All tests for the phylogenetic signal were done on the tree used for generating independent contrasts (i.e., with all branch lengths equal to 1, see below).

COMPARATIVE METHODS

The program Systat 10.2 was used for all statistical analyses that did not correct for phylogeny, such as least-squares regressions. Independent contrasts were calculated using the PDAP module v. 1.07 (Midford et al. 2005) in the program Mesquite v. 1.12 (Maddison and Maddison 2006). Independent contrasts must be standardized by branch lengths in units of the expected variance in character change so that contrasts involving longer periods of time are not given greater weight in the analysis (Garland et al. 1992). For each trait, the absolute values of the standardized independent contrasts were plotted against their standard deviations to determine what branch lengths adequately standardized the data (Garland 1992; Garland et al. 1992). Branch lengths based on genetic distance did not adequately standardize the data. Adequate standardization was achieved by setting all branch lengths equal to 1, which corresponds to a punctuational model of character change (Garland et al. 1992). As recommended by Diaz-Uriarte and Garland (1996, 1998), we subtracted two degrees of freedom from all analyses of independent contrasts to account for estimation of the best branch length transformation. This approach can sometimes be overly conservative (Diaz-Uriarte and Garland 1998), but retaining the two degrees of freedom did not change our results in any substantial way (results not shown). The tree was pruned of populations with missing data before calculating contrasts as was recommended for PDAP (Midford et al. 2008). The tree for contrasts in clutch size had 26 remaining populations and the tree for tail breaks had 30 populations. After pruning the tree of missing data, all branch lengths were reset to equal 1 because this improved the standardization of SSD on the tree. All polytomies were regarded as hard polytomies for the analyses (Garland and Diaz-Uriarte 1999).

The analyses of independent contrasts were based on the phylogenetic relationships from the reduced dataset analysis (Fig. 3). The sole exception was that the Zion population was constrained to be monophyletic with other *U. s. uniformis* populations because this tree provides the most parsimonious reconstruction in changes in numbers of morphs and is suggested by similarities between

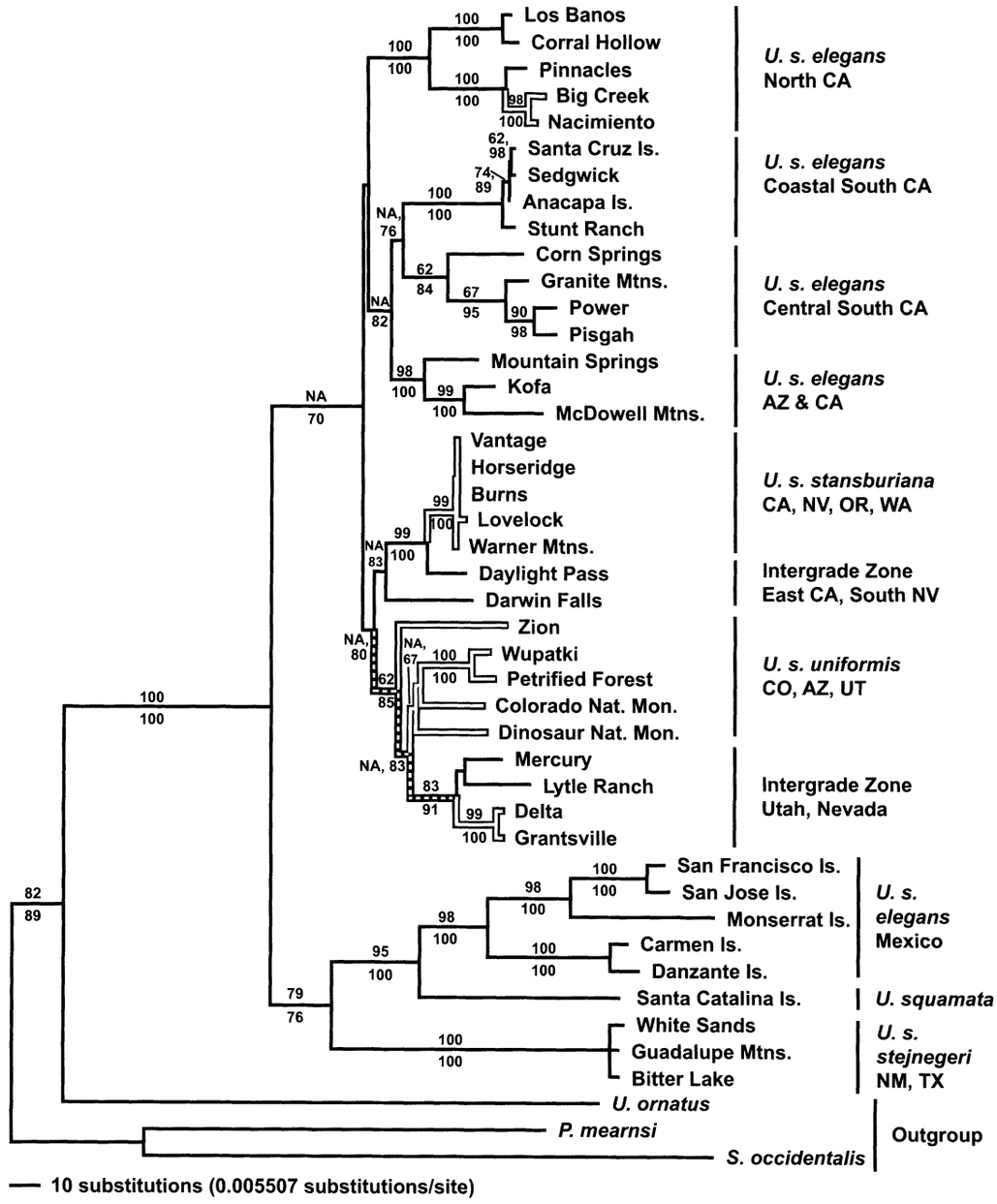

Figure 3. Phylogram depicting the relationships among *U. stansburiana* populations. Numbers above branches show likelihood bootstrap values and numbers below a branch show Bayesian posterior probabilities. Where space did not allow, these values are shown adjacent to a node, with the likelihood bootstrap value given first. A value of "NA" is given when one of the analyses did not give a value above 50. Geographic groupings of the populations are shown to the right and labeled with their respective subspecies. The population on Santa Catalina Island in Mexico is considered a different species (*Uta squamata*). The most parsimonious ancestral state reconstruction of transitions in morph number from Corl (2007) is depicted, where solid branches designate polymorphic lineages and hollow branches designate monomorphic lineages. There are four transitions to monomorphism across the tree when the uncertainty in the reconstruction (dashed branches) is resolved by constraining Zion to be monophyletic with other *U. s. uniformis* populations.

Zion throat coloration and other *U. s. uniformis* populations (Corl 2007). The likelihood of the constrained tree is not significantly different from the unconstrained tree (Corl 2007). We compared the results from the constrained tree with independent contrasts calculated on a tree in which Zion was not constrained to be monophyletic with other *U. s. uniformis* populations and across the three alternative phylogenetic topologies obtained from the complete dataset analysis (see the Supporting Information). All

possible combinations between the original tree and these four alternative topologies were tested, providing a range of *P*-values.

We first used PDAP to test for correlations among variables and to assess how robust these correlations were across different tree topologies. One-tailed *P*-values are given for these correlations because we had a priori predictions for the sign of the slope. Next, independent contrasts were exported to Systat to test whether monomorphic and polymorphic (i.e., dimorphic and trimorphic) populations had different slopes for the correlations. This was done following the methods outlined in Garland et al. (1992) for doing analyses of covariances (ANCOVAs) with independent contrasts. First, we made a dummy variable with polymorphic populations coded as 1 and monomorphic populations coded as 0. Then, a crossproduct term (named "Morph") was computed by multiplying an independent variable by the dummy variable. The independent variable and Morph term were entered into a multiple regression, but the dummy variable was not tested in the model because including it would violate the requirement that all independent contrasts regression lines must pass through the origin. A significant Morph term indicated that monomorphic and polymorphic populations had different slopes. We tried other codings for the dummy variable (such as trimorphic = 1, dimorphic and monomorphic = 0), but the major effects were between monomorphic and polymorphic populations, so the results of other codings are not shown. Two-tailed *P*-values are given for these multiple regressions and the ones described below.

We conducted more complex multiple regressions with our independent contrasts to assess what combination of predictors best explained changes in SSD. Male size and female size could not be entered into the same model as they were highly collinear. Therefore, we assessed one model that included male size and a possible predictor of female size (clutch size) and another model with female size and a possible predictor of male size (sex-biased tail breaks). For both models, we included crossproduct Morph terms for all variables and then conducted backward stepwise elimination of nonsignificant variables. Although these more complex models were useful for assessing how multiple variables may predict SSD, these analyses were not as powerful as the less complex analyses described above because the degrees of freedom for the complex model was determined by the independent variable with the lowest sample size.

Independent contrasts can test how changes in two phenotypic variables are correlated, but they do not show the direction of phenotypic change (e.g., whether SSD in a population has increased or decreased from the ancestral state). We assessed the direction of SSD evolution in monomorphic populations in multiple ways. First, we assessed evolutionary trajectories of SSD following fixation of morphs by using a paired *t*-test to compare independent sets of taxa in which one set was monomorphic and the other polymorphic. We calculated the average phenotype for multiple populations in each monomorphic/polymorphic set, rather than using a single representative population, to account for variability among populations. These tests had low statistical power because there were only four independent monomorphic sets of populations.

Second, we used PDAP and the methods of Garland and Ives (2000) to test whether monomorphic populations deviated from the allometric predictions of polymorphic populations. Monomorphic populations were pruned from the tree and then an independent contrasts regression line and 95% confidence intervals (CI) were computed for the remaining polymorphic populations. The regression line and 95% CI were mapped back on to plots of the uncorrected data (e.g., measurements of SVL and SSD) for all populations. We then observed whether monomorphic populations tended to deviate in a specific direction from the polymorphic predictions and whether they lay outside the 95% CI and thus were significantly different from the polymorphic allometric relationship (Garland and Ives 2000). This test allowed us to assess the proportion of monomorphic populations that had significant changes in SSD and to observe whether any populations had new, outlying phenotypes.

Third, we tested whether monomorphic and polymorphic populations on average differed in SSD by conducting a phylogenetic ANOVA (Garland et al. 1993). We first used Systat to obtain an *F*-statistic from a conventional ANOVA that tested for a difference between monomorphic and polymorphic populations. Next, we used the program PDSIMUL (Garland et al. 1993) to perform 1000 simulations of SSD evolving on our phylogeny according to gradual Brownian motion, with upper and lower bounds dictated by the highest and lowest SSD observed in our data (see Table S3), and the bounds enforced by the Replace function. We converted the simulated data to a null distribution for *F*-statistics using the program PDANOVA (Garland et al. 1993). Finally, we observed whether the *F*-ratio from the real data exceeded the 95% percentile of the null distribution, which would indicate statistical significance.

Results

PHYLOGENETIC ANALYSES

Phylogenetic analyses revealed 10 major groups of lineages that corresponded to separate geographic regions (Figs. 2 and 3, Fig. S1). Seven of these groupings had high bootstrap support for monophyly (Fig. 3). Three of these lineages corresponded to subspecies that were proposed based on morphological characters (Pack and Tanner 1970; Ballinger and Tinkle 1972). Populations in New Mexico and Texas, which are members of *U. s. stejnegeri,* formed a highly divergent and allopatric monophyletic lineage. Populations in northern Nevada, Oregon, and Washington, the proposed range of *U. s. stansburiana,* were also a well-supported

Table 1. Results from the tests for phylogenetic signal. Traits are ordered from high to low phylogenetic signal, as quantified by the *K*-statistic. The *P* signal column gives the *P*-value resulting from the randomization test for phylogenetic signal. The last two columns give the estimate of the *d*-statistic and whether it is significantly different than zero.

Trait	*K*	*P* signal	*d*	*P* *d*=0
Clutch size	0.789	0.001	0.919	0.003
Male SVL	0.650	<0.001	0.893	<0.001
SSD	0.645	<0.001	0.707	<0.001
Sex-biased tail breaks	0.523	0.023	0.251	0.050
Female SVL	0.435	0.011	0.702	0.073
Male tail	0.426	0.088	0.083	0.119
Female tail	0.347	0.558	0.000	0.566

monophyletic group. Populations in Utah, Colorado, and northern Arizona, the proposed range of *U. s. uniformis,* were monophyletic, with the possible exception of the Zion population, which was of ambiguous affinity. In contrast, the subspecies *U. s. elegans*, as currently recognized, was multiply paraphyletic because all the other subspecies of *U. stansburiana* were nested within it.

Although several distinct and well-supported clades were recovered in our phylogenetic analysis, the relationships among clades generally had poor support. This suggests that the lineages originated in rapid succession. The only relationship among clades that had moderate support was a sister group relationship between the Mexican and *U. s. stejnegeri* clades (Fig. 3, likelihood bootstrap = 79%, Bayesian posterior probability = 76), which together are sister to the remaining clades of *U. stansburiana*. At the highest phylogenetic level, the monophyly of *U. stansburiana* with respect to the outgroup taxa was strongly supported (Fig. 3, bootstrap and Bayesian = 100%).

Within geographic clades, there was a strong influence of geography on the clustering of populations (Fig. 3). Typically, geographically close populations were sister taxa, often with high bootstrap support. However, genetic differentiation was weak or nonexistent in two areas: (1) between populations of *U. s. stejnegeri* from New Mexico and Texas and (2) between populations of *U. s. stansburiana* in Washington, Oregon, and northern Nevada, at the northern limit of the distribution of the species. The lack of structure in these areas could indicate recent range expansion into these regions. Accordingly, relationships among populations in these regions were considered hard polytomies in the comparative analyses.

PHYLOGENETIC SIGNAL

Significant phylogenetic signal was detected for male size, female size, SSD, and clutch size (Table 1). Male and female tail breaks did not show significant phylogenetic signal, but sex-biased tail breaks did show significant signal. All *K*-values were less than 1, which indicated that relatives were less similar than expected from Brownian motion. A star phylogeny was rejected for male size, SSD, and clutch size because *d*-values were significantly different than zero. Phylogenetic corrections were therefore justified for these traits. For female size and sex-biased tail breaks, *d*-values bordered on being significantly different than zero. Therefore, phylogenetic corrections were likely to be necessary for these traits, but noncorrected tests were also done to assess the sensitivity of the analyses to changing the tree to a star phylogeny. A star phylogeny was confidently accepted only for measures of tail break frequency within each sex, the two traits with no significant phylogenetic signal.

COMPARATIVE ANALYSES

Independent contrasts indicated a significant positive correlation between contrasts in the mean male size (snout-vent length) and SSD (Table 2, $P = 0.003$). No significant interaction with Morph was initially identified ($P = 0.22$). However, the contrast between

Table 2. Results from different methods of statistical analysis. All *P*-values are one-tailed. The "*P*-value range" is the range of *P*-values obtained for different topologies of the phylogeny. *P*-values in bold in the last column indicate a disagreement between the statistics not corrected for phylogeny and the independent contrasts about whether a correlation was significant or not.

Comparison	Independent contrasts					Statistics not corrected for phylogeny			
	DF	Slope	r^2	*P*-value	*P*-value range	DF	Slope	r^2	*P*-value
SSD×male SVL	37	0.005	0.182	0.003	0.001–0.004	39	0.008	0.378	0.000
SSD×female SVL	37	−0.003	0.037	0.115	0.097–0.125	39	0.001	0.000	0.384
Male SVL×sex-biased tail breaks	26	7.729	0.123	0.029	0.029–0.033	28	12.614	0.240	0.002
SSD×sex-biased tail breaks	26	0.104	0.182	0.010	0.006–0.011	28	0.163	0.281	0.001
Male SVL×male tail	26	7.676	0.173	0.011	0.011–0.018	28	10.015	0.180	0.006
Female SVL×female tail	26	2.330	0.019	0.233	0.232–0.275	28	1.732	0.000	0.308
Female SVL×clutch size	22	1.323	0.159	0.022	0.022–0.024	24	0.076	0.002	**0.158**
SSD×clutch size	22	−0.010	0.058	0.117	0.094–0.121	24	−0.018	0.139	**0.017**

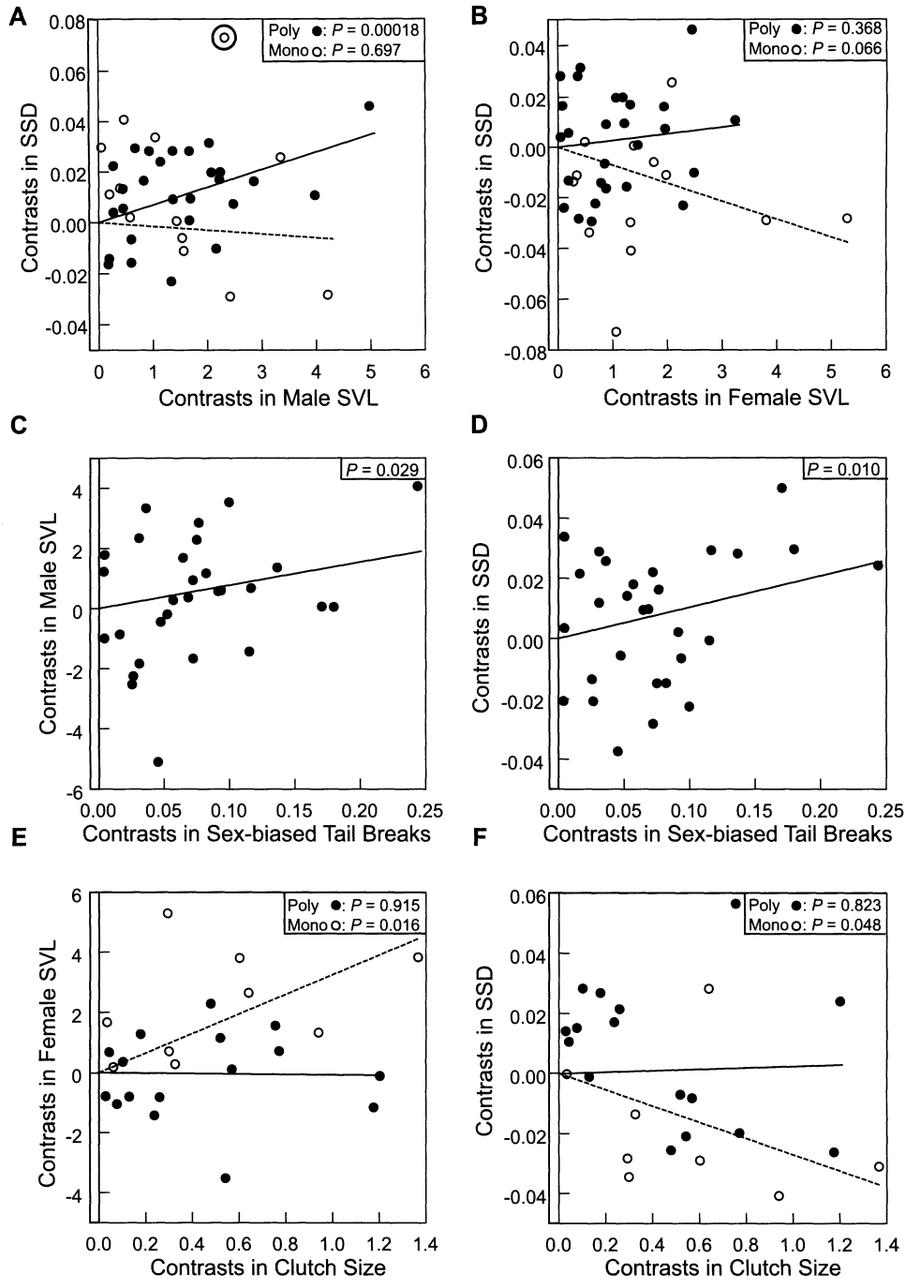

Figure 4. Results from analyses of independent contrasts based on the tree from Figure 3, but with Zion made monophyletic with other *U. s. uniformis* populations. Male and female sizes are snout-vent lengths (SVL) in millimeters. Significant interactions with Morph were found for panels A, B, E, and F. For these panels, contrasts for polymorphic populations are filled circles with a solid regression line and contrasts for monomorphic populations are unfilled circles with a dashed regression line. The interaction with Morph for panel A was significant only when an outlying contrast (circled point at top) was excluded. Panels C and D did not have an interaction with Morph, so both polymorphic and monomorphic contrasts are depicted by filled circles.

the monomorphic populations of Big Creek and Nacimiento was identified as a significant outlier. Big Creek has the smallest sample size of our sampled populations (Table S3) and therefore size data from this population may be poorly estimated. When the outlying contrast was removed (circled point, Fig. 4A), then a significant interaction with numbers of morphs was detected (df = 35, $t = 2.49$, $P = 0.018$, $r^2 = 0.253$). Polymorphic populations had a positive correlation between male size and SSD (Fig. 4A, $P = 0.00018$, $r^2 = 0.423$) whereas monomorphic populations had no significant correlation ($P = 0.697$).

Independent contrasts indicated a negative trend between female size and SSD (Table 2, $P = 0.115$). A significant interaction with Morph was identified (df = 36, $t = 2.26$, $P = 0.030$, $r^2 = 0.128$), and this effect remained significant if the outlying contrast between Big Creek and Nacimiento was removed ($P = 0.033$). Monomorphic populations had a negative correlation between female size and SSD (Fig. 4B, $P = 0.066$, $r^2 = 0.263$ with all points, $P = 0.045$, $r^2 = 0.330$ with outlier removed) whereas polymorphic populations had no significant correlation ($P = 0.368$).

Independent contrasts indicated a significant positive correlation between sex-biased tail breaks and male size (Fig. 4C, $P = 0.029$) and between sex-biased tail breaks and SSD (Fig. 4D, $P = 0.010$). Male size was correlated with male tail breaks (Table 2, $P = 0.011$), but female size was not correlated with female tail breaks ($P = 0.233$). No significant interactions with Morph were found for any of the above correlations (all $P > 0.10$).

Independent contrasts indicated a significant positive correlation between female size and clutch size ($P = 0.022$). There was a significant interaction with Morph (df = 21, $t = -3.08$, $P = 0.006$, $r^2 = 0.379$). Monomorphic populations had a significant positive correlation between clutch size and female size (Fig. 5E, $P = 0.016$, $r^2 = 0.582$), whereas polymorphic populations had no significant correlation ($P = 0.915$). There was a negative trend between clutch size and SSD (Table 2, $P = 0.117$). The interaction with Morph approached significance (df = 21, $t = -1.88$, $P = 0.074$, $r^2 = 0.149$) and became significant once changes in male size were included in the model (see below). Monomorphic populations had a significant negative correlation between clutch size and SSD (Fig. 5F, $P = 0.048$, $r^2 = 0.433$), whereas polymorphic populations had no significant correlation ($P = 0.823$).

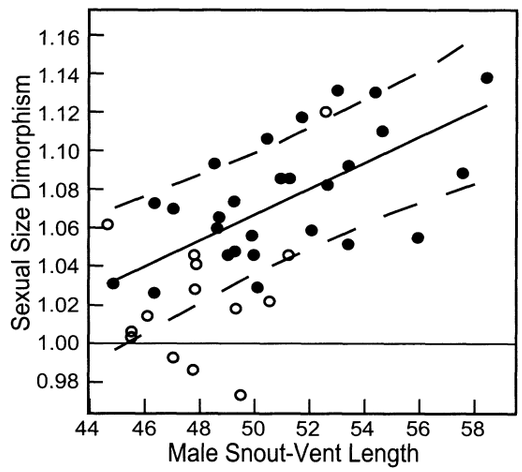

Figure 5. The correlation from independent contrasts between male size and SSD mapped onto uncorrected population data. A value of SSD = 1 indicates a lack of sexual size dimorphism. The regression line and 95% confidence intervals (dashed lines) were obtained from an analysis of only polymorphic populations (see the text). Filled points are polymorphic populations and unfilled points are monomorphic populations. No phylogenetic corrections have been done on the population data so the points do not represent independent evolutionary transitions. The graph allows an assessment of whether monomorphic populations have significantly outlying phenotypes relative to the allometric predictions of polymorphic populations. It also allows an assessment of whether monomorphic populations tend to have higher or lower SSD than polymorphic populations.

To determine how multiple factors may explain variance in SSD, we conducted a multivariate regression with male size, clutch size, and crossproduct Morph terms for both variables. Backward stepwise elimination of nonsignificant variables resulted in a model that included an effect of male size (df = 20, $t = 3.34$, $P = 0.003$), an effect of clutch size (df = 20, $t = -3.79$, $P = 0.001$) and a significant interaction between clutch size and Morph (df = 20, $t = 3.13$, $P = 0.005$). This model explained 41% of the variation in SSD (adjusted $r^2 = 0.409$). We conducted another multivariate regression that included female size, sex-biased tail breaks, and crossproduct Morph terms. Backward stepwise elimination using a threshold of $P = 0.05$ only retained an effect of sex-biased tail breaks. However, if the threshold was relaxed to $P = 0.10$, then this resulted in a model with an effect of sex-biased tail breaks (df = 24, $t = 2.29$, $P = 0.031$), an effect of female size (df = 24, $t = -1.90$, $P = 0.069$), and an interaction between female size and Morph (df = 24, $t = 1.75$, $P = 0.093$). This model explained 24% of the variation in SSD (adjusted $r^2 = 0.237$).

TESTS OF THE DIRECTION OF SSD EVOLUTION

Pairwise comparisons of independent sets of monomorphic and polymorphic populations suggested that SSD may decrease in monomorphic populations (Table 3). In three of the four comparisons the average SSD in monomorphic populations was lower than the average SSD in trimorphic populations. In the fourth comparison, the averages of the paired populations were equal. A paired t-test for these comparisons approached significance (df = 3, $t = -2.35$, $P = 0.100$).

An alternative way to observe trends in SSD evolution in monomorphic populations was to test whether monomorphic populations differed from the allometric predictions obtained from comparisons among polymorphic populations. A plot of the population data showed that all polymorphic populations had male-biased SSD and populations with larger males tended to have greater SSD (Fig. 5). Monomorphic populations differed from this pattern in several ways. Many monomorphic populations (6 of 14) lay outside the 95% CI, suggesting that they did not follow the allometric predictions of polymorphic populations. Although these population data were not independent (because they had not been phylogenetically corrected), the populations lying

Table 3. Direction of the change in SSD in monomorphic populations. The numbers following the geographic regions correspond to the populations in Figure 2. The SSD listed are averages for the populations.

Monomorphic populations		Polymorphic populations	Monomorphic SSD	Polymorphic SSD
Northern UT (33, 34)	vs.	Southern UT/NV (31, 32)	0.994	1.05
Coastal, North CA (4, 5)	vs.	Central, North CA (1–3)	1.07	1.07
U. s. stansburiana (37–41)	vs.	Western intergrade (35, 36)	1.03	1.05
U. s. uniformis (26–30)	vs.	Coastal and Central CA, AZ (6–16)	1.01	1.07

outside the 95% CI included representatives from all four of the independent evolutions of a monomorphic state. Another pattern was that most monomorphic populations (12 of 14) fell below the regression line, which indicated that they had lower SSD for a particular male size than expected, and therefore relatively large females. In addition, three monomorphic populations had female-biased SSD and two had essentially no SSD, which are phenotypes not observed in any polymorphic population. These monomorphic populations have evolved novel SSD phenotypes, because polymorphic populations with male-biased SSD are ancestral.

An ANOVA performed with conventional statistics showed that SSD significantly differed among monomorphic and polymorphic populations ($F_{1,39} = 20.74$; $P = 0.00005$), with monomorphic populations having lower SSD (mean = 1.026) than polymorphic populations (mean = 1.076). The F-ratio obtained from the observed data ($F_{1,39} = 20.74$) lies beyond the 95% percentile of the null distribution of F-values obtained by simulation on our phylogeny ($F_{\text{critical}} = 16.9$). Therefore, the phylogenetic ANOVA indicates that SSD is significantly lower in monomorphic than that in polymorphic populations ($P = 0.028$).

ALTERNATIVE ANALYSES

The correlations observed above were robust to changes in the tree topology. Changing the topology of the tree made only minor changes to the P-values of the correlations (see P-value range, Table 2). In no case did an alteration of the topology change a nonsignificant P-value to a significant one. In contrast, regressions that did not correct for phylogeny often differed in levels of significance from the analyses of independent contrasts, sometimes to the degree that one method was significant and the other was not (Table 2). For example, independent contrasts found a significant correlation between female size and clutch size, but this was not significant in the uncorrected analysis. The uncorrected analysis was confounded because it regarded the low clutch sizes of Mexican populations as independent from one another; when these populations were removed, a significant correlation was found ($P = 0.02$).

Analyses that did not correct for phylogeny did not find the significant interaction terms observed in the analyses of independent contrasts. In a general linear model predicting SSD that included male size, Morph, and an interaction between male size and Morph, the interaction term was not significant ($F_{1,37} = 0.041$; $P = 0.842$). In a similar model for female size, the interaction between female size and Morph was not significant ($F_{1,37} = 2.71$; $P = 0.108$). When predicting female size with a model that included clutch size, Morph, and an interaction term, the interaction was not significant ($F_{1,22} = 0.937$; $P = 0.343$).

Discussion

ALTERNATIVE MATING STRATEGIES AND THE EVOLUTION OF SEXUAL DIMORPHISM

Our analyses suggested that populations that have diverged in their alternative mating strategies have faced different selective pressures. Increases in male body size were correlated with increases in SSD in polymorphic populations, following the predictions of the intrasexual selection hypothesis. In contrast, increases in female body size were correlated with decreases in SSD in monomorphic populations, consistent with the predictions of the fecundity selection hypothesis. Analyses of other traits were consistent with both of these hypotheses. Levels of sex-biased tail breaks were positively correlated with larger males and more male-biased SSD, which was consistent with the hypothesis that male–male aggression varies among populations, causing different selection pressures on body size. In monomorphic populations, increases in clutch size were correlated with increases in female size and decreases in SSD, which was consistent with the predictions of the fecundity selection hypothesis. The likely result of these differences in selection among populations is that some monomorphic populations have developed no SSD or female-biased SSD, phenotypes not observed in polymorphic populations. Overall, these observations supported the hypothesis that changes to the number of alternative mating types within populations may be associated with phenotypic diversification among populations.

Studies of the polymorphic population at Los Banos suggest two reasons why sexual selection may favor the evolution of large male size and male-biased SSD. Females prefer high thermal quality territories from which they gain direct benefits (Calsbeek and Sinervo 2002b) and body size is an important factor determining the ability of males to control territories (Calsbeek and Sinervo

2002a). Therefore, male–male competition for territories can favor the evolution of large male size. Intersexual selection may also promote large male body size. Females at Los Banos have a preference for large males (Calsbeek and Sinervo 2002b), which may reflect selection for good genes, because sons of large males have increased survival (Calsbeek and Sinervo 2004). Thus, both intrasexual and intersexual selection may explain why polymorphic populations have male-biased SSD.

The variation in levels of tail breaks that we observed may reflect different levels of aggression among populations, provided that some tail breaks are caused by the male–male combat. Consistent with this idea, male *U. stansburiana* from a polymorphic population in Texas were described as quite aggressive, whereas males from a monomorphic population in Colorado were described as less aggressive (Tinkle 1967). In addition, lizards in a monomorphic population from Oregon were described as exhibiting low levels of intraspecific aggression (Wilson 1991). Such changes in male–male aggression could help explain some of the variation in tail breaks, male size, and SSD that we observed among populations.

It is important to note that many other factors may influence the relative frequencies of tail breaks among populations, including differences in predation pressure and longevity. One previous study interpreted an observed decrease in tail break frequency from southern to northern populations of *U. stansburiana* as arising primarily from a higher density and diversity of predators in the south, and partially from greater aggression within southern populations (Parker and Pianka 1975). However, a later demographic study found no correlation between levels of tail breaks and levels of mortality across multiple populations of *U. stansburiana* (Wilson 1991). This result is inconsistent with the predation hypothesis and suggests that male–male aggression may be an important factor influencing the frequency of tail breaks within populations. In addition, we observed that while changes in male tail break frequency were correlated with changes in male size, changes in female tail break frequency were not correlated with female size. This suggests that longevity differences among populations have not resulted in a general correlation between size and tail breaks in both sexes, but instead that there have been changes in either male–male aggression or male longevity. Changes in male longevity could occur because males may be more exposed to predation during activities such as territorial defense. Given that multiple factors may influence tail breaks, correlations involving tail breaks must be interpreted with care. However, our results do suggest that studying levels of male–male aggression among populations could be a fruitful area for future research.

The ecology of *U. stansburiana* may provide clues as to why the selective environment for SSD has changed to favor fecundity selection in monomorphic populations. Local ecology can have direct effects on the intensity of sexual selection and the form of sexually selected traits (Emlen and Oring 1977). For example, sexual selection consistently favored large male size in marine iguanas, but local food supply and climatic variability sometimes caused the largest males to have low survivorship, resulting in variation in SSD among island populations (Wikelski et al. 1997; Wikelski and Trillmich 1997). Similar ecological constraints may affect sexual selection and levels of SSD in *U. stansburiana*. It is notable that all monomorphic lineages occur in areas where temperatures can be cool and seasonal, such as northern regions and the coastal environment. Cool conditions greatly limit the amount of time available for ectotherms to be active. Females in northern regions have less opportunity to lay multiple clutches during the year, as is commonly done in southern areas (Sinervo et al. 2000b; Zani 2005). This could select for larger females with increased female fecundity per clutch, which would result in a decrease in male-biased SSD. This sort of ecological effect has been observed in the lizard *Sceloporus undulatus,* in which decreases in temperature increase female size, which in turn increase clutch size (Angilletta et al. 2006). Future work that relates clutch size and frequency to environmental variables among populations would be useful to better understand the ecological conditions that affect body size.

In addition to ecological differences among populations, fixation on a single morph may have changed the selective regime in monomorphic populations. All monomorphic populations have fixed on throat color genotypes associated with r-strategy females, which are selected for offspring quantity (Sinervo et al. 2000b; Corl 2007). Fixation on the r-strategy may have allowed the spread of alleles for further specialization on fecundity that were disadvantageous in populations with both female life-history types. This scenario is in line with West-Eberhard's concept of character release (West-Eberhard 1986). In addition, fecundity selection in polymorphic populations may primarily select on the frequencies of the two female morphs (Sinervo et al. 2000b; Sinervo and Svensson 2002). Fixation on a single morph may result in female size becoming the target of fecundity selection, which may explain why we only observe a correlation between female size and fecundity for comparisons among monomorphic populations.

Loss of alternative male mating strategies likely resulted in a new competitive environment for sexual selection because morph fitness depends upon the frequency of other strategies within a population. The observations described above of lower male aggression in monomorphic populations suggest that selection favoring large male size in monomorphic populations may be weaker than in more aggressive polymorphic populations. These observations are at first surprising, because some monomorphic populations are fixed for the orange allele that is associated with aggressive male morphs in a trimorphic population (Sinervo et al. 2000a; Corl 2007). However, a monomorphic orange population could have strong selection to deescalate aggression because the

costs of male fighting may be higher when all males are on equal footing. Alternatively, trimorphic populations may have strong selection for large, aggressive males because of fights with invading, sneaker males, but this selection may be reduced in monomorphic populations because they are missing the yellow allele for sneaker males. Such changes in the male competitive environment are important to consider because SSD could have remained unchanged in the face of fecundity selection if genetic correlations between the sexes caused male size to change along with female size. Relaxed intrasexual selection could have allowed female size to surpass male size in monomorphic populations.

Associations between the presence and absence of mating strategies and levels of sexual dimorphism are likely to be found in many other systems. Polymorphic and polyphenic mating strategies are increasingly recognized within species (reviews in Gross 1996; Oliveira et al. 2008). In many cases, sexually dimorphic traits vary among male mating strategies and may be integral to their mating behavior. For example, male mating types in dung beetles (*Onthophagus acuminatus*) vary in sexual dimorphism for horns: large, horned males aggressively defend tunnels containing females whereas small, hornless males sneak into tunnels (Emlen 1997). The intensity of intrasexual selection on such sexually dimorphic traits is likely to be a function of the prevalence of other male types. For example, European earwigs (*Forficula auricularia*) use forceps for fighting and have two male types, a large-bodied morph with long forceps and a small-bodied morph with short forceps. Males with long forceps are competitively superior and are more likely to be found in dense populations where there is a high probability of having to fight other males. Thus, changes in the frequency and density of male morphs may determine whether sexually dimorphic traits are observed.

Phenotypic divergence associated with changes in numbers of mating strategies could have important implications for species formation (West-Eberhard 1986; Sinervo and Svensson 2002; Gray and McKinnon 2007). In *Uta,* morph phenotypes have evolved in response to their social competitors, so monomorphic populations have different fitness optima. For example, if aggression is reduced in monomorphic orange populations, such males would have low fitness in a trimorphic population where aggression is necessary for the orange mating strategy. Such interpopulational divergence in social environment could limit mating and gene flow between populations. Reproductive isolation can also form when genetic divergence leads to low hybrid fitness among populations due to epistatic interactions among the divergent alleles (i.e., Dobzhansky–Muller incompatibilities) (Coyne and Orr 2004). Divergence in the genes for traits such as body size and clutch size could result in Dobzhansky–Muller incompatibilities between polymorphic and monomorphic populations. At our focal trimorphic study population (at Los Banos, CA), we have also observed large numbers of traits to be associated in complex ways with throat color alleles and many of these associations are maintained by correlational selection generated by interactions among morphs (Sinervo et al. 2001; Sinervo and Svensson 2002; Sinervo et al. 2006). The chance of Dobzhansky–Muller incompatibilities increases with the number of associations among genes and with the number of genes that diverge (Coyne and Orr 2004), so genetic changes resulting from morph fixation have the potential to generate a large number of incompatibilities. Genetic crosses are needed to establish if and how reproductive isolation forms between populations differing in numbers of mating strategies.

Overall, our study finds support for both the intrasexual selection and fecundity advantage hypotheses. Support for both hypotheses of SSD evolution has also been found in more macroevolutionary studies. For instance, analyses of independent contrasts in stalk-eyed flies revealed that evolutionary changes in male, but not female allometry, were responsible for the evolution of SSD, supporting the hypothesis that eye stalks are used in sexual selection (Baker and Wilkinson 2001). In spiders, independent contrasts in clutch size were related to changes in both female size and SSD, supporting the fecundity advantage hypothesis (Prenter et al. 1999). Independent contrasts between 302 species of lizards showed that changes in male aggression and territoriality were correlated with SSD, supporting the intrasexual selection hypothesis (Cox et al. 2003). The same study also showed that changes in clutch size, reproductive mode, and reproductive frequency were correlated with SSD, consistent with the fecundity advantage hypothesis (Cox et al. 2003). Our study provides an important population-level link for explaining such macroevolutionary patterns in SSD.

METHODS OF ANALYSIS AT THE POPULATION LEVEL

Our results suggest that intraspecific comparative studies may need to correct for statistical nonindependence of population data due to shared ancestry. Substantial phylogenetic structure was observed among populations of *U. stansburiana*, a pattern found across many other species (e.g., Edwards and Kot 1995; Zamudio 1998; Avise 2000; Kuchta et al. 2009). The K-values quantifying phylogenetic signal in our data (Table 1) are comparable to K-values calculated for body size in other intraspecific studies, which ranged from 0.39 to 0.79 (Ashton 2004). The significant phylogenetic signal in our data and the generally poor fit of a star phylogeny to our data suggested that methods accounting for shared evolutionary history among populations were necessary for comparative analyses.

Phylogenetic corrections had substantial effects on the interpretation of our data. Statistical analyses that did not correct for phylogeny sometimes differed from independent contrasts about whether a correlation was significant or not (Table 2). Also, without phylogenetic corrections, we would not have understood that male size, female size, and clutch size have changed

differently among monomorphic and polymorphic populations because noncorrected statistics failed to detect interactions with the Morph term. Thus, our conclusions about how the presence/absence of morphs affects morphological evolution would have changed greatly had phylogenetic corrections not been done. Differences between the two statistical methods are likely the result of phylogenetic methods having smaller standard errors for correlation coefficients, which leads to Type I error rates closer to the desired levels and more powerful tests when the parameters are not equal to zero (Rohlf 2006).

Many phylogenetic studies of intraspecific variation have similarly concluded that it is necessary to take shared ancestry into account (Edwards and Kot 1995; Radtkey et al. 1997; Zamudio 1998). However, other studies have concluded that phylogenetic history within species is not a confounding factor (Ashton 2001; Niewiarowski et al. 2004). A possible reason for these differences in opinion is the fact that more than 20 operational taxonomic units are needed to adequately detect phylogenetic signal (Blomberg et al. 2003; Ashton 2004). Thus, the fact that we observed significant effects of phylogeny may partially result from our sampling of a sufficient number of populations (41) to detect phylogenetic effects.

It could be argued that our analysis is not solely intraspecific, because the highly divergent mtDNA clades we observed could indicate that *U. stansburiana* is in fact a species complex. However, regardless of whether our analysis is partially interspecific, determining whether cryptic species and/or phylogenetic structure exist within a species is precisely the point of conducting a phylogenetic analysis for population-level comparisons. For example, no significant trends in body size were found for the Western rattlesnake (*Crotalus viridus*) unless two well-differentiated clades or cryptic species were taken into account, because the clades had opposing trends in body size in relation to the mean annual temperature (Ashton 2001). Even simple recognition of phylogenetic history can be vital in determining the questions to ask. In our study, recognition that alternative mating strategies had been repeatedly lost allowed us to investigate the phenotypic consequences of this loss. Similarly, a phylogenetic analysis of skinks of the *Eumeces skiltonianus* species group revealed parallel evolution of a large-bodied morphotype, and subsequent tests with independent contrasts showed a significant correlation between changes in body size and color pattern evolution (Richmond and Reeder 2002). All of these factors suggest that phylogenetic structure should be investigated as a possible confounding factor before the analysis of variation within a species.

Phylogenetic analyses depend upon accurate reconstruction of the relationships among populations or species. It is important to note that our mtDNA phylogeny only gives a maternal evolutionary history and thus the amount of gene flow and phylogenetic structure for other loci could differ. However, mtDNA gene trees are particularly good at tracking bifurcations in the species tree because mtDNA has a shorter coalescence time than nuclear genes (Moore 1995; Hudson and Coyne 2002; Zink and Barrowclough 2008). Also, three of the mtDNA clades of *U. stansburiana* corresponded with subspecies designated by morphological characters (Pack and Tanner 1970; Ballinger and Tinkle 1972). These morphological characters are presumably governed by nuclear loci, which suggest that loci independent from mtDNA have diverged among geographic regions. Overall, the concordance of geography, morphological classifications, and mtDNA gene tree structure supports the validity of our mtDNA phylogeny for use in comparative analyses. In addition, our comparative analyses proved robust to some minor changes in the mtDNA tree topology. Future studies using multiple nuclear loci to obtain gene trees independent of the mtDNA tree could be useful for verifying our hypothesized relationships among populations.

Phylogenetic comparative studies can both reveal patterns of evolutionary change as well as test whether changes in phenotypic traits are consistent with particular hypotheses of evolution. However, it is important to note that no correlational study can ascertain the causative factors of evolutionary change. For example, although all changes in SSD occur because of changes in body size, selection may not be on body size, but on correlated traits. In *Uta palmeri*, a closely related species to *U. stansburiana*, head depth and territory quality were found to be the direct targets of selection for reproductive success, whereas selection on male size was likely due to a correlation with the direct targets of selection (Hews 1990). Body size may change for many reasons including direct selection, developmental trade-offs, differential survival among populations, and differential food availability in disparate environments. This complexity suggests that inferences about the mode of selection on body size and other traits should be done cautiously. However, correlations from comparative analyses are useful for identifying plausible factors affecting evolutionary change that can then be tested by further experiments. For example, selection experiments on *Drosophila melanogaster* have demonstrated that SSD can evolve in response to fecundity selection (Reeve and Fairbairn 1999). In *U. stansburiana*, lizard density and clutch size could be manipulated in different populations to elucidate how selection differs among locations (Sinervo 1999; Svensson and Sinervo 2000).

A fundamental goal of evolutionary biology is to understand the patterns and processes involved in phenotypic diversification. Our study revealed that even within a single species, multiple evolutionary forces have shaped SSD, causing it to vary from male-biased SSD to female-biased SSD. These results suggest that variation within species can be used to test how multiple forms of selection interact in the process of phenotypic diversification. Incorporating data on morphs proved to be vital in predicting and interpreting patterns of phenotypic evolution across the range of

the species. Thus, studies within populations on the presence or absence of alternative mating strategies and the selective forces maintaining polymorphisms can provide important information about how phenotypic diversity arises across populations. Overall, our study shows that investigations of population-level variation offer an important way to link microevolutionary selection within populations to more macroevolutionary patterns of phenotypic divergence.

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Supporting Information

The following supporting information is available for this article:

Supporting text. Methods, analysis, and discussion of the multiple individuals per population phylogeny.

Figure S1. Phylogram of *U. stansburiana* populations from the complete dataset that included multiple individuals per population.

Table S1. Population locations and years sampled.

Table S2. Tail break frequency data.

Table S3. Sexual size dimorphism (SSD) observed within populations.

Table S4. Clutch size data for *Uta* populations.

Supporting Information may be found in the online version of this article.
(This link will take you to the article abstract).

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