



Does habitat disturbance promote geographical parthenogenesis in whiptail lizards?

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Abstract

Sexual and asexual organisms often vary in their distribution and abundances among habitats. These patterns of “geographical parthenogenesis” can shed light on ecological conditions underlying the evolution of sex. Habitat disturbance is hypothesized to be a mechanism that generates geographical parthenogenesis. Parthenogens are predicted to be more prevalent in disturbed habitats than sexuals due to the greater colonizing ability of parthenogens and the tendency of parthenogens to avoid competition with sexuals in undisturbed habitat. We tested whether habitat disturbance (i.e., a rapid state transition between vegetation communities) causes geographical parthenogenesis in whiptail lizards in the Chihuahuan Desert of southern New Mexico. Non-experimental approaches have shown the parthenogenetic *Aspidoscelis uniparens* commonly occurs in habitat with a history of vegetation disturbance from shrub removal, whereas the sexual *A. marmorata* occurs more often in undisturbed shrubland habitat. We used a field experiment replicated across 16 sites to test whether the parthenogen *A. uniparens* and sexual *A. marmorata* differ in their response to vegetation disturbance from shrub removal. The sites were distributed across a broad region of southern New Mexico, and we used a paired design with each site including a shrub-removal treatment and a control on 9-ha plots. Using a co-abundance model that accounts for imperfect detection, we found the parthenogen *A. uniparens* and sexual *A. marmorata* both responded positively to disturbance, but only when the congener was rare. Our results are inconsistent with the idea that parthenogens exploit disturbed habitat to avoid competition with sexuals. In our study system, *A. uniparens* often dominates older disturbed sites, especially two decades or more after shrub removal. Collectively, these results indicate geographical parthenogenesis emerges from biotic interactions in heterogeneous landscapes that include disturbed habitats used by sexual and asexual species alike.

Keywords Competition · Desert · Disturbance · Evolution of sex · Niche partitioning · Parthenogenesis

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Introduction

Investment in males by sexual organisms bears a twofold fitness cost relative to asexual organisms, assuming equal fecundity of sexual and asexual females and survival of their offspring (Maynard Smith 1978; Gibson et al. 2017). This cost of males, along with other costs of sex (Meirmans et al. 2012), raises the question of why sexual reproduction is so widespread. Solving this quandary in part requires understanding how ecological conditions in the field govern the cost–benefit ratio of sex (Lively and Morran 2014; Neiman et al. 2018). Insight into ecological conditions favoring the evolution of sex can be gained by identifying the mechanisms underlying geographical parthenogenesis—when sexual and asexual organisms have different distributions or abundances among areas (Vandel 1928).

Patterns of geographical parthenogenesis include parthenogens occurring at higher latitudes and altitudes and in areas with a history of glaciation compared with their sexual relatives (Tilquin and Kokko 2016). Cuellar (1977) proposed that parthenogens are more often associated with habitat disturbance (e.g., fire, anthropogenic habitat change) than sexuals because parthenogens have a greater ability to colonize newly available habitat. Parthenogens have a demographic advantage during colonization because populations can be established by a single clonal individual, eliminating Allee effects. However, greater colonization ability is insufficient to explain why parthenogens, with a twofold reproductive advantage, do not outcompete sexuals in undisturbed habitat (Glesener and Tilman 1978). Cuellar's (1977) hypothesis assumes that parthenogens are poor competitors due to their limited genetic variability and evolutionary potential. When genetic variation is limited in parthenogens, sexuals could be favored in undisturbed habitat if biotic interactions drive evolutionary arms races (i.e., Red Queen Hypothesis; Jaenike 1978; Hamilton 1980; Bell 1982). Greater habitat heterogeneity in undisturbed habitat could also favor genetically diverse populations of sexuals that are more effective than clonal populations at exploiting a wide range of resources (i.e., Tangled Bank Hypothesis; Bell 1982). Although hypotheses for the association of parthenogens with disturbance are abundant (see Tilquin and Kokko 2016), experimental investigation of how such patterns arise in the field are rare (Neiman et al. 2018).

Among living species, reptiles are the only vertebrates that have evolved true parthenogenesis (i.e., not sperm-dependent), which is especially common among whiptail lizards (Teiidae; Kearney et al. 2009). In the Chihuahuan Desert of southern New Mexico, parthenogenetic and sexual whiptails occur in a dramatically changing landscape. Since the nineteenth century, the dominant vegetation shifted from semiarid grassland to shrubland, representing a state transition driven by drought, livestock overgrazing, and altered fire regimes (Bestelmeyer et al. 2018). Management agencies have applied herbicides to approximately 300,000 ha to remove shrubs as a restoration strategy since the 1980s, with >60% of treatments applied from 2007 to 2014. Treatments greatly reduce shrub cover in <8 years (Perkins et al. 2006), resulting in novel savanna habitats with increased grass cover (Coffman et al. 2014). The sharp contrast between shrub-encroached areas and shrub-removal areas presents a rare opportunity to test how parthenogenetic and sexual species respond to rapid vegetation disturbance.

Disturbance is often vaguely defined in the geographical parthenogenesis literature (Tilquin and Kokko 2016). Here, we define disturbance as an unusually rapid state transition between vegetation communities. The formation of the current shrubland state occurred over the past 150 years (Bestelmeyer et al. 2018), and over that time faunal

communities have re-assembled in response to these gradual changes in vegetation structure (e.g., Eldridge et al. 2011, Schooley et al. 2018). In contrast, shrub removal is an abrupt and powerful disturbance to shrubland habitats. These rapid state transitions could create habitat that is newly available for colonization, or they could change environmental conditions in a way that alters the cost–benefit ratio of sex. Vegetation structure is an important driver of resource diversity for lizards (e.g., microhabitat heterogeneity, prey diversity; Pianka 1966, 1967), so shifts in vegetation structure from disturbance could be particularly important for affecting the benefits of genetic diversity associated with sex (i.e., Tangled Bank Hypothesis).

We used a field experiment to determine how the distributions and abundances of two closely related whiptail species respond to habitat disturbance from shrub removal. Our focal species were the parthenogenetic (all female) *Aspidoscelis uniparens* and the sexual *A. marmorata*. *Aspidoscelis uniparens* is a triploid of hybrid origin, although *A. marmorata* is not one of the parental species. Parthenogenetic whiptails are viewed as fugitive species that occur in disturbed habitats because of their colonization ability and avoidance of competition with sexual species (Wright and Lowe 1968; Cuellar 1977). In our study area, non-experimental approaches indicate *A. uniparens* is associated with areas historically treated for shrub removal, whereas *A. marmorata* is more abundant in shrublands (Cosentino et al. 2013). Responses of *A. uniparens* and *A. marmorata* to experimental disturbance should clarify whether disturbance is a key mechanism underlying geographical parthenogenesis. If *A. uniparens* is a fugitive parthenogen that uses disturbed habitat to avoid competition with *A. marmorata*, then *A. uniparens* should be more abundant in experimentally disturbed sites, whereas *A. marmorata* should be more abundant in undisturbed sites. We used a novel co-abundance model that accounts for imperfect detection to test how *A. uniparens* and *A. marmorata* respond to vegetation disturbance. We also examined the potential for interspecific competition by testing for a negative association between the abundances of the two species while controlling for variation related to vegetation disturbance and habitat variables.

Methods

Study species

Aspidoscelis uniparens occurs in the Chihuahuan Desert of southern New Mexico and northern Mexico, and in the Sonoran Desert west along the Mogollon Rim of Arizona (Jennings 2009). *Aspidoscelis marmorata* is restricted to the Chihuahuan Desert in southern New Mexico, western Texas, and northern Mexico (Dixon 2009). Although *A. marmorata* is recognized as a distinct species, it was previously considered a subspecies of *A. tigris*, and hybridization with *A. tigris* occurs in southwestern New Mexico outside our study area (Painter et al. 2017). Previous reports on whiptail lizards in our study area refer to *A. marmorata* as *A. tigris* (e.g., Cuellar 1979; Price et al. 1993; Menke 2003; Cosentino et al. 2013).

Aspidoscelis uniparens and *A. marmorata* are wide-ranging, active foragers that specialize on fossorial prey and have extensive niche overlap in diet and phenology (Mitchell 1979). Body size is larger for *A. marmorata* (snout-vent length = 68–94 cm; Mata-Silva et al. 2010) than *A. uniparens* (snout-vent length = 47–78 cm; Cuellar 1993). *Aspidoscelis marmorata* is bisexual, whereas *A. uniparens* is a triploid of hybrid origin with meiotic

parthenogenesis (Cuellar 1971). The parental lineage of *A. uniparens* includes *A. inornata* (maternal; Densmore et al. 1989) and *A. burti* (paternal; Wright 1993). The F1 hybrid between these parental species backcrossed with *A. inornata* resulting in the triploid *A. uniparens* (Reeder et al. 2002). Despite the difference in body size and reproductive mode, other reproductive characteristics are similar between the species. Females of both species produce two or more clutches between late spring and mid-summer (Cuellar 1981; Cuellar 1984; Mata-Silva et al. 2010). Clutch size is typically 2–4 for *A. marmorata* (Mata-Silva et al. 2010) and 3–5 for *A. uniparens* (Congdon et al. 1978; Cuellar 1984), and egg masses are 0.30–0.75 g for *A. marmorata* (Schall 1978) and 0.45–0.76 g for *A. uniparens* (Cuellar 1984).

Study area and experimental design

We conducted the experiment at 16 sites in the Chihuahuan Desert in a large region extending west and north of Las Cruces, New Mexico (Fig. 1). Each site consisted of two 300×300-m plots (9 ha each). One plot was treated with the herbicide tebuthiuron to remove creosotebush (*Larrea tridentata*), the dominant shrub. The second plot was a control that was never treated. Treatment and control plots were randomly assigned within a pair, separated by 0.3–1.3 km, and located within a larger area treated with herbicide. A single application of tebuthiuron (0.56 kg/ha) was activated by summer rains at six plots in 2010 and 10 plots in 2011.

We measured vegetation cover at each plot five years after treatment using line-point intercept sampling (Herrick et al. 2017). Sampling was conducted on two 50-m transects oriented perpendicular to the slope and offset by 20 m. We quantified the mean percentage cover of six vegetation categories on each plot: perennial grasses, perennial forbs, shrubs, sub-shrubs, litter (herbaceous and woody), and bare ground.

We performed lizard surveys at treatment and control plots at each site on a single day between 12 June and 7 July 2017. Each plot was divided into 10 belt transects that were 300×30 m, and we counted lizards via visual surveys between 7:15 and 13:15 in each belt transect (Cosentino et al. 2013). Binoculars were used to identify lizards to species. Two observers surveyed treatment and control plots concurrently. Observers switched between treatment and control plots after surveying five belt transects each to avoid confounding observer with treatment. We recorded search time for each belt transect. We used a Kestrel 3000 weather meter (Kestrel Instruments, Boothwyn, PA) to measure air temperature, relative humidity, and wind speed for 30 s at the start and end of each belt transect, and then we averaged the two measurements.

The remote nature of our sites covering a broad geographic region prohibited repeated sampling of lizards within an active season. Instead, we focused our efforts on extensive spatial replication of disturbance treatments, and use of abundance models that account for imperfect detection, to produce strong inferences. Sampling for multiple, consecutive years was also unlikely to quantify relevant temporal changes in lizard abundances that can take many years to unfold (see “Discussion” section).

Statistical analyses

We used principal component analysis (PCA) with varimax rotation to describe covariation in the six vegetation cover categories among plots. We retained principal components with eigenvalues > 1. The PCA was conducted with the *psych* package (Revelle 2018) in R

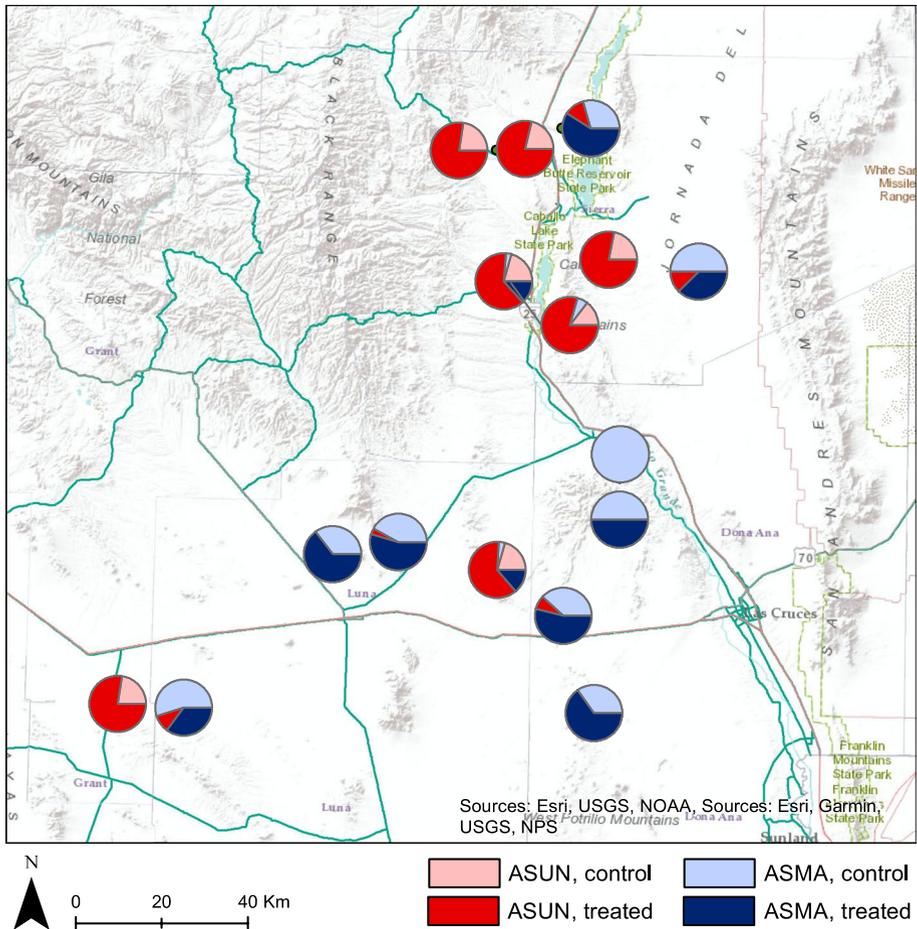


Fig. 1 Map of the study area. Sites ($n = 16$; pie charts) include a plot treated for shrub removal and a control plot. Pie charts represent the relative abundances of the parthenogen *Aspidooscelis uniparens* (ASUN; red) and the sexual *A. marmorata* (ASMA; blue) at treated and control plots predicted from a co-abundance model (Table 1). (Color figure online)

3.5.1 (R Core Team 2018). We used paired t -tests in R to test for differences in vegetation cover as reflected in the principal components between treatment and control plots.

We used a two-species N -mixture model (Brodie et al. 2018) to test for a relationship between the abundances of *A. uniparens* and *A. marmorata* while accounting for imperfect detection and the responses of each species to shrub removal. N -mixture models are used to jointly estimate the latent (i.e., unobserved) abundances (N_{ij}) and individual detection probabilities (p_{ijk}) of species i based on repeated counts k at each location j (Royle 2004). We used counts of each species from the 10 belt transects at each plot as repeated counts. We defined the latent abundances as $N_{ij} \sim \text{Poisson}(\lambda_{ij})$, where λ_{ij} is the expected abundance of species i at location j . To test for a relationship between species abundances, the abundance of one species is used as a covariate in the model of the second species. We arbitrarily chose *A. uniparens* as species 1 because the model allowed us to infer a correlation

in latent abundances rather than a directional competitive effect (Brodie et al. 2018). We defined the model of abundance for *A. uniparens* ($i = 1$) as

$$\log(\lambda_{1j}) = \beta_0 + \beta_1 * \text{treatment}_j + \beta_2 * \text{site}_j$$

where β_0 is the intercept, β_1 is the effect of shrub removal treatment, and β_2 is a random effect of site to account for the pairing of treatment and control plots. The model of abundance for *A. marmorata* ($i = 2$) was defined with separate parameters as

$$\log(\lambda_{2j}) = \beta_0 + \beta_1 * \text{treatment}_j + \beta_2 * N_{1j} + \beta_3 * \text{treatment}_j * N_{1j} + \beta_4 * \text{site}_j$$

where β_0 is the intercept, β_1 is the effect of shrub removal treatment, β_2 is the effect of the latent abundance of *A. uniparens*, β_3 is an interaction effect of treatment and latent abundance of *A. uniparens*, and β_4 is a random effect of site.

We described the detections y_{ijk} of species i at location j during repeated count k as $y_{ijk} | N_{ij} \sim \text{Binomial}(N_{ij}, p_{ijk})$. We defined the models of detection probability for both species as

$$\begin{aligned} \text{logit}(p_{ijk}) = & \alpha_{0i} + \alpha_{1i} * \text{temperature}_{jk} + \alpha_{2i} * \text{temperature}_{jk}^2 + \alpha_{3i} * \text{humidity}_{jk} \\ & + \alpha_{4i} * \text{wind}_{jk} + \alpha_{5i} * \text{survey_time}_{jk} + \alpha_{6i} * \text{site_survey}_{jk} \end{aligned}$$

where α_0 is the intercept, α_1 is the effect of air temperature, α_2 is a quadratic effect of air temperature, α_3 is the effect of humidity, α_4 is the effect of wind, α_5 is the effect of time surveyed, and α_6 is a site-by-survey random effect (Kéry and Royle 2016).

To test whether treatment effects on lizard abundance were related to changes in vegetation, we fit a second co-abundance model using principal components describing vegetation cover. The abundance model for *A. uniparens* was defined as

$$\log(\lambda_{1j}) = \beta_0 + \beta_1 * \text{PC1}_j + \beta_2 * \text{PC2}_j + \beta_3 * \text{site}_j$$

where β_0 is the intercept, β_1 is the effect of a principal component representing low-lying vegetation, β_2 is the effect of a principal component representing shrub and grass cover, and β_3 is a random effect of site. The model of abundance for *A. marmorata* ($i = 2$) was defined with separate parameters as

$$\log(\lambda_{2j}) = \beta_0 + \beta_1 * \text{PC1}_j + \beta_2 * \text{PC2}_j + \beta_3 * N_{1j} + \beta_4 * \text{PC2}_j * N_{1j} + \beta_5 * \text{site}_j$$

where β_0 is the intercept, β_1 is the effect of a principal component representing low-lying vegetation, β_2 is the effect of a principal component representing shrub and grass cover, β_3 is the effect of the latent abundance of *A. uniparens*, β_4 is an interaction effect of a principal component representing shrub and grass cover with latent abundance of *A. uniparens*, and β_5 is a random effect of site. We included an interaction effect of *A. uniparens* abundance with a principal component describing shrub and grass cover because shrub and grass cover are the primary targets of herbicide treatment (see “Results” section). The model of detection probability was identical to that used for the first co-abundance model.

We fit the co-abundance models with a Bayesian approach with Markov chain Monte Carlo using JAGS 4.3.0 (Plummer 2017) and the *R2jags* package (Su and Yajima 2015) in R. A Bayesian approach allowed us to estimate latent abundances of *A. uniparens* and to propagate the error in those estimates when estimating latent abundances of *A. marmorata* (Brodie et al. 2018). All continuous covariates were standardized prior to analysis. As derived parameters, we estimated the difference in abundance of each species between treatment and control plots at each site, and the mean of the differences in abundance between treatment and control plots across sites.

We used normal prior distributions that were noninformative for regression coefficients and uniform prior distributions for standard deviation parameters (Gelman and Hill 2007). For each model, we ran three chains with 501,000 iterations each. We discarded the first 1000 iterations as burn-in and thinned the remaining samples by 100, leaving 15,000 iterations to describe the posterior distribution of each parameter. Convergence of parameter estimates was confirmed with the Gelman–Rubin statistic ($R\text{-hat} < 1.1$; Gelman and Hill 2007). We used the posterior distribution to quantify 95% credible intervals (CI) for each parameter, and we discuss only the factors for which the 95% CI of the parameter estimates excluded zero.

Results

The PCA revealed two components of vegetation cover accounting for 62% of the variation (Table S1 in supplementary information). We interpreted PC1 as an index of “low-lying vegetation” with positive loadings for litter, perennial grass, perennial forbs, and sub-shrubs, and a negative loading for bare ground. Low-lying vegetation cover did not differ between treated and control plots (paired t -test, $t=0.24$, $df=15$, $P=0.81$). PC2 largely represented shrub cover based on its strong positive loading. Perennial grass also had a high negative loading on PC2. PC2 values were lower at treated than control plots (paired t -test, $t=7.28$, $df=15$, $P<0.001$), indicating treatments successfully decreased shrub cover and increased grass cover (Fig. S1 in supplementary information).

We counted 748 lizards representing 13 species across the 32 plots. There were 118 *A. uniparens* and 465 *A. marmorata*, accounting for 78% of all lizard observations. The range in the number of individuals counted on belt transects was 0–6 for *A. uniparens* and 0–13 for *A. marmorata*. Detection probability was positively related to survey time for both species (Table 1; Fig. S2 in supplementary information). Detection probability for *A. uniparens* was positively related to humidity, and detection probability for *A. marmorata* was a negative quadratic function of air temperature (Table 1; Fig. S2 in supplementary information).

Abundances of *A. uniparens* and *A. marmorata* were both greater at plots treated for shrub removal than at control plots (Table 1, Fig. 2a). However, the model of *A. marmorata* revealed a significant interaction effect of treatment and *A. uniparens* abundance. The abundance of *A. marmorata* was greater at treated than control plots only when *A. uniparens* was rare (Fig. 2b). Similarly, the positive response of *A. uniparens* abundance to treatment occurred primarily when *A. marmorata* was rare (Fig. 2c).

The co-abundance model with vegetation cover covariates revealed that *A. uniparens* abundance was negatively related to shrub cover (Table 1, Fig. 2d), whereas there was no relationship between *A. marmorata* abundance and shrub cover (Table 1). There was no effect of low-lying vegetation on abundances for either whiptail species. Abundances of *A. marmorata* and *A. uniparens* were negatively correlated, but there was no interaction effect of *A. uniparens* abundance and shrub cover on *A. marmorata* (Table 1). The posterior distribution of the standard deviation parameter for the random effect of site was > 0 for both co-abundance models, indicating significant variation in abundance of *A. uniparens* and *A. marmorata* among site pairs (Table 2, Fig. 1).

Table 1 Parameter estimates and 95% credible intervals (CI) for fixed effects on abundance and detection probability in co-abundance models of *Aspidoscelis uniparens* and *Aspidoscelis marmorata* using shrub removal treatment or indices of vegetation cover as a predictor of both species

Model	Response variable	Explanatory variable	Estimates (95% CI)		
			<i>Aspidoscelis uniparens</i> (unisexual)	<i>Aspidoscelis marmorata</i> (sexual)	
Shrub removal treatment	Abundance	Treatment	1.25 (0.66, 1.86)	0.34 (-0.11, 0.79)	
		<i>A. uniparens</i>	-	-0.40 (-0.95, -0.08)	
	Detection	Treatment * <i>A. uniparens</i>	-	0.30 (0.05, 0.74)	
		Survey time	0.61 (0.25, 1.02)	0.39 (0.16, 0.63)	
		Temperature	0.40 (-0.12, 0.91)	-0.04 (-0.33, 0.25)	
		Temperature ²	-0.21 (-0.46, 0.02)	-0.35 (-0.55, -0.17)	
		Humidity	1.22 (0.47, 1.97)	0.04 (-0.30, 0.39)	
		Wind	-0.07 (-0.50, 0.39)	-0.21 (-0.48, 0.06)	
		Vegetation cover	Abundance	0.07 (-0.60, 0.72)	-0.27 (-0.80, 0.28)
			Abundance	-0.58 (-0.94, -0.23)	-0.17 (-0.58, 0.23)
Vegetation cover	Abundance	<i>A. uniparens</i>	-	-0.21 (-0.56, -0.01)	
		PC2 * <i>A. uniparens</i>	-	-0.06 (-0.20, 0.03)	
	Detection	Survey time	0.61 (0.22, 1.06)	0.40 (0.16, 0.64)	
		Temperature	0.40 (-0.17, 0.94)	-0.03 (-0.33, 0.27)	
		Temperature ²	-0.21 (-0.47, 0.05)	-0.35 (-0.56, -0.17)	
		Humidity	1.21 (0.14, 2.09)	0.06 (-0.30, 0.42)	
		Wind	-0.04 (-0.50, 0.44)	-0.20 (-0.48, 0.06)	

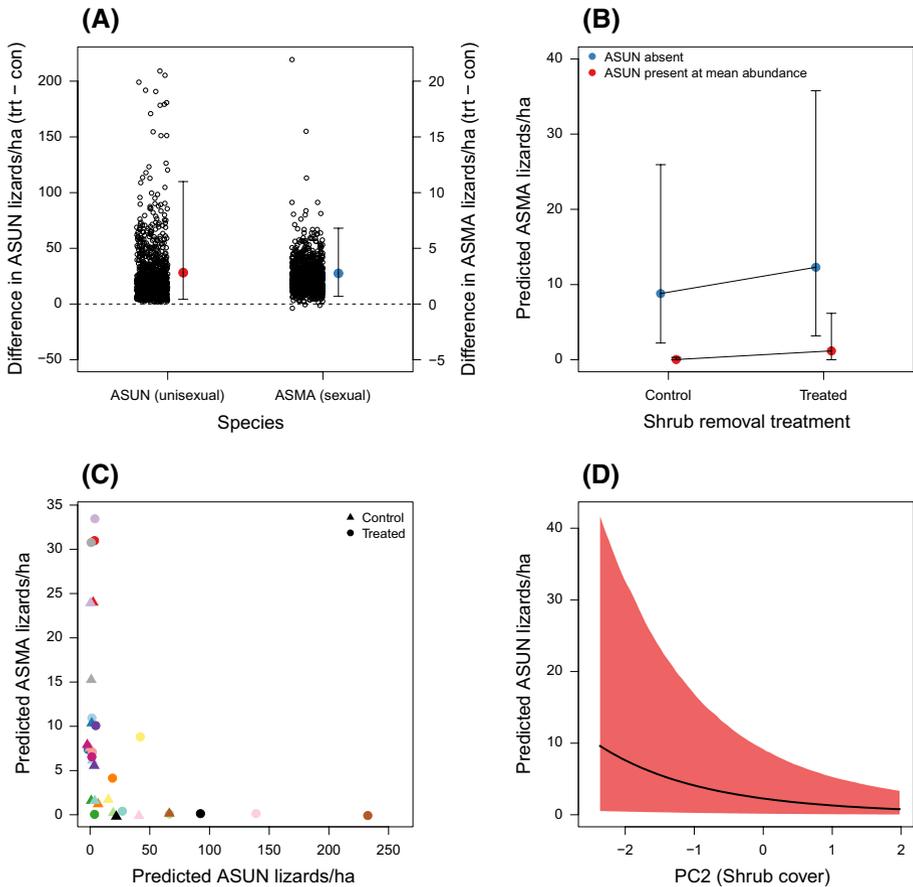


Fig. 2 Relationships among shrub removal treatments that created habitat disturbance and abundances of *Aspidoscelis uniparens* (ASUN) and *A. marmorata* (ASMA) including **a** difference in abundance between paired plots treated for shrub removal and untreated controls. Posterior means (filled circles), 95% credible intervals (CI), and a sample of 1000 draws from the posterior distribution (open circles) are shown. Note the difference in y-axis scales for ASUN and ASMA. **b** Relationship of predicted mean *A. marmorata* abundance to treatments when *A. uniparens* is absent (filled blue circles) or present at mean abundance (filled red circles). Error bars represent 95% CIs. **c** Relationship of predicted mean *A. marmorata* abundance to *A. uniparens* abundance at treated (circles) and control (triangles) plots. Colors represent treatment–control pairs. **d** Relationship of *A. uniparens* abundance to shrub cover. Best-fit line (solid) and 95% CI (red fill) were generated from the posterior distribution holding PC1 (low-lying vegetation) at its mean. (Color figure online)

Discussion

In contrast to the expectation from geographical parthenogenesis, we found the parthenogen *A. uniparens* and sexual *A. marmorata* both can respond positively to habitat disturbance. Each species was more abundant in disturbed plots than in controls, but only when its congener was rare. Vegetation disturbance had no effect on abundance of either species when its congener was common. *Aspidoscelis uniparens* was most abundant at plots with

Table 2 Parameter estimates and 95% credible intervals (CI) for standard deviation estimates of the random effect of site on abundance of *Aspidoscelis uniparens* and *A. marmorata*

Model	Standard deviation estimates (95% CI) for site	
	<i>Aspidoscelis uniparens</i> (unisexual)	<i>Aspidoscelis marmorata</i> (sexual)
Shrub removal treatment	3.06 (1.63, 5.59)	1.37 (0.66, 2.60)
Vegetation cover	2.81 (1.37, 5.52)	1.51 (0.58, 3.25)

Estimates are from co-abundance models using shrub removal treatment or vegetation cover as a predictor of both species (Table 1)

high grass and low shrub cover, which is consistent with *A. uniparens* preferring grassland habitat (Menke 2003; Cosentino et al. 2013). Although abundance of *A. marmorata* was unrelated to vegetation cover, its positive response to shrub removal when *A. uniparens* was rare suggests environmental conditions at recently disturbed sites can be favorable for *A. marmorata*.

Our study highlights the importance of experimental manipulation in the field to test ideas about geographical parthenogenesis, and more broadly about the evolution of sex (Neiman et al. 2018). Previously we showed that the parthenogen *A. uniparens* predominates at sites with a history of vegetation disturbance (Cosentino et al. 2013), which is consistent with a key prediction of geographical parthenogenesis. However, hypotheses to explain geographical parthenogenesis often characterize parthenogens as fugitive species that escape competition with sexuals by colonizing disturbed habitats (Vrijenhoek and Parker 2009). Our experimental habitat disturbance at a landscape scale does not support this depiction. Instead, the parthenogen and sexual can both increase after disturbance, illustrating the parthenogen is not simply a fugitive species that avoids competition with the sexual species in newly created habitat.

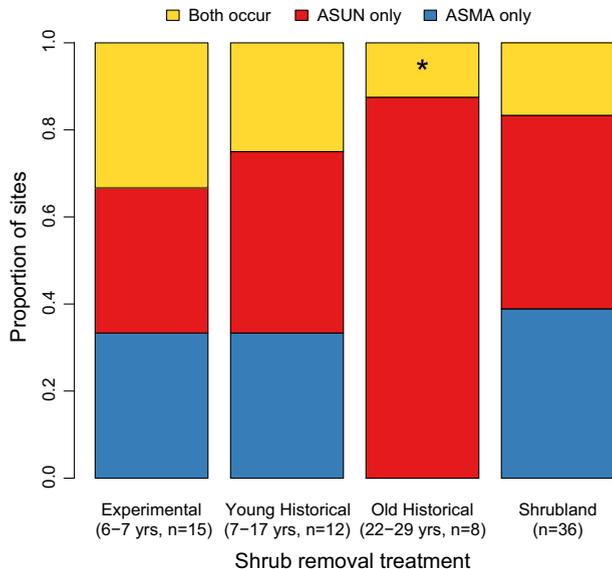
One of the critical assumptions of hypotheses to explain the predominance of parthenogens in disturbed areas is that parthenogens are weaker competitors than sexuals due to their limited genetic diversity (Wright and Lowe 1968; Cuellar 1977). Parthenogens could escape competition with sexuals by being the first to colonize newly created habitat after disturbance. This mechanism is unlikely in our study system. Our previous work showed that *A. marmorata* and *A. uniparens* can both occur in shrublands (Cosentino et al. 2013), so remnant populations of both species likely occur at sites recently treated for shrub removal. Alternatively, models of the Tangled Bank Hypothesis predict that parthenogens can persist in disturbed habitats that are structurally simple with low resource diversity, which causes sexuals to lose their competitive advantage associated with high genetic diversity (Case and Taper 1986; Gaggiotti 1994). Empirical comparison of resource diversity is needed between shrublands and sites treated for shrub removal, but we would predict that resource diversity for lizards is lower in shrublands than treated sites. Creosotebush shrublands are structurally simple with uniform dispersion of shrubs at small spatial scales (< 2 m; Fuentes-Ramirez et al. 2015) that create resource islands separated by areas of bare ground (Schlesinger et al. 1990). Shrub removal causes a massive state transition producing intermediate levels of grass and shrub cover compared with shrublands and remnant grasslands (Coffman et al. 2014). Shrub removal also can increase net primary production, especially of herbaceous plants (RLS, unpublished data), which may increase the diversity or abundance of insect prey used by sexual and asexual whiptails. This productivity pulse

may explain why *A. uniparens* and *A. marmorata* both respond positively to shrub removal in the short-term.

What is the evidence for competition between *A. uniparens* and *A. marmorata* in our study system? The negative relationship between abundances of *A. uniparens* and *A. marmorata* is suggestive of interspecific competition. However, inferring competition from observed abundances is difficult because negative correlations can emerge from differential responses by species to environmental conditions rather than from direct interactions between species (Brodie et al. 2018). Indeed, one whiptail species often dominated both treatment and control plots at each site (Table 2), creating a striking checkerboard pattern of abundances that was likely established on the landscape before our experiment (Fig. 1). However, there was no obvious spatial pattern of dominance in the region (Fig. 1), suggesting the variation in abundances among sites was not driven by broad spatial gradients in environmental conditions. Furthermore, when we control for spatial variation in abundance among sites in our co-abundance models, as well as local effects of disturbance and vegetation structure, we still detect a negative relationship between the species' abundances suggestive of competition.

Despite having extensive niche overlap (Kearney et al. 2009), parthenogenetic and sexual whiptails often coexist geographically with little covariation in abundance (e.g., Case 1990; Paulissen et al. 1992), making *A. uniparens* and *A. marmorata* an exceptional example. Inferring competition, and whether competition is asymmetric, requires experimental manipulation of abundances. However, our results together with those from Cosentino et al. (2013) are indicative of *A. uniparens* being the superior competitor. Species composition at sites treated for shrub removal clearly shifts towards dominance by *A. uniparens* over a timespan of nearly three decades (Fig. 3), which is consistent with *A. uniparens* outcompeting *A. marmorata* over time. Although we cannot rule out the possibility that this change in species dominance is due to changing habitat conditions, limited experimental evidence also points to *A. uniparens* being the superior competitor. Cuellar (1979, 1993) found that *A. marmorata* invaded habitat where *A. uniparens* was experimentally removed, but then *A. marmorata* declined when *A.*

Fig. 3 Relationship of co-occurrence of *Aspidoscelis uniparens* (ASUN) and *A. marmorata* (ASMA) to age of shrub removal treatments and shrubland references at experimental sites (this study) and sites historically treated for shrub removal (Cosentino et al. 2013). Treatments at historical sites were classified as young (treatments 7–17 years before lizard sampling) or old (treatments 22–29 years before lizard sampling). *Only a single *A. marmorata* individual was counted. (Color figure online)



uniparens was allowed to recover. These results suggest *A. uniparens* can exclude *A. marmorata*, but inferences are limited due to lack of replication and control populations.

What explains the long timespan required for geographical parthenogenesis to emerge in our study system? In the current study, the constraints on *A. uniparens* by shrub cover means that the species was likely absent or rare at some sites when shrub removal treatments were applied. Limited abundance of *A. uniparens* may allow a potentially inferior competitor like *A. marmorata* to persist at treated sites temporarily due to stochasticity overriding competition, and competitive exclusion may take many generations (Orrock and Fletcher 2005). Increasing abundance of *A. uniparens* at treated sites over time may explain why *A. marmorata* responded positively to recent shrub removal treatments but not to older treatments (see Cosentino et al. 2013).

Models of resource competition between sexual and asexual populations show the outcome hinges largely on the degree of genetic variation within populations, and whether niche width is driven by genetic differences among individuals (Case and Taper 1986). Sexual populations can overcome the costs of sex when genetic variation is high and genetically based differences among individuals translate into greater use of the resource base than by asexuals. High clonal diversity in asexual populations can counteract this advantage (Lavanchy et al. 2016), but clonal diversity is likely low or nonexistent in *A. uniparens* (Cuellar 1976). The extent to which the hybrid origin and polyploid genome of *A. uniparens* confers a fitness advantage is unknown. Asexuals can competitively exclude sexuals when individuals have a large niche width relative to sexuals (Hanley et al. 1994), or when between-individual variation in niche width is driven by the environment such that a single clone produces many offspring that collectively use a broad range of resources (Case and Taper 1986). Niche differentiation is an important mechanism maintaining sexual and asexual lineages (Neiman et al. 2018), and Case and Taper's (1986) model predicts coexistence between sexual and asexual populations can occur through character displacement. In our study system, the minimal co-occurrence of *A. uniparens* and *A. marmorata* in all habitats (Fig. 3) suggests character displacement is unlikely.

The ability of *A. marmorata* to persist in shrublands where *A. uniparens* occurs at low abundance may allow the maintenance of sexual and asexual lineages at a landscape scale through spatial niche partitioning that potentially evolved before shrub removal treatments. The preference of *A. uniparens* for grassland habitat is consistent with its maternal ancestor (*A. inornatus*; Cosentino et al. 2013), suggesting that its adaptation to grasslands is a consequence of its hybrid origin. The sexual *A. marmorata* appears more general in its habitat use and may have exploited increasing shrub cover in the region over the last 150 years to avoid competition with *A. uniparens*. This scenario is speculative but illustrates how habitat transitions resulting from disturbance could favor sexual or asexual lineages depending on the match of newly created habitat to the fundamental niche of those lineages.

In conclusion, our experiment revealed that both sexual and parthenogenetic lizards have the potential to respond positively to disturbance, counter to expectations from hypotheses on geographical parthenogenesis. These results are inconsistent with the idea that disturbance creates habitat uniquely exploited by parthenogens. Rather, geographical parthenogenesis may emerge directly from biotic interactions within heterogeneous landscapes that include disturbed habitats used by sexuals and asexuals alike.

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Author contributions BJC, RLS, and BTB designed the study. HC and LMB collected the data. BJC analyzed the data and wrote the manuscript. All authors edited the manuscript.

Data availability The data and code for our models are available at <https://github.com/bcosentino/whiptail-coabundance>.

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