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Habitat Loss and Local Extinction: Linking Population Declines of Eastern Collared Lizards (*Crotaphytus collaris*) to Habitat Degradation in Ozark Glades

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ABSTRACT.—Habitat loss and degradation are the leading causes of local extinctions, making preservation and restoration of remaining habitat increasingly critical to conserving biodiversity. Mechanisms driving species extinction, however, often begin with habitat loss and seldom are well understood, which greatly limits our ability to mitigate their impacts. The first step in understanding mechanisms that drive local extinction is to identify vital rates affected by habitat degradation. Here we provide a case study of the impact of habitat degradation on individual growth and reproductive rates of Eastern Collared Lizards (*Crotaphytus collaris*), a species of special concern in the Ozark Mountains. Our data suggest that *C. collaris* in habitats encroached by dense woody vegetation have reduced age-specific body size, primarily as a result of depressed individual growth rates in their first 2 yr of life. In turn, female *C. collaris* in habitats with high woody vegetation density have delayed age of maturity (by 1 yr in 70% of females), smaller age-specific clutch size and reduced clutch frequency (up to a 50% decrease in population annual fecundity). We conclude that depressed reproductive rates of *C. collaris* in degraded habitats likely contribute to population declines in Ozark glades. Our study provides the basis for understanding mechanisms driving population declines of *C. collaris* in the Ozarks and highlights an underutilized perspective that can be used to link causal factors to local extinction.

Effective conservation strategies aimed at ameliorating the negative impacts of habitat loss on biodiversity require explicit information on cause-and-effect and consequence of species declines (Cooke and O'Conner, 2010). Mechanism-based inquiry allows investigators to better understand not only the root cause of population declines (Dunham and Beupre, 1998; Carey, 2005; Tuff et al., 2016) but also a greater predictive power under future scenarios (Kearney and Porter, 2009; Huey et al., 2012). Unfortunately, causal relationships driving population declines are seldom well understood, limiting our ability to mitigate impacts of environmental change. Fortunately, the most direct mechanisms associated with any change in population size (including extinction) are vital rates (birth, death, emigration, and immigration rates; Dunham et al., 1989; DeAngelis et al., 1991; Beupre, 2002). Therefore, studies that examine causal relationships among habitat loss and factors that influence the four fundamental rates provide invaluable information for determining effective conservation strategies (Cooke and O'Conner, 2010). Here we provide a case study that investigates the causal factors driving population declines in Eastern Collared Lizards (*Crotaphytus collaris*), a species of special concern in Arkansas and Missouri (S2 and S4, respectively), as a result of habitat degradation in Ozark glade habitats.

Ozark glades are insular habitats consisting of xeric limestone prairies with exposed bedrock and thin soils within a savannah-woodland matrix (Baskin and Baskin, 2000). Historically, Ozark glades were maintained by natural and anthropogenic fire regimes (Strausberg and Hough, 1997). However, wildfires were excluded almost completely from the Ozarks throughout the 20th century (Jenkins et al., 1995; Verble, 2012) allowing invasion of fire intolerant species into glade habitats (e.g., Eastern Red Cedar, *Juniperus virginiana*) and providing conditions suitable for succession of other woody plants (Laughlin, 2004). Encroachment of woody plants has resulted in habitat degradation of many Ozark glades (Jenkins et al., 1995; Laughlin, 2004) and, in turn, substantial population declines in a glade-dependent predator, *C. collaris*.

Previous studies on declining *C. collaris* populations in the Ozarks have provided a compelling argument that habitat degradation through anthropogenic fire suppression is an important driver of population declines (Templeton et al., 1990; Grimsley, 2012; Neuwald and Templeton, 2013); however, no studies have investigated mechanisms that link habitat degradation to population declines. One study (Sexton et al., 1992) on a central Missouri population inhabiting a glade encroached by woody vegetation (encroached glade) reported reduced age-specific growth rates, compared to *C. collaris* in glade habitat with low woody vegetation density (intact glade). The central Missouri population, however, represents the only reported case of reduced body size in *C. collaris*; thus, the generality of this phenomenon is unknown. Furthermore, Sexton et al. (1992) did not provide data quantifying vegetation encroachment, how habitat degradation affected reproductive rates, or any effects on population size. Therefore, the effect of woody vegetation encroachment and the mechanisms by which it might cause a decrease in age-specific body size of *C. collaris* remain unclear. Additionally, the long-term consequences of reduced body size and its effect on life-history traits (i.e., reproductive potential) have not been examined.

Examining complex mechanisms driving population declines such as that of *C. collaris* in Ozark glades can be a daunting task, but investigating impacts to vital rates provides a relatively straightforward starting point to address the most probable explanatory factors driving local extinctions. Our approach in this study was to test for an association between woody vegetation encroachment and reproductive rates in female *C. collaris* across multiple populations. If *C. collaris* in encroached glades do not have reduced reproductive rates, then this implies that population declines in these habitats are driven primarily by a reduction in survival rates (or increased emigration rates); and further investigation should follow this line of questioning. Conversely, if reproductive rates are reduced, the study then turns to investigating casual mechanisms that could explain a decline in reproduction as a result of habitat degradation. Hence, our line of questioning was threefold. First, we compared habitat characteristics among three Ozark glade

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types (intact, encroached, and glades recently extirpated of *C. collaris*) to quantify any important structural differences. Next, we compared age-specific body size, growth, and female reproduction rates between *C. collaris* in intact versus encroached glades. Finally, we compared body condition (males) and the clutch size to body size relationship (females) of *C. collaris* from both glade types (intact and encroached) to uncover potential explanatory factors driving population declines in Ozark glades.

MATERIALS AND METHODS

Study Sites.—We sampled 10 glade sites and designated each site into one of three categories: 1) intact glades: extant population of *C. collaris*, with observably low levels of woody vegetation ($N = 3$); 2) encroached glades: extant population of *C. collaris*, with observably high levels of woody vegetation encroachment ($N = 4$); and 3) extirpated glades: recently extirpated of *C. collaris*, with observably high levels of woody vegetation encroachment ($N = 3$). Sites were deemed extirpated after we made a minimum of four visits to each of the sites over a 2-yr span where no *C. collaris* were observed, and animals were known to have been captured in the previous 10 yr. All sites were naturally occurring glades located in the Ozark St. Francis National Forest (along the White River and Buffalo River), within a radius of 80 km in north-central Arkansas. We excluded the exact locality of populations in this study to reduce the possibility of human exploitation of *C. collaris* at these sites.

Habitat Variables.—All habitat variables were measured in late May and early June in 2014 and 2015 to reduce potential differences in plant biomass associated with seasonality. We measured 10 total habitat variables including density of large (>15 cm diameter at breast height; dbh) and small (2.5–15 cm dbh) trees; percent cover of canopy, grass, shrubs, exposed rock, litter, shade on the ground surface at solar noon, and rocks ≥ 30 cm above the surface (the microhabitat used most frequently by *C. collaris* in this study); and area of total continuous glade habitat. We chose these 10 habitat variables with the goal of 1) capturing the most important habitat variables in Ozark glade habitats and 2) providing an approximately even representation of variables assumed to be related to woody vegetation density (tree densities, canopy, shrub, and shade cover) and variables not necessarily related to woody vegetation density (total area, and percent cover of rock, litter/moss, grass, and 30 cm rock). We used randomly designated (randomizing compass direction and distance) 100 m² blocks, with a minimum of eight blocks/site, to estimate density and percent cover variables (except for percent shade), and used the mean of these estimates per site to quantify habitat variables. Each 100 m² block was partitioned into four even quadrants and subsampled for each of the cover variables. Total habitat area was estimated using aerial imagery. For percent canopy cover, we scored the number of times canopy was observed through a densitometer along five 10-m transects (~2.5 m resolution) within the 100 m² sampling blocks (25 measurements/block). Percent cover of shade was estimated as the fraction of 200 randomly designated points (~2 m resolution) along a linear transect where a 4-cm object (a painted rock) was either covered or not covered with shade, at solar noon (± 30 min). All other percent cover estimates are the mean estimated percentage of each variable that covered the ground surface (or the sky, for canopy cover) in a block. Density estimates are the mean number of trees per 10-m² block converted to density/hectare.

Data Analysis: Habitat Variables.—We used a correlation matrix to assess collinearity among habitat variables. We used $r < 0.75$ as the maximum threshold for variables used to test for differences among glade types (intact, encroached, and extirpated) in a MANOVA. In the case where multiple variables were correlated with one another ($r \geq 0.75$), we used a single variable to represent correlated variables. We also used linear discriminant analysis (LDA; Cottenie, 2005), a form of discriminant-function analysis (Williams, 1983) in the R statistical software package, to assess priority of habitat variables in distinguishing among the three glade types.

Lizard Capture and Age Classification.—Although some *C. collaris* were originally captured and marked in 2013, the majority of data used here are from captures spanning 2014–2016. Animals were captured using a noose, toe-clipped to give a unique permanent mark and released at the capture location. Upon capture we recorded SVL (snout–vent length) to the nearest millimeter using a metric ruler and mass to the nearest 0.5 g using a spring scale (60 g Pesola™). For each initial capture, we classified individuals as young-of-the-year (YOY), one-year-olds (1YO) or at least two years-old and older (adult) using conspicuous coloration patterns unique to the three age groups (McCoy et al., 1997). To classify adult age classes (2YO–4YO), we used only individuals that were originally captured as YOY or 1YOs or when minimum age was known to be at least 4YO (e.g., classified as adult in 2014, recaptured in 2016). Although we did find individuals known to be at least 5YO, these instances were rare. Furthermore, most *C. collaris* tend to asymptote in size by 4YO (Sexton et al., 1992); hence, we grouped animals known to be 4YO and animals known to be at least 4YO into one age class (4YO+). *Crotaphytus collaris* is sexually dimorphic at maturity, and we determined sex of juveniles by the presence (males) or absence (females) of enlarged post-anal scales (Telemeco and Baird, 2011).

Age- and Sex-Specific Body Size and Growth.—For comparisons of age- and sex-specific body size of 1YO and adults, we used only body-size estimates obtained 1–30 May of each year. We used a narrow range of capture dates to reduce confounding variation in age-specific body size associated with time of year. Because YOY typically do not start hatching until mid to late July in Arkansas (Brewster et al., 2013), age-specific body size of the YOY age class was estimated from captures dated between 20 August and 20 September. We also compared age- and sex-specific differences of within-season SVL growth rate (mm/day). In all but the YOY age class, we used a minimum of 30 days between recaptures to reduce the influence of investigator measurement error in growth rate estimates. We observed our lowest recapture rate in the YOY age class. Therefore, to increase sample size in growth rate estimates in the YOY age class, we used a minimum of 14 days between recaptures. The YOY age class has the fastest growth rates of any of the age classes in *C. collaris* (Brewster et al., 2014), reducing potential impacts of measurement error over the shorter recapture interval.

Age-Specific Female Reproduction.—We attempted to recapture females once every 2 weeks through the peak of the reproductive season (early May to early July) to track reproductive condition (e.g., nondetectable, small follicles, large follicles, shelled oviductal eggs, postoviposition, and clutch size; Sloan and Baird, 1999). Females typically reach maturity at 1YO, but smaller females may not reach maturity until 2YO (Trauth, 1978; Ballinger and Hipp, 1985). Reproductive condition was assessed by physical palpation or when knowledge of a clutch had been previously identified through palpation, the presence of dried mud on the

dorsum, and recent significant weight loss, which are both indicative of recent oviposition (Baird et al., 2001). Although physical palpation has been used to estimate clutch size in lizards (Cueller, 1971; Turner et al., 1982; Olsson et al., 2002), in our experience with *C. collaris*, the only palpation estimates in which we are confident are those made once eggs have been shelled (large, turgid, and distinct). Therefore, we made clutch size estimates only when females had shelled oviductal eggs; however, we did use all reproductive condition categories to assess clutch frequency (zero, one, two, or three clutches/season), as long as a female had been captured a minimum of three times in a reproductive season.

Data Analysis: Body Size, Growth, and Reproduction.—In all age-specific comparisons of body size, growth, and reproduction (clutch size/clutch frequency), we used linear mixed models (“nlme” package in R; Bates et al., 2015) to test for a difference between glade types (intact and encroached). *Crotaphytus collaris* is sexually size dimorphic as adults (Fitch, 1956; McCoy et al., 1997; Brewster et al., 2014); thus, to reduce model complexity, models were fit separately for males and females. All response variables (SVL, mass and change in SVL) were log transformed, except for clutch frequency and clutch size, where we used raw data. To estimate the predicted annual age-specific fecundity (F_x) between glade types, we multiplied the annual mean clutch frequency for each age class times the corresponding mean clutch size of each age-class (Cole, 1954). To estimate the predicted cumulative age-specific fecundities (ΣF_x), we summed the estimated F_x over each age-class from 1YO–4YO animals. Annual and cumulative age-specific fecundities (F_x and ΣF_x) are derived estimates; therefore, we did not use these two estimates for statistical comparison.

We tested for interactions of fixed effects among glade type, site, and age (\log_{10} age+1; for growth rate, we used initial SVL as a covariate). Data on individual *C. collaris* were repeated over multiple years in many instances; hence, animal “ID” was included as a random factor. Model selection for fixed effects was based on AICs derived from maximum-likelihood estimation (Bozdogan, 1987) and random effects based on restricted maximum-likelihood estimates (Pinheiro et al., 2017). In all mixed model comparisons, positive general-definite covariance structure provided the best fit to our models. We report values for resulting parameter estimates with \pm SE.

Body Condition and Clutch Size to Body Size.—To test for differences in body condition between glade types, and the clutch size to body size relationship, we used linear mixed models with ID as a random factor. For body condition, we used the \log_{10} of mass as the response variable and \log_{10} of SVL as the predictor (testing for interactions among age, glade type, and SVL). We used only male *C. collaris* for body condition comparisons because body mass of females can be confounded by variation in timing of gravidity. For the clutch size to body size comparison, we used the \log_{10} of clutch size (number of eggs) as the response variable, and \log_{10} of SVL as the predictor variable (testing for interactions among age, glade type, and SVL).

RESULTS

Habitat Variables.—All five woody vegetation density variables (large tree density, small tree density, canopy, shrub, and shade cover) were highly correlated with one another ($r > 0.80$), whereas none of the other habitat variables (total area, and rock, litter/moss, grass, and 30-cm rock cover) were highly correlated

with one another ($r < 0.71$). We chose to use shade cover in our analysis over the other variables because shade cover is a result of all of the other woody vegetation variables. We combined shade cover with the other five nonwoody vegetation variables in the MANOVA and LDA (Table 1). The MANOVA suggested a significant difference among glade types ($Pillai = 1.86$, $F_{1,5} = 6.645$, $P = 0.0147$), although the only statistically different variable among types was shade cover ($P < 0.001$). Similarly, the LDA indicated shade cover as the leading discriminant variable (coefficient of linear discriminant, Table 1). A post hoc Tukey test of shade cover among glade types suggested a statistical difference between the intact and either encroached or extirpated glade types ($P < 0.001$ in both comparisons) but no statistical difference between encroached and extirpated glade types ($P = 0.49$; Table 1). We provide a full summary of all habitat variables among sites in Appendix 1.

Age-Specific Female Reproduction.—In all of our mixed models, REML indicated models that used ID alone as random effects were the most appropriate models. Low replication of individuals in adult age classes (3 and 4 YO) in some of the encroached sites ($N \leq 5$ in multiple age classes in two of the glade sites) precluded models that included both site and glade type as fixed effects. We found no statistically significant “age \times glade type” interactions on clutch size or clutch frequency. Age-specific clutch frequency (number clutches/female) was significantly lower in females from encroached glades compared to intact glades (intercept = -0.34 ± 0.174 ; slope = 0.71 ± 0.218 ; $F_{1,82} = 21.63$, $P < 0.001$; Fig. 1A). Similarly, age-specific clutch size (number eggs/clutch) was lower in encroached glades (intercept = 3.85 ± 0.603 ; slope = 1.17 ± 0.810 ; $F_{1,40} = 20.53$, $P < 0.0001$; Fig. 1B).

Age- and Sex-Specific Body Size and Growth.—We found no statistically significant “age \times glade type” interactions in the four age-specific body size comparisons (male or female SVL, and male or female mass). Both male and female age-specific SVL was significantly greater in *C. collaris* from intact glades than in encroached glades (males, intercept = 1.75 ± 0.011 ; slope = 0.059 ± 0.014 ; $F_{1,90} = 25.99$, $P < 0.0001$ and females, intercept = 1.77 ± 0.009 ; slope = 0.050 ± 0.012 ; $F_{1,103} = 24.5$, $P < 0.0001$; Fig. 2A,B). The average difference in mean SVL across age classes was 7.7 mm for females, and 8.2 mm for males. Similarly, age-specific mass for both sexes was significantly greater for *C. collaris* in intact glades (males, intercept = 0.86 ± 0.031 ; slope = 0.158 ± 0.040 ; $F_{1,90} = 32.95$, $P < 0.0001$ and females, intercept = 0.89 ± 0.033 ; slope = 0.144 ± 0.043 ; $F_{1,103} = 28.13$, $P < 0.0001$; Fig. 2C,D). The average difference in mean mass across age classes was 7.8 g for females, and 7.9 g for males. We observed a significant “age \times glade type” interaction on both male and female within-season growth rates (“age \times glade type” interaction for males, $F_{1,27} = 9.81$, $P = 0.0041$ and females, $F_{1,26} = 17.58$, $P = 0.0003$; Fig. 3). We provide raw summary data of age-specific body size and growth of all animals used in the study in Appendix 2.

Body Condition and Clutch Size to Body Size.—We observed no interactions among fixed effects (SVL, age, and glade type) as they related to body condition or clutch size to body size. Male body condition was not significantly different between glade types ($F_{1,50} = 2.6$, $P = 0.115$; Fig. 4A). Similarly, the clutch size to body size relationship was not significantly different between glade types ($F_{1,39} = 0.43$, $P = 0.516$; Fig. 4B).

DISCUSSION

The goal of this study was to investigate factors that link habitat degradation in Ozark glades to population declines in *C.*

TABLE 1. Group means of six habitat variables among three glade types and coefficients of linear discriminant one (LD1) showing leading discriminant variable (% cover shade). Four highly correlated variables not shown (see Appendix 1). Density (number of lizards/hectare) of *Crotaphytus collaris* aged 1YO and above. Percent cover of shade at solar noon (shade), exposed bedrock (rock), rocks ≥ 30 cm above surface (bask. rock), grass, and leaf litter or moss (litter). Total glade habitat area (habitat) in hectares. Percent cover shade used in post hoc Tukey test: intact versus encroached, $P < 0.001$; intact versus extirpated, $P < 0.001$; encroached versus extirpated, $P = 0.49$.

Glade type	N	Density lizards	% Shade	% Rock	% Litter	% Grass	% Bask. rock	Area habitat
Intact	3	7.7	18.7	46.8	21.2	26.7	0.4	3.4
Encroached	4	2.2	61.6	31.4	27.9	24.6	0.5	3.9
Extirpated	3	0.0	65.5	32.5	21.2	19.5	0.5	2.8
		LD1	6.64	-1.4	-1.4	-0.8	-0.7	-0.1

collaris. Our first line of questioning was designed to quantify important habitat differences between encroached and intact sites. We recognize that the 10 habitat variables used in this study are not exhaustive, and one could hypothesize other potentially important habitat variables associated with Ozark glades (e.g., soil depth, plant composition, geological charac-

teristics). Regardless, our habitat variable assessments allowed us to provide a quantifiable justification of our a priori delineation of glade types (intact and encroached). Not surprisingly, all five woody vegetation variables were highly correlated and substantially different between intact and non-intact (encroached and extirpated) sites. The LDA (coeff. LD1;

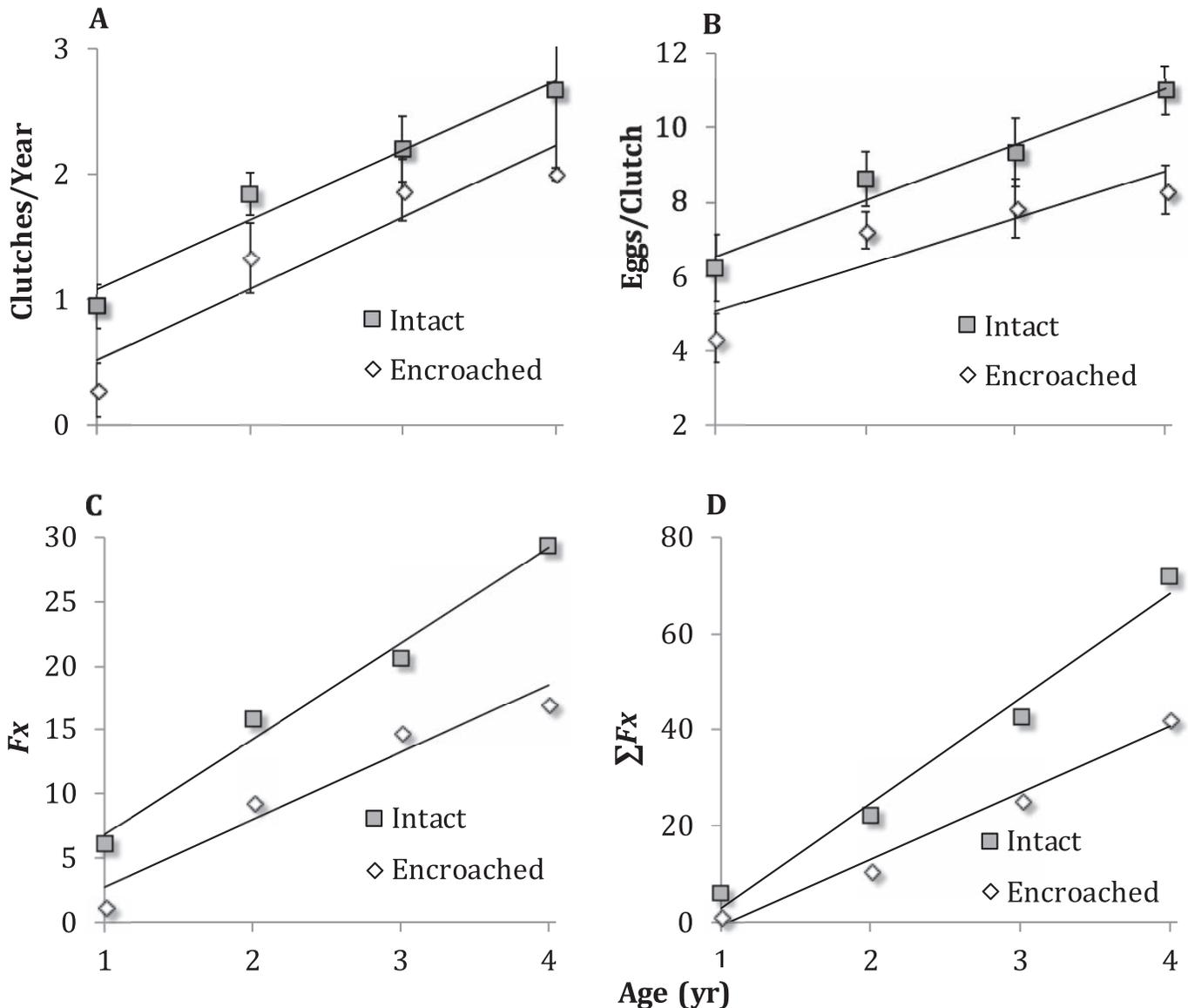


FIG. 1. Adjusted means and $\pm 95\%$ CI of age-specific (A) clutch frequency, (B) clutch size, (C) predicted number of eggs per season (F_x), and (D) the cumulative sum of F_x (ΣF_x). F_x and ΣF_x are estimates derived from clutch frequency and clutch size and not used to assess statistical differences.

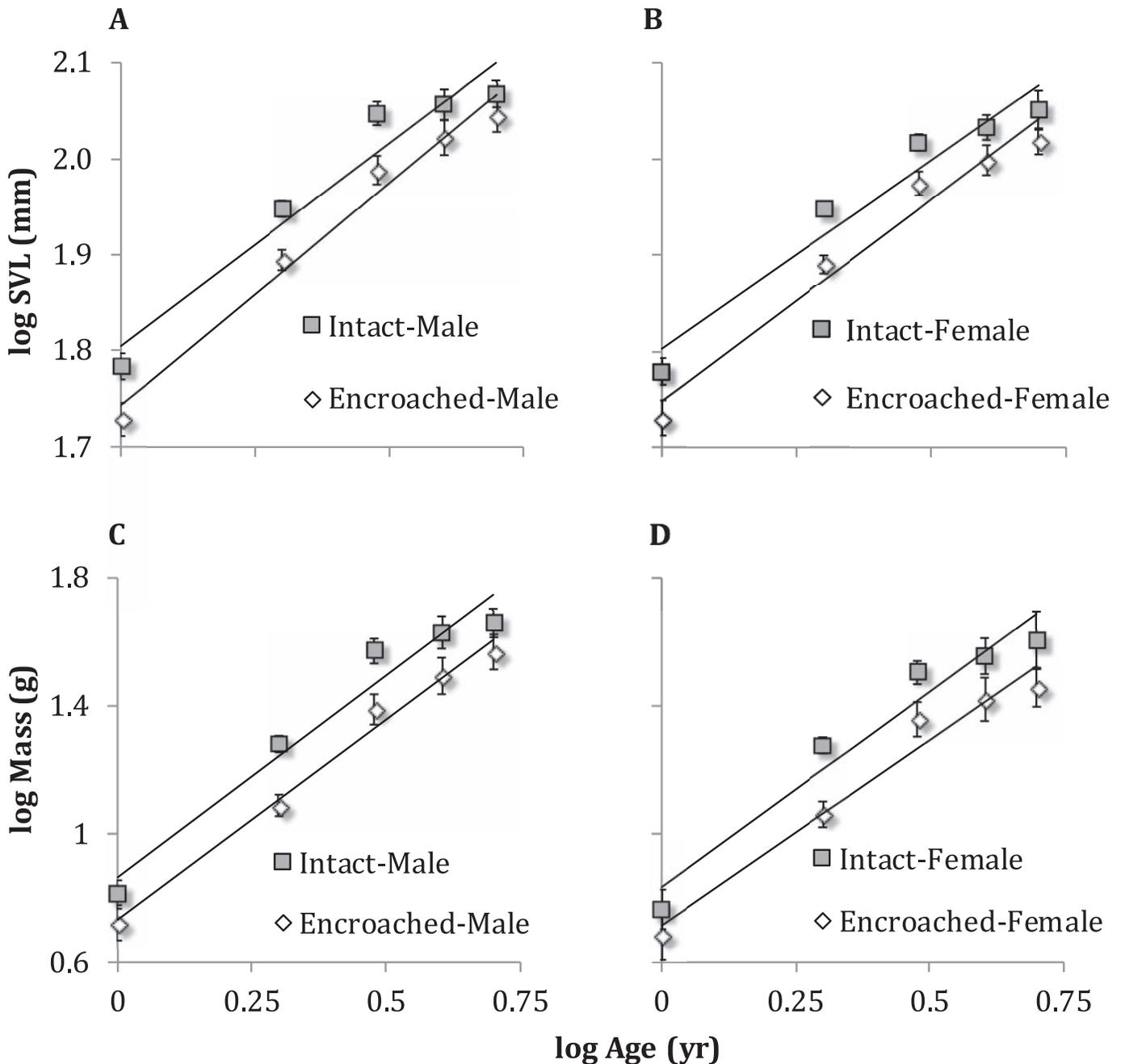


FIG. 2. Adjusted means and $\pm 95\%$ CI for age-specific body size (log transformed) between glade types (encroached and intact) for (A) male SVL, (B) female SVL, (C) male mass, and (D) female mass. $\log \text{Age} = \log_{10}(\text{no. yr} + 1)$.

Table 1) indicated shade as the best discriminant habitat variable among glade-types, and MANOVA suggested a significant difference among glade types in the six habitat variables. However, the only variable that was significantly different was shade, and this variable was statistically indistinguishable between encroached and extirpated glade types (Table 1). Similarly, we found no statistical difference in nonwoody vegetation variables among sites. Therefore, other nonwoody vegetation variables that should be important to *C. collaris* (e.g., size of the habitat, availability of basking rocks, or amount of grasses that should provide necessary densities of Orthoptera, a primary prey source) were similar among all sites (Table 1; Appendix 1). We interpret our habitat assessment results to suggest that the most important difference between

intact and nonintact glades was density of woody vegetation encroachment and resulting shade cover.

Our second line of questioning was designed to determine whether *C. collaris* in encroached glades had reduced age-specific growth, body size, or reproductive rates. Both age-specific clutch size and clutch frequency were significantly lower in *C. collaris* from encroached sites. In fact, 70% of females in encroached sites did not produce their first clutch until 2YO, a full year later than 98% of females in intact sites. Similarly, females in encroached sites had smaller clutch sizes than females in intact sites. The potential impacts of these differences are apparent in the predicted cumulative number of eggs (ΣFx) of a 4YO female in an intact versus an encroached glade (72.0 and 42.5 eggs, respectively; Fig. 1D). Taking the approximate

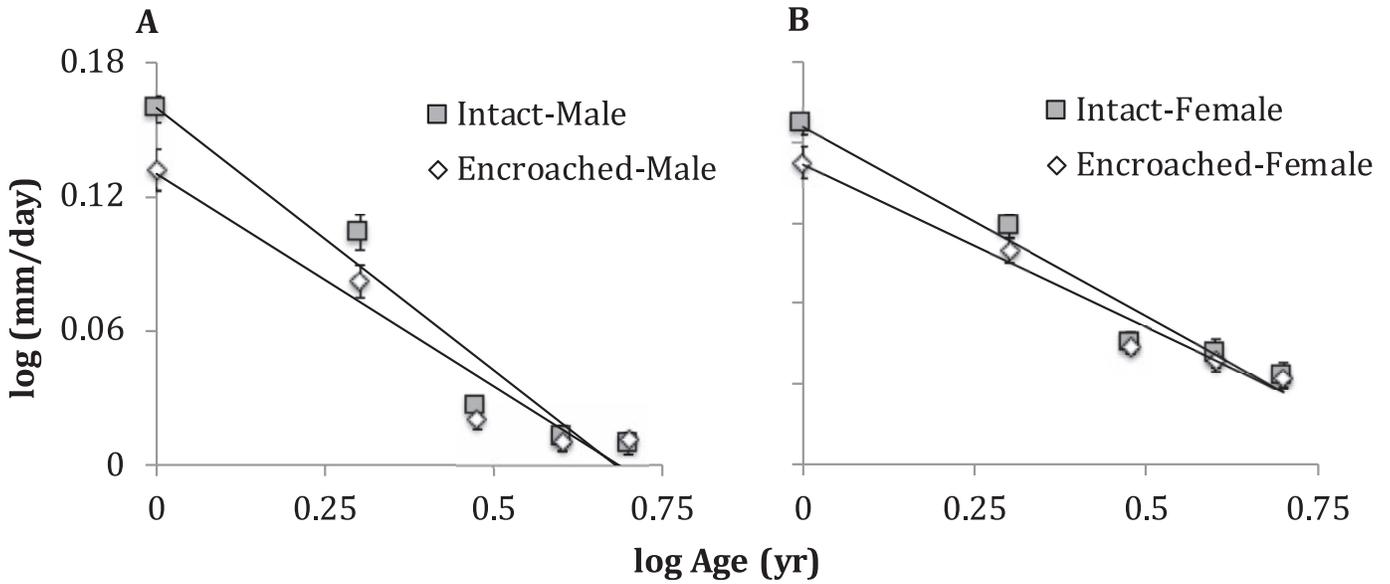


FIG. 3. Within season growth rate (log of mm/day) of male (A) and female (B) lizards from intact and encroached glades. $\log \text{Age} = \log_{10}(\text{no. yr}+1)$.

mean age structure of all sites (55% 1YO, 30% 2YO, 20% 3YO, 5% 4YO) multiplied by the estimated number of eggs per season for each age class (F_x ; Fig. 1C), yields an ~50% decrease in annual population fecundity in an encroached glade compared to an intact glade (assuming the same initial population size). Depending on age-specific survival rates in encroached populations, the estimated deficits in reproduction would be consistent with population declines in encroached sites.

Age- and sex-specific body sizes were smaller in encroached glades compared to intact glades (Fig. 2; Appendix 2); however, in our within-season growth rate comparisons, we observed a significant interaction between glade type and age. Hence, the effect of age on growth rates was different between glade types (intersecting slopes; Fig. 3A,B). The “age \times glade type” interaction is likely because of the large difference between glade-types in growth rates of younger age classes (YOY and

1YO) compared to the similar growth rates of older age classes (3YO and 4YO; Fig. 3; Appendix 2). Superficially and surprisingly, we did not observe an “age \times glade type” interaction with body size but did with within-season growth rates. We note, however, that body sizes of *C. collaris* in intact glades were still substantially larger than *C. collaris* in encroached glades at the older age classes (3YO and 4YO; Fig. 2; Appendix 2) even though within-season growth rates were not. Therefore, our data suggest that animals in intact glades approach asymptotic body size (where growth rates would naturally decline) at a younger age than animals in encroached glades by experiencing greater growth rates at younger age classes.

Unfortunately, we currently do not have data that could explain how or why *C. collaris* would exhibit this difference in growth patterns between glade types. One explanation could be that *C.*

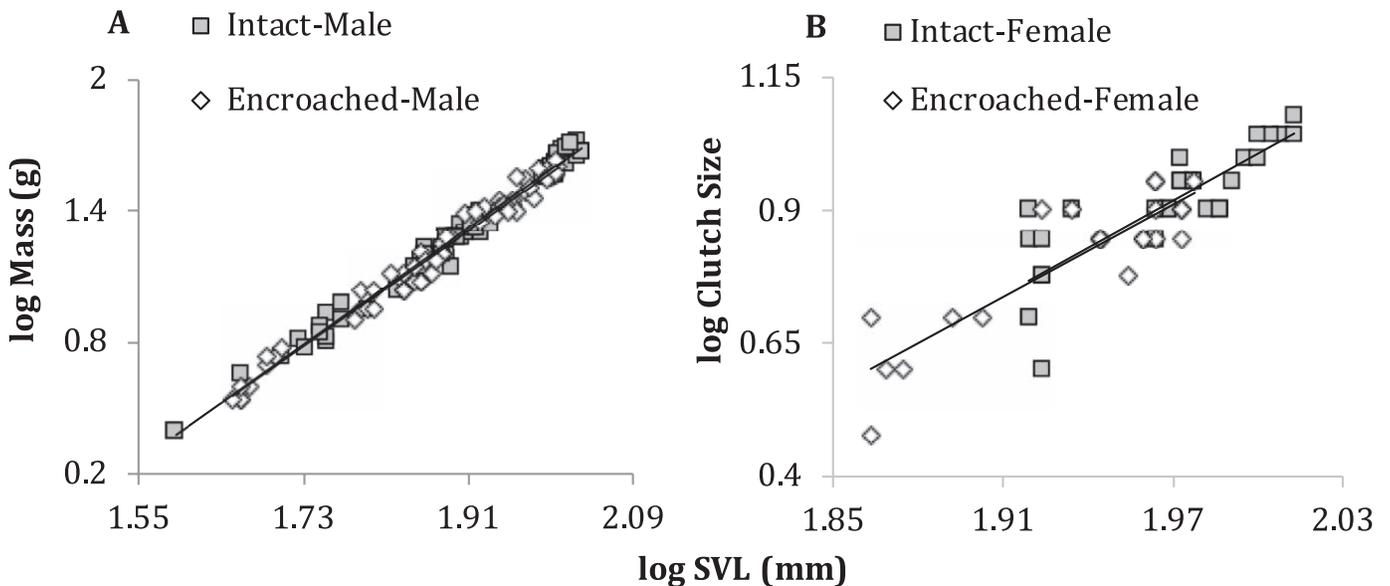


FIG. 4. Comparison of (A) male body condition and (B) female SVL to clutch size between lizards from intact and encroached glades.

collaris in encroached sites experience some factor (e.g., reduced energy acquisition or digestive processing) that leads to lower total assimilated energy per unit time than do *C. collaris* in intact glades. If we assume that all *C. collaris*, regardless of glade type, allocate proportionally less energy to growth with increasing body size, then this would lead to an earlier decline in growth of *C. collaris* (i.e., declines at younger ages) in intact glades compared to *C. collaris* in encroached glades. This explanation is consistent with our observation of an “age × glade type” interaction in growth rates of *C. collaris* (i.e., intersecting slopes for age-specific growth) and a significant difference of body size between glade types (with no “age × glade type” interaction). Without a better mechanistic understanding of variables driving differences in growth between glade types, however, the causal link between these patterns remains unclear. What is clear, however, is that reduced growth rates, primarily in their first 2 yr of age, result in reduced age-specific body sizes in encroached glades compared to intact glades and ultimately lead to reduced age-specific reproductive rates.

Our third line of questioning was designed to investigate potential factors, other than differences in age-specific body size that could explain population declines of *C. collaris* in encroached sites. First, we found no statistical difference in body condition of males between glade types (Fig. 4A). Therefore, factors potentially linked to poor body condition (e.g., starvation) would appear to be similar between *C. collaris* in intact and encroached glades. Next, we tested for a difference in the SVL to clutch size relationship between glade types (Fig. 4B) to determine whether factors other than reduced age-specific body size contribute to reduced reproductive rates. Had we found a significant interaction (i.e., among SVL, age, or glade type), or a significant difference in intercepts (clutch size as a function of SVL), this would have suggested that some factor other than age-specific body size contributes to clutch size variation. For example, if females in degraded glades had significantly lower clutch sizes as a function of SVL than females in intact glades, this would have indicated that animals differed in their proportions of allocation between growth and reproduction and that differences in reproductive rates were not necessarily explained solely by age-specific body size differences. Because we found no statistical interaction, and no difference in clutch size as a function of SVL, we conclude that reduced age-specific body size is the primary factor driving reduced reproductive rates in *C. collaris* from degraded sites.

Our data suggest that *C. collaris* restricted to habitats with dense woody vegetation exhibit a shift in life-history traits (body size, growth, and reproduction) that is consistent with explaining observed population declines. Specifically, we conclude that depressed growth rates within their first 2 yr of life leads to smaller age-specific body sizes and reduced reproductive rates. Our findings provide a compelling argument that anthropogenic fire suppression in Ozark glades is driving extensive population declines in an important glade predator. Our results also underscore the importance of habitat restoration through prescribed fire and mechanical removal of dense woody vegetation in Ozark glade habitats. Indeed, the only reported cases of *C. collaris* population recoveries have been projects that included glade restoration through prescribed fire (Brisson et al., 2003; Neuwald and Templeton, 2013).

We recognize that multiple interacting factors likely drive variation in life histories among *C. collaris* populations in Ozark glades, and some of these factors may be linked to variables other than woody vegetation density or shade cover. Future

research will need to focus on the causal link between dense woody vegetation and reduced growth. For example, one of the authors (CLB) is currently investigating the impact of increased shade in encroached glades on available operative temperatures (Bakken, 1992), surface activity-time budgets (Grant and Dunham, 1988), and animal body temperatures as well as any differences in prey densities between glade types. We also note that dense woody vegetation may cause a decline in survival rates, as well as reproductive rates. Because understanding population level impacts requires data on all four fundamental rates, we cannot infer the entire impact of habitat degradation on *C. collaris* populations from the data presented here. Regardless, because migration is extremely limited for this species through most of the Ozarks (Templeton et al., 1990; pers. obs.), unless dense woody vegetation increases survival rates substantially, the observed decline in reproduction of *C. collaris* in encroached sites will likely lead to population declines and extirpations of this species throughout the Ozarks.

We have provided a case study aimed at understanding the link between habitat degradation and local extinctions of an at-risk species. Our study shows the effectiveness of using mechanism-based inquiry to investigate complex conservation issues and highlights the utility of investigating vital rates to uncover casual factors contributing to local extinctions. Projects such as ours are important not only to understanding how habitat loss and degradation are influencing at-risk species, but also to identifying effective strategies that can slow or even reverse current declines. For example, data from this project have helped prompt state level funding for conservation of *C. collaris* and will be used to guide habitat restoration efforts on five of the seven nonintact sites in this study.

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LITERATURE CITED

- BAIRD, T. A., C. L. SLOAN, AND D. K. TIMANUS. 2001. Intra- and inter-seasonal variation in the socio-spatial behavior of adult male collared lizards, *Crotaphytus collaris* (Reptilia, Crotophytidae). *Ethology* 107: 15–32.
- BAKKEN, G. S. 1992. Measuring and application of operative and standard operative temperatures in ecology. *American Zoology* 32: 194–216.
- BALLINGER, R. E., AND T. G. HIPP. 1985. Reproduction in the collared lizard, *Crotaphytus collaris*, in west central Texas. *Copeia* 1985:976–980.
- BASKIN, J. M., AND C. C. BASKIN. 2000. Vegetation of limestone and dolomite glades in the Ozarks and midwest regions of the United States. *Missouri Botanical Garden* 87:286–294.
- BATES, D. M., M. MAECHLER, B. BOLKER, AND S. WALKER. 2015. Fitting linear mixed-effects models using lme4. *Journal of Statistical Software* 67:1–48.
- BEAUPRE, S. J. 2002. Modeling time-energy allocation in vipers: individual responses to environmental variation and implications for popula-

- tions. Pp. 463–481 in G. W. Schuett, M. Hoggren, M. E. Douglas, and H. W. Greene (eds.), *Biology of the Vipers*. Eagle Mountain Publishing, USA.
- BOZDOGAN 1987. Model selection and Akaike's information criterion (AIC): the general theory and its analytical extensions. *Psychometrika* 52:345–370.
- BREWSTER, C. L., R. S. SIKES, AND M. E. GIFFORD. 2013. Quantifying the cost of thermoregulation: thermal and energetic constraints on growth rates in hatchling lizards. *Functional Ecology* 27:490–497.
- BREWSTER, C. L., R. S. SIKES, AND M. E. GIFFORD. 2014. Body size and growth of the eastern collared lizard (*Crotaphytus collaris*) in central Arkansas. *Herpetological Review* 45:580–583.
- BRISSON, J. A., J. L. STRASBURG, AND A. R. TEMPLETON. 2003. Impact of fire management on the ecology of collared lizard (*Crotaphytus collaris*) populations living on the Ozark Plateau. *Animal Conservation* 6: 247–254.
- CAREY, C. 2005. How physiological methods and concepts can be useful in conservation biology. *Integrative and Comparative Biology* 45:4–11.
- COLE, L. C. 1954. The population consequences of life history phenomena. *Quarterly Review of Biology* 29:103–137.
- COOKE, S. J., AND C. M. O'CONNOR. 2010. Making conservation physiology relevant to policy makers and conservation practitioners. *Conservation Letters* 3:159–166.
- COTTENIE, K. 2005. Integrating environmental and spatial processes in ecological community dynamics. *Ecology Letters* 8:1175–1182.
- CUELLAR, O. 1971. Reproduction and the mechanism of meiotic restitution in the parthenogenetic lizard *Cnemidophorus uniparens*. *Journal of Morphology* 133:139–165.
- DEANGELIS, D. L., L. GODBUT, AND B. J. SHUTER. 1991. An individual-based approach to predicting density-dependent dynamics in smallmouth bass populations. *Ecological Modelling* 57:91–115.
- DUNHAM, A. E., AND S. J. BEAUPRE. 1998. Scale, phenomenology, mechanism, and the illusion of generality. Pp. 27–49 in J. Bernardo and W. Reserits (eds.), *Ecological Experiments: Issues and Perspectives*. Oxford University Press, USA.
- DUNHAM, A. E., B. W. GRANT, AND K. L. OVERALL. 1989. Interfaces between biophysical and physiological ecology and the population ecology of terrestrial vertebrate ectotherms. *Physiological Zoology* 62:335–355.
- FITCH, H. S. 1956. An ecological study of the collared lizard (*Crotaphytus collaris*). University of Kansas Publications, Museum of Natural History 8:213–274.
- GRANT, B. W., AND A. E. DUNHAM. 1988. Thermally imposed time constraints on the activity of the desert lizard *Sceloporus merriami*. *Ecology* 69:167–176.
- GRIMSLEY, A. 2012. A Reexamination of the Eastern Collared Lizard (*Crotaphytus collaris*) in Arkansas. Unpubl. master's thesis. University of Arkansas, USA.
- HUEY, R. B., M. R. KEARNEY, A. KROCKENBERGER, J. A. M. HOLTUM, M. JESS, AND S. E. WILLIAMS. 2012. Predicting organismal vulnerability to climate warming: roles of behaviour, physiology and adaptation. *Philosophical Transactions of the Royal Society B: Biological Sciences* 367:1665–1679.
- JENKINS, S. E., R. GUYETTE, AND A. J. REBERTUS. 1995. Vegetation-Site Relationships and Fire History of a Savanna-Glade-Woodland Mosaic in the Ozarks. *Proceedings of the 11th Central Hardwood Forest Conference*; 1997 March 23–26; Columbia, MO: U.S. Department of Agriculture, Forest Service, North Central Forest Experiment Station. 184–201.
- KEARNEY, M., AND W. PORTER. 2009. Mechanistic niche modelling: combining physiological and spatial data to predict species' ranges. *Ecology Letters* 12:334–350.
- LAUGHLIN, D. C. 2004. Woody plant invasion and the importance of anthropogenic disturbance within xeric limestone prairies. *Journal of the Pennsylvania Academy of Science* 78:12–28.
- MCCOY, J. K., J. H. HARMON, T. A. BAIRD, AND S. F. FOX. 1997. Geographic variation in sexual dimorphism in the collared lizard, *Crotaphytus collaris* (Sauria: Crotophytidae). *Copeia* 1997:565–571.
- NEUWALD, J. L., AND A. R. TEMPLETON. 2013. Genetic restoration in the eastern collared lizard under prescribed woodland burning. *Molecular Ecology* 22:3666–3679.
- OLSSON, M., R. SHINE, E. WAPSTRA, B. UJVARI, AND T. MADSEN. 2002. Sexual dimorphism in lizard body shape: the roles of sexual selection and fecundity selection. *Evolution* 56:1538–1542.
- PINHEIRO, J., D. BATES, S. DEBROY, D. SARKAR, S. HEISTERKAMP, AND B. VAN WILLIGEN. 2017. Package "nlme". Linear and nonlinear mixed effects models, 3–1. Available from: <http://cran.rapporter.net/web/packages/nlme/nlme.pdf>.
- SEXTON, O. J., R. M. ANDREWS, AND E. BRAMBLE. 1992. Size and growth rate characteristics of a peripheral population of *Crotaphytus collaris*. *Copeia* 1992:968–980.
- SLOAN, C. L., AND T. A. BAIRD. 1999. Is heightened post-ovipositional aggression in female collared lizards (*Crotaphytus collaris*) nest defense? *Herpetologica* 55:516–522.
- STRAUSBERG, S., AND W. A. HOUGH. 1997. The Ouachita and Ozark-St. Francis National Forests: A History of the Lands and USDA Forest Service Tenure. USDA Forest Service General Technical Report SO-121. Asheville, NC.
- TELEMCO, R. S., AND T. A. BAIRD. 2011. Capital energy drives production of multiple clutches whereas income energy fuels growth in female collared lizards *Crotaphytus collaris*. *Oikos* 120:915–921.
- TEMPLETON, A. R., K. SHAW, E. ROUTMAN, AND S. K. DAVIS. 1990. The genetic consequences of habitat fragmentation. *Annals of the Missouri Botanical Garden* 77:13–27.
- TRAUTH, S. E. 1978. Ovarian cycle of *Crotaphytus collaris* (Reptilia, Lacertilia, Iguanidae) from Arkansas with emphasis on corpora albicantia, follicular atresia, and reproductive potential. *Journal of Herpetology* 12:461–470.
- TUFF, K. T., T. TUFF, AND K. F. DAVIES. 2016. A framework for integrating thermal biology into fragmentation research. *Ecology Letters* 19:361–374.
- TURNER, F. B., P. A. MEDICA, K. W. BRIDGES, AND R. I. JENNICH. 1982. A population model of the lizard *Uta stansburiana* in southern Nevada. *Ecological Monographs* 52:243–259.
- VERBLE, R. M. 2012. Effects of Prescribed Fire on Ozark Ant Ecology. Unpubl. PhD diss., University of Arkansas at Little Rock, USA.
- WILLIAMS, B. K. 1983. Some observations of the use of discriminant analysis in ecology. *Ecology* 64:1283–1291.

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APPENDIX 1. Summary data of habitat variables used to characterize three glade types (intact, encroached, and extirpated). Density (number/hectare) of one-year-old and above *Crotaphytus collaris* (lizards), trees with diameter at breast height (dbh) of 2.5–15.0 cm (Sm.tree), and dbh of 15 cm+ (Lg.tree). Percent cover of mid- and overstory (canopy), understory (shrubs), shade on ground surface at solar noon (shade), exposed bedrock (rock), rocks ≥ 30 cm above surface (bsk. rock), leaf litter or moss (litter), and grass and forbs (grass). Total continuous glade habitat area (habitat) in hectares. Predicted values from linear discriminant analysis (predicted LD1 values; proportion of trace, LD1 = 0.927, LD2 0.0783).

Glade type	Lizards	Sm.tree	Lg.tree	Canopy	Shrub	Shade	Rock	Litter	Grass	Habitat	Bsk.rock	LD1
Intact	8.2	5.0	3.4	8.4	4.2	16.3	52.0	20.4	23.3	3.9	0.6	-13.0
Intact	7.9	2.9	5.1	10.9	7.3	17.9	40.1	16.9	34.9	4.3	0.3	-10.3
Intact	6.8	2.4	2.6	6.8	3.4	21.8	48.2	26.2	22.0	1.9	0.4	-10.6
Encroached	2.2	39.1	18.0	49.8	18.4	64.4	37.4	24.1	20.0	6.4	0.6	4.3
Encroached	2.4	29.7	7.6	36.8	11.6	56.2	36.4	11.5	40.2	4.1	0.3	3.1
Encroached	1.3	11.4	18.2	42.8	15.8	58.8	23.8	39.8	20.2	3.8	0.4	2.6
Encroached	2.9	28.8	19.6	54.4	17.4	66.8	28.0	36.1	17.8	1.4	0.8	4.4
Extirpated	0.0	24.4	8.8	36.6	29.7	60.5	26.8	20.2	22.4	1.2	0.3	6.3
Extirpated	0.0	28.8	21.2	61.1	28.6	69.8	40.4	18.1	12.1	2.4	0.9	6.6
Extirpated	0.0	38.3	18.3	56.4	18.9	66.2	30.2	25.4	24.1	1.8	0.3	6.7

APPENDIX 2. Summary table of mean, 95% CI, and *N* of age- (yr) and sex-specific SVL (mm), mass (g), and within season growth rate (mm/day) of *Crotaphytus collaris* from encroached and intact glades.

Glade-type by sex and age	SVL			Mass			Growth Rate		
	Mean	95% CI	<i>n</i>	Mean	95% CI	<i>n</i>	Mean	95% CI	<i>n</i>
Age 0 yr									
Female									
Intact	54.12	2.33	27	6.63	1.67	27	0.45	0.02	12
Encroached	48.12	3.01	15	5.12	2.05	15	0.39	0.03	10
Male									
Intact	54.12	2.33	23	6.63	1.67	24	0.44	0.02	15
Encroached	48.12	3.01	17	5.12	2.05	16	0.36	0.03	11
Age 1 yr									
Female									
Intact	79.40	1.80	41	19.71	1.57	41	0.25	0.02	23
Encroached	69.22	1.93	24	11.71	1.82	24	0.21	0.02	14
Male									
Intact	79.53	1.75	43	19.42	1.37	43	0.27	0.02	21
Encroached	69.97	1.65	24	12.80	1.45	25	0.21	0.02	15
Age 2 yr									
Female									
Intact	93.07	1.38	30	31.88	1.64	30	0.06	0.02	19
Encroached	84.52	2.04	12	23.43	2.46	12	0.05	0.02	10
Male									
Intact	99.28	1.89	19	36.49	1.48	18	0.06	0.01	19
Encroached	86.89	2.30	12	25.55	1.81	12	0.05	0.01	8
Age 3 yr									
Female									
Intact	95.88	2.13	12	36.23	2.57	12	0.04	0.02	9
Encroached	89.26	2.55	10	26.88	3.13	9	0.03	0.02	9
Male									
Intact	101.42	2.45	13	43.66	1.90	13	0.03	0.01	12
Encroached	94.27	2.77	9	31.91	2.21	9	0.03	0.01	7
Age 4 yr									
Female									
Intact	100.44	3.45	8	40.91	3.83	7	0.01	0.01	6
Encroached	93.18	2.23	9	29.27	2.68	9	0.01	0.01	8
Male									
Intact	104.36	2.21	9	46.65	1.68	9	0.02	0.01	10
Encroached	98.71	2.67	11	38.04	2.09	11	0.03	0.01	4