EFFECT OF URBANIZATION ON ABUNDANCE OF JOLLYVILLE PLATEAU SALAMANDERS (*EURYCEA TONKAWAE*)

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Abstract.—Urbanization causes havoc to native ecosystems, resulting in population declines or extirpation of sensitive taxa. This can be devastating to narrow-range endemics whose distributions overlap or are enveloped by urban development. Jollyville Plateau Salamanders (*Eurycea tonkawae*) are aquatic neotenes restricted to karst-associated waters in a small, highly urbanized area of central Texas. *Eurycea tonkawae* was recently listed as threatened under the U.S. Endangered Species Act due to threats from urbanization, although the published literature on their population status is limited to a single, short-term study. Here, we attempt to remedy this dearth of knowledge by summarizing population survey data from sites that span the breadth of *E. tonkawae*'s range. We analyzed count data using Bayesian inference and generalized linear models, first to determine trends in abundance at eight sites from 1996–2011. Secondly, we examined differences in salamander density at these and an additional nine sites (*n* = 17) among urbanized and non-urbanized catchments from 2009–2012. Study sites occurred in catchments that ranged from undeveloped to completely built-out, from no-change in development to > 20% increases in development. Accounting for climatic variation, we found that counts of *E. tonkawae* declined in areas that had the largest increases in residential development (a metric of urbanization) over a 15-y period. Additionally, densities of *E. tonkawae* were negatively correlated with residential development across their range. We discuss several possible mechanisms responsible for declines of *E. tonkawae* and highlight likely causes and potential areas of future research to aid in conservation efforts for this and other central Texas *Eurycea* salamanders.

Key Words.—Edwards Aquifer; endangered species; habitat loss; land-use change; Plethodontidae; population ecology

INTRODUCTION

Urbanization has myriad impacts on ecosystems worldwide, changing land cover, biodiversity, and hydrosystems (Grimm et al. 2008). Aquatic ecosystems are particularly vulnerable to urbanization; impervious surfaces increase stream flashiness, altering stream morphology, in-stream habitats, and community structure (Paul and Meyer 2001; O'Driscoll et al. 2010). In response to these impacts, amphibians have experienced declines or extirpation in urban areas, exhibiting low survival (Barrett et al. 2010; Price et al. 2012), occupancy (Price et al. 2011), abundance (Orser and Shure 1972; Riley et al. 2005; Price et al. 2006; Miller et al. 2007), and species richness (Rubbo and Kiesecker 2005; Barrett and Guyer 2008; for review, see Scheffers and Paszkowski 2011). While amphibians with broad geographic distributions may persist in undisturbed portions of their range, those with restricted ranges in or near metropolitan areas face a greater risk of extinction. The latter case is best exemplified by the spring and cave-dwelling *Eurycea* (Plethodontidae) salamanders of the Edwards Plateau in central Texas (clade *Paedomolge*; Hillis et al. 2001). At least seven species in this group (of 13) are threatened by, and in some cases, completely surrounded by development from an ever-growing human population (Chippindale et al. 2000; Chippindale and Price 2005; U.S. Fish and Wildlife 2012). For species whose ranges are engulfed by urbanization, understanding their response to anthropogenic threats is critical for developing a conservation strategy.

Eurycea tonkawae (Jollyville Plateau Salamander) along with three other congeners endemic to central Texas were recently listed (*E. tonakwae* as threatened; *E. waterlooensis* as endangered) or await final determination for listing (*E. chisholmensis* and *E. naufragia*) under the U.S. Endangered Species Act, with anthropogenic threats to water quantity and quality being the primary impetus for the proposed federal rulemaking (U.S. Fish and Wildlife Service 2012). *Eurycea tonkawae* inhabits a range of groundwater-associated habitats including small hillside seeps, large water-filled caves and spring-fed streams across eight watersheds in northwestern Travis and southern Williamson counties, Texas (Chippindale et al. 2000), an area of approximately 233 km². A large portion of their known localities occur within the Balcones Canyonlands

Preserve, a sanctuary system created to protect and manage the breeding habitats of numerous rare and endangered species. However, at least half of the range of *E. tonkawae* occurs within, or downstream of, highly urbanized areas within the City of Austin and its suburbs. In contrast, *E. naufragia* and *E. chisholmensis* (Georgetown and Salado Salamanders, respectively) occur in less developed areas (as of this writing) compared to *E. tonkawae*, but where the human population is expected to increase considerably in comparison to the national average over the coming decades (Texas State Data Center. 2012. Population projections for the State of Texas and Counties. http://txsdc.utsa.edu/Data/TPEPP/Projections/Index.aspx [accessed 26 July 2013]; U.S. Census Bureau. 2012. 2012 National Population Projections, Middle Series. http://www.census.gov/population/projections/data/natio nal/2012/summarytables.html [accessed 26 July 2013]). Thus, understanding the response of *E. tonkawae* populations to urbanization may provide insights into how other, closely-related species will fare as development continues in this region of central Texas.

Despite conservation concern for central Texas *Eurycea* species (Chippindale and Price 2005) and ample scientific interest in the group (particularly with respect to taxonomy and systematics, e.g., Sweet 1984; Chippindale et al. 1993, 2000; Hillis et al. 2001; Wiens et al. 2003; Bendik et al. 2013) only four studies of their population ecology have been published. This literature is generally limited to short-term (i.e., based on a single collection event or a single year of observation) studies of one or two populations (Bruce 1976; Tupa and Davis 1976; Pierce et al. 2010). In the case of *E. tonkawae,* available information on their ecology is limited to a single published study (Bowles et al. 2006) and multiple unpublished government reports (U.S. Fish and Wildlife 2012 and references therein). From 1996–1998, fewer *E. tonkawae* were found at five developed sites compared to three undeveloped sites (Bowles et al. 2006). This difference was attributed to the effects of urbanization, possibly due to increased scouring of habitat at developed sites (Bowles et al. 2006). Since that time, however, development has continued to occur throughout their range, potentially impacting these and numerous other populations.

Our goal is to provide an up-to-date summary of the population status of *E. tonkawae* as well as to elucidate factors that may contribute to current patterns and past trends in abundance. By documenting the response of *E. tonkawae* to urbanization, we hope to gain a better understanding of the areas and populations most impacted in order to aid future conservation efforts of this and other central Texas neotenic salamanders. To that end, we examine trends in counts of *E. tonkawae* at eight sites from 1996 to 2011 in the context of a changing urban landscape. We ask whether

development upstream of our study sites corresponds to long-term trends in surface abundance of salamanders. Additionally, we assess the effect of urbanization on more recent estimates (2009–2012) of salamander density using a broad sample of sites from across the range of *E. tonkawae*. Lower densities of *E. tonkawae* have been associated with low cover availability caused by urban development (e.g., due to scouring from flash floods; Bowles et al. 2006), so we ask whether development negatively affects *E. tonkawae* density when differences in cover availability are accounted for. We used hierarchical generalized linear models and Bayesian inference to examine counts of *E. tonkawae* in response to climatic variation and changes in land use over time, and also in response to cover availability and differences in land use across their range.

METHODS

Sites.—City of Austin and Travis County biologists selected sites non-randomly, but coverage was spatially comprehensive, as the geographic distribution of our study sites spans the majority of the known range of *E. tonkawae*. Researchers initially delineated sites based on the presence of *E. tonkawae* at a spring or within a spring-dominated stream channel (Bowles et al. 2006), since presence of central Texas *Eurycea* is associated with spring discharge (Sweet 1982). Our study sites include eight sites originally delineated by Bowles et al. (2006) in 1996, as well as an additional nine sites we added to the study between 2007 and 2009. Researchers divided sites into sections according to different stream habitat types (e.g., riffles, runs, shallow pools). Geologically, study sites range from small Edwards Aquifer springs with short spring-runs to larger, spring-dominated stream channels within the Glen Rose and Walnut limestone formations. Most sites occur within Bull Creek (11 of 17 sites) or one of its tributaries (denoted by number, e.g., "Trib 5"), and the remaining study sites are within Brushy, Cypress, Long Hollow, and Shoal Creek watersheds.

Area surveyed among sites and sections varied, although the size and location of the area surveyed remained consistent within each site throughout the study period. The size of survey areas varied widely among sites due to differences in stream morphology, habitat types, and spring locations among sites and sections. Survey boundaries were subjective due to the difficulty of determining *a priori* what area within the creek channel constituted optimal habitat that would be appropriate for equivalent comparisons of *E. tonkawae* density among sites. Due to variation in survey areas (among sites and sections) and the potential for differences in coverage of optimal habitat, we tested for correlations between survey area and explanatory variables (see below) to determine whether area could be

a confounding variable.

Surveys.—City of Austin and Travis County biologists directed surveys from late 1996 through 2012. Researchers surveyed on a monthly or semi-monthly basis from 1996 through 1998 (Bowles et al. 2006), and generally on a quarterly basis thereafter. However, there was some variability in survey frequency for several reasons. Central Texas climate is unpredictable and periodic droughts and floods introduced variability in spring and stream flow patterns resulting in partial surveys (e.g., when some sections within a site were dry) and inconsistency between survey intervals. Another source of variation was due, in part, to changes in staff availability and priorities.

Observers surveyed each site by exhaustively searching all cover objects on the surface of the stream (e.g., rock cover, leaf litter, woody debris), counting each salamander observed and visually estimating their size (total length: < 25 mm, 25–50 mm, ≥ 50 mm). This was done as a drive survey, whereby observers would begin downstream removing cover objects to create an open "line" perpendicular to the bank that moved upstream until all cover objects were searched. To avoid double-counts, only salamanders that were chased (or captured and moved) downstream below the observer line were tallied. It was not possible to search the subsurface habitat for salamanders. Where we use the term "abundance," we are specifically referring to surface or relative abundance.

Land use.—We delineated surface drainage basins from the downstream end of each site using the watershed tool and a flow-direction raster (City of Austin, unpubl. data) in ArcGIS v9.2 (ESRI, Redlands, California, USA). For the purpose of examining the effect of urbanization on salamander populations, we assumed that surface drainage basins (hereafter, "catchments") approximated the area most likely to influence water quality and quantity (and thus, habitat quality) at each site. We used land parcel data from the City of Austin and Travis Central Appraisal District to calculate land use and median development age for each catchment—the spatial resolution being limited by the size of each parcel. We chose to use land parcels to quantify urbanization because datasets were available for the years 1995, 2000, 2006, and 2010, roughly spanning the time period of our study and allowing us to examine changes in urbanization over time. A preliminary analysis also indicated close correspondence of development based on parcel data to impervious cover estimates (an oft-used metric of urbanization) from building and road footprint data (these data were not available for all years of interest; results not shown). Therefore, we were confident that parcels would be an adequate surrogate of impervious cover for quantifying urbanization, with one exception—large developed properties with relatively low impervious cover could positively bias estimates of developed land within a catchment. For example, some large parcels categorized as developed (e.g., industrial use) consist mostly of undeveloped land or preserves. While this is merely an artifact of parcel ownership and organization of the available land use datasets, it could bias our results. Therefore, we chose instead to represent urbanization within a catchment as the proportion of land developed for residential use (calculated from parcel area) and excluded other types of development from the statistical analysis. Residential development in the study area primarily consists of small-plot, single-family homes in large subdivisions as well as apartment complexes, and represented a large portion of the total developed area (see Results). Because these parcels are small and collectively represent most of the development within our study area, any single parcel is unlikely to weigh heavily on the total estimates of developed land, in contrast to larger parcels typical of other development types.

Environmental variables.—Changes in hydrologic conditions can influence *E. tonkawae* abundance at the surface, particularly in cases of extreme drought where salamanders are forced to retreat to subterranean refugia as their surface habitat dries out (Bendik and Gluesenkamp 2013). To account for the influence of changing hydrologic conditions in our trend analysis, we used the National Oceanic and Atmospheric Administration's monthly Palmer Z-Index (a measure of short-term drought) and Temperature Index for the Texas Edwards Plateau, climate division 6 (available from http://www.ncdc.noaa.gov/). We also obtained 90-day median flow rates from USGS station 08154700, Bull Creek at Loop 360, Travis Co., Texas (available from http://waterdata.usgs.gov/nwis). While point estimates of stream discharge were usually available for each survey, we chose instead to use period-averaged data since they represent the range of environmental conditions between surveys.

High in-stream water velocities created by stormwater runoff from impervious surfaces can wash away habitat (e.g., cobble substrate) for both salamanders and their prey, in addition to flushing salamanders themselves downstream into potentially unsuitable habitat. Bowles et al. (2006) found lower cover availability at sites in urbanized drainages which could have contributed to comparatively lower salamander densities in their study. Therefore, we accounted for differences in rock cover availability among sites in our density analysis by visually estimating the proportion of area covered by rocks ranging in size from gravel (> 8 mm) to boulders (> 256 mm). We assumed the amount of cover remained constant within our study sections between 2009 and

2012, with one exception. High storm flow within one of the sites resulted in substantial cover loss, in which case, we moved the survey area to an adjacent section downstream to keep habitat type and cover availability consistent.

Data analysis.—Our goals were to model changes in salamander counts over time, and differences in salamander density in response to development. We used a separate dataset for each task. To examine changes in abundance (i.e., population trend) we used count data from eight sites (seven catchments) collected from 1996–2011 (referred to as long-term monitoring sites); this included data from Bowles et al. (2006). To evaluate differences in salamander density across varying levels of residential development within catchments we included count data from both long-term monitoring sites and nine additional sites surveyed from 2009–2012 ($n = 17$). We compiled datasets using SAS Enterprise Guide v4.3 (SAS Institute, Cary, N.C., USA) and analyzed the counts using Poisson generalized linear models in OpenBUGS (Lunn et al. 2009) via the BRugs package (Thomas et al. 2006) in R (R Development Core Team 2012). We chose a Bayesian modeling approach because of its convenience for fitting complex hierarchical models.

While our study uses counts as indices for population size, we recognize that the assumption of constant detection probability is unrealistic, particularly for amphibians (Hyde and Simons 2001; Bailey et al. 2004; Dodd and Dorazio 2004). We do not believe this assumption is necessary to make inferences from our data, although we do make two critical assumptions about detection error. Firstly, there were no long-term trends in detection probability and secondly, differences in detection among sites were random. Random noise in the data from observation error could reduce statistical power to detect differences among treatments, but is unlikely to result in long-term trends or systematic biases among sites when sample sizes are large.

We applied several adjustments to the long-term dataset prior to analysis. First, we included only large salamanders ($\geq$ 25 mm total length; includes both large juveniles and adults) in the trend analysis due to the high frequency of zeroes in the small salamander dataset ($<$ 25 mm total length; small juveniles) during the 15-year time period (however, small salamanders were included in the density analysis). We combined section-specific counts for each site or excluded them if they were surveyed inconsistently. Finally, we summarized survey periods by month, so that surveys occurring within the same month were treated as being taken at the same time and assumed to be subject to the same climatic conditions. The one exception was the 90-day median flow rate, which we estimated based on the actual survey date.

For the trend analysis, we regressed counts against time as well as climatic factors that may control salamander abundance or our ability to observe them. We further modeled trend in time for each site as a function of change in development (within a catchment) over time. Because time-series data typically exhibit serial dependence, it was necessary to account for this in our model. However, unequal sampling intervals and gaps within the time-series precluded the use of commonly used auto-regressive error structures such as AR-1, which typically require even sampling intervals and do not accommodate missing data. To model serial dependence of counts with uneven sampling intervals, we included an auto-regressive term that scaled with time interval between surveys, following Saveliev et al. (2009). Formally, we modeled counts (Y_{jt}) at site j time t as Poisson-distributed random variables with expected mean λ_{jt}. We modeled the log Poisson mean counts [$\log(\lambda_{jt})$] as being dependent on the linear predictor η_{jt} plus the random effect ε_{jt}, specifying the auto-regressive error structure

$$\varepsilon_{jt} = \rho_j^{|W_{\text{dist}}|} \times \varepsilon_{j,t-1} + u_{jt},$$

where ρ_j is the auto-correlation parameter at site j and W_{dist} is the time lag in months between data points t-1 and t. We assumed that the errors u_{jt} were independent and normally distributed with mean 0 and variance σ_u^2. The linear predictor η_{jt} was a function of the fixed effects factors Temperature Index (tmp), Palmer Z-index (Z-index), 90-day median flow rate (flow) and time (t). Thus,

$$\eta_{jt} = \alpha_j + \beta_1 \times \text{tmp}_t + \beta_2 \times \text{flow}_t + \beta_3 \times \text{Z-index}_t + \gamma_j \times t.$$

Furthermore, we modeled γ_j as a function of the change in development at each site (Δdev_j) during the study period:

$$\gamma_j = \alpha_\gamma + \beta_\gamma \times \Delta\text{dev}_j$$

We defined population trend as the geometric mean rate of change during the 15-year study period and calculated the geometric rate of change from a baseline model (with time as the only covariate) in terms of percent change per year. We also report a statistic representing the probability of population decline as the proportion of the posterior distribution where the geometric mean rate of change is < 0.

For the density analysis, we applied a Poisson generalized linear mixed model which included random effects to account for sections nested within sites, as well as site-to-site heterogeneity. We also included a random effects term for year, to account for year-to-year

variation within the unbalanced data set (some sites were sampled more than others within a given year). Additionally, because each section differed in the size of habitat surveyed, we included log-transformed survey area in our model as an offset. This effectively allows us to model density (instead of counts) as a response (for explanation on use of offset, see Kéry 2010). We tested the importance of residential development (dev) and rock cover (cov) as explanatory variables of small and large salamander counts. We modeled the logged Poisson mean counts, which vary according to the size of the survey area, (λ_{icjk}), as being dependent on the fixed effects of development (which varied by site), cover (which varied by section) and the random effects for section (a_{cj}), site (b_j), year (c_k), and individual survey (ε_{icjk}). Thus,

$$\log(\lambda_{icjk}) \sim (\log(\text{area}_c)) + \beta_1 \times \text{dev}_j + \beta_2 \times \text{cov}_{cj}$$
$$+ \beta_3 \times \text{dev}_j \times \text{cov}_{cj} + a_{cj} + b_j + c_k$$
$$+ \varepsilon_{icjk},$$

where $a_{cj} \sim Normal(0, \sigma^2_a)$, $b_j \sim Normal(0, \sigma^2_b)$, $c_k \sim Normal(0, \sigma^2_c)$, and $\varepsilon_{icjk} \sim Normal(0, \sigma^2_\varepsilon)$, with subscripts i, j, c, and k representing indices for survey, site, section, and year, respectively. We centered explanatory variables such that their means equaled zero.

We assigned all α and β parameters standard vague priors with normal distributions (mean = 0, variance = 1000), all inverse variance parameters $(1/\sigma^2)$ were given priors of $Gamma(0.001, 0.001)$, and ρ_j were assigned uniform priors from -1 to 1. We ran four Markov chains simultaneously for 50,000 generations, with samples from the first 5,000 generations discarded as burn-in and assessed convergence using the Brooks-Gelman-Rubin convergence diagnostic implemented in BRugs. To assess model fit, we qualitatively examined a posterior predictive check of the Pearson residuals from actual versus ideal data (Kéry 2010). We tested for auto-correlation among residuals in the trend analysis (with up to 3 lags) using the Ljung-Box statistic Q_j (Ljung and Box 1978); the lag-k auto-correlation was calculated following Congdon (2005). We report 95% Bayesian credible intervals for model parameters. OpenBUGS code is available from the corresponding author by request.

To check whether the trend analysis was confounded by multicollinearity of predictors, we graphed and visually examined temporal trends in explanatory variables and tested for correlations among them. We also tested for correlations among explanatory variables and catchment size for the density analysis. We tested all correlations using Pearson product-moment correlation analysis in R. Where applicable, we assessed significance at $\alpha = 0.05$.

RESULTS

Land use.—Catchments used to calculate land use cover ($n = 17$) ranged in size from 23 to 726 ha (mean = 214; Table 1). Approximately 48% of the total area within the associated stream catchments was developed for residential, office, manufacturing, or other use (Fig. 1). Urbanized catchments predominantly consisted of residential developments which were built, on

TABLE 1. Summary of land use for all catchment areas and survey results from 2009–2012. Sites are ordered from those with the least to most residential development as of 2010. Mean values of rock cover and salamander density (by total length category) were weighted by survey area for sites with more than one section. Asterisks indicate sites included in long-term trend analysis. NA indicates not applicable.

Site	% Residential development	Catchment area (ha)	Median year built	Survey area (m²)	n surveys	n sections	Mean % rock cover	Density mean #/m² (SD) < 25 mm	Density mean #/m² (SD) ≥ 25 mm
Wheless	0	119.3	NA	90.5	4	4	68	0.26 (0.14)	1.17 (0.52)
SAS	0	46.7	1989	59.0	9	2	24	0.04 (0.04)	0.15 (0.17)
Franklin*	5	725.7	1999	95.7	13	2	84	0.13 (0.04)	0.69 (0.30)
Lanier	6	634.3	1999	64.5	6	3	48	0.20 (0.04)	1.27 (0.44)
Lower Ribelin	7	210.3	2000	52.4	6	1	65	0.01 (0.01)	1.00 (0.29)
Upper Ribelin	14	105.0	2000	43.8	9	1	70	0.15 (0.09)	1.74 (0.46)
MacDonald Well	17	214.8	1980	61.9	9	1	75	0.22 (0.04)	1.65 (0.82)
Hill Marsh	18	64.6	2005	19.7	9	1	70	0.51 (0.22)	3.64 (4.10)
Avery Deer	26	116.2	2001	7.5	6	2	68	2.60 (11.50)	3.47 (9.20)
Trib 5*	39	313.8	1997	52.7	12	3	56	0.01 (< 0.01)	0.01 (< 0.01)
Stillhouse*[†]	52	22.6	1985	28.9	16	3	38	0.02 (0.01)	0.11 (0.02)
Spicewood*	58	153.7	1980	40.0	15	2	76	0	0.08 (0.01)
Trib 6*	60	492.3	1992	109.5	14	3	19	0.03 (<0.01)	0.16 (0.02)
Troll	63	51.4	1984	17.6	8	1	70	0.06 (0.01)	0.52 (0.08)
Trib 3*	67	256.1	1993	201.9	3	3	10	< 0.01 (< 0.01)	0.03 (< 0.01)
Tanglewood*	67	59.0	1982	23.4	12	2	41	0.03 (< 0.01)	0.02 (0.01)
Barrow	76	49.9	1974	33.3	12	3	52	0.04 (0.01)	0.29 (0.12)

[†]Two sections within this catchment were treated as different sites for the analysis of trend
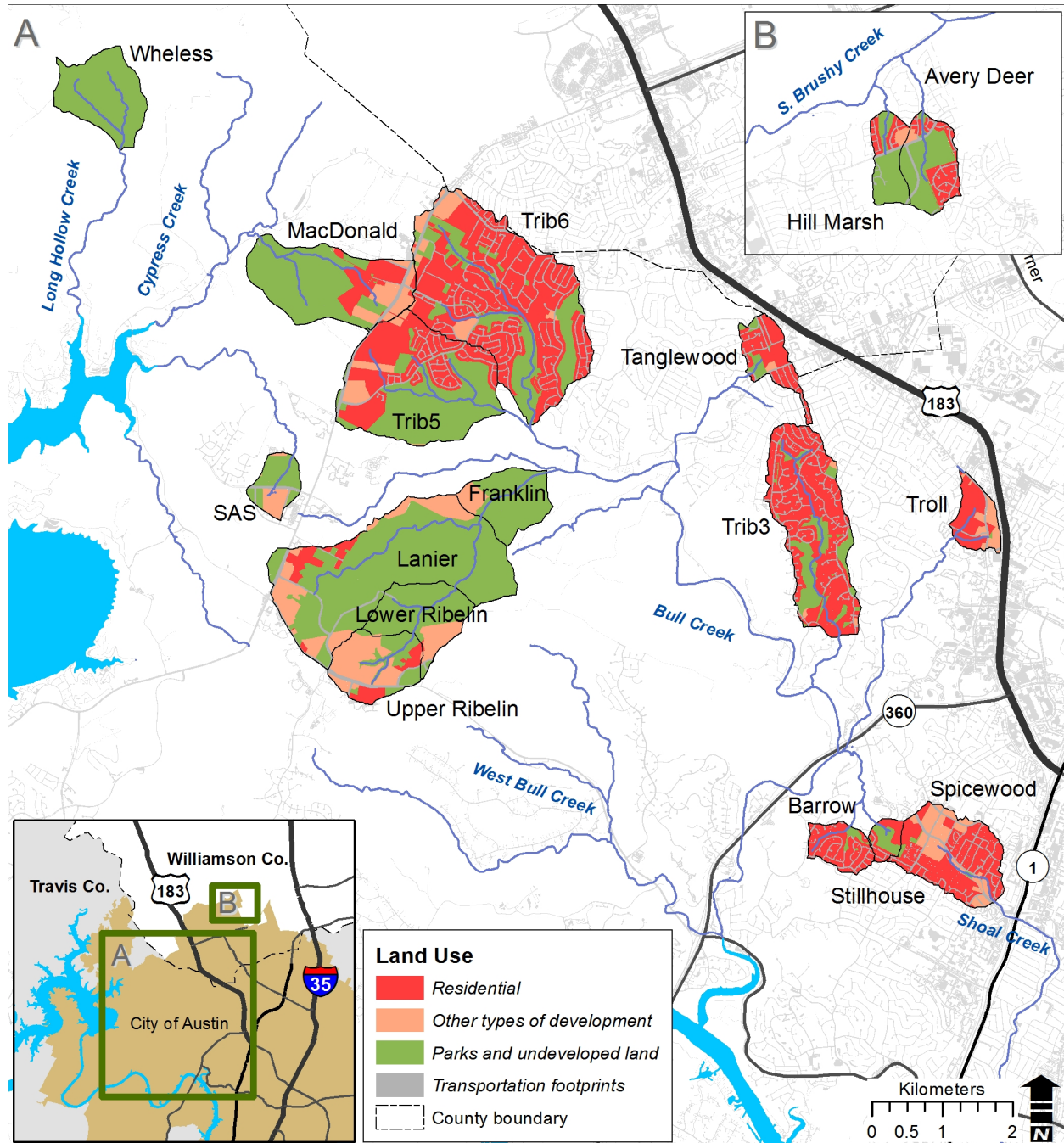
FIGURE 1. Land use in *Eurycea tonkawae*-inhabited catchments. Each catchment is outlined in black. The residential land use category includes both single family and multi-family housing. Other types of development include office space, retail, manufacturing, and schools. Parks and undeveloped land also includes golf courses. Survey sites are located (approximately) at the downstream end of each delineated catchment.

average, between 1974 and 2005 (based on median structure age per catchment). Structures were typically older in highly developed catchments (top 50% of the data range; year built grand mean = 1986) compared to those with less development (excluding catchments with no residential development; year built grand mean = 1998).

Residential housing development covered 68% of the total developed land area, ranging from 0 to 76% (mean = 35%, S.D. = 27%; Table 1) per catchment. Five
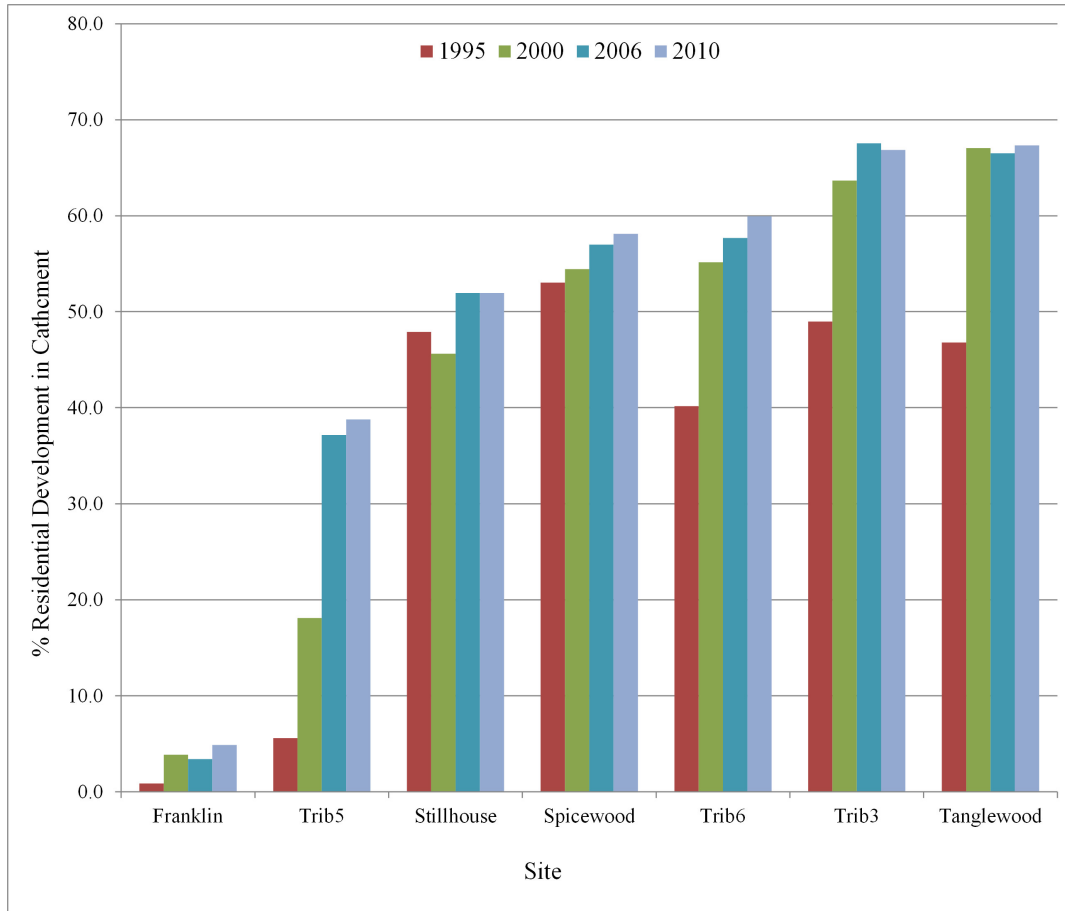
FIGURE 2. Percentage of residential development over time for stream catchments of long-term monitoring sites ordered from least- to most-developed.

TABLE 2. Auto-regressive parameter estimates and 95% Bayesian credible intervals (CI) from Poisson GLM of trends in *E. tonkawae* counts at long-term monitoring sites from 1996–2011. Ljung-Box statistic estimates for each site-specific time series (Q_j) fall within the $\chi_2(3)$ critical region (0.22, 9.35) for $\alpha = 0.05$, indicating a lack of auto-correlation among the *k*-lag residuals. Parameter ρ indicates the strength of auto-correlation for each site-specific time series and σ_u^2 is the error variance.

Parameter	Mean	SD	95% CI
σ_u^2	0.47	0.06	0.37, 0.60
Q_j			
Franklin	3.01	2.38	0.23, 9.11
Stillhouse trib	2.09	1.66	0.16, 6.33
Stillhouse spring	2.66	2.10	0.20, 8.05
Trib 3	0.97	0.77	0.07, 2.94
Tanglewood	1.21	0.96	0.09, 3.67
Spicewood	1.32	1.04	0.10, 3.99
Trib 5	2.38	1.88	0.18, 7.19
Trib 6	2.31	1.82	0.18, 6.98
ρ_j			
Franklin	0.08	0.09	0.01, 0.33
Stillhouse trib	0.39	0.25	0.04, 0.95
Stillhouse spring	0.50	0.24	0.08, 0.95
Trib 3	0.57	0.27	0.06, 0.97
Tanglewood	0.56	0.28	0.05, 0.98
Spicewood	0.46	0.29	0.02, 0.95
Trib 5	0.89	0.11	0.57, 1.00
Trib 6	0.45	0.28	0.04, 0.98

catchments had less than 10% residential land use (all predominantly within the Balcones Canyonlands Preserve), while seven had over 50% (Table 1). For sites included in the long-term trend analysis, most development during our study occurred between 1995 and 2000, although even larger increases in residential development continued at Trib 5 through 2005 (Fig. 2). There were no significant correlations between catchment size and explanatory variables (development: $r = -0.26$, $P = 0.31$; rock cover: $r = -0.01$, $P = 0.96$).

Model adequacy.—Convergence was achieved for all parameters prior to the burn-in period and the posterior predictive check indicated good model fit for both trend and density models. We did not observe any clear trends or detect any significant correlations among climatic variables ($r = 0.15$, $P = 0.26$ for Z-index and flow; $r = -0.21$, $P = 0.12$ for tmp and flow; $r = -0.12$, $P = 0.39$ for Z-index and tmp) nor did we detect any strong patterns in our visual examination of Pearson residuals. The Ljung-Box test did not indicate significant serial auto-correlation in the residuals of the count data (Table 2). The random effects auto-correlation parameters (ρ) were
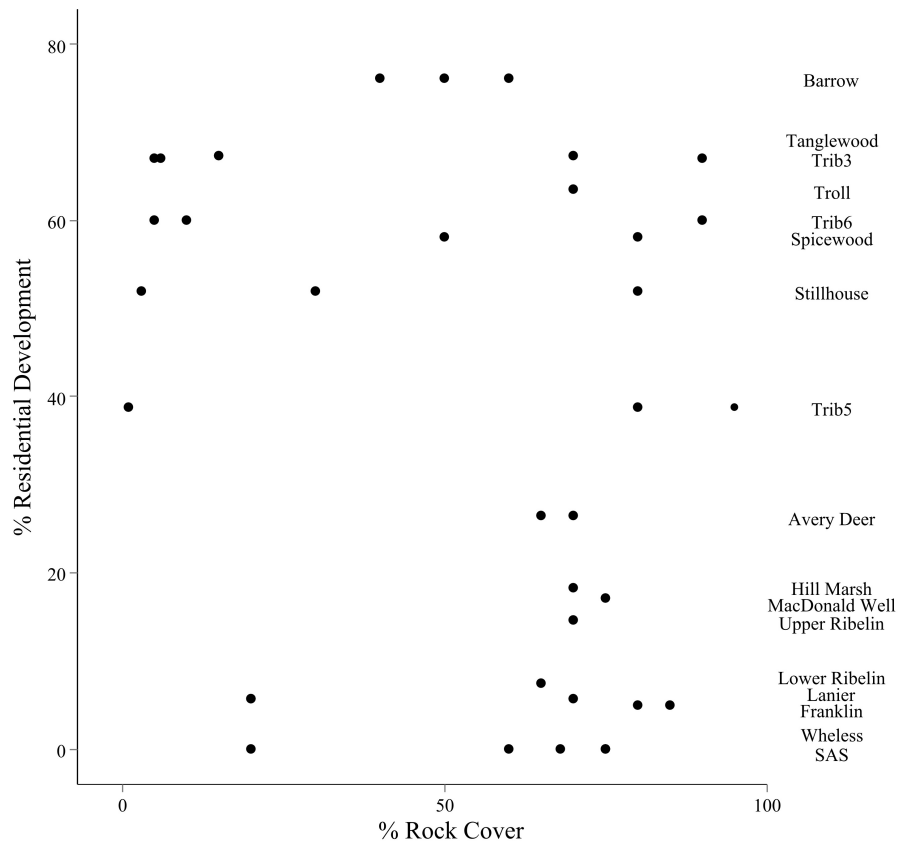
FIGURE 3. Relationship between residential development and rock cover for all sections and catchments. Site names on the right side correspond to the data points from their respective sections (also see Table 1). Sites in highly developed catchments had a wide range of cover, including heavily scoured sections with little to no available rock cover.

significant for each site (Table 2), suggesting that including these terms in the model was warranted.

There was a small but significant negative correlation ($r = -0.13$, $P = 0.02$) between available rock cover within a section and proportion of land cover with residential development (Fig. 3). There were no significant correlations between survey area and development or rock cover (development: $r = -0.04$, $P = 0.89$; rock cover: $r = -0.20$, $P = 0.24$).

Trends.—From 417 surveys at eight sites over a 15-year period, trends in counts ranged from no-change to steep declines. Declines were strongly correlated with increasing development during the same time period (Table 3 and Fig. 4). Average monthly air temperature and 90-day median stream flow were positively correlated with *E. tonkawae* counts, while monthly drought Z-index was negatively correlated (Table 3). The 95% credible intervals for these parameters excluded zero, suggesting that these climatic variables were important predictors of salamander surface abundance.

Trib 5 had the highest percentage increase in development (33%; Fig. 4) which was coupled with the steepest decline in counts (48% decline per year), followed by Tanglewood, Trib 3, and Trib 6 (Table 3). Franklin, Stillhouse trib, Stillhouse spring, and Spicewood did not exhibit statistically significant changes in surface abundance (although the probability of decline for Spicewood was over 90%). Change in development was relatively low at these sites (4–5%) compared to sites with declining populations (18–33%; Fig. 4).

Surveys from one section each at Franklin, Trib 5, and Trib 6 were excluded from the trend analysis due to infrequent sampling during the 15-year study period (although these were included in the density analysis).

Density.—We found a strong negative effect of development on density of *E. tonkawae* (Table 4) estimated from 163 surveys at 17 sites (mean no. surveys per site = 10, range = 3–16; Table 1) between 2009 and 2012. The effect of development was not confounded by differences in available rock cover among sites, as

TABLE 3. Linear predictor parameter estimates and 95% Bayesian credible intervals (CI) from Poisson GLM of trends in *E. tonkawae* counts at long-term monitoring sites from 1996–2011. Trend is the geometric rate of population change displayed as percent change per year and was estimated from the baseline model. Mean estimates with 95% credible intervals excluding zero are displayed in bold.

Variable (parameter)	Mean	SD	95% CI	Baseline Trend (%)
Tmp (β_1)	**0.015**	**0.004**	**0.007, 0.022**	NA
Flow (β_2)	**0.023**	**0.006**	**0.012, 0.035**	NA
Z-index (β_3)	**-0.047**	**0.019**	**-0.083, -0.009**	NA
Δdev (β_γ)	**-0.695**	**0.358**	**-1.573, -0.121**	NA
Time (γ_j)				
Franklin	0.018	0.034	-0.050, 0.084	4.4
Stillhouse trib	0.017	0.034	-0.050, 0.083	0.9
Stillhouse spring	0.017	0.034	-0.050, 0.083	10.5
Trib 3	**-0.079**	**0.045**	**-0.186, -0.003**	**-14.1**
Tanglewood	**-0.097**	**0.052**	**-0.225, -0.012**	**-16.1**
Spicewood	0.010	0.033	-0.054, 0.073	-6.6
Trib 5	**-0.092**	**0.050**	**-0.214, -0.010**	**-47.9**
Trib 6	**-0.185**	**0.093**	**-0.421, -0.042**	**-8.2**
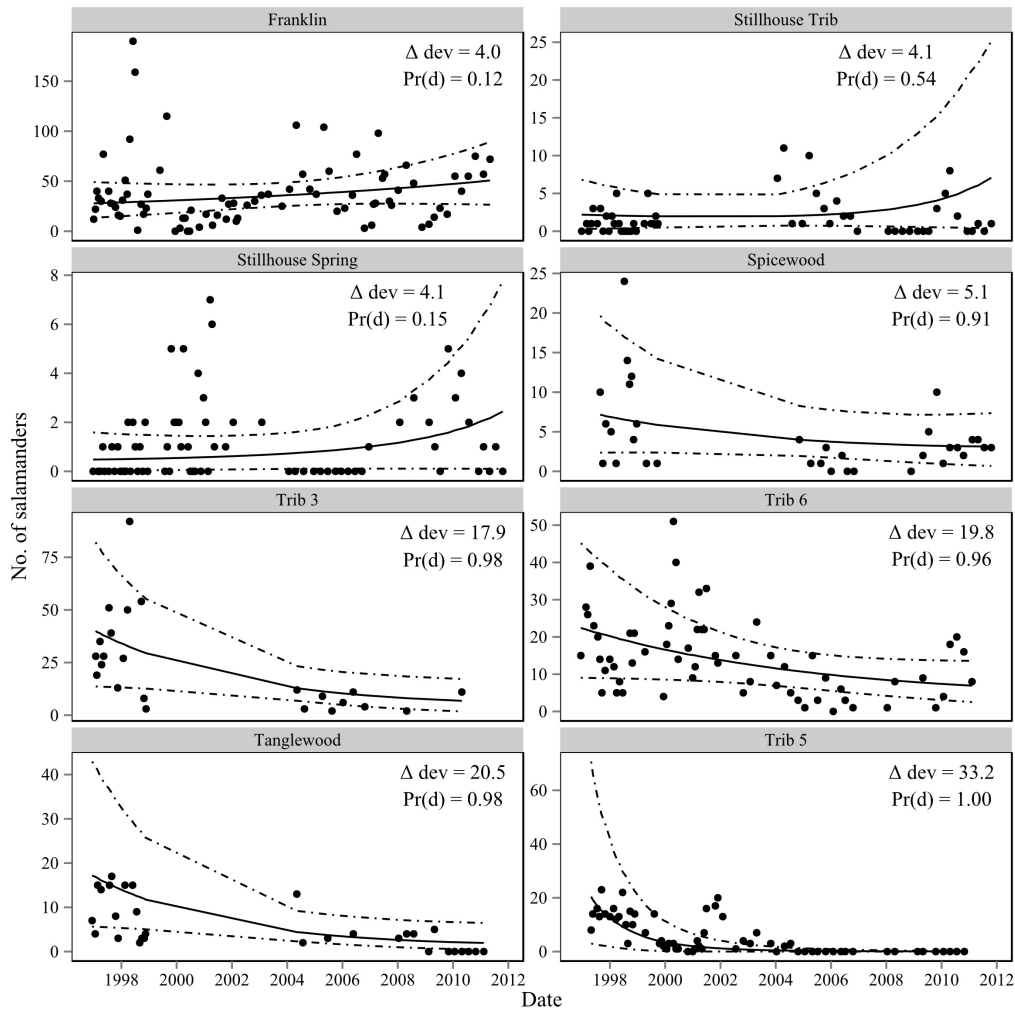
FIGURE 4. Scatterplots of salamander counts over time at eight long-term monitoring sites from 1996–2011 with baseline trend (solid line) and 95% credible interval (dashed lines). Each plot has unique y-axes but identical x-axes. Sites are ordered (increasing from top left to bottom right) by percent change in residential development (Δ dev) between 1995 and 2010 (also see Figure 2). Pr(d) is the posterior probability that the trend is < 0.

indicated by the lack of an interaction between these variables (Table 4). Density of *E. tonkawae* ranged from 0 to 10.97 large salamanders/m^2 and 0 to 10.73 small salamanders/m^2 over the 3.5-year sampling period. Sites with residential development $\geq$ 39% tended to have lower densities of salamanders from both size classes (Table 1; Fig. 5). Variation in density not explained by development or cover was due in large part to within-section and within-site variation, compared to within-year variation (Table 4). However, there was still a considerable amount of unexplained variation in the model (Table 4), possibly due to observation error and/or unmeasured environmental variables.

DISCUSSION

Population declines.—Counts of *E. tonkawae* are lower in highly urbanized catchments throughout their range and have declined in response to increases in development. Although our sample size was small (*n* = 8 sites), we detected a strong negative correlation between change in development and trends in surface abundance of large salamanders. The greatest decline occurred at Trib 5 which exhibited the largest increase in development, but it was also the only site that went from relatively undeveloped to developed during the study period. In comparison, Trib 3, Trib 6, and Tanglewood were already partially developed though development continued during our study; these populations may have already been in decline prior to monitoring. Three long-term monitoring sites in urbanized

catchments did not exhibit substantial changes in surface abundance of *E. tonkawae* (Stillhouse Spring, Stillhouse Trib, and Spicewood). Median residential structure ages within the Stillhouse and Spicewood drainages indicate that most development occurred, on average, 10–15 years before population monitoring began. Counts of *E. tonkawae* were low throughout our study (we typically observed fewer than 10 individuals), and previous observations of *E. tonkawae* at Stillhouse suggest that they were once more abundant prior to pollution from a petroleum leak in 1993 (Paul Chippindale, David Hillis, and Andrew Price, unpubl. report). Thus, declines in *E. tonkawae* abundance at these sites may have occurred prior to our study.

Because data were only available from a subset of sites to assess long-term trends, we also tested whether short-term estimates of *E. tonkawae* density were related to the amount of development in catchments throughout their range. We found a strong negative relationship between residential development and *E. tonkawae* density, unconfounded by differences in cover availability. This could be an artifact of sampling, such that sites with naturally lower densities just happen to coincide with urban areas. However, we do not believe that is the case, given the evidence of declines in response to development from our trend analysis. Low densities of *E. tonkawae* in highly developed drainages are most likely a result of population declines from the negative impacts of urbanization, which is consistent with findings from other studies of stream-dwelling salamanders (Orser and Shure 1972; Willson and Dorcas

TABLE 4. Parameter estimates and 95% Bayesian credible intervals (CI) from Poisson GLMMs of *E. tonkawae* density at 17 sites from 2009–2012. Development was the only strong predictor of salamander density for both large and small size classes. Fixed-effects estimates with 95% credible intervals excluding zero are displayed in bold.

Parameter	Estimate	SD	95% CI
Small salamanders (< 25 mm)			
development (β_1)	**-4.86**	**1.85**	**-8.77, -1.47**
cover (β_2)	0.55	1.32	-2.15, 3.19
dev*cover (β_3)	0.02	5.68	-11.06, 11.13
section effects SD (σ_a)	1.59	0.54	0.58, 2.74
site effects SD (σ_b)	1.12	0.71	0.04, 2.56
year effects SD (σ_c)	0.49	0.47	0.04, 1.66
survey effects SD (σ_ε)	1.85	0.20	1.49, 2.28
Large salamanders ($\geq$ 25mm)			
development (β_1)	**-4.16**	**1.34**	**-6.94, -1.58**
cover (β_2)	0.79	0.87	-0.94, 2.51
dev*cover (β_3)	-1.22	3.54	-8.36, 5.69
section effects SD (σ_a)	1.24	0.30	0.78, 1.93
site effects SD (σ_b)	1.08	0.51	0.06, 2.01
year effects SD (σ_c)	0.15	0.15	0.03, 0.52
survey effects SD (σ_ε)	0.88	0.06	0.77, 1.02
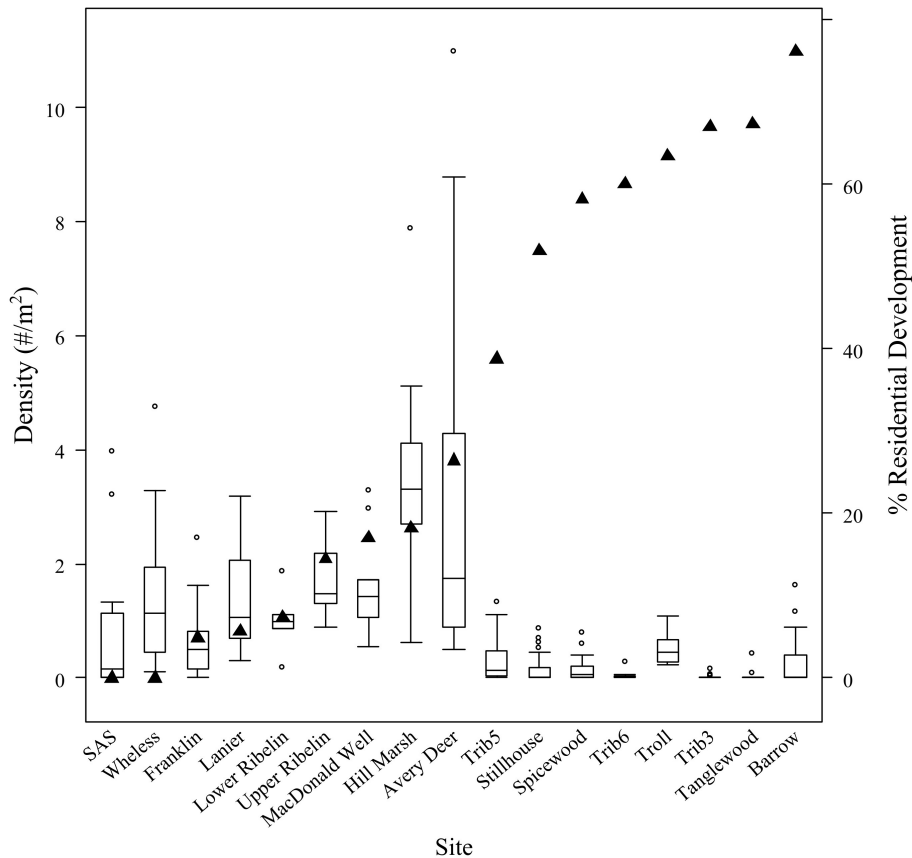
FIGURE 5. Box and whisker plots for density of large (≥ 25 mm) *Eurycea tonkawae* and % residential development (triangles) at 17 sites from 2009–2012. Box plots represent median (horizontal line within box), first and third quartiles (box), extreme values ≤ interquartile range x 1.5 (whiskers), and outliers (open circles).

2003; Price et al. 2006, 2011, 2012; Miller et al. 2007).

In light of these results, conservation planners may be interested in determining what levels of development result in declines of *E. tonkawae* and what levels have no impact. In our study, sites with ≥ 39% residential development appear to have much lower densities compared to those with ≤ 26 % development (although no catchments in our study had development levels between those values; Fig. 5). For example, four sites in highly urbanized drainages had extremely low densities of *E. tonkawae* (average of < 0.10 individuals/m^2), as much as two orders of magnitude lower compared to less developed catchments. In contrast, two sites with moderate levels of development (Hill Marsh and Avery Deer; 18% and 26%, respectively) exhibited the highest average salamander densities (> 3 large individuals/m^2). However, these high density sites may have yet to be impacted by urbanization, as development within these catchments is recent compared to all other study sites (Table 1). Although negative impacts from urbanization to other stream-dwelling salamanders have occurred in as little as four years (Price et al. 2011), older water

transmission and sewer pipes are more likely to leak, and structure age in Austin is strongly correlated with urban leakage, a source of water quality degradation (Christian et al. 2011). Furthermore, differences in landscape features (natural or modified) between catchments such as geomorphology or storm-water control methods may result in differential impacts from urbanization. For example, some catchments have improved storm-water control methods compared to developments built prior to the City of Austin's Comprehensive Watershed Ordinance in 1986. As we discuss below, potential mechanisms responsible for population declines due to urbanization are varied and may also differ between catchments. Finally, our study used residential development from land-parcel data as a metric of urbanization, and these results must be interpreted within that context; our analysis does not fully account for, nor rule out, the effects of other types of urbanization. Thus, to define a specific threshold of urbanization protective of *E. tonkawae* populations (if one even exists) would be fraught with caveats, and is beyond the scope of this study.

Instead, the goal of this study was to elucidate a general pattern of *E. tonkawae* abundance through time and across space in relation to urbanization, and to identify populations of the greatest conservation concern. We demonstrated that development has a strong negative correlation with both population trends and density of *E. tonkawae*. Populations remain robust in areas untouched by development, but could be in danger of extirpation in several, highly developed catchments. Populations that exhibit low apparent population sizes and/or cessation of reproduction and recruitment are under the greatest threat, because small populations are more vulnerable to extinction from demographic and environmental stochasticity (Morris and Doak 2002). For example, it is now uncommon to observe any salamanders at two sites (Trib 5 and Tanglewood) where they were frequently encountered in the late 1990's. Relative abundance of small juveniles is also lower in highly developed catchments, indicating either a reduction in reproduction, or lower juvenile-specific survival rates, e.g., if they are more susceptible to mortality from flood events (Barrett et al. 2010) or more sensitive to pollutants compared to adults.

Recovery of these low-abundance populations will depend upon understanding both the reasons for declines as well as their continued persistence at very low densities. For example, at long-term monitoring sites where few individuals are observed, it is difficult to know whether these are source populations that are nearly extirpated, or persist through migration from other populations (e.g., from subterranean refugia), thereby operating as a population sink. The former case may represent a point of no return (for natural population recovery) whereas in the latter, recovery may be possible through restoration and protection of the surface habitat and water quality. Although little is known about the aquifer ecology in this region, primary production is typically low within subterranean ecosystems (Gibert et al. 1994; Culver and Pipan 2009) and surface populations of *E. tonkawae* become emaciated and show other signs of energetic stress when confined to subterranean refugia for long periods of time (Bendik and Gluesenkamp 2013). Additionally, subterranean habitats in urban areas are unlikely to provide refuge from degraded water quantity and quality, since these tend to be closely linked between the surface and subsurface in karst systems. Furthermore, habitat fragmentation from impoundments, reduced cover availability, and other impacts to natural stream hydrology and morphology may limit migration from both subterranean and surface populations. On the other hand, subterranean habitat may provide refuge from the physical impacts of storm flow, which is detrimental to aquatic salamanders (Barrett et al. 2010). Thus, the fates of urban *E. tonkawae* populations are likely determined by a complex set of factors which includes the population and meta-population dynamics that govern population growth and migration as well as the external mechanism(s) that cause population declines.

Potential mechanisms.—There are numerous possible mechanistic links between urbanization and *E. tonkawae* declines, and determining cause and effect is difficult when the various impacts from urbanization often occur simultaneously. For example, more frequent flooding from impervious surfaces alters stream hydrology and in-stream habitat and can deliver high pollutant loads, greatly impacting aquatic ecosystems (Walsh et al. 2005). Below we discuss several factors that may play a role in declines of *E. tonkawae* in urban areas, but where further research is needed to quantify and elucidate their effects.

Chemical pollutants harmful to amphibians, such as heavy metals (Linder and Grillitsch 2000), pesticides (Howe et al. 1998; Larson et al. 1998; Hayes 2000), and organic compounds (Bryer et al. 2006) have been documented at our study sites (City of Austin 2001) and other urbanized streams in Austin (Scoggins et al. 2007; Glick 2009) at potentially dangerous concentrations (Hayes et al. 2002; Macías et al. 2007; Bommarito et al. 2010). However, the effects of these pollutants on *E. tonkawae* populations are unclear. Obvious, physical ailments such as spinal deformities have been observed in the past at Stillhouse and Barrow; however, it is uncertain whether water-borne pollutants are to blame or if this was a naturally occurring phenomenon (Bowles et al. 2006). Pollutants may also have non-apparent effects (such as endocrine disruption) or cause negligible harm, and further study is needed to determine how *E. tonkawae* are affected.

Chytridiomycosis (caused by the chytrid fungus *Batrachochytrium dendrobatidis*) has been implicated in worldwide amphibian declines (primarily frogs; Skerratt et al. 2007). Although chytrid fungus has been detected in 15 populations of *E. tonkawae* (including several sites with relatively little anthropogenic disturbance), all individuals appeared to be asymptomatic (Lisa O'Donnell et al., unpubl. report; Gaertner et al. 2009). The incidence of chytrid fungus was highest at Stillhouse (the site most impacted by urbanization in the study) compared to other populations (including four other neotenic *Eurycea* species), suggesting there may be a relationship between disease prevalence and environmental degradation (Gaertner et al. 2009).

Although rock cover was not an important predictor of *E. tonkawae* density in our analysis, the few scoured areas we surveyed had low salamander densities and these sections were only present at sites downstream of dense development (Fig. 3). Catchments with high impervious surface cover have storm flows that are more frequent and greater in magnitude compared to those with less impervious cover, altering natural stream

hydrology (Poff et al. 2006). Flashy storm flows (spates) in urban drainages can have direct impacts on stream-dwelling salamanders. For example, spates flush stream-dwelling *Eurycea cirrigera* larvae from their preferred habitat resulting in low survival (Barrett et al. 2010). Spates in urban streams may impact the behavior of *E. tonkawae*, limit dispersal and migration, or result in increased juvenile mortality.

Changes in water quantity and anthropogenic groundwater recharge may also have negative impacts on *E. tonkawae* populations. Impervious cover reduces natural recharge that occurs from precipitation, potentially resulting in lower overall baseflow of springs and streams. However, urban leakage may mitigate reduction in natural recharge caused by runoff from impervious cover and even increase the amount of recharge above natural conditions (Lerner 2002). Urban recharge from leaking water supply, sewer lines, detention ponds, and storm drains as well as from over-irrigation provides artificial baseflow to groundwater catchments (Sharp 2010) and is a significant source of baseflow to streams in Austin (Christian et al. 2011). However, these water sources (e.g., chlorinated water, raw sewage, irrigation water) contain pollutants and, aside from possibly causing direct harm to salamanders, may be less likely to facilitate energy input (e.g., detritus or dissolved organic matter) into groundwater ecosystems with the same manner and efficiency as natural recharge from precipitation and percolation.

The community structure of fishes and invertebrates in spring-run habitats is also affected by urbanization (Paul and Meyer 2001). Loss of intolerant/sensitive taxa and replacement with more tolerant taxa changes in-stream communities, potentially altering the prey base and presence of predators in *E. tonkawae* habitat. For example, changes in channel morphology from scouring floods and additional baseflow from anthropogenic water may lead to deeper, permanent pools, providing habitat for predatory fishes. Thus, any potential mitigating benefit of urban leakage (as a replacement for natural recharge) may be offset by other environmental stressors associated with it.

Counts as indices of population size.—While count data have been commonly used to assess population trends in hundreds of amphibian studies (Houlahan et al. 2000 as cited by Schmidt 2003), it has been widely recognized that potentially unrealistic assumptions are made when count data are interpreted as indices for population size (Hyde and Simons 2001; Bailey et al. 2004; Dodd and Dorazio 2004). We observed high short-term variation in counts, which could be an indication of high-observer error, although we do not believe this is the case. Capture-recapture surveys of *E. tonkawae* indicate that temporary migration can be high, and estimates of population size vary widely from month

to month even when accounting for changes in detection probability (Nathan Bendik, unpubl. report). This suggests that a large component of short-term variation is likely due to natural population processes (e.g., migration to and from subterranean refugia; Bendik and Gluesenkamp 2013), and therefore many surveys are required to adequately sample the surface population at a given site. Despite the potential pitfalls of using counts as population indices (though see Johnson 2008), we believe that the strong downward trends we observed are unlikely to be caused by concordant trends in observation error. We did not observe correlated downward trends in environmental variables that may affect detection during our study period, nor are we aware of factors that could result in spatially discordant patterns of detection probability that correspond to our treatment groups. We argue that while observer error almost certainly contributes to some variability in our dataset, it is unlikely to fully explain consistent differences in counts between urbanized and non-urbanized sites, particularly when they differ by several orders of magnitude.

Conservation implications.—Species endemic to small, highly populated areas such as *E. tonkawae* are at greater risk of extinction due to the effects of urbanization. *Eurycea tonkawae* appears to have suffered substantial declines throughout its range based on both direct observations of declining surface abundance and much lower densities in urbanized catchments, a pattern common among amphibians in urban areas (for review, see Scheffers and Paszkowski 2011). With much of its range within already highly developed catchments, conservation efforts for *E. tonkawae* must focus on mitigating the impacts of urbanization, highlighting the need for further research to determine what mechanisms (as outlined above) drive declines. On the other hand, other endemic central Texas salamanders such as *E. naufragia* and *E. chisholmensis* face similar threats, but occur in (currently) less developed areas. In these cases, conservation efforts may be better suited to protecting and preserving watersheds and water sources yet to be degraded by urban development.

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