City of Austin
WATERSHED PROTECTION

JOLLYVILLE PLATEAU SALAMANDER STATUS REPORT

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ABSTRACT

In this report, we summarize the current status of the Jollyville Plateau salamander (*Eurycea tonkawae*) drawing upon data gathered from two different survey methods, count surveys and capture-mark-recapture (CMR) surveys. We examined short term trends in count data from 2008-2010 in the context of the 2008-2009 drought at thirteen monitoring sites, and long term trends at eight of those sites from 1996-2009. We also analyzed CMR data for three sites from 2007-2009 to estimate detection probability, population size, temporary emigration, and survival. Regarding overall status of the species, the analysis of long-term count data indicated that urban sites have a significant declining population trend overall, compared to rural sites. However, our ability to detect salamanders when they are present (detection probability) varies among sites and over time, and should be accounted for when interpreting count data. With respect to the response of *E. tonkawae* to the drought, we detected significantly lower total and juvenile salamander counts during 2008 through part of 2009, in comparison to post-drought counts. At CMR sites, population size did not significantly decrease during the longest dry period at each site, and reproduction was also observed at one site during this period. These results indicate a resiliency of *E. tonkawae* to dry surface conditions caused by drought.

INTRODUCTION

Broad scale amphibian declines have been recognized as a major conservation issue for several decades, the common denominator among them being threats of anthropogenic origin (Blaustein 1994; Blaustein & Wake 1990). The Edwards Plateau of central Texas is home to many endemic *Eurycea* salamanders (Chippindale 2000; Chippindale et al. 2000; Hillis et al. 2001), but is also an area that has experienced rapid urbanization around major cities such as Austin and San Antonio. These species have very restricted distributions, and the health of the ecosystems they inhabit is threatened by human activities (Chippindale & Price 2005).

Eurycea tonkawae (the Jollyville Plateau salamander) is a neotenic salamander, endemic to springs, headwater streams and caves in northwest Austin, Texas and surrounding areas (Bowles et al. 2006; Chippindale et al. 2000). Threats to *E. tonkawae*, due to the rapid urbanization of Austin, were identified even before the species was formally recognized (Chippindale et al. 2000); however there was a dearth of quantitative information on these threats and the status of the species (Cole et al. 1995). To address this knowledge gap, the City of Austin (COA) initiated a monitoring program from 1996-1998 at

nine sites to identify the physical, chemical, and biological factors that potentially affect the distribution and abundance of *E. tonkawae* (City of Austin 2001). Because its range encompasses areas with two very distinct land-uses, urban development and biological preserves (Figure 1), sites were surveyed in rural, developing, and developed spring watersheds. Sites within urbanized watersheds were found to have lower salamander densities, compared to those in rural areas (Bowles et al. 2006; City of Austin 2001). Subsequent studies have identified declining trends in counts at some urban sites between 1996 and 2006 (O'Donnell et al. 2006; O'Donnell et al. 2007b; Turner 2003). Due to low count-based estimates of population size, *E. tonkawae* populations in urbanized watersheds have high predicted probabilities of extirpation (Bendik 2008). Depressed populations are more vulnerable to extirpation from the effects of random events, such as demographic and environmental stochasticity (Bull et al. 2007; Drake & Lodge 2004; Morris & Doak 2002). The primary threat to *E. tonkawae* has been cited as degraded water quality due to pollution in urbanized watersheds (Bowles et al. 2006; Chippindale 2000; O'Donnell et al. 2007b). Degraded water quality and other threats have prompted a "warranted but precluded" ruling for protection under the Endangered Species Act by the U.S. Fish and Wildlife Service (USFWS 2007), and it currently remains a candidate species.

Here, we summarize the current status of the Jollyville Plateau salamander drawing upon data gathered from two different survey methods, count surveys and capture-mark-recapture surveys. Most of the previous research on the conservation status of *E. tonkawae* relied upon count data (Bendik 2008; Bowles et al. 2006; City of Austin 2001; O'Donnell et al. 2006; O'Donnell et al. 2007b; Turner 2003), whereby salamanders are counted as they are observed within a given area. These studies comprise the bulk of the available knowledge on the ecology of *E. tonkawae*, and form the basis of its candidate species status (USFWS 2007).

Count data have been collected since late 1996 with variable frequency and number of sites. For this reason, count data are analyzed here in several distinct groups. Most count data from 2008-2010 were collected on a regular basis, at approximately 3 month intervals. We report results from this period at 13 monitoring sites in the context of the 2008-2009 drought, and compare drought and post-drought survey results to test the hypothesis that juvenile recruitment and total counts differ between these two periods.

Data from two and three year intervals (as above) are less useful for understanding temporal trends, because natural variation in populations from one year to the next may confound any long-term signal. To estimate differences in long-term trends between urban and rural *E. tonkawae* populations, we use a Poisson regression of count data collected from eight long-term monitoring sites, from 1996 through 2009. This is a novel approach to analyzing *E. tonkawae* count data that tests the hypothesis of a significant difference between urban and rural population trends by comparing trends at sites with high and low levels of impervious cover. We use a hierarchical model that can incorporate different covariates (such as impervious cover), and demonstrate the utility of Bayesian modeling for analyzing *E. tonkawae* count data. Finally, we examine whether salamander total counts and juvenile counts are higher in spring and summer months, a pattern noted by Bowles et al. (2006). Their study only included

data for a two year period, and we extend this include all available data from 1996 through 2010 to statistically test this hypothesis.

While count data has also been commonly used to assess population trends in many other studies (e.g. Link & Sauer 1998), it has been widely recognized that potentially unrealistic assumptions are made when count data are interpreted as indices for population size (Bailey et al. 2004b; Dodd & Dorazio 2004; Hyde & Simons 2001). For example, it is assumed that detectability remains constant over time, that there is a linear relationship between counts and population size (Hyde & Simons 2001). Not accounting for detectability can lead to a compromised monitoring scheme (Bailey et al. 2004b; Pollock et al. 2002; Yoccoz et al. 2001).

Capture-mark-recapture (CMR) surveys, a recent addition to the *E. tonkawae* monitoring program (O'Donnell et al. 2007a), incorporate estimates of detectability that are missed by count surveys. An eight month CMR study was conducted in 2007 in the Bull Creek watershed in order to gather baseline data and assess the future impact of a proposed water treatment plant in upper Bull Creek on populations of *E. tonkawae* (O'Donnell et al. 2007a). The location of this plant was eventually moved, and CMR monitoring has continued on a less intensive basis through 2009. Although fewer surveys were conducted from 2008 through 2009 in comparison to the initial 2007 study due to resource limitations and drought conditions, they incorporate additional temporal variation and allow for comparisons of vital rates before and after the 2008-2009 drought.

In order to examine spatial and temporal variation in detection probabilities, and estimate vital rates, we reanalyze CMR data from the initial CMR study (O'Donnell et al. 2007a), in combination with recent results. In addition to modeled estimates of survival, temporary emigration (movement in and out of the study site between surveys), population size and detection probability (as included in O'Donnell et al. 2007), we also calculate the "effective capture probability" (Kendall 1999), an estimate of detection probability that is commonly reported in other studies of plethodontid salamanders (Bailey et al. 2004a; Smith & Petranka 2000). Effective capture probability is analogous to what might be expected as a proportion of the population observed during a count-based survey. Patterns in detection probability from the CMR study have implications for how count data are interpreted. This is critical, because count data are the predominant source of information available for *E. tonkawae*.

Finally, we compare estimates of population size pre and post-drought to determine what effect prolonged dry surface conditions had at two CMR sites. These CMR sites experienced prolonged periods without surface water, forcing salamanders to either follow the retreating groundwater as springs were drying, or face desiccation on the surface. Surveys were conducted before, during and after the drought, allowing a unique opportunity to study how a long dry spell impacts *E. tonkawae* populations.

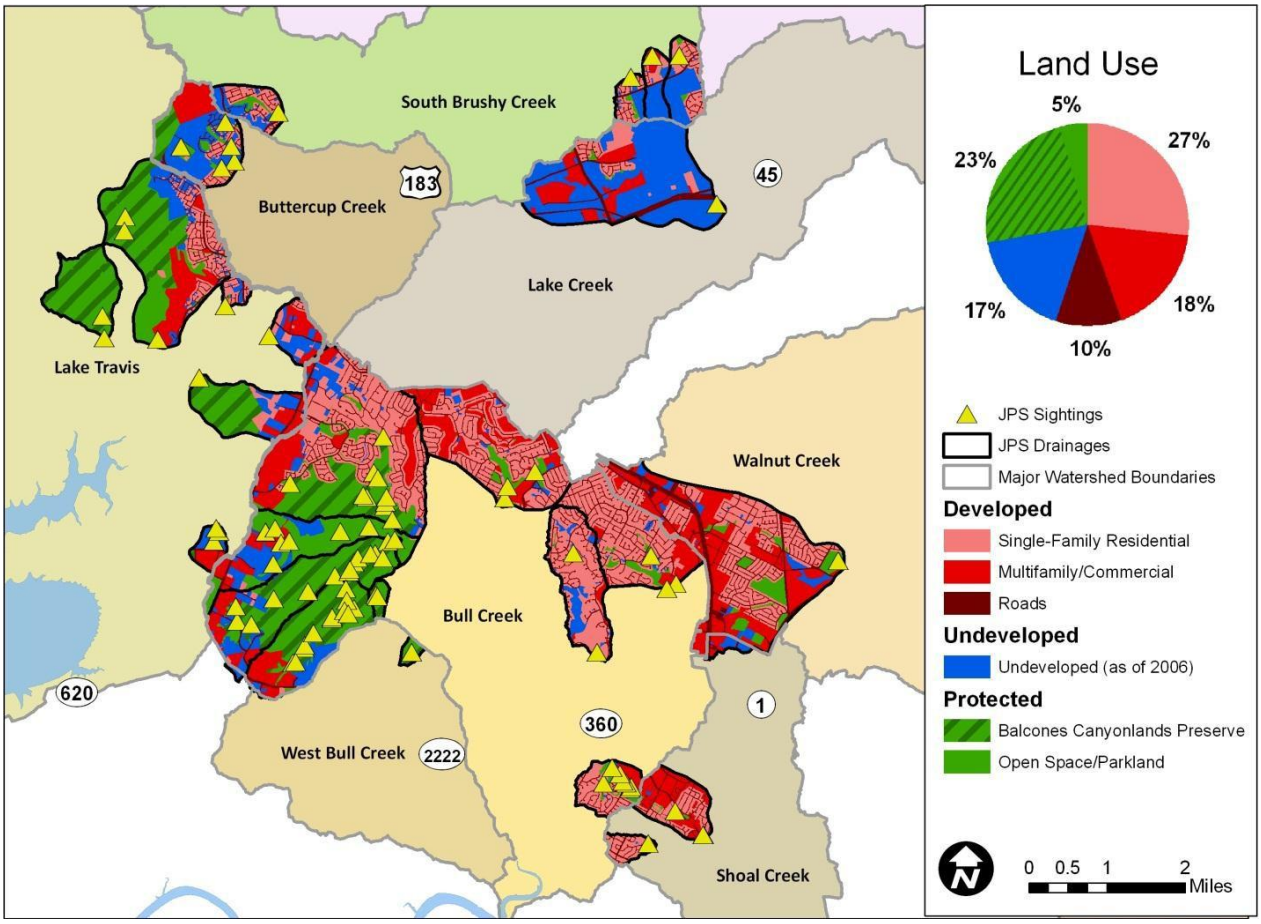


Figure 1. Land use practices within drainage basins inhabited by the Jollyville Plateau salamander (*E. tonkawae*).

STUDY AREA

Sites included in this study occur in five watersheds (Bull Creek, Walnut Creek, Brushy Creek, Shoal Creek, and Lake Travis) in the Jollyville Plateau and surrounding area of Travis County, Texas. However, the trend analysis is restricted to sites within Bull, Shoal and Lake Travis watersheds because the remaining sites do not have long enough time series of data to predict a biologically meaningful trend. The CMR study was conducted at three sites, two occurring in the Bull Creek watershed, the other within Lake Travis watershed.

Sites were classified as urban or rural based on the percentage of impervious cover within their respective drainages following designations of USFWS (2007; see METHODS). Percent of impervious cover (IC) was calculated for each site used within the trend or CMR data analysis. Table 1 shows IC based on land use data (Bendik 2008) for the corresponding drainage basin of each site (Figure 2). Of the count survey sites, only two of these can be considered rural (Franklin and Wheless, IC <5%), while for the remaining six sites, IC ranges from 18-46%, indicating high levels of urbanization (Table 1). All three mark-recapture sites are part of the Balcones Canyonland Preserve, and are considered rural (IC <1%; Figure 2, Table 1).

Table 1. Summary of sites surveyed. Impervious cover percentages are based on land use. For additional information on impervious cover calculations, see Bendik (2008). Impervious cover category was assigned following the same criteria as USFWS (2007). For the trend analysis, high and very high groups were combined. nc=not calculated; trend=Poisson regression of 1996-2009 count data; CMR=capture-mark-recapture analysis of 2007-2009 data; count=analysis of 2008-2010 count data.

Site	Site #	2006 Impervious Cover (%)	Analysis	Impervious Cover Category	Watershed
Franklin	349	1	trend	low	Bull
Trib 3	926	26	trend	high	Bull
Trib 5	1164	18	trend	high	Bull
Trib 6	151	22	trend	high	Bull
Spicewood	930	46	trend	very high	Shoal
Stillhouse	927	22	trend	high	Bull
Tanglewood	928	34	trend	high	Bull
Wheless	1045	<1	CMR/trend	low	Lake Travis
Lanier	3963	<1	CMR	low	Bull
Ribelin	4035	<1	CMR	low	Bull
Balcones DP Spr	445	nc	count	nc	Walnut
Upper Ribelin	4184	nc	count	nc	Bull
Baker Spring	3959	nc	count	nc	Lake Travis
Barrow Hollow	929	nc	count	nc	Bull
Troll Spring	4457	nc	count	nc	Bull
Avery Deer Spr	1355	nc	count	nc	Brushy

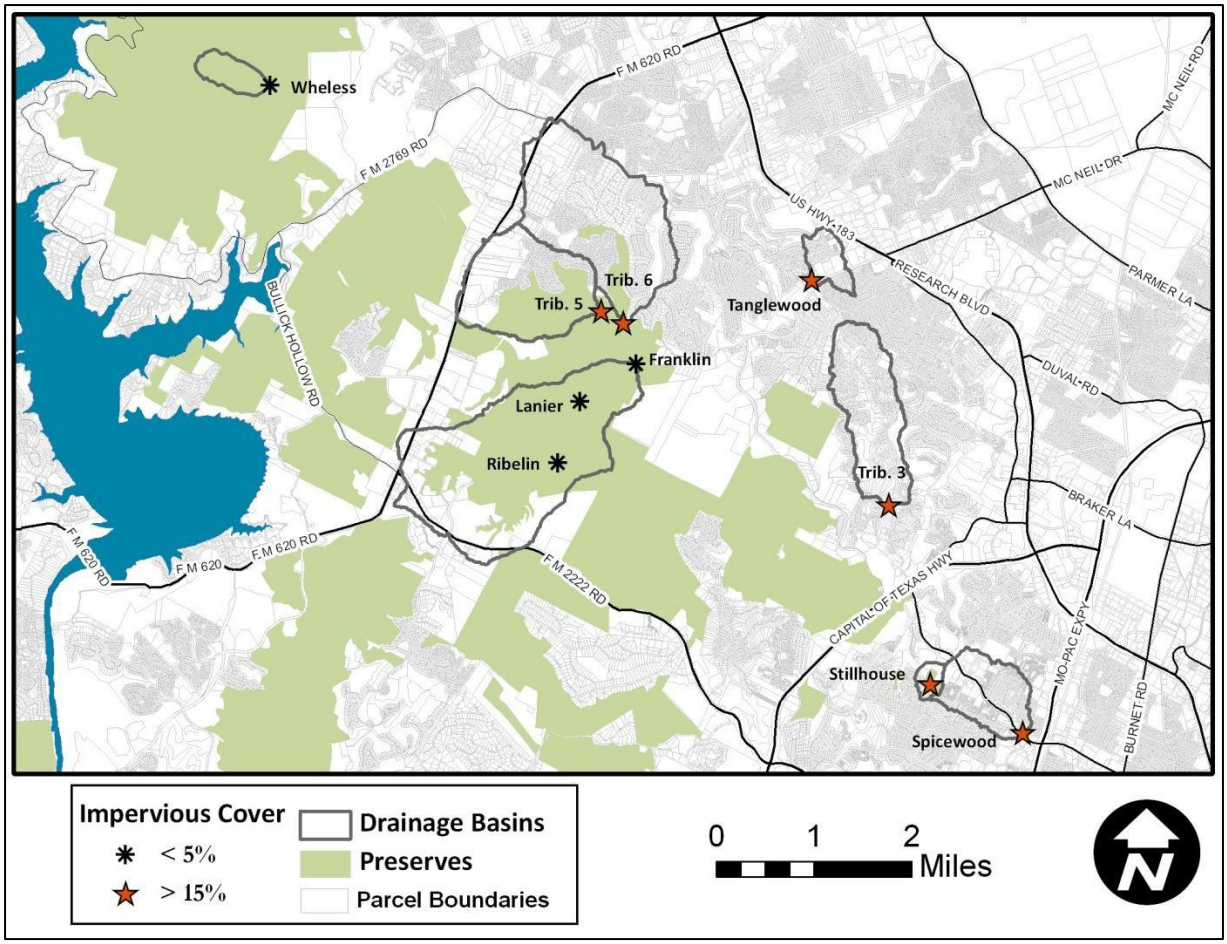


Figure 2. Site locations (star or asterisk) and their associated drainage basins (grey borders) used for calculating percent impervious cover. Shaded great areas indicate development density.

There are some differences in natural habitat which should be considered when directly comparing survey results among sites. For example, the Tanglewood site (928) is bedrock dominated, while Franklin (349) and Spicewood Spring (930) have abundant cobble and gravel substrate. Additional information on site characteristics can be found in O'Donnell et al. (2007a) and City of Austin (2001).

METHODS

SURVEYS

Count surveys have varied in frequency since monitoring of *E. tonkawae* populations began. In general, surveys were on a monthly or semi-monthly basis from late 1996 through 1998 (City of Austin 2001), and varied in survey frequency thereafter (O'Donnell et al. 2007b). From 2008 to 2009, most sites were surveyed quarterly, with the exception of Trib. 3, Avery Deer Spring, Troll Spring, which were surveyed once a year. Quarters are three month periods starting in January and denoted QI, QII, QIII, and QIV.

Most surveys were conducted during the beginning of each quarter, so that consecutive surveys at the same site would have approximately the same time interval (3 months) between them. Counts were conducted in a fixed survey area at each site by searching under all cover objects, and noting the size class of the salamander (≤1 inch, 1-2 inches, ≥ 2 inches). Double counting of individuals was minimized by using a drive survey technique, whereby all observers search together in a line, moving from downstream to upstream, flushing salamanders downstream as they are counted. During each survey, specific conductance (SpC), dissolved oxygen, pH, and temperature of the water were measured.

Capture-mark-recapture surveys were conducted monthly from March through October, 2007 at three sites: Lanier, Wheless and Ribelin. Subsequently, surveys were conducted less frequently through 2008 and 2009, at two of the three sites (Wheless and Lanier). The two surveys conducted at Wheless (Mar. 2008 and Dec. 2009) encompass a drought period, when the spring was dry for most of the time in between. Surveys were conducted at Lanier during the following months: Mar. 2008; Mar., June, and Dec. 2009. Surface conditions were generally wetter at Lanier Spring during this period than at Wheless Spring, although site conditions were dry or mostly dry for the latter half of 2008 at Lanier. CMR data were collected using Pollock's robust design (Pollock 1982), whereby salamanders were captured and marked (or identified) for several consecutive "secondary sessions," (= three days in this study) during which the survey area is presumed to be closed to migration, births and deaths. Within this group of surveys, population size and detection probability are estimated. Each group of secondary sessions is referred to as a "primary period," between which populations are treated as open, and estimates of survival and temporary emigration can be obtained. Additional details on the survey method and study design can be found in O'Donnell et al. (2007a).

Table 2. Primary periods used in CMR analyses. *March 2007 was dropped from Wheless analysis; see Results. Ribelin was not sampled after 2007 due to resource limitations. Although quarterly surveys were planned, sampling was sparse for 2008 and 2009 due to dry site conditions.

	Sample Periods			
Site	**2007**	**2008**	**2009**	**total**
Lanier	March-October (monthly)	March	March, June, December	12
Wheless*	April-October (monthly)	March	December	9
Ribelin	May-October (monthly)	none	none	6

DATA ANALYSIS

COUNT DATA

Juvenile recruitment (i.e. counts) and total counts were compared between two seasons, spring/summer and fall/winter. We refer to juvenile recruitment simply as any juvenile (<1") being in a free-living state (i.e. has hatched). Counts from all available data (1996-2010) were summed by site, date and size class. An average was taken for two groups among all Winter/fall (Oct. through Mar.) and spring/summer (Apr. through Sept.) months to generate a balanced dataset. Those with fewer than 10 records per site/season combination were removed from the analysis. This resulted in datasets for total counts and juveniles containing the following sites: 151, 349, 445, 926, 927, 928, 929, 930, and 1164. Differences in average count by site/season were tested for significance using a non-parametric Wilcoxon signed rank test in SAS 9.1 (SAS Institute, Inc.)

To compare juvenile recruitment rate and total salamander count during and after the drought, results from quarterly monitoring (sites 151, 349, 445, 926, 927, 928, 929, 930, 1164, 4184), and yearly monitoring (sites 1355 and 4457) were summed across 5 survey-quarters each of drought (QIII 2008- QIII 2009) and post-drought (QIV 2009- QIV 2010) conditions. Drought and post-drought counts were also tested for a significant difference using a non-parametric Wilcoxon signed rank test in SAS 9.1 (SAS Institute, Inc.) because differences were not normally distributed (`univariate` procedure; Shapiro-Wilk, $P<0.001$).

Trend analyses (described below) were used to evaluate the status of eight *E. tonkawae* populations using results from direct count surveys conducted periodically from 1996-2009 (other summaries are available in: Bendik 2008; City of Austin 2001; O'Donnell et al. 2006; O'Donnell et al. 2007b; Turner 2003). These count data pose challenging problems for statistical analysis. Counts are highly erratic and time series for most long term monitoring sites have missing data, some as high as 4 years between visits. Perhaps most challenging is that the time series lengths are fairly short, whereas longer time series are generally preferable (Hovestadt & Nowicki 2008). These problems have resulted in very wide confidence intervals for estimates of population growth rate in previous analyses of *E. tonkawae* count data that have made accurate assessments of population status and viability difficult (Bendik 2008).

Although count surveys have been conducted at several different study sites to assess the status of Jollyville Plateau salamanders since 1996, most previous analyses of these data relied on simple linear regression analysis of the raw data to predict trends. However, a simple linear regression using raw data requires some assumptions that may not be supported (e.g., homoscedasticity), particularly when dealing with count data. Several alternative methods to estimate population size trends are used here in an effort to provide an overall status assessment for *E. tonkawae*.

First, count data were summarized in program R v 2.11.0 (R Core Development Team 2010) using a general additive model (GAM) smoothing method to present a trend (package mgcv 1.6-2) of counts,

including all size classes, summed by site and survey (all code is provided in Appendix A). The GAM models provide a summary of the raw counts at each site, but are not as useful for hypothesis testing.

These data were also analyzed using loglinear Poisson regression, accounting for overdispersion of the Poisson distributed log-counts, to test the hypothesis of a difference in trend between sites with low and high impervious cover:

$$\log(\lambda_t) = \alpha_j + \beta_c (t - t^*) + \varepsilon_{jt}$$

Here, λ_t is the expected count at time *t* (in months since beginning of study), α_j is a constant intercept of site *j*, β_c is the slope of impervious cover group *c*, and ε is the overdispersion effect for site *j* at time *t*. Change is indexed relative to base month *t**. This model incorporates a different intercept as a random effect for each site and fits a common slope among sites within the same impervious cover category. Using a common slope for sites from the same group is a way of summarizing the overall population trend for a given group. The random site-effects parameterization of the model (i.e. site-specific α levels) accounts for inherent differences in the baseline population size due to differences (natural and by study design) between sites (e.g. see STUDY AREA).

The Poisson model was fit to data from each site using a Bayesian analysis implemented in the program OpenBUGS (Thomas et al. 2006). All models implemented in OpenBUGS were adapted from Sauer et al. (2010). In a Bayesian analysis, all model parameters are treated as random variables. Poisson models are useful for modeling count data because counts are ‘‘discrete, positive valued, and typically exhibit strong mean-variance relationships’’ (Royle et al. 2002 as cited in Thogmartin et al. 2004). Poisson regressions have been used in numerous studies of count-based population data (e.g. Link et al. 2006; Royle & Nichols 2003; Sauer & Link 2002; Thogmartin et al. 2004, 2007).

The overall trend, i.e., the geometric rate of change in counts since the inception of this study, was calculated as

$$B = \left(f[1] / f[\mathrm{t}] \right)^{(t-1)} ,$$

where *f* is the expected average count at the initial and final time *t*. The derived parameter *B* provides a single summary estimate of the average rate of change for all monitored populations combined between 1997 and 2009. We grouped sites by impervious cover (IC) category (low, moderate, high, very high), as defined in USFWS (2007) from 2006 estimates of IC (Table 1) based on land use data. However, there were no sites in the moderate level IC, and only a single very high site, so sites were categorized as either low (rural) or high to very high (urban), to compare estimates of *B* (Table 1).

Water quality degradation, which is linked to impervious cover, has been cited as a potential cause of decline in Jollyville Plateau salamander populations (USFWS 2007). To represent overall water

chemistry differences between sites that may be associated with urbanization, the average specific conductance (SpC) for each site was incorporated as a covariate. Additionally, average percent IC across all site-years during the study was calculated using combinations of IC estimates by land use type and Travis County Appraisal District records (Herrington 2008). Average IC and SpC (Table 3) were imposed as covariates on the intercept α, as

$$\mu(\alpha_j) = \mu_\alpha + \beta^i(i_j - i^*) + \beta^s(s_j - s^*)$$

where μ_α is a site specific intercept, and β^i and β^s are slopes for IC and SpC, respectively. Parameters *i* and *s* are the average IC and SpC respectively, at site *j*, and *i** and *s** represent the averages across all sites. These parameters were scaled to facilitate computation by subtracting the mean from each original value. Although averaging these covariates is an over simplification (because IC and SpC have increased over time in some watersheds), it nevertheless allows us to determine whether these are important covariates in predicting the base population level, independent of the population trend. This covariate model was analyzed separately from the preceding model, although the overall model structure was similar (Appendix A).

Standard, non-informative priors (Gilks et al. 1996) were used for the Bayesian analyses in OpenBUGS. The inverse variances were assigned gamma distributions with a mean =1 and variance = 1000. Parameters α, β, β^i, β^s, and μ_α were assigned normal distributions with mean = 0 and variance = 1000^2. The overdispersion parameter was assigned a normal distribution with mean =0 and variance = σ^2. Burn-in (number of iterations that are thrown out) was set at 50000 Markov chain Monte Carlo generations, and four chains were run for an additional 200,000 iterations. Convergence of parameter estimates was evaluated by the BGR (Brooks-Gelman-Rubin) statistic implemented in OpenBUGS. Full descriptions of both Bayesian models and corresponding OpenBUGS code are provided in Appendix A.

Table 3. Average impervious cover (% of land within drainage) and average specific conductance (µS/cm) estimates used in covariate model. Site ID refers to the dummy variable assigned to each site in the analysis (see Appendix A).

Site	Site #	Site ID	1996-2009 Average IC	1996-2009 Average SpC (µS/cm)	Category
Franklin	349	7	0.04	550	Rural
Trib 3	926	3	0.13	795	Urban
Trib 5	1164	6	0.11	631	Urban
Trib 6	151	1	0.13	941	Urban
Spicewood	930	2	0.30	862	Urban
Stillhouse	927	4	0.15	929	Urban
Tanglewood	928	5	0.18	841	Urban
Wheless	1045	8	0	625	Rural

CAPTURE-MARK-RECAPTURE DATA

CMR data were analyzed with the program MARK version 6.0 (White & Burnham 1999). Although estimates of detection probability can be obtained with closed population models, it is confounded by temporary emigration and can bias estimates of population size (Kendall et al. 1997). Pollock's robust design allows for accounting of temporary emigration parameters, and is used to examine a suite of models in order to test hypotheses about variation in detection probability and the movement of salamanders in and out of the study area. All analyses were conducted using the "Robust design with closed captures" option in MARK. A single dataset was also fit using the Huggins method (Huggins 1989), which conditions out estimates of *N* (population size), and calculates *N* as a derived parameter. However there were no major differences between the two methods, and so the results reported here are from the "standard" closed population estimation method as implemented in MARK.

Median $\hat{c}$ was estimated in MARK for each model to assess goodness-of-fit (GOF) for a general full time varying Cormack-Jolly-Seber model (CJS; Pollock et al. 1990; Lebreton et al. 1992). Since there is no current way to test GOF for a robust design, the data were reduced to an open design CJS model, where all secondary periods were collapsed for each primary period into a single event. This is analogous to how the robust design handles survival and temporary emigration estimation. Akaike's Information Criterion corrected for small samples and overdispersion (QAICc) was used to select for the best model. Occasionally, MARK was unable to fit parameters reliably, so parameter estimates were only included if the estimate was greater than its standard error.

A variety of models were fit to the data that incorporated time-variability or constant parameterizations of φ (survival), γ' (probability being off the study area given it *was not* present during prior trapping session), γ'' (probability being off the study area given that it *was* present during prior trapping session), *p* (conditional capture probability), and *c* (conditional recapture probability) for Lanier, Ribelin and Wheless separately. Population size (*N*) was estimated for each primary period in all models. Additionally, models with no temporary emigration (γ=0), random temporary emigration[1] ($\gamma' = \gamma''$), Markovian temporary emigration ($\gamma' \neq \gamma''$), and with *p*=*c* (recapture rate is equivalent to capture rate) were also evaluated. Both *p* and *c* were allowed to vary within periods or set constant within periods. Models with full time varying detection [i.e. $p(t,t)\ c(t,t)$] were constrained on the last *p* for each session as *p*=*c* to enable identifiability of all parameters. Similarly, fully time varying survival and temporary emigration models were constrained on the last γ, such that $\gamma_t = \gamma_{t-1}$ to allow identifiability of all survival parameters. Table 4 contains an explanation of notation and the possible combination of parameters. This method resulted in a total of 60 possible models tested for each dataset. Parameter estimates
were obtained from model weighted averaging using QAICc weights (unless otherwise specified) in order to account for uncertainty in the model selection process.

[1] Random temporary emigration means that the location of an individual during the previous primary period has no bearing on its location during the current period. Markovian emigration is when the current location of the animal depends on the last location.

Table 4. Model notations used. A total of 60 models were tested using two possible parameterizations for survival, six for conditional capture and recapture probability, and five for temporary emigration.

Parameters	Type of Time Variation		
	Time invariant	**Between Periods**	**Within and Between Periods**
Monthly Survival	φ (.)	φ (*t*)	NA*
Conditional Capture (*p*) and Conditional Recapture (*c*) Pr			
Capture Pr = Recapture Pr	*p*(.)=*c*(.)	*p*(*t*)=*c*(*t*)	*p(t,t)=c(t,t)*
Capture Pr ≠ Recapture Pr	*p*(.) *c*(.)	*p*(*t*) *c*(*t*)	*p*(*t*,*t*) *c*(*t*,*t*)
Temporary Emigration			
Random Temporary Emigration ($\gamma' = \gamma''$)	random (.)	random (*t*)	NA
Markovian Temporary Emigration ($\gamma' \neq \gamma''$)	Markov (.)	Markov (*t*)	NA
No Temporary Emigration ($\gamma' = \gamma'' = 0$)	no mov	NA	NA

Parameter estimates generated by the best random temporary emigration models for each site, according to the lowest QAICc score, were used to calculate effective capture probabilities. Effective capture probability (p^{js}) differs from the conditional capture probability (p^*). Conditional capture probability represents the probability of capture, given an individual is present in the sampled area. Effective capture probability is the probability of capture given an individual is present in the superpopulation (the population including both observable and unobservable individuals, i.e. those that have temporarily emigrated), regardless of its presence in the sampled area (Kendall et al. 1997). Under the completely random emigration model, effective capture probability was calculated as $p^{js}\ t = 1-\gamma\ t \quad p^*(t)$, (Kendall et al. 1997; Bailey et al. 2004a), where $p^*(t)$ is the composite of conditional capture probabilities during primary period *t,* or the average conditional capture probability among secondary samples. Estimates of effective capture probabilities were calculated using a composite $p^*(t)$ to examine temporal trends in detection probability and compare site averages. We also calculated effective capture probabilities on a per-sample basis, so that estimates would be analogous a single-count survey and other estimates of detection probability in salamanders.

RESULTS

COUNT SURVEYS

We confirmed previous observations (Bowles et al. 2006) of higher counts during the spring and summer months using a larger, 13-year dataset. Both total (signed rank W=21.5, P=0.008) and juvenile (W=22.5, P=0.004) counts were significantly higher by site, on average, during the spring/summer than the winter/fall season. Looking at a subset of this data (from 1997-2000), where surveys were conducted on a monthly or bi-monthly basis, average total counts and juvenile counts (≤1") were highest during the month of April overall (Figure 3). In contrast, the month of December had the lowest mean total and mean juvenile counts (Figure 3).

The 2008-2010 count data also show pronounced effects of the 2008-2009 drought on salamander counts. Total counts for the 5-quarter period during the drought were significantly lower than total counts in the following 5-quarter period, when site was accounted for (W=33.5, P=0.005). Recruitment was also significantly greater during post-drought conditions (W=31.5, P=0.003). Although counts were higher on average for 2010 (post-drought), zero salamanders were observed on at least one occasion at two sites (Trib. 5 and Tanglewood; Figure 4). These results are consistent with a pattern of very low salamander density at these sites (Figure 4g and 5h; O'Donnell et al. 2007b). In contrast, salamanders were observed at Balcones District Park Spring for the first time since 2005 (Figure 4a). Although there was only a total of six salamanders observed from three surveys conducted in 2010, this site has a very small amount of surface habitat (<9 sq. m). In comparison, counts continue to be high at Franklin and Upper Ribelin (Figures 4c and 4d), which are both low IC "rural" sites (Table 1).

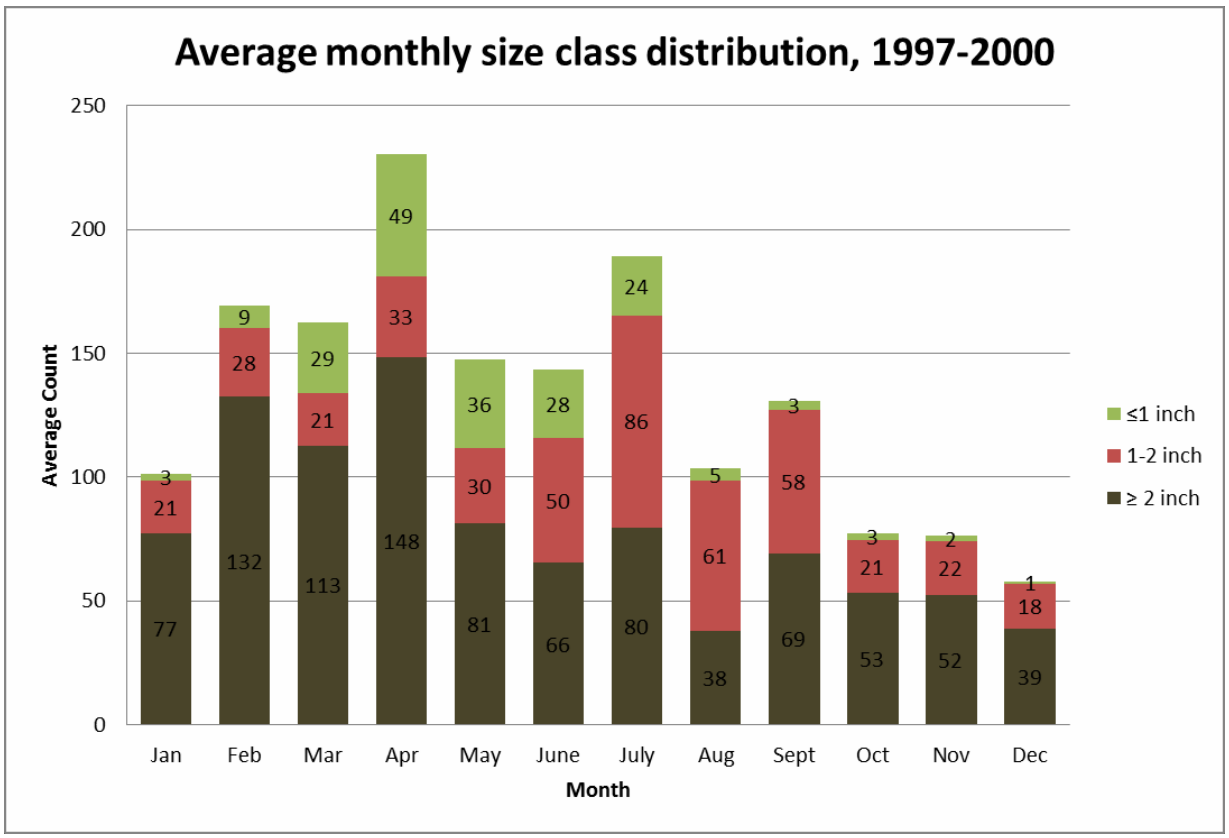
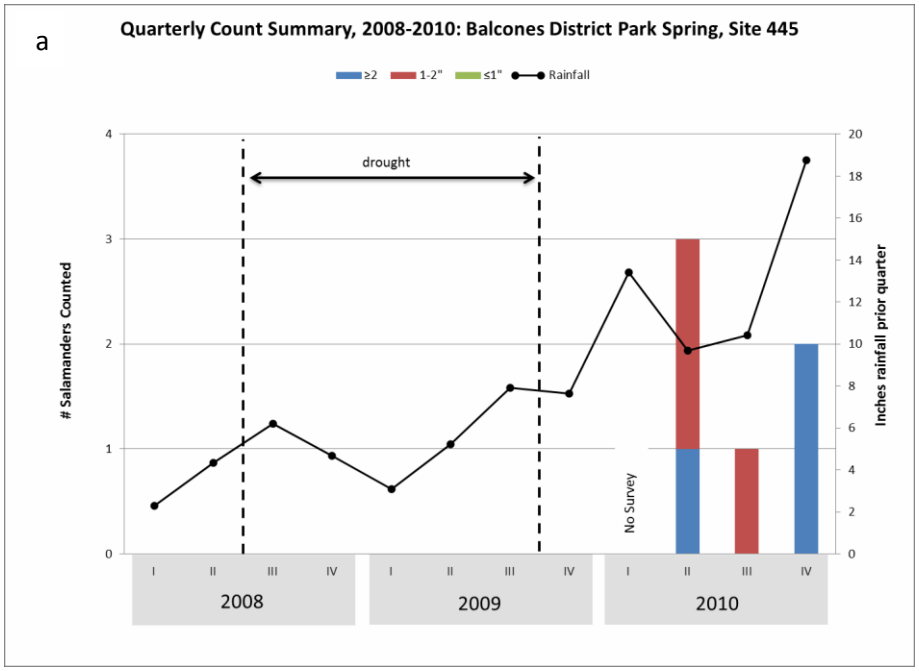
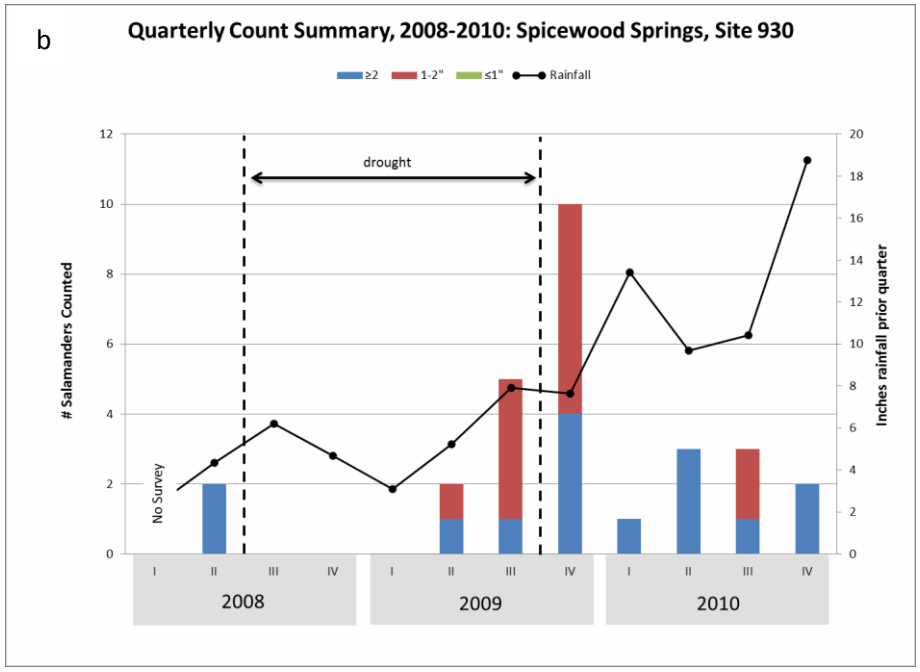


Figure 3. The average monthly size class distribution of *E. tonkawae* observed during count surveys for seven sites between 1997 and 2000.

Figure 4. **Quarterly Count Summary.** Below are the quarterly results of count surveys conducted at ten sites between 2008 and 2010. Total salamander counts are partitioned by size class: ≤1 inch, 1-2 inches, and ≥2 inches. Each graph has the same x-axis and secondary y-axis, but different primary y-axes (left side) are scaled by salamander count. Missing data are noted on each graph, and it is noted when surveys were skipped due to an absence of flowing water. Otherwise, blanks on the chart represent survey totals of zero salamanders. The drought of 2008-2009 is also indicated in each graph. The time period for the drought was based on discharge levels at Barton Springs (Barton Springs/Edwards Aquifer Conservation District). Rainfall is shown as lagging 3 months prior to the first day of each quarter (secondary y-axis).





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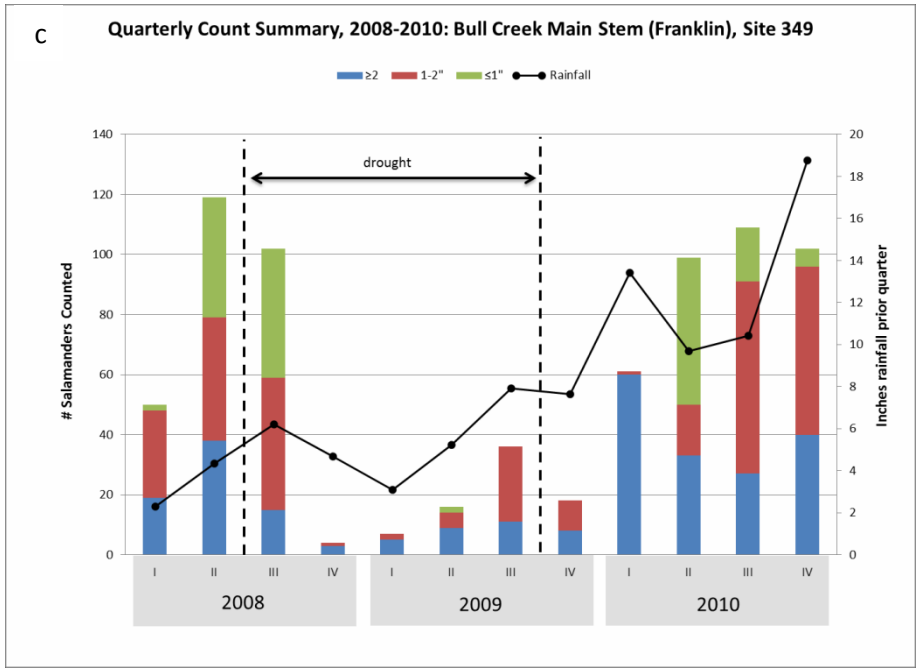

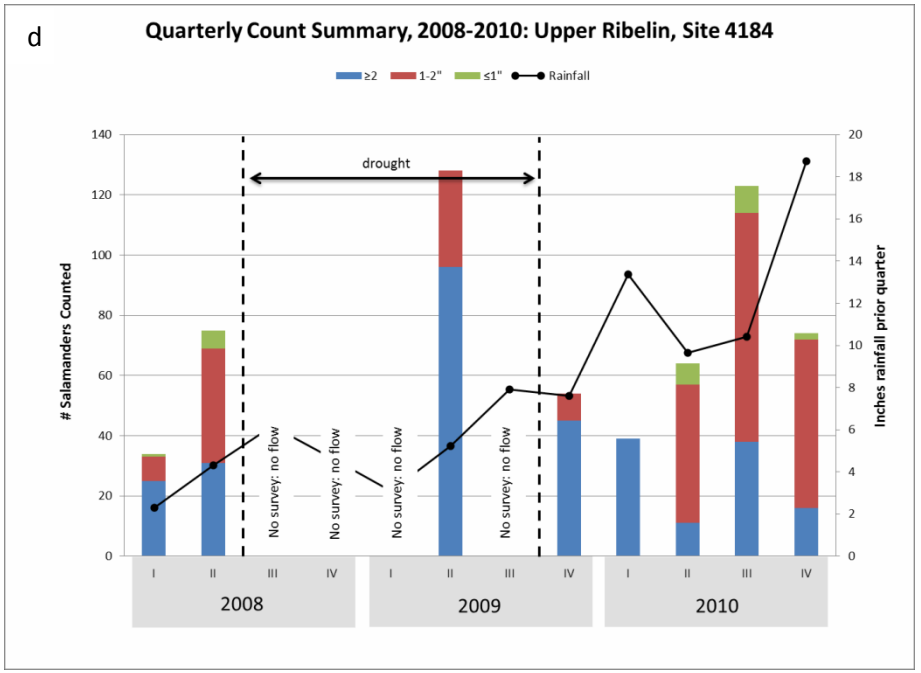

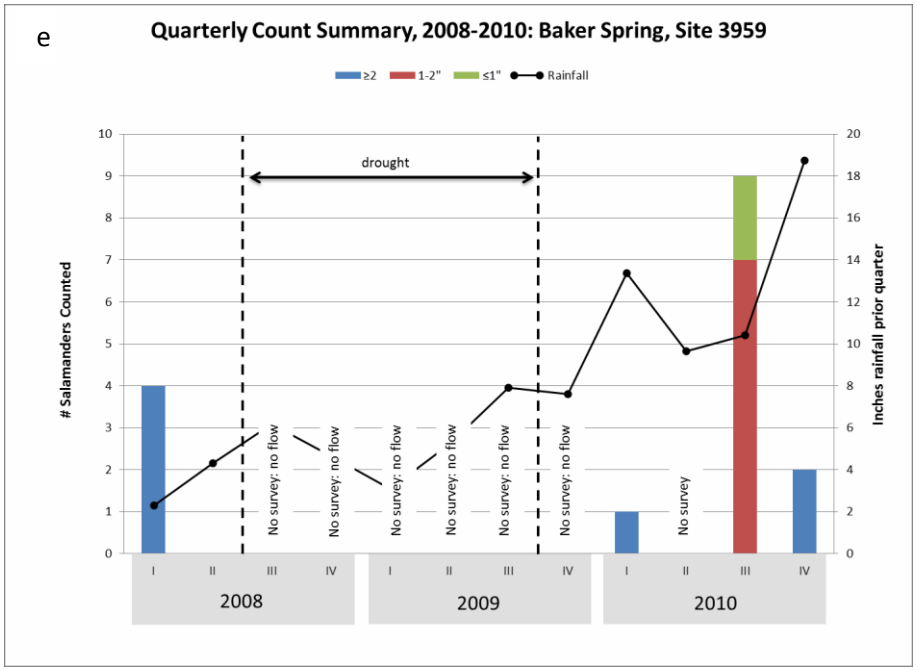

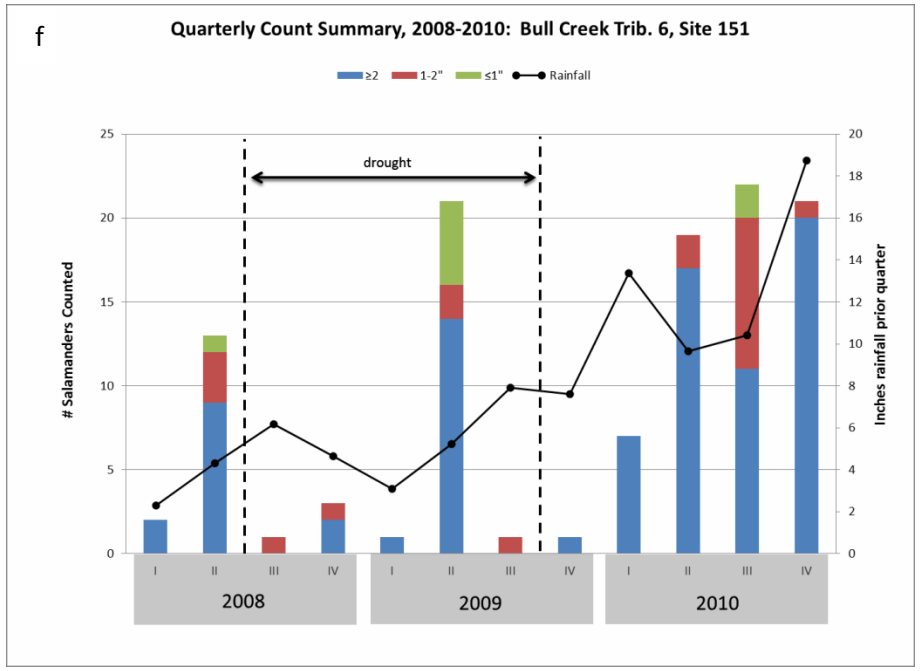

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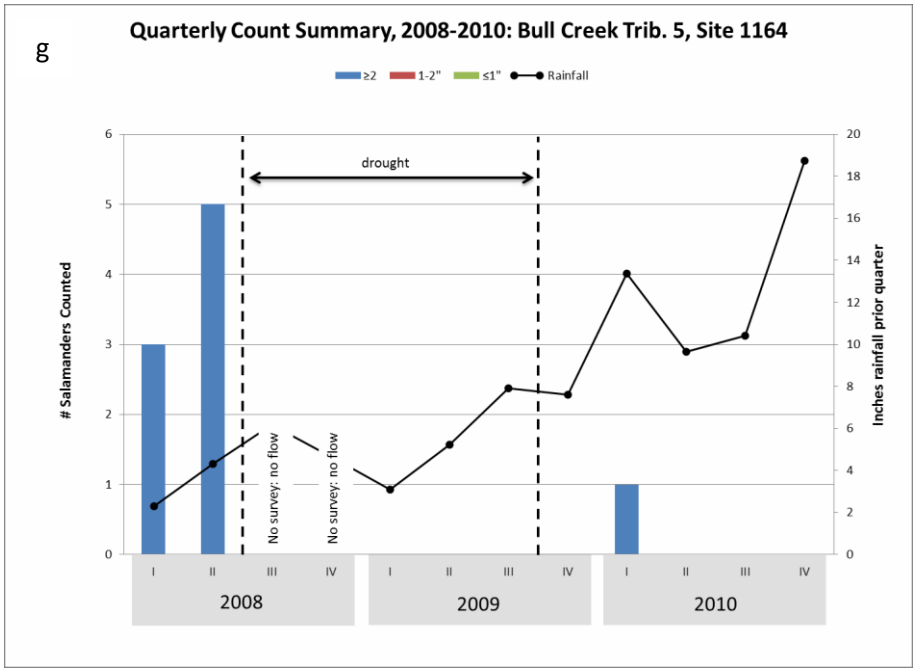
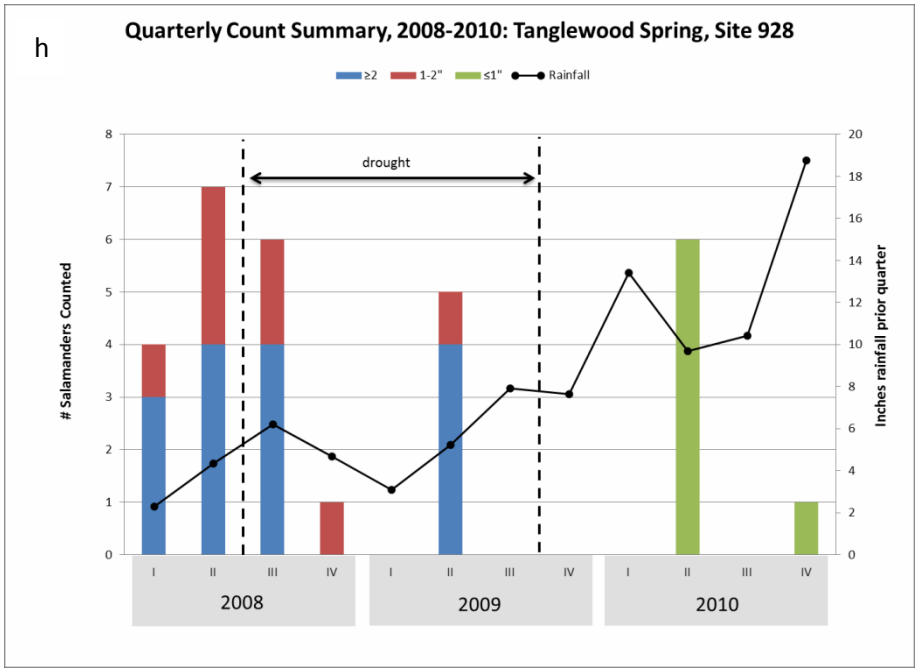
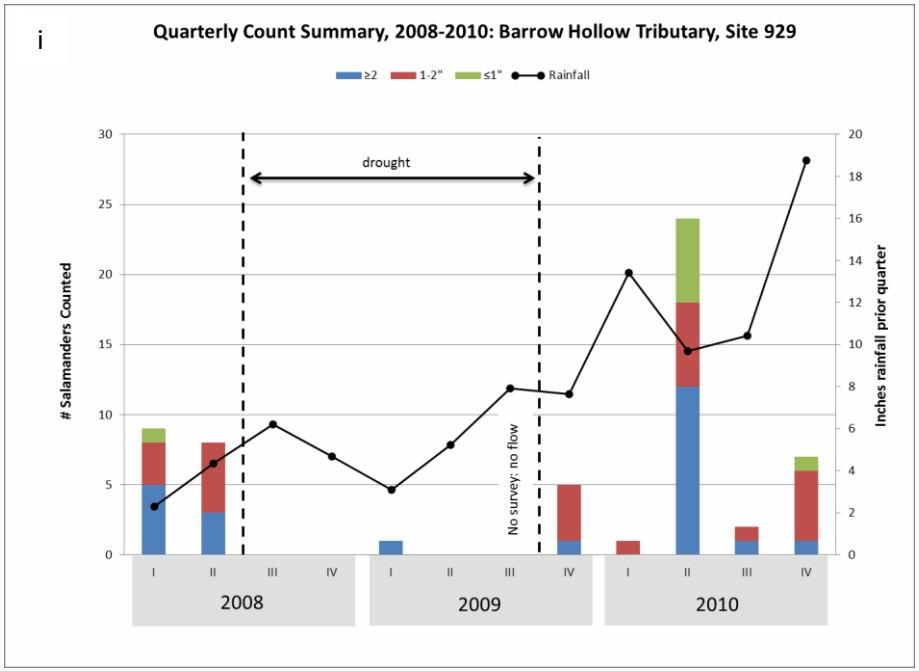






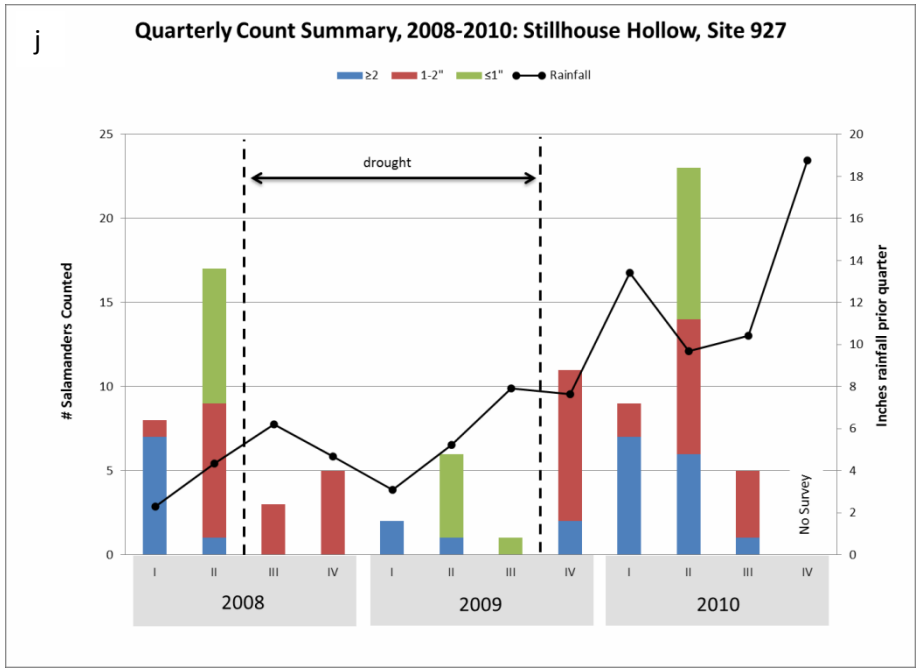
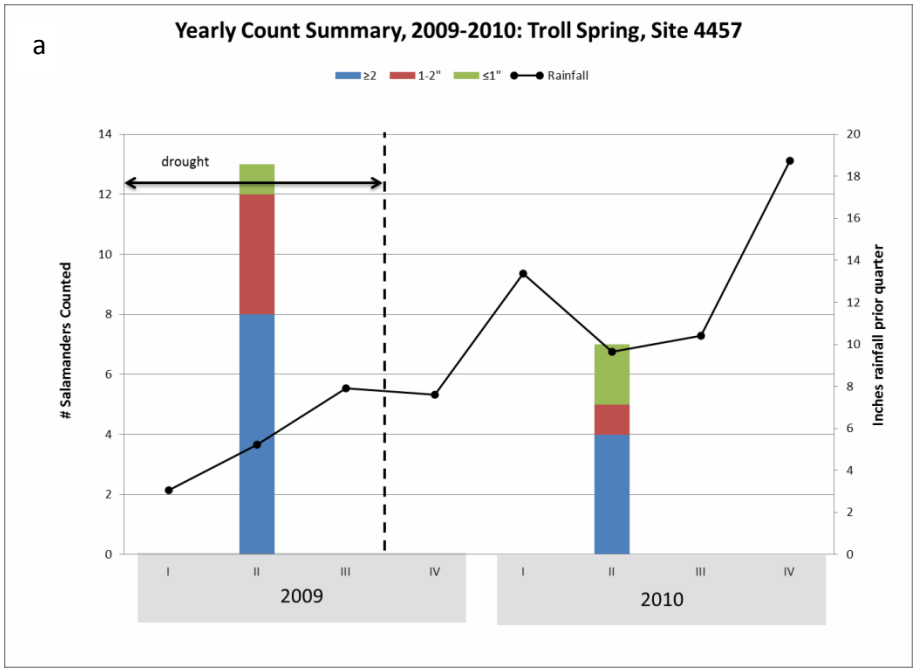


Figure 5. **Yearly Count Summary**. Below are the yearly results of count surveys conducted at three sites between 2008 and 2010. These sites are surveyed only once per year, during quarter II. Surveys were initiated for sites 4457 and 1355 in 2009. Graph notation is the same as Figure 4.

a



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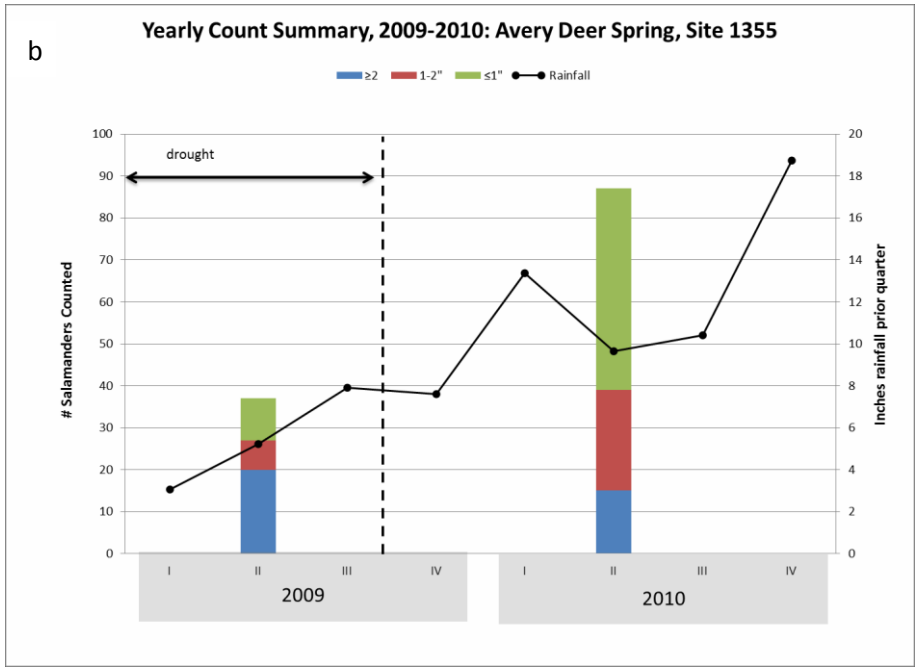

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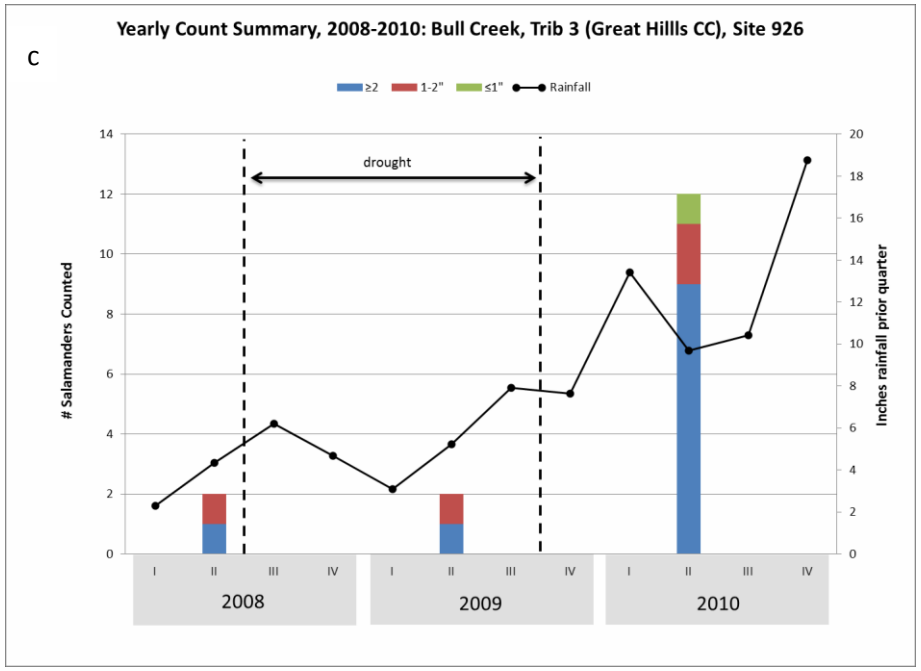


Figure 6. Smooth trend lines using a general additive model (GAM) through count data from surveys conducted at eight sites since 1996. Six of the eight sites occur in drainage basins with higher than 15% impervious cover, the other two having less than 5% of impervious cover, as measured from land use data in 2006. Trends are mostly negative for the 15% impervious cover sites, although counts for all sites are highly variable. Data are sparse for several sites (928, 926, 1045), especially between the years 2000 and 2004.

Rural Sites

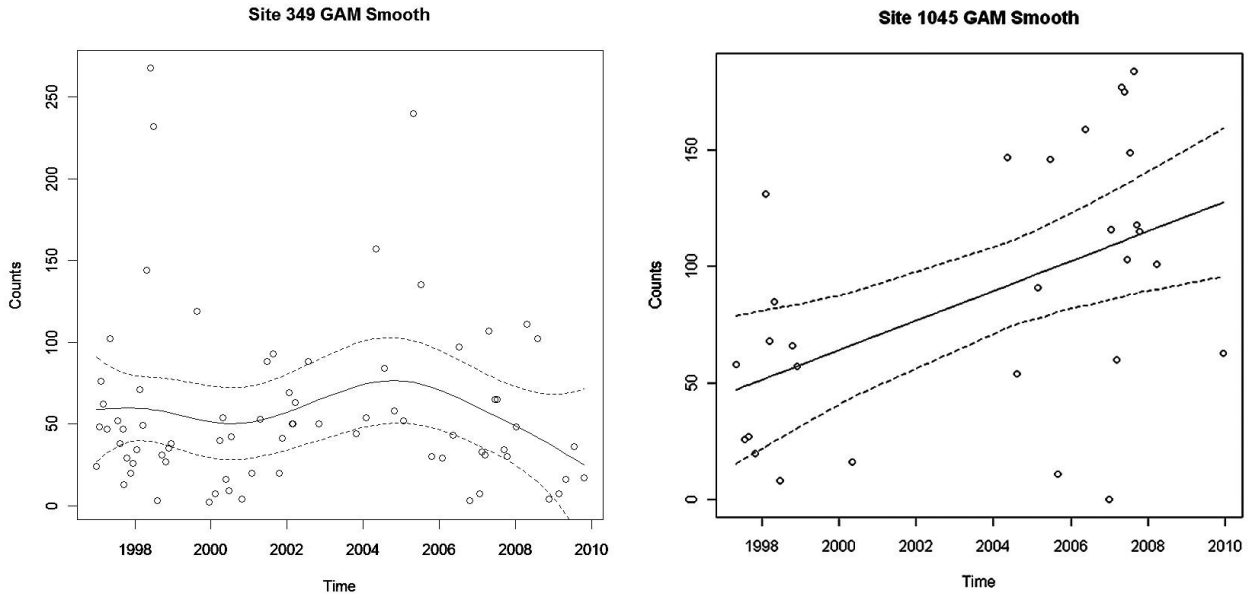
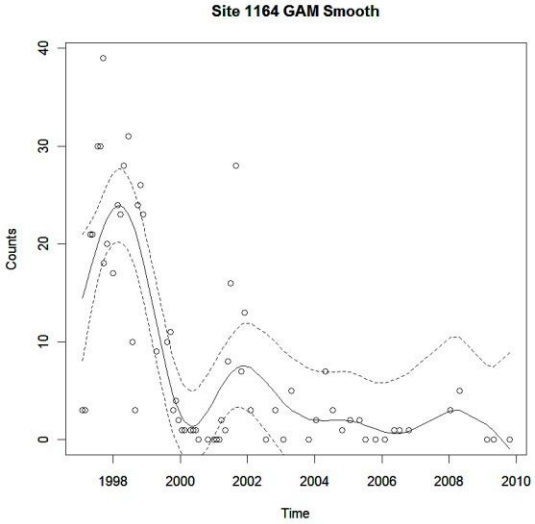
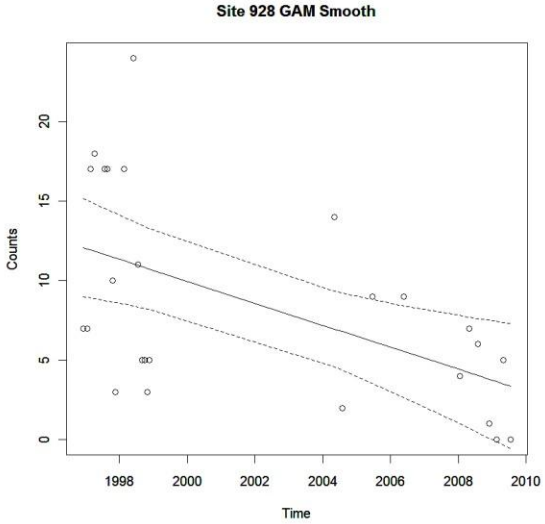
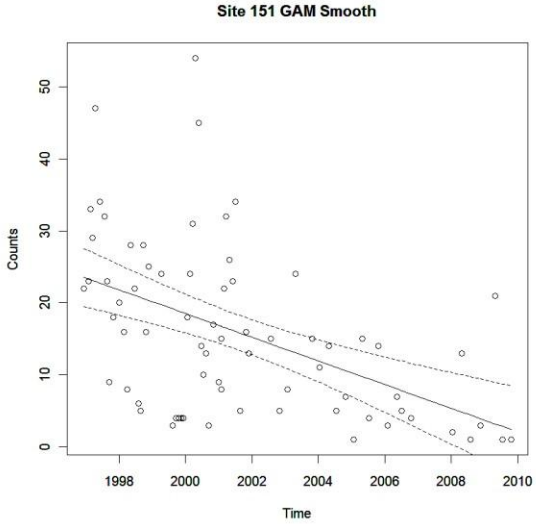


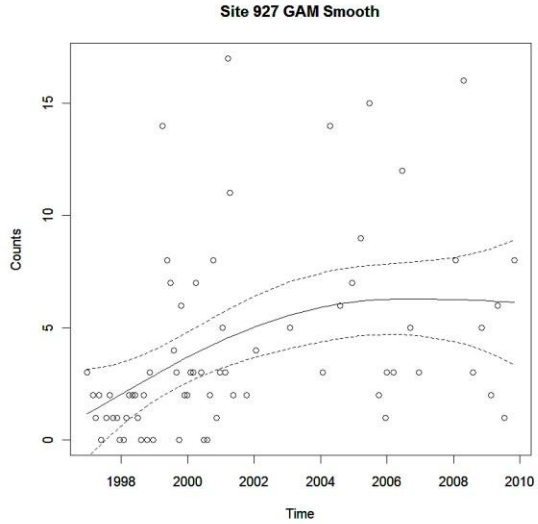
Figure 6 continued

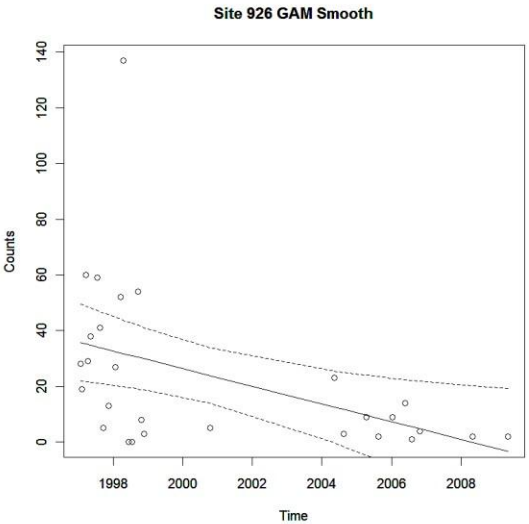
Urban Sites

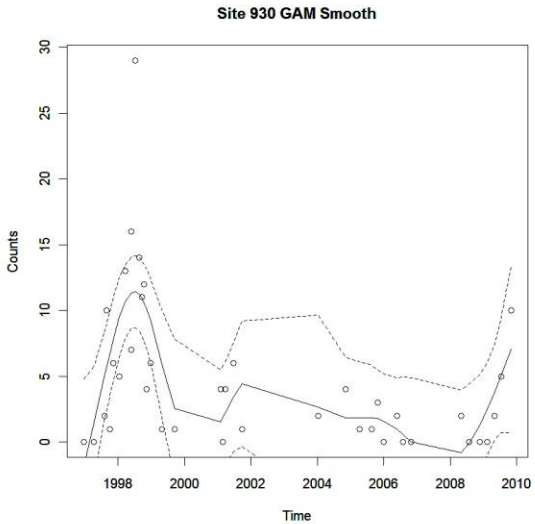












GAM TRENDS

General additive model (GAM) smooth trends provide a summary of the general population trend at each site (Figure 6). Plots indicate general decreasing pattern in the high impervious cover category, with the exception of site 927 (Stillhouse Hollow) and site 930 (Spicewood Spring), which shows an increase in counts since the 2008-2009 drought, but not as high as previous levels. Site 151 (Trib 5) shows a very stark decline in salamander counts and is the largest dataset of the high IC category sites. Only two time series were considered in the low impervious cover category. Site 349 (Franklin), reveals high variation counts and an overall variable trend that is decreasing in the near term likely due to drought conditions during that period. Site 1045 (Wheless) shows a strong upward trend, however this may be partly biased by the change in collection method used at this site post 2006. Initial captures from CMR were used as a surrogate for direct counts and may be positively biased because salamanders were captured using nets and a slightly more intensive search method.

POISSON REGRESSION MODELS

The results of the Poisson regression model indicate a declining trend overall for sites in the high impervious cover category. The estimate of *B* (the geometric rate of change) is -0.87%, and the associated 95% credible interval (Bayesian correlate to confidence interval) does not include zero (Table 5). In contrast, the low IC group (including site 349 and 1045), indicate a positive trend, with *B* estimated at 0.54% per year (credible interval above zero). Because site 1045 may be heavily influencing the positive trend due to a positive bias in counts (see above), we conducted an analysis on site 349 alone. This resulted in estimates of *B* with a 95% credible interval that includes zero, indicating a population trend that is neither increasing nor decreasing.

As an alternative method to examine the effects of impervious cover, average impervious cover estimates were imposed as a covariate on the model intercept. Additionally, to represent one potential chemical effect of urban watersheds, specific conductance (SpC) was also included as a covariate. Adding covariates to just the intercept, as opposed to the entire model, allows us to examine site-specific effects of the covariates. Given the results of the trend analysis above, impervious cover was expected to be an important covariate. Additionally, since sites in highly urbanized watersheds tend to have high SpC on average (Bendik 2008), SpC was expected to also have a similar effect on the model as IC. This did not turn out to be the case. The estimate of β^s (slope of SpC on the site specific intercept, μ_α) was close to zero (Table 6). Impervious cover, on the other hand, shows a large effect on the intercept (Table 6), although the 95% credible interval just barely includes zero.

Table 5. Results of Poisson regression for estimates of B, the geometric rate of change per month by sites grouped by low (<5%) and high (>15%) impervious cover.

IC group	Mean *B*	Lower CI	Upper CI
< 5%	0.54%	0.09	0.99
> 15%	-0.87%	-1.18	-0.55

Table 6. Poisson regression with impervious cover and specific conductivity as covariates on the model intercept, as β^i and β^s, respectively.

Parameter	Mean	Lower CI	Upper CI
β^i	-11.37	-22.81	0.1026
β^s	-0.0007	-0.0076	0.0061

MARK-RECAPTURE

Goodness-of-fit estimates for median c were fairly close to 1 for both Ribelin (1.04) and Lanier (1.19) datasets, indicating acceptable model fit. Wheless had a median c of 2.72, which was considered to have a potentially poor fit (with values of $c > 3$ considered unacceptable). However, the correction for overdispersion with c (QAICc) did not alter the order of the best models in any of the analyses.
The best models from the selection process are listed in Table . Appendix B contains a list of all CMR models analyzed in MARK.

Table 7. The best models chosen for each dataset and their corresponding QAICc values and weights. The top three models are listed Ribelin, while a single best model was chosen for the Wheless and Lanier dataset.

Dataset	Model	QAICc	QAICc Weight	No. Par.
Lanier	$\varphi(.)\ p(t,t) = c(t,t)$ Markov(t)	-2938.0	0.99	70
Wheless	$\varphi(.)\ p(t,t) = c(t,t)$ Markov(t)	-3763.3	1.00	52
Ribelin	$\varphi(.)\ p(t,t) = c(t,t)$ no mov	-729.9	0.34	25
Ribelin	$\varphi(.)\ p(t,t) = c(t,t)$ random(.)	-728.2	0.15	26
Ribelin	$\varphi(.)\ p(t)\ \ c(t)$ random(.)	-272.1	0.08	20

There are several differences, aside from the addition of new data, between this analysis and the previous one (O'Donnell et al. 2007a). First, additional QA/QC has been conducted on the 2007 dataset, such as corrections of misidentified individuals or data entry errors. Second, for the Wheless dataset, the first primary period of March 2007 was removed because of a violation of closure due to increased rainfall and migrants entering the survey area. Third, the model selection process was different. The previous study, for example, did not include any within primary period time variation of p or c; these were the best models selected in the current analysis for all three sites (i.e. models of $p(t,t)\ c(t,t)$. The current approach was an "all combinations" model selection procedure drawing from a large number (60) of candidate models, which did not arbitrarily excluded time-variance of parameters. The previous approach used an ad-hoc model selection procedure, which does not perform as well as an "all combinations" approach (Doherty et al. 2010). Lastly, the standard estimation procedure was used rather than the Huggins formulation, as was used in O'Donnell et al. (2007a). We did not find any difference from the Huggins results for one selected dataset (Wheless) in numerical convergence or model selection.

Among all three sets of analyses, models with *p(t,t)=c(t,t)* (equal capture and recapture rates with full time variation) and constant survival [φ(.)] were the best (Table 7). Model averaged conditional capture probabilities [*p*(*t,t*)] from each dataset ranged from 10-50% among sites and secondary sessions (Table 8). Average effective capture probabilities, estimated using parameters from the best random temporary emigration models, ranged from 0.03 to 0.63. Effective capture probability varied temporally (Figure 7), but mean estimates were fairly similar at Wheless (0.21) and Lanier (0.18), and much higher at Ribelin (0.47).

Average monthly survival estimates were 0.97, 1.00, and 0.73 for Lanier, Wheless and Ribelin, respectively, corresponding to annual estimates of 0.65, 1.00, and 0.02. The unusually high estimate of survival at Wheless was due to problems of numerical estimation of survival and temporary emigration. The period of March 2008 at Wheless resulted in zero subsequent recaptures; removing this period from the analysis yielded a survival estimate of 0.92 (0.37 annually), which was equivalent to the survival estimate from the next best model including March 2008. Because of these numerical convergence problems resulting in spurious estimates of survival and temporary emigration, we used the next best model selected for Wheless [φ (.) p(.) c(.) Markov (t)] for estimates of those parameters.

Another problem was encountered with the Ribelin analysis, whereby setting *p=c* for fully time varying models resulted in a spurious estimate of *p* and *N* for the first period. These were not included in the model averaged results for these parameters. Population size estimates were fairly similar to previous results (O'Donnell et al. 2007a), where Wheless had the largest mean population size, followed by Lanier and then Ribelin, which roughly corresponds with the total surface area surveyed at each site. Population sizes ranged from 86 at Lanier to 845 at Wheless (Table 9). Population size estimates directly before and after prolonged dry periods remained stable at Wheless and showed a surprising increase at Lanier, followed by a decrease in population size (Figure 9).

Models with time-invariant Markovian movement were heavily favored for both Lanier and Wheless datasets, while the best model for the Ribelin dataset was a no-movement model. The relationship and magnitude of mean γ' and γ'' estimates are very similar between Lanier and Wheless (Table). During the course of this study, there was a much higher probability for an individual outside the sampling area at time *t*-1 to remain outside the sampling area, than for an individual within the sampling area, at time *t*-1, to emigrate to outside that area, at time *t* (Figure 8). These results are in contrast to results of the prior study (O'Donnell et al. 2007a), which identified the random (.) movement model as the best for all sites. However, the random (.) model had half the support of the best model for Ribelin in this analysis, with a QAICc weight of 0.15 (Table 6). Model averaged estimates of γ for Ribelin were fairly low (0.11-0.15), suggesting temporary emigration is much lower at there, if present at all, compared to Lanier and Wheless.

Table 8. Summary of model averaged estimates of conditional capture probabilities, *p*.

Site	n	Range	Mean
Lanier	36	0.010-0.500	0.26
Wheless	27	0.087-0.329	0.19
Ribelin	18	0.181-0.448	0.26

Table 9. Summary of model averaged estimates of population size, *N*.

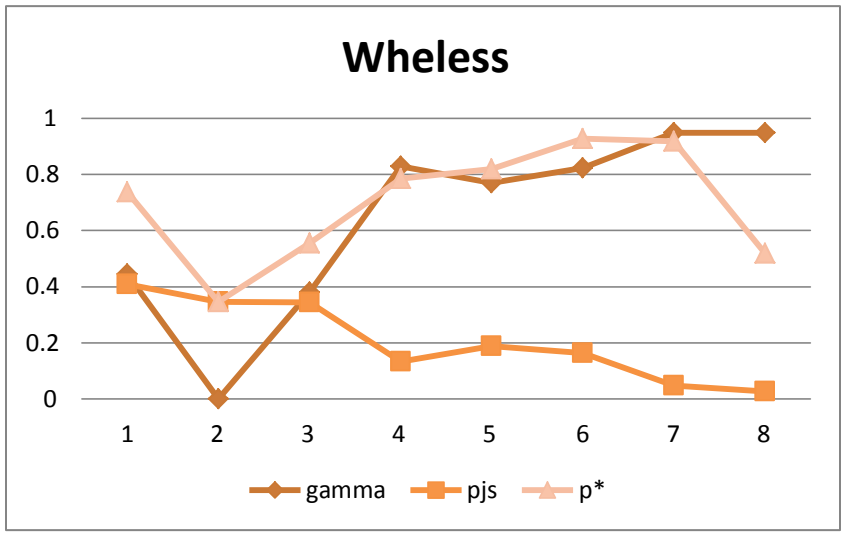
Site	n	Range	Mean
Lanier	12	86-655	225
Wheless	9	365-845	581
Ribelin	6	107-166	144

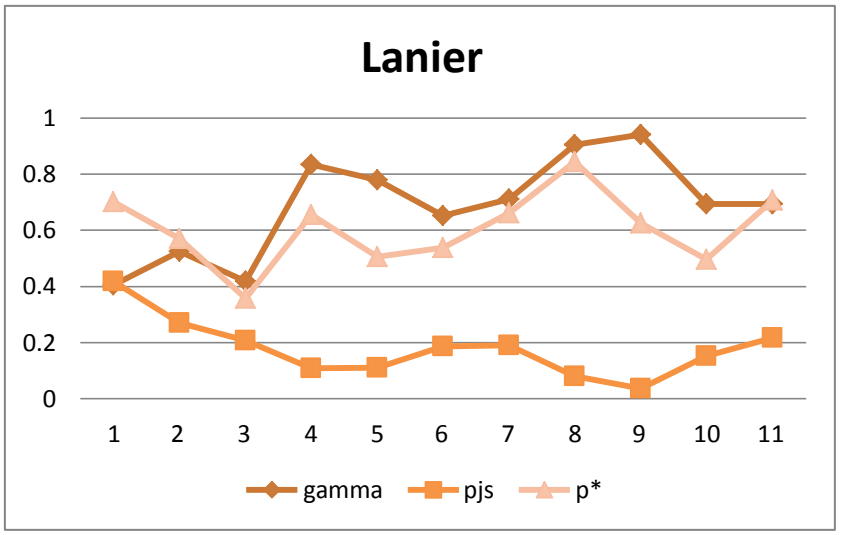
Table 10. Mean estimates of temporary emigration for each site using the variance components method (White et al. 2001). Estimates from Wheless are using the second best model. Two γ'' and one γ' were excluded from Wheless and Lanier averages, respectively, because they had spurious standard errors. *The no movement model was the best model at Ribelin, so estimates of temporary emigration are zero.

Site	γ'	SE γ'	γ''	SE γ''
Lanier	0.95	<0.01	0.53	0.05
Wheless	0.95	<0.01	0.60	0.01
Ribelin*	0.00		0.00	

Table 11. Estimates of the average effective capture probability p^{js} calculated from the parameter estimates of the best random temporary emigration models ($\gamma' = \gamma''$) for each site; * γ was calculated from an average of the time-varying temporary emigration model using the variance components method (White et al. 2001). Average conditional capture probabilities, p, were calculated across all secondary samples (i.e. from all $p(t,t)$) using the variance components method. The best model for Ribelin was a no movement model, indicating that effective capture probability equals conditional capture probability.

Site	p	SE p	γ	SE γ	p^{js}	SE p^{js}
Lanier	0.27	0.079	0.71*	0.03	0.078	0.001
Wheless	0.15	0.071	0.61*	0.11	0.142	0.002
Ribelin*	0.20	0.067	0	0	0.20	0.067





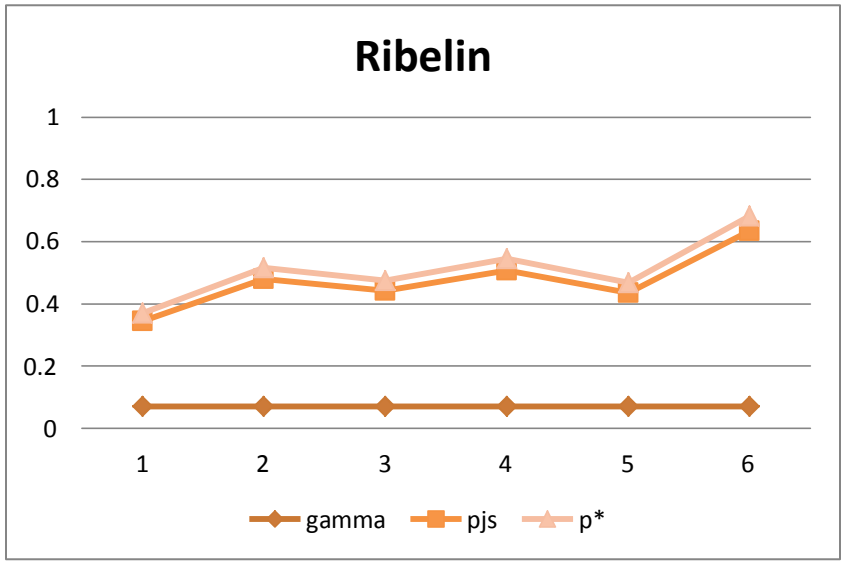
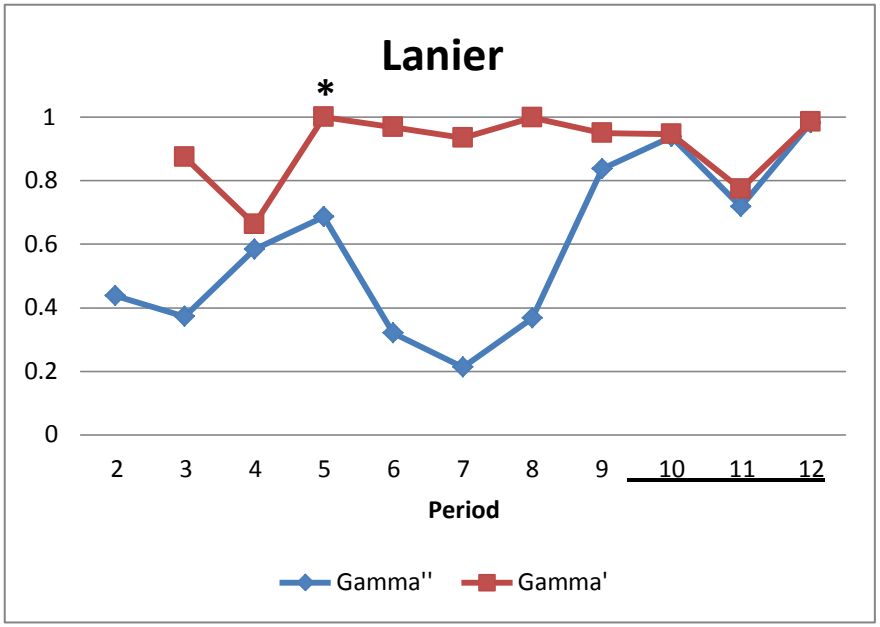


Figure 7. Estimates of temporary emigration (gamma), composite conditional capture probability (p*), and effective capture probability (pjs) from the best random temporary emigration models. Effective capture probabilities vary temporally, showing a decreasing trend at both Lanier and Wheless. Conditional capture probabilities mirror effective capture probabilities at Ribelin because of constant temporary emigration (gamma) in that model.



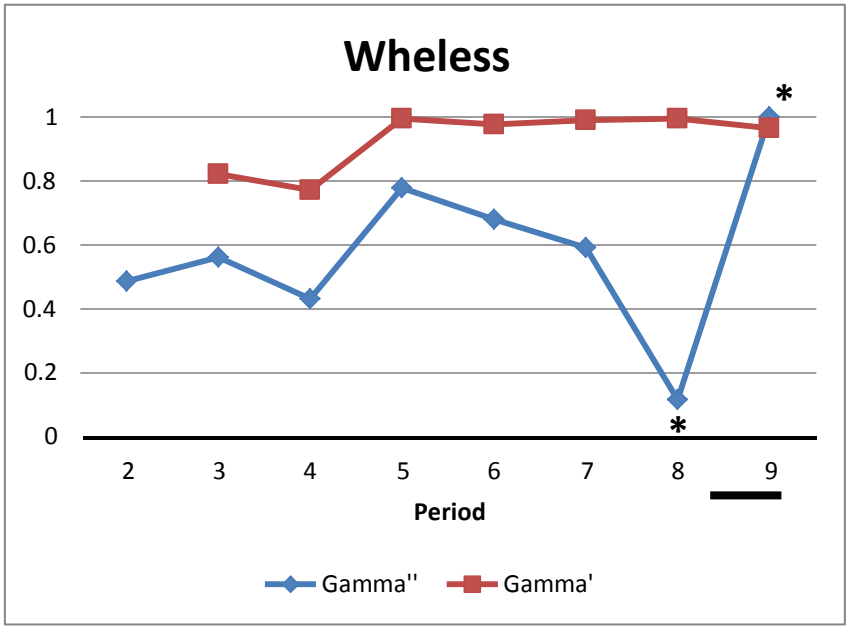


Figure 8. Markovian movement patterns at Lanier and Wheless. * indicate estimates had spurious standard errors. Both sites exhibit consistently high γ' indicating that individuals are unlikely to return to the sample site once they have left. Estimates of $\gamma''$are highest towards the later periods, suggesting that individuals left the site at a higher rate after the drought (indicated by black bar). Future surveys will determine whether temporary emigration patterns return to pre-drought levels.

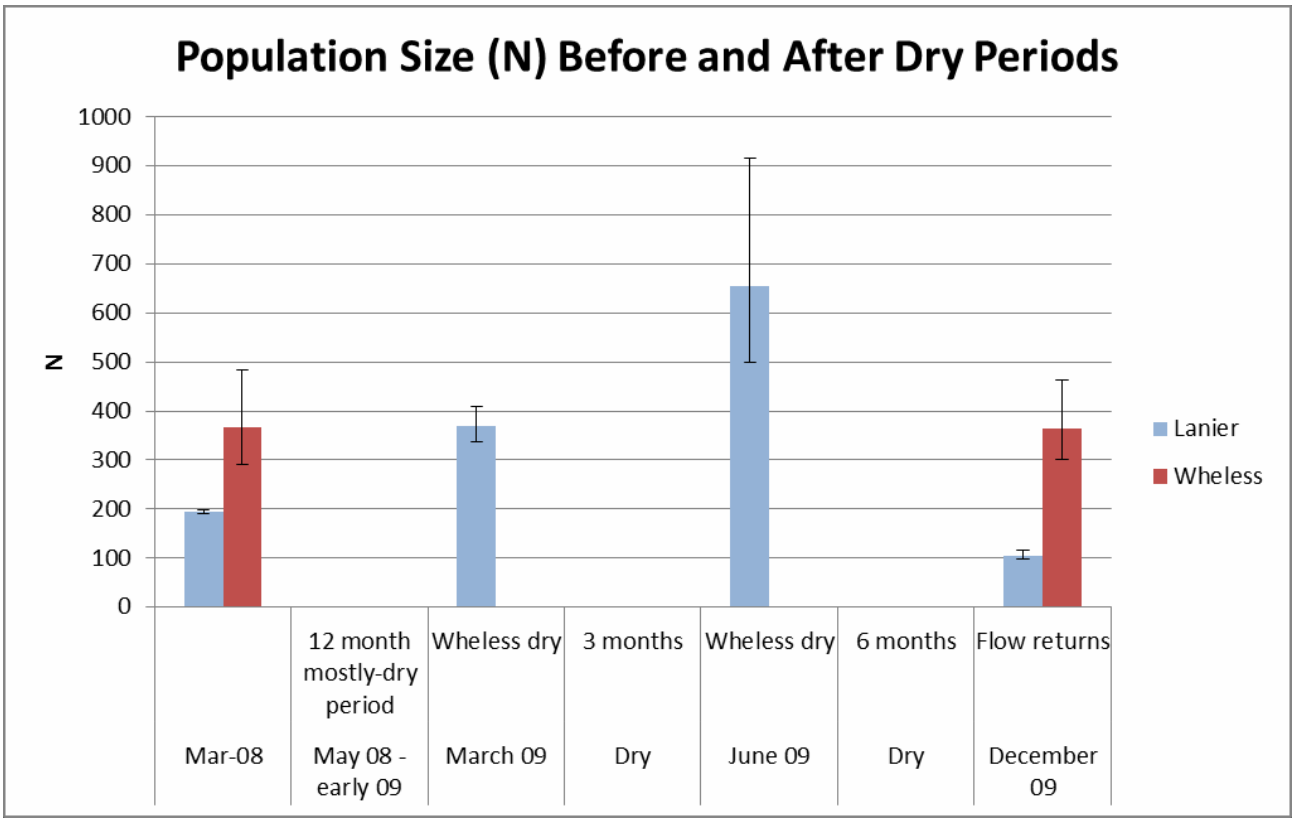


Figure 9. Model averaged estimates of population size (*N*) at Lanier and Wheless springs. Error bars represent 95% confidence intervals. After an approximately 18-month period between surveys where Wheless Spring remained without flowing water for the majority of that period, estimates of population size remained relatively constant. The longest dry period at Lanier lasted for approximately 10 months between March 2008 and March 2009. Population size estimates were higher after this period, and the subsequent shorter dry period in late spring of 2009, but then declined substantially after another short dry spell in the fall.

DISCUSSION

COUNT STUDY

Total counts and juvenile counts of *E. tonkawae* are statistically higher, on average, in the spring and summer months. While juvenile abundance is generally highest during the spring/summer, juveniles may be observed any time of year. These results are consistent with the previous findings of Bowles et al. (2006). While there is some indication of a seasonal effect on reproduction, these results confirm that reproduction can occur year-round, similar to observations of the closely related Barton Springs salamander (City of Austin 2009).

While previous studies have shown that sites with higher impervious cover (i.e. higher urbanization within their associated drainage basins) tend to have declining population trends (O'Donnell et al. 2006; O'Donnell et al. 2007b), a statistical correlation between impervious cover and *E. tonkawae* population trends had never been formally tested. This relationship has been confirmed by the

results of the Poisson regression analysis, indicating that declining trends in counts are correlated with high levels of impervious cover. The covariate analysis also shows a negative effect of impervious cover on base-level counts (i.e. the model intercept). This is consistent with the results of Bowles et al. (2006), who found lower densities of *E. tonkawae* at urbanized sites.

Several studies have reported lower densities of stream-dwelling salamanders or salamander larvae in urbanized watersheds (Barrett et al. 2010; Orser & Shure 1972; Price et al. 2006; Willson & Dorcas 2003); however the mechanism of population degradation has not been well studied. Barrett et al. (2010) demonstrate that higher storm velocities in streams contribute to decreased density of larval *Eurycea cirrigera*, and that degraded water quality was also a likely factor. Watershed urbanization alters numerous aspects of a stream's chemical, biological, and physical characteristics, which can have multiple complex interactions (Walsh et al. 2005). Separating cause from effect under such circumstances is difficult, if not impossible, using only observational studies. The challenge of determining the mechanism of decline as a result of urbanization lies not only in the practical difficulty of designing and conducting manipulative experimentation to separate out those effects, but also the fact that it must be done, in this case, on a species of conservation concern. Experimental research may be required to determine the cause and effect relationships between water quality degradation and *E. tonkawae* population declines.

CAPTURE-MARK-RECAPTURE STUDY

VARIATION IN DETECTION PROBABILITY

Count survey data, by themselves, can be a useful benchmark for the status of a population only if counts are accurate estimates of the actual population size. If that is the case, counts may be useful as indices to population size in order to determine population trends and to investigate factors that control population dynamics. The problem that often occurs is that variation observed in counts is not only due to natural fluctuations in population size (due to environmental or demographic factors), but from observation error as well. Studies of terrestrial salamanders have indicated that detection probability can vary widely across space and time (Bailey et al. 2004b; Dodd & Dorazio 2004; Hyde & Simons 2001; Jung et al. 2000) and it may be inappropriate to use count data to assess population trends without accounting for detection probability (Bailey et al. 2004a, b; Dodd & Dorazio 2004; Hyde & Simons 2001). Although the aforementioned studies were conducted on terrestrial salamanders, there are several commonalities between the terrestrial and aquatic plethodontid study systems. For example, both terrestrial and aquatic plethodontids are found under cover objects, such as rocks, and both have access to subterranean habitat (whether in the stream bed or within the forest floor). Also, both are detected in a similar manner with respect to how they are captured (e.g. one is not captured using traps, and the other hand captured- both are captured by hand or net). Therefore we had reason to suspect that detection probability for *E. tonkawae* may vary across space and time, as it does for terrestrial plethodontids. In order to better understand population changes from count data, we must first understand how detection probability varies, and identify what factors are influencing detection probability. Prior to this study (and O'Donnell et al. 2007a), *p* had never been estimated for any *E.*

tonkawae population, so it was impossible to say anything about how *p* might vary over time or across different sites.

In this study, models of full time varying conditional capture probability were chosen for all analyses using QAICc. This is in contrast to a previous analysis of these data (O'Donnell et al. 2007a) and one study of plethodontid salamanders (Bailey et al. 2004a), where full time-varying detection probabilities models were not considered. These results show that detection probability was variable within and between primary sessions. Between primary periods, environmental conditions can change drastically, such as spring discharge or water temperature. These changes are likely to be more pronounced, for example, between surveys conducted during different seasons. Although we did not test for a seasonal effect (only one year with more than 3 primary periods), data from count surveys suggest that salamander surface abundance is lower during the winter months (Figure 3, Figure 4), indicating that a lower proportion of salamanders may be available for capture at the surface during these times. Additional data and analyses are needed to determine whether there is a seasonal effect on detectability and whether environmental factors can be correlated to changes in detection. This will aid understanding and interpretation of previously collected count data if corresponding environmental data are available for those periods.

We calculated the effective capture probability in order to examine variation among sites and through time, and also to compare estimates of capture probability to other salamander studies. Effective capture probability is analogous to capture probability from open-design Jolly-Seber models, and is associated with the entire superpopulation, not just the area exposed to capture efforts (Kendall et al. 1997). To calculate effective capture probability γ must be estimated from a random temporary emigration model. In this case, models with Markovian movement were heavily favored over models with random movement (Table 6). While the random temporary emigration models were not favored in any of the analyses, estimates of conditional capture probability were not drastically different from the estimates from the best models. For this reason we believe that our estimates of effective capture probability are reasonable. To compare temporal trends and averages among sites, we calculated effective capture probability from the composite conditional capture probabilities across all secondary samples within a primary period, $p(t)$ (Figure 7). To compare effective capture probabilities to results from other studies, and to generate estimates analogous to single-count survey data, we used the individual secondary sample estimates of conditional capture probability, $p(t,t)$ (Table 11).

Effective capture probabilities at Lanier and Wheless exhibit a downward trend, although this is likely due to the effect of the drought during periods 7 and 8 at Wheless and period 9 at Lanier (Figure 7), which showed low effective capture probabilities and high temporary emigration rates. Overall, Wheless and Lanier have similar average effective capture probabilities (Lanier, 0.18; Wheless, 0.21). Ribelin had the highest effective capture probability (0.47) due to the fact that temporary emigration was zero in the top model.

Compared to studies of terrestrial plethodontid salamanders (Bailey et al. 2004a; Jung et al. 2000; Smith & Petranka 2000), our estimates of effective capture probability are generally higher based on our

overall averages across all secondary samples (Table 11). For example, Bailey et al. (2004a) estimated an average detection probability of 0.03 across all site-years. If these results can be generalized to all count survey sites, we expect our single-count survey data to exhibit a similar range of effective capture probabilities, approximately 6 to 20% on average (Table 11) for a given survey.

The presence of temporary emigration has a profound effect on estimates of effective capture probability. Effective capture probabilities exhibit substantial temporal variation over time at Lanier and Wheless (Figure 7), underscoring the difficulty of using counts as indices of population size. This is in contrast to the findings of Bailey et al. (2004b), who found that temporary emigration and conditional capture probabilities were inversely related, showing little temporal variation in effective capture probability in terrestrial plethodontid salamanders. Temporal variation in detection probability has several important and previously overlooked implications for how the count data are interpreted. First, counts cannot be reliably interpreted as some constant proportion of the true population size, as this and several studies of terrestrial and biphasic plethodontid salamanders demonstrate (Dodd & Dorazio 2004; Hyde & Simons 2001; Jung et al. 2000; Smith & Petranka 2000). Such an interpretation would require a constant detection probability over time, and this is clearly not supported by these results. Thus, changing or stable counts over a short period of time do not necessarily imply a changing or stable population. Secondly, counts likely represent a small fraction of the total population size at a given site. Therefore, it is incorrect to assume that a site with low counts necessarily has a very small population size. Thirdly, uncertainty in detection probability for count surveys increases uncertainty in the magnitude and significance of population trends. While long-term trends in counts may be a real reflection of trends in population size (the alternative being a long term trend in detection), uncertainty in detection results in lower confidence in how large or small those declines or increases actually are in the population. Variation in detection that is unaccounted for also increases the possibility that trends deemed statistically significant, are not. Exploring the potential effects of variation in detection probability over time on the interpretation of count data will be the focus of a future study.

Movement Patterns

Temporary emigration was prevalent and variable at Lanier and Wheless. This is demonstrated by variation in $\gamma'$and γ'' (under the Markovian models) and the effect of γ on effective capture probability (under the random models; Figure 7). Temporary emigration was low at Ribelin, indicated by a no-movement model having the highest QAICc weight, and lower weighted models with small temporary emigration estimates.

The biological significance of the Markovian pattern of emigration at Lanier and Wheless is unclear. In other species, Markovian temporary emigration may relate to the breeding status of an individual, whereby its presence at a breeding site is related to whether it was a breeder in the previous year. This is probably not a realistic explanation of the results because Jollyville Plateau salamanders likely breed year round. Additionally, most of the data analyzed were from a single year, meaning that temporary emigration is primarily occurring between months, not years. Consistently high estimates of γ' at Wheless and Lanier may indicate that salamanders away from the study area are less likely to return

over time, even though the models only consider first-order Markovian movement. Thus, some of these individuals may eventually become permanent emigrants, resulting in lower population persistence. Persistence is reflected in estimates of annual survival because death and permanent emigration are confounded. Estimates of survival were 0.65 and 0.37 for Lanier and Wheless, respectively. In contrast, Ribelin had a much lower annual survival estimate (0.02), and very low temporary emigration. This variation in survival and temporary migration may be partially due to differences in habitats among sample sites. The study site at Ribelin may confine salamanders horizontally: downstream of the study site consists of bedrock with almost no surface cover, and there is a small travertine waterfall at the upstream end (where the spring emerges). These features may prevent easy horizontal movement to and from the study area. When horizontal movement does occur, it is more likely to be permanent due to those same barriers, thus resulting in a very low temporary emigration rate but a higher permanent emigration rate, i.e. low survival. In contrast, both Lanier and Wheless feature contiguous stretches of cover-dominated habitat within the stream bed, perhaps facilitating temporary emigration, allowing salamanders to move to and from the study area more easily. Emigrants at Lanier or Wheless are less likely to be permanent emigrants than at Ribelin, where it would be more difficult to return to the sample area due to the physical site conditions. However, high estimates of γ' at Lanier and Wheless indicate that once a salamander is away from the study area, it is less likely to return than if it had just left the study area (γ''). Since γ' was consistently high for both study sites, the combined effect may be that the longer a salamander is away from a study site, the less likely it is to return.

Whether salamanders were temporarily emigrating outside of the study area, below the stream surface, or through spring orifices, is not entirely clear. Jollyville Plateau salamanders have been observed within the stream substrate, 8-12" below the surface, during wet and dry surface conditions (N. Bendik, personal observation). Movement to and from this subsurface habitat may be regulated by cues from environmental conditions, such as surface water temperature, or other seasonal changes. However, the results presented here suggest that temporary movements below the subsurface (or along the surface) may be more frequent than seasonal, because models with temporary emigration were supported for both Lanier and Wheless. Other *Eurycea* species are also known to inhabit interstitial spaces of the gravel bed below the stream surface (Tumlison & Cline 1997; Tumlison et al. 1990), and some populations of *Eurycea tynerensis* have independently evolved a neotenic life history adapted to this subsurface habitat (Bonett & Chippindale 2006). Whether temporary movements of *E. tonkawae* occur below or above the surface, these results indicate that either (a) salamanders frequently shift between habitats above or below the surface of the stream and not just during periods of fluctuating spring flow, or (b) that they frequently disperse outside the immediate vicinity of springs (our sampling areas) and return, or (c) some combination of a and b. Bailey et al. (2004a) have shown that a large proportion of terrestrial plethodontid populations occur below the surface and are unavailable to capture due to temporary emigration. However, it was impossible to distinguish between emigration below surface or upstream/downstream of the study area since it is impractical to leave net barriers in place for longer than a few days. In the future, searches outside the boundary of the survey area might shed light on how frequently salamanders are migrating along the surface.

EFFECTS OF DROUGHT

The recent drought that spanned most of 2008 and 2009 in the central Texas region was the worst drought since the drought of record in the 1950's. Prolonged periods of low or no rainfall resulted in numerous Jollyville Plateau salamander spring sites going dry (Figure 4). Salamanders may experience several potential negative effects as a result of this process, the most obvious of which is desiccation. When surface waters run dry, *E. tonkawae* can avoid desiccation by following the water table as it recedes. Assuming groundwater refugia are fairly localized, some population losses may be expected because of competition for space or failure of some individuals to reach refugia. For example, during previous dry periods salamanders have been found desiccated or stranded in shrinking pools of stagnant water (O'Donnell et al. 2007b; Mark Sanders, personal communication). For those able to recede with the water table, prey availability is expected to be lower within local groundwater refugia because of reduced ecosystem production and reliance on autotrophic input from surface waters (Gilbert et al. 1994) that may be practically nil during times of drought. The negative effects of drought may be countered in part by reduced predation pressure from macroinvertebrates and centrarchid fishes, which are temporarily extirpated when streams run dry (with the possible exception of burrowing crayfish). Furthermore, groundwater refugia may be much larger and less localized than expected (e.g. Hauwert & Warton 1997), which could also mitigate the effects of drought on surface populations.

Based on the results presented here, the negative effects of the drought were not significant enough to decimate populations, as might be expected from such prolonged periods without surface water. In fact, results from both CMR and count based data confirm that *E. tonkawae* populations are relatively resilient to dry surface conditions. Post-drought response was generally positive among all count-only sites, indicated by significantly higher total salamander counts and juvenile counts. However, the CMR results give a more detailed account of how population sizes were affected by the drought because they provide point estimates just before the springs went dry and just after they resumed flowing.

Population size remained relatively stable at Wheless, even after 18 months of predominantly dry surface conditions (Figure 9). Ten months of dry surface conditions at Lanier yielded an almost doubling of population size (Figure 8), perhaps reflecting a concentration of salamanders at the spring just after flow resumed, whereby a greater majority of the superpopulation was available for capture than is available during normal flow conditions. That salamanders may become more concentrated at the source of the spring when the water level recedes was also reflected in the unprecedented high number of recaptures (~44%) during the first post-drought Wheless survey. Unlike Wheless Spring, which had one prolonged dry period, Lanier Spring experienced several periods where flow would resume and then recede during 2009. Between July and December, estimates of population size were much lower (N=106±12) than the prior period (N=656±74) at Lanier (Figure 9). A pattern of lower survival was observed in models with time-varying survival (i.e. persistence) for this time period at Lanier, although φ (.) models were more highly supported. While purely speculative, it is possible that this pattern is the result of dispersal following emergence from refugia. This is also supported by higher estimates of temporary emigration at both sites after the drought period (Figure 8). Alternatively it may reflect a

cumulative negative effect of repeated wet and then dry surface conditions, potentially being more stressful to the population than a single long dry period, as observed at Wheless.

Observations of juvenile recruitment indicate that reproduction did not completely cease during the drought. In one case, several juveniles (0.5-1 inch) were observed only a few weeks following completely dry surface conditions (March 2009, Lanier Spring). Estimates of incubation period for the Barton Springs Salamander, a closely related species, range from three to four weeks (City of Austin 2002). Assuming *E. tonkawae* egg development incubation time is similar, these eggs were laid before spring flow resumed. This is remarkable, considering that Lanier Spring is estimated to have been "dry" for approximately 10 months. In contrast, no juveniles were observed at Wheless following the 18-month dry period at the end of 2009, although they were observed the following March. At count study sites, total juvenile counts were higher during the 5 quarters following the drought, including sites which did not "dry up." These results suggest a resiliency of *E. tonkawae* to natural drought conditions, and in some cases, that they are also able to allocate energy towards reproduction (e.g. egg development) before surface flow resumes. Given the frequency of droughts in central Texas, the evolutionary history of central Texas *Eurycea*, and the frequency with which springs on the Jollyville Plateau go dry (O'Donnell et al. 2007b), it is unsurprising to learn that *E. tonkawae* are adapted to such conditions.

CONCLUSIONS

In this report, we examined trends in count data using a different approach than previous analyses of *E. tonkawae* data. While the Bayesian Poisson regression used in this study is a relatively simplistic analysis that did not incorporate interaction effects or additional covariates (other than conductance or impervious cover), it shows promise because additional model complexity can be included relatively easily. On the other hand, its simplicity facilitates generalizations about the effects of different land use practices while accounting for differences in baseline population levels. Using this method, we were able to detect a statistically significant difference in trends of salamander counts between sites with high and low levels of impervious cover. This supports previous conclusions that high impervious cover is negatively correlated with *E. tonkawae* salamander counts (Bowles et al. 2006; USFWS 2007).

As previous analyses of the CMR data have shown (O'Donnell et al. 2007a), detection probability is highly variable, posing problems for interpreting count data and analyses based on them. Despite this problem, both counts and CMR data were consistent when considering the predominantly positive post- drought response of *E. tonkawae* populations. Reproduction increased following the drought, and salamander counts were higher. We also found that population size did not appear to change drastically at CMR sites between long periods with dry surface conditions. These results show that *E. tonkawae* populations can be resilient to natural drought conditions, even when springs run dry.

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APPENDIX A- **Count Data Models**

$$
\left.\begin{array}{rcl}
\log(\lambda_k) & = & \alpha_{\text{site}_k} + \beta_{\text{cover}_k} \cdot (\text{month}_k - \text{fixedmonth}) + \epsilon_k \\
\epsilon_k & \sim & \text{dnorm}(0.0, \tau_\epsilon) \\
\text{count}_k & \sim & \text{dpois}(\lambda_k)
\end{array}\right\} 1 \le k \le \text{ncounts}
$$

$$
\begin{array}{rcl}
\tau_\epsilon & \sim & \text{dgamma}(0.001, 0.001) \\
\sigma_\epsilon & = & 1/\tau_\epsilon^{0.5}
\end{array}
$$

$$
\left.\begin{array}{rcl}
\alpha_i & \sim & \text{dnorm}(\mu_{\text{site}}, \tau_{\text{site}})
\end{array}\right\} 1 \le i \le \text{nosites}
$$

$$
\begin{array}{rcl}
\mu_{\text{site}} & \sim & \text{dnorm}(0, 1.0\text{E-}6) \\
\tau_{\text{site}} & \sim & \text{dgamma}(0.001, 0.001) \\
\sigma_{\text{site}} & = & 1/\tau_{\text{site}}^{0.5}
\end{array}
$$

$$
\left.\begin{array}{rcl}
\beta_j & \sim & \text{dnorm}(0, 1.0\text{E-}6)
\end{array}\right\} 1 \le j \le \text{ncovertypes}
$$

$$
\left.\begin{array}{rcl}
\text{loglambda}_k & = & \alpha_{\text{site}_k} + \beta_{\text{cover}_k} \cdot (\text{month}_k - \text{fixedmonth}) \\
\text{fit}_k & = & e^{\text{loglambda}_k + 0.5 \cdot \sigma_\epsilon \cdot \sigma_\epsilon}
\end{array}\right\} 1 \le k \le \text{ncounts}
$$

$$
\begin{array}{rcl}
\mu.\alpha 1 & = & \text{mean}(\alpha_{\text{cover}_1}) \\
\mu.\alpha 2 & = & \text{mean}(\alpha_{\text{cover}_2})
\end{array}
$$

$$
\left.\begin{array}{rcl}
\text{fitted}_{1,t} & = & e^{\mu.\alpha 1 + \beta_{\text{cover}_1} \cdot (t - \text{fixedmonth}) + 0.5 \cdot \sigma_\epsilon \cdot \sigma_\epsilon + 0.5 \cdot \sigma_{\text{site}} \cdot \sigma_{\text{site}}}
\end{array}\right\} 1 \le t \le \text{nmonths}
$$

$$
\left.\begin{array}{rcl}
\text{fitted}_{2,t} & = & e^{\mu.\alpha 2 + \beta_{\text{cover}_2} \cdot (t - \text{fixedmonth}) + 0.5 \cdot \sigma_\epsilon \cdot \sigma_\epsilon + 0.5 \cdot \sigma_{\text{site}} \cdot \sigma_{\text{site}}}
\end{array}\right\} 1 \le t \le \text{nmonths}
$$

$$
\begin{array}{rcl}
B_1 & = & 100 \cdot ((\text{fitted}_{1,\text{nmonths}} / \text{fitted}_{1,1})^{1/(\text{nmonths}-1)} - 1) \\
B_2 & = & 100 \cdot ((\text{fitted}_{2,\text{nmonths}} / \text{fitted}_{2,1})^{1/(\text{nmonths}-1)} - 1)
\end{array}
$$

Bayesian model of trends in counts over time, grouped by impervious cover category, with site effects and overdispersion.

OPENBUGS MODEL CODE FOR FIGURE A:

```
Model{
      #### counts and overdispersion effects  ######
      for( k in 1 : ncounts ) {
            log(lambda[k]) <- alpha[site[k]] + beta[type[k]] * (month[k] -
fixedmonth) + epsilon[k]
            epsilon[k] ~ dnorm(0.0, tau.epsilon)
            count[k] ~ dpois(lambda[k])}
      tau.epsilon ~ dgamma(0.001,0.001)
      sd.epsilon <- 1 / pow(tau.epsilon,0.5)
      #### Site effects  ######
      for( i in 1 : nosites ){
            alpha[i] ~ dnorm(mu.obs,tau.obs)}
            mu.obs~dnorm(0,1.0E-6)
            tau.obs~dgamma(0.001,0.001)
            sd.obs <- 1 / pow(tau.obs, 0.5)
```

```
      #### Slope  ######
      for (j in 1:notypes)
      {beta[j] ~ dnorm( 0,1.0E-6)}
      #### Summary Statistics  ######
      for( k in 1 : ncounts ) {
            loglambda[k] <- alpha[site[k]] + beta[type[k]] * (month[k] -
fixedmonth)
            fit[k] <- exp(loglambda[k] + 0.5*sd.epsilon*sd.epsilon)}
      mu.alpha1<-mean(alpha[1:6])
      mu.alpha2<-mean(alpha[7:8])
      for( t in 1 : nmonths ){
            fitted1[t] <- exp(mu.alpha1 + beta[1]*(t-fixedmonth)
                  + 0.5*sd.epsilon*sd.epsilon + 0.5*sd.obs*sd.obs)}
            for( t in 1 : nmonths ){
            fitted2[t] <- exp(mu.alpha2 + beta[2]*(t-fixedmonth)
                  + 0.5*sd.epsilon*sd.epsilon + 0.5*sd.obs*sd.obs)}
      B1 <- 100*(pow(fitted1[nmonths]/fitted1[1],1/(nmonths-1))-1)
      B2<- 100*(pow(fitted2[nmonths]/fitted2[1],1/(nmonths-1))-1)}
```

$$
\left.\begin{array}{rcl}
\log(\lambda_k) & = & \alpha_{\text{site}_k} + \beta \cdot (\text{month}_k - \text{fixedmonth}) + \epsilon_k \\
\epsilon_k & \sim & \text{dnorm}(0.0, \tau_\epsilon) \\
\text{count}_k & \sim & \text{dpois}(\lambda_k)
\end{array}\right\} 1 \le k \le \text{ncounts}
$$

$$
\begin{array}{rcl}
\tau_\epsilon & \sim & \text{dgamma}(0.001, 0.001) \\
\sigma_\epsilon & = & 1/\tau_\epsilon^{0.5} \\
\beta & \sim & \text{dnorm}(0.0, 1.0\text{E-}6) \\
\beta_i & \sim & \text{dnorm}(0.0, 1.0\text{E-}6) \\
\beta_s & \sim & \text{dnorm}(0.0, 1.0\text{E-}6)
\end{array}
$$

$$
\left.\begin{array}{rcl}
\mu_{\alpha,i} & = & \mu_{\text{site}} + \beta_i \cdot \text{Scaled}_{\text{impc},i} + \beta_s \cdot \text{Scaled}_{\text{spc},i} \\
\alpha_i & \sim & \text{dnorm}(\mu_{\alpha,i}, \tau_{\text{site}})
\end{array}\right\} 1 \le i \le \text{nosites}
$$

$$
\begin{array}{rcl}
\mu_{\text{site}} & \sim & \text{dnorm}(0.0, 1.0\text{E-}6) \\
\tau_{\text{site}} & \sim & \text{dgamma}(0.001, 0.001) \\
\sigma_{\text{site}} & = & 1/\tau_{\text{site}}^{0.5} \\
\overline{x}_{\text{impc}} & = & \text{mean}(\text{impc}_{1\ldots\text{nosites}}) \\
\overline{x}_{\text{spc}} & = & \text{mean}(\text{spc}_{1\ldots\text{nosites}})
\end{array}
$$

$$
\left.\begin{array}{rcl}
\text{Scaled}_{\text{impc},i} & = & \text{impc}_i - \overline{x}_{\text{impc}} \\
\text{Scaled}_{\text{spc},i} & = & \text{spc}_i - \overline{x}_{\text{spc}}
\end{array}\right\} 1 \le i \le \text{nsites}
$$

Bayesian model of trends in count data over time (as above) with impervious cover and specific conductance covariates imposed on the intercept.

OPENBUGS MODEL CODE FOR FIGURE B:

```
Model{
      #### standardize habitat variables ######
      xbar.impc <- mean(impc[1:nosites])
      xbar.spc<-mean(spc[1:nosites])
      for( i in 1 : nosites ) {
            Scaled.impc[i]<-impc[i]-xbar.impc
            Scaled.spc[i]<-spc[i]-xbar.spc}
      #### counts and overdispersion effects ######
      for( k in 1 : ncounts ) {
            log(lambda[k]) <- alpha[site[k]] + beta * (month[k] - fixedmonth)
+ epsilon[k]
            epsilon[k] ~ dnorm(0.0, tau.epsilon)
               count[k] ~ dpois(lambda[k]) }
      tau.epsilon ~ dgamma(0.001,0.001)
      sd.epsilon <- 1 / pow(tau.epsilon, 0.5)
      #### impervious cover effects ######
      # Comment out node or constant definition to decide inclusion #
      beta.i ~ dnorm(0.0, 1.0E-6)
      beta.s~ dnorm(0.0, 1.0E-6)
      #beta.i<-0
      #beta.s<-0
      #### Site effects ######
      for( i in 1 : nosites ) {
            mu.alpha[i] <- mu.obs +
beta.i*Scaled.impc[i]+beta.s*Scaled.spc[i]
            alpha[i] ~ dnorm( mu.alpha[i],tau.obs)}
      mu.obs ~ dnorm(0.0, 1.0E-6)
      tau.obs ~ dgamma(0.001,0.001)
      sd.obs <- 1 / pow(tau.obs, 0.5)
   mean.obs <- mean(mu.alpha[1:nosites ])
      #### slope ######
      beta ~ dnorm( 0.0,1.0E-6)
      ### Expected average counts (derived)###
            for( t in 1 : nmonths ){
            fitted[t] <- exp(mean.obs + beta*(t-fixedmonth)
                  + 0.5*sd.epsilon*sd.epsilon + 0.5*sd.obs*sd.obs)}}
```

EXAMPLE OF R-CODE FOR GAM SMOOTH:

```
#GAM(mgcv) Generalized additive models with integrated smoothness
#df is a relative measure of smoothing
#gam fits using splines

library(mgcv)
```

APPENDIX A

```
sites <- read.table("928.txt", header = TRUE, sep = "\t", quote="\"",
dec=".")
p<-as.Date(sites$date, origin="1960-01-01")
sgam1 <- gam(sites$y ~ s(sites$date))
sgam <- predict(sgam1, se=TRUE)
plot(p,sites$y, xlab='Time', ylab='Counts',main="Site 928 GAM Smooth")
 lines(p,sgam$fit, lty = 1)
 lines(p,sgam$fit + 1.96* sgam$se, lty = 2)
 lines(p,sgam$fit - 1.96* sgam$se, lty = 2)

savePlot(filename = "928 GAM smooth",
         type = "png",
         device = dev.cur(),
         restoreConsole = TRUE)
sink("928 GAM summary.txt")
summary(sgam1)
sink()
```

APPENDIX B- **CMR model results**

LANIER

Model	QAICc	Delta QAICc	AICc Weights	Model Likelihood	Num. Par
φ(.) p(t,t) =c(t,t) Markov (t)	-2938.0397	0	0.99105	1	70
φ(t) p(t,t) =c(t,t) Markov (t)	-2927.3483	4.2669	0.00473	0.0048	78
φ(.) p(t,t) c(t,t) Markov (t)	-2927.1164	4.4988	0.00421	0.0042	82
φ(t) p(t,t) c(t,t) Markov (t)	-2916.0794	15.5358	0.00002	0	90
φ(t) p(t) c(t) Markov (t)	-2908.5895	23.0257	0	0	66
φ(.) p(t)=c(t) Markov (t)	-2904.8825	26.7327	0	0	46
φ(t) p(t)=c(t) Markov (t)	-2894.5167	37.0985	0	0	54
φ(t) p(t,t) c(t,t) Markov (.)	-2894.0205	37.5947	0	0	73
φ(t) p(t,t) =c(t,t) Markov (.)	-2891.2754	40.3398	0	0	61
φ(.) p(t) c(t) Markov (t)	-2885.9469	45.6683	0	0	58
φ(.) p(.) c(.) Markov (t)	-2875.0362	56.579	0	0	36
φ(t) p(t) c(t) Markov (.)	-2871.6445	59.9707	0	0	49
φ(.) p(t) c(t) Markov (.)	-2868.0515	63.5637	0	0	39
φ(t) p(.) c(.) Markov (t)	-2867.9357	63.6795	0	0	44
φ(t) p(t)=c(t) Markov (.)	-2858.8477	72.7675	0	0	37
φ(.) p(.)=c(.) Markov (t)	-2857.8189	73.7963	0	0	35
φ(.) p(t,t) c(t,t) Markov (.)	-2857.7956	73.8196	0	0	63
φ(t) p(t,t) =c(t,t) random (t)	-2851.3051	80.3101	0	0	69
φ(t) p(.)=c(.) Markov (t)	-2843.3739	88.2413	0	0	43
φ(t) p(t,t) c(t,t) random (t)	-2835.9298	95.6854	0	0	81
φ(t) p(t) c(t) random (t)	-2834.2872	97.328	0	0	57
φ(.) p(t,t) =c(t,t) random (t)	-2827.078	104.5372	0	0	60
φ(.) p(t,t) =c(t,t) Markov (.)	-2824.1779	107.4373	0	0	51
φ(t) p(t)=c(t) random (t)	-2817.5116	114.1036	0	0	45
φ(.) p(t,t) c(t,t) random (t)	-2811.9413	119.6739	0	0	72
φ(t) p(.)=c(.) Markov (.)	-2811.2828	120.3324	0	0	26
φ(.) p(t) c(t) random (t)	-2809.8261	121.7891	0	0	48
φ(t) p(.) c(.) Markov (.)	-2809.2284	122.3868	0	0	27
φ(t) p(.) c(.) random (t)	-2803.0042	128.611	0	0	35
φ(t) p(t) c(t) random (.)	-2794.8738	136.7414	0	0	48
φ(.) p(t)=c(t) random (t)	-2792.8203	138.7949	0	0	36
φ(.) p(t)=c(t) Markov (.)	-2791.5469	140.0683	0	0	27
φ(t) p(t,t) c(t,t) random (.)	-2790.9005	140.7147	0	0	72
φ(.) p(.) c(.) random (t)	-2778.1246	153.4906	0	0	26
φ(t) p(.)=c(.) random (t)	-2775.6263	155.9889	0	0	34
φ(t) p(t,t) =c(t,t) random (.)	-2772.6083	159.0069	0	0	60
φ(t) p(t) c(t) no mov	-2758.8803	172.7349	0	0	48
φ(.) p(t) c(t) random (.)	-2756.5632	175.052	0	0	38
φ(t) p(t)=c(t) random (.)	-2738.9819	192.6333	0	0	36
φ(t) p(t,t) c(t,t) no mov	-2731.1789	200.4363	0	0	71
φ(.) p(t) c(t) no mov	-2724.2892	207.326	0	0	38
φ(.) p(t,t) c(t,t) random (.)	-2718.0881	213.5271	0	0	62
φ(t) p(.)=c(.) random (.)	-2707.8224	223.7928	0	0	25
φ(t) p(.) c(.) random (.)	-2705.9155	225.6997	0	0	26

φ(.) p(t,t) =c(t,t) random (.)	-2665.6601	265.9551	0	0	50
φ(.) p(t,t) c(t,t) no mov	-2649.5851	282.0301	0	0	61
φ(t) p(t,t) =c(t,t) no mov	-2646.9525	284.6627	0	0	60
φ(.) p(.) c(.) Markov (.)	-2644.1107	287.5045	0	0	17
φ(.) p(t)=c(t) random (.)	-2631.7635	299.8517	0	0	26
φ(.) p(.)=c(.) Markov (.)	-2631.7183	299.8969	0	0	16
φ(.) p(.)=c(.) random (t)	-2631.0254	300.5898	0	0	24
φ(t) p(.) c(.) no mov	-2629.8839	301.7313	0	0	25
φ(t) p(t)=c(t) no mov	-2621.3585	310.2567	0	0	36
φ(.) p(t,t) =c(t,t) no mov	-2520.6865	410.9287	0	0	50
φ(.) p(.)=c(.) random (.)	-2518.6453	412.9699	0	0	15
φ(.) p(.) c(.) random (.)	-2517.6092	414.006	0	0	16
φ(.) p(t)=c(t) no mov	-2497.3304	434.2848	0	0	25
φ(.) p(.) c(.) no mov	-2445.3628	486.2524	0	0	15
φ(t) p(.)=c(.) no mov	-2444.8526	486.7626	0	0	24
φ(.) p(.)=c(.) no mov	-2174.1402	757.475	0	0	14

WHELESS

Model	QAICc	Delta QAICc	AICc Weightt	Model Likelihood	Num. Par
φ(.) p(t,t)=c(t,t) Markov (t)	-3763.3169	0	0.99875	1	52
φ(.) p(.) c(.) Markov (t)	-3749.5185	13.7984	0.00101	0.001	27
φ(.) p(t,t) c(t,t) Markov (t)	-3746.2625	17.0544	0.0002	0.0002	61
φ(.) p(t) c(t) Markov (t)	-3743.4578	19.8591	0.00005	0.0001	43
φ(.) p(.)=c(.) Markov (t)	-3723.3601	39.9568	0	0	26
φ(.) p(t)=c(t) Markov (t)	-3711.0238	52.2931	0	0	32
φ(t) p(t,t)=c(t,t) Markov (t)	-3707.6532	55.6637	0	0	57
φ(t) p(t,t)=c(t,t) Markov (.)	-3698.9296	64.3873	0	0	46
φ(t) p(t,t) c(t,t) Markov (t)	-3697.2644	66.0525	0	0	65
φ(t) p(t) c(t) Markov (t)	-3694.563	68.7539	0	0	48
φ(t) p(t,t) c(t,t) Markov (.)	-3687.9559	75.361	0	0	55
φ(.) p(t,t) c(t,t) Markov (.)	-3678.1763	85.1406	0	0	48
φ(t) p(.) c(.) Markov (.)	-3672.6318	90.6851	0	0	21
φ(t) p(t) c(t) Markov (.)	-3668.6455	94.6714	0	0	37
φ(.) p(t,t)=c(t,t) Markov (t)	-3667.5586	95.7583	0	0	50
φ(t) p(.)=c(.) Markov (t)	-3664.9301	98.3868	0	0	30
φ(t) p(t)=c(t) Markov (t)	-3661.5945	101.7224	0	0	38
φ(.) p(t) c(t) Markov (.)	-3655.3698	107.9471	0	0	30
φ(.) p(.) c(.) Markov (.)	-3653.6298	109.6871	0	0	14
φ(t) p(t)=c(t) Markov (.)	-3651.8357	111.4812	0	0	28
φ(t) p(.)=c(.) Markov (.)	-3646.6189	116.698	0	0	20
φ(.) p(t)=c(t) Markov (.)	-3638.2156	125.1013	0	0	21
φ(.) p(.)=c(.) Markov (.)	-3628.1661	135.1508	0	0	13
φ(t) p(.) c(.) Markov (t)	-3622.9848	140.3321	0	0	30
φ(t) p(t) c(t) random (t)	-3611.8359	151.481	0	0	42
φ(t) p(t,t)=c(t,t) random (t)	-3610.7341	152.5828	0	0	51
φ(t) p(.) c(.) random (t)	-3608.5458	154.7711	0	0	26
φ(t) p(t,t)=c(t,t) random (.)	-3604.9776	158.3393	0	0	45
φ(t) p(t,t) c(t,t) random (t)	-3599.3158	164.0011	0	0	60

φ(t) p(t,t) c(t,t) random (.)	-3594.5124	168.8045	0	0	54
φ(t) p(t,t)=c(t,t) no mov	-3586.1842	177.1327	0	0	44
φ(t) p(t,t) c(t,t) no mov	-3585.3844	177.9325	0	0	53
φ(.) p(t) c(t) random (t)	-3583.3675	179.9494	0	0	35
φ(.) p(t,t)=c(t,t) random (t)	-3581.7223	181.5946	0	0	44
φ(.) p(.) c(.) random (t)	-3581.3507	181.9662	0	0	19
φ(t) p(.)=c(.) random (t)	-3571.4954	191.8215	0	0	25
φ(.) p(t,t) c(t,t) random (t)	-3570.7759	192.541	0	0	53
φ(t) p(t) c(t) random (t)e (.)	-3569.0351	194.2818	0	0	36
φ(t) p(t)=c(t) random (t)	-3563.4693	199.8476	0	0	33
φ(t) p(t)=c(t) random (.)	-3560.08	203.2369	0	0	27
φ(t) p(.) c(.) random (.)	-3552.4348	210.8821	0	0	20
φ(t) p(t) c(t) no mov	-3548.8317	214.4852	0	0	35
φ(.) p(t,t) c(t,t) random (.)	-3546.7057	216.6112	0	0	47
φ(t) p(.)=c(.) random (.)	-3545.137	218.1799	0	0	19
φ(t) p(t)=c(t) no mov	-3543.561	219.7559	0	0	26
φ(.) p(t,t)=c(t,t) random (.)	-3543.3611	219.9558	0	0	38
φ(.) p(.)=c(.) random (t)	-3539.5434	223.7735	0	0	18
φ(t) p(.) c(.) no mov	-3534.3803	228.9366	0	0	19
φ(.) p(t)=c(t) random (t)	-3533.9274	229.3895	0	0	26
φ(t) p(.)=c(.) no mov	-3528.5907	234.7262	0	0	18
φ(.) p(t,t) c(t,t) no mov	-3525.942	237.3749	0	0	46
φ(.) p(t) c(t) random (t)e (.)	-3524.3773	238.9396	0	0	29
φ(.) p(t) c(t) no mov	-3512.6571	250.6598	0	0	28
φ(.) p(t,t)=c(t,t) no mov	-3501.2915	262.0254	0	0	37
φ(.) p(t)=c(t) random (.)	-3500.0002	263.3167	0	0	20
φ(.) p(t)=c(t) no mov	-3459.9842	303.3327	0	0	19
φ(.) p(.) c(.) random (.)	-3434.0682	329.2487	0	0	13
φ(.) p(.)=c(.) random (.)	-3412.613	350.7039	0	0	12
φ(.) p(.) c(.) no mov	-3380.6126	382.7043	0	0	12
φ(.) p(.)=c(.) no mov	-3317.7674	445.5495	0	0	11

RIBELIN

Model	QAICc	Delta QAICc	AICc Weights	Model Likelihood	Num. Par
φ(.) p(t,t)=c(t,t) no mov	-729.9427	0	0.34492	1	25
φ(.) p(t,t)=c(t,t) random (.)	-728.2333	1.7094	0.14673	0.4254	26
φ(.) p(t) c(t) random (.)	-727.1362	2.8065	0.08478	0.2458	20
φ(.) p(t,t)=c(t,t) Markov (.)	-726.5937	3.349	0.06464	0.1874	27
φ(t) p(t,t)=c(t,t) random (.)	-726.1016	3.8411	0.05054	0.1465	30
φ(t) p(t) c(t) random (.)	-725.9579	3.9848	0.04704	0.1364	24
φ(t) p(t,t)=c(t,t) no mov	-725.8037	4.139	0.04355	0.1263	29
φ(.) p(t) c(t) Markov (.)	-725.0018	4.9409	0.02916	0.0845	21
φ(.) p(t) c(t) no mov	-724.6433	5.2994	0.02438	0.0707	19
φ(t) p(t) c(t) Markov (.)	-724.4345	5.5082	0.02196	0.0637	25
φ(t) p(t,t)=c(t,t) Markov (.)	-724.3678	5.5749	0.02124	0.0616	31
φ(.) p(t,t) c(t,t) random (.)	-724.1433	5.7994	0.01898	0.055	32
φ(.) p(t,t) c(t,t) no mov	-724.0595	5.8832	0.01821	0.0528	32
φ(.) p(t) c(t) random (t)	-723.7058	6.2369	0.01525	0.0442	24

φ(t) p(t,t) c(t,t) no mov	-723.5232	6.4195	0.01392	0.0404	34
φ(.) p(t,t)=c(t,t) random (t)	-722.8917	7.051	0.01015	0.0294	30
φ(.) p(t,t) c(t,t) Markov (.)	-722.5175	7.4252	0.00842	0.0244	33
φ(t) p(t,t) c(t,t) random (.)	-722.2238	7.7189	0.00727	0.0211	35
φ(t) p(t,t) c(t,t) Markov (.)	-722.0678	7.8749	0.00673	0.0195	35
φ(t) p(t) c(t) no mov	-721.5419	8.4008	0.00517	0.015	23
φ(t) p(t) c(t) random (t)	-720.9931	8.9496	0.00393	0.0114	27
φ(t) p(t,t)=c(t,t) random (t)	-720.3451	9.5976	0.00284	0.0082	33
φ(t) p(.) c(.) random (.)	-719.5534	10.3893	0.00191	0.0055	14
φ(t) p(t) c(t) Markov (t)	-719.3269	10.6158	0.00171	0.005	29
φ(.) p(t,t) c(t,t) random (t)	-718.887	11.0557	0.00137	0.004	35
φ(.) p(.) c(.) random (t)	-718.6317	11.311	0.00121	0.0035	14
φ(.) p(t) c(t) Markov (t)	-718.15	11.7927	0.00095	0.0028	28
φ(t) p(.) c(.) Markov (.)	-718.0398	11.9029	0.0009	0.0026	15
φ(.) p(t,t)=c(t,t) Markov (t)	-717.9202	12.0225	0.00085	0.0025	34
φ(t) p(t,t) c(t,t) random (t)	-715.9344	14.0083	0.00031	0.0009	38
φ(t) p(t,t)=c(t,t) Markov (t)	-715.4785	14.4642	0.00025	0.0007	36
φ(t) p(.) c(.) random (t)	-714.9657	14.977	0.00019	0.0006	17
φ(.) p(t,t) c(t,t) Markov (t)	-714.4718	15.4709	0.00015	0.0004	39
φ(.) p(.) c(.) random (.)	-714.259	15.6837	0.00014	0.0004	10
φ(.) p(.) c(.) Markov (t)	-714.1723	15.7704	0.00013	0.0004	18
φ(.) p(.) c(.) Markov (.)	-712.2268	17.7159	0.00005	0.0001	11
φ(t) p(.) c(.) Markov (t)	-712.0043	17.9384	0.00004	0.0001	20
φ(t) p(t,t) c(t,t) Markov (t)	-710.94	19.0027	0.00003	0.0001	41
φ(.) p(t)=c(t) no mov	-699.9556	29.9871	0	0	13
φ(t) p(.) c(.) no mov	-698.1531	31.7896	0	0	13
φ(.) p(t)=c(t) random (.)	-698.1237	31.819	0	0	14
φ(t) p(.)=c(.) no mov	-697.8988	32.0439	0	0	12
φ(t) p(.)=c(.) random (.)	-697.2033	32.7394	0	0	13
φ(.) p(t)=c(t) Markov (.)	-696.5973	33.3454	0	0	15
φ(t) p(t)=c(t) no mov	-696.4072	33.5355	0	0	17
φ(t) p(t)=c(t) random (.)	-696.336	33.6067	0	0	18
φ(t) p(.)=c(.) Markov (.)	-695.3743	34.5684	0	0	14
φ(.) p(.) c(.) no mov	-694.9823	34.9604	0	0	9
φ(t) p(t)=c(t) Markov (.)	-694.5827	35.36	0	0	19
φ(.) p(.)=c(.) no mov	-693.1375	36.8052	0	0	8
φ(.) p(t)=c(t) random (t)	-692.8708	37.0719	0	0	18
φ(.) p(.)=c(.) random (t)	-692.6754	37.2673	0	0	13
φ(t) p(.)=c(.) random (t)	-692.637	37.3057	0	0	16
φ(.) p(.)=c(.) random (.)	-691.881	38.0617	0	0	9
φ(t) p(t)=c(t) random (t)	-690.8655	39.0772	0	0	21
φ(.) p(.)=c(.) Markov (t)	-690.8024	39.1403	0	0	17
φ(.) p(.)=c(.) Markov (.)	-689.8697	40.073	0	0	10
φ(.) p(t)=c(t) Markov (t)	-688.7736	41.1691	0	0	22
φ(t) p(.)=c(.) Markov (t)	-687.7023	42.2404	0	0	19
φ(t) p(t)=c(t) Markov (t)	-686.2001	43.7426	0	0	24