

USING SPATIOTEMPORAL MODELS AND DISTANCE SAMPLING TO MAP THE SPACE USE AND ABUNDANCE OF NEWLY METAMORPHOSED WESTERN TOADS (*ANAXYRUS BOREAS*)

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Abstract.—High variability in abundance, cryptic coloration, and small body size of newly metamorphosed anurans have limited demographic studies of this life-history stage. We used line-transect distance sampling and Bayesian methods to estimate the abundance and spatial distribution of newly metamorphosed Western Toads (*Anaxyrus boreas*) in terrestrial habitat surrounding a montane lake in central Washington, USA. We completed 154 line-transect surveys from the commencement of metamorphosis (15 September 2009) to the date of first snow accumulation in fall (1 October 2009), and located 543 newly metamorphosed toads. After accounting for variable detection probability associated with the extent of barren habitats, estimates of total surface abundance ranged from a posterior median of 3,880 (95% credible intervals from 2,235 to 12,600) in the first week of sampling to 12,150 (5,543 to 51,670) during the second week of sampling. Numbers of newly metamorphosed toads dropped quickly with increasing distance from the lakeshore in a pattern that differed over the three weeks of the study and contradicted our original hypotheses. Though we hypothesized that the spatial distribution of toads would initially be concentrated near the lake shore and then spread outward from the lake over time, we observed the opposite. Ninety-five percent of individuals occurred within 20, 16, and 15 m of shore during weeks one, two, and three respectively, probably reflecting continued emergence of newly metamorphosed toads from the lake and mortality or burrow use of dispersed individuals. Numbers of toads were highest near the inlet stream of the lake. Distance sampling may provide a useful method for estimating the surface abundance of newly metamorphosed toads and relating their space use to landscape variables despite uncertain and variable probability of detection. We discuss means of improving the precision of estimates of total abundance.

Key Words.—*Anaxyrus boreas*; Bayesian estimation; distance sampling; juvenile; metamorphosis; variable-distance line-transect; Western Toad; WinBUGS

INTRODUCTION

Once abundant throughout much of western North America, Western Toads (*Anaxyrus boreas*) have declined dramatically in portions of their range, especially in montane areas where they were historically most abundant (Corn et al. 1989; Leonard et al. 1993; Carey et al. 2005; Muths and Nanjappa 2005). Declines have been most dramatic for southern Rocky Mountain populations (Muths et al. 2003; Carey et al. 2005), and there is some evidence of declines in the Pacific Northwest (Davis and Gregory 2003; Wentz et al. 2005; Pearl et al. 2009). Disease-related mortality of adult toads has been implicated in some declines (Muths et al. 2003). However, mortality of adults must be put into the context of the entire life-cycle for a full understanding of population-level dynamics.

To date, demographic research on Western Toads has focused on the adult stage or on evidence of breeding (Muths and Nanjappa 2005). Little is known of newly metamorphosed toads in terms of their abundance relative to other life-history stages, factors affecting survival and growth, preferred habitats, or space use

(Bull 2009). Considering the potential for explosive population growth (mature females can lay as many as 12,000 eggs [Wright and Wright 1949; Samollow 1980; Leonard et al. 1993]), the larval and early terrestrial stages have been under-studied. Small differences in survival rates to sexual maturity could greatly affect numbers recruited to breeding populations and population growth. Understanding factors affecting space use of newly metamorphosed toads may help to clarify the relative importance of risks such as road mortality (Bull 2009), cannibalism at the natal pond (Child et al. 2008b), and desiccation mortality in habitats having different temperature and humidity extremes (Child et al. 2008a, 2009; Hossack et al. 2009). While mark-recapture and radiotelemetry work well for studying adult toads, the effectiveness of these methods is limited for earlier life-stages due to their small size and high variability in abundance. Better methods, therefore, are needed to study the early life-history stages *in situ*.

Several factors make distance sampling a useful method for studying the abundance and spatial distribution of cryptic, newly metamorphosed toads.

Distance sampling, also known as variable-distance line-transect or point-transect sampling (Buckland et al. 1993), is suitable for the study of animal populations because it can be used to estimate density or abundance under minimal assumptions while accounting for variation in the probability of detection. Distance sampling may be accomplished relatively quickly, as there is no need to mark individuals or to revisit sites. Newly metamorphosed toads are diurnally active (Black and Black 1969; Lillywhite et al. 1973; Pizzato et al. 2008), facilitating surveys during daylight, and because of their low mobility, reactive movements should be minimal. They may also be easily captured to avoid double-counting, and the distance data may be measured directly rather than estimated as in avian point counts. Hence, newly metamorphosed toads on the ground surface meet many of the assumptions of distance sampling. However, the assumption that detection of individuals on the centerline is certain may be problematic. Violation of this assumption may occur when individuals are underground in burrows, for example, or otherwise unexposed to the physical search methods. In this case, unbiased estimates of surface abundance may still be made.

While newly metamorphosed toads on the ground surface may be amenable to the physical methodology of distance sampling, the conventional statistical framework for analysis of distance sampling data can be limiting. Conventional design-based distance sampling estimators (i.e., estimators reliant strictly on random sampling) preclude directly relating covariate data to abundance (Hedley et al. 2004; Royle et al. 2004). Yet, relating explanatory covariates to abundance is desirable from the standpoint of addressing hypotheses about habitat use, animal movement, and other aspects of spatial ecology, especially for variables that may be measured on a continuous scale. To address this issue, Royle et al. (2004) developed a model-based method (i.e., relying on a sample and its modeled relationship with other data) for distance sampling that facilitates relating explanatory variables to abundance. The method embodies the constructs of Poisson regression, the generalized-linear-model for count data, wherein a linear combination of potential explanatory variables is linked to the expectation of abundance at a small spatial scale. By adding random effect terms to the linear combination and adopting a Bayesian approach to estimation, the model of Royle et al. (2004) can be adapted to accommodate dependencies, as can occur when sites are repeatedly surveyed over time. Further, by modeling the spatial correlation among sites, small-area abundance estimates can be smoothed, leading to better clarity of spatial patterns (Elliott et al. 2000). This can be helpful in generating new hypotheses about space use and movement, improving local prediction, and producing abundance maps when important drivers of space use are

unknown *a priori*.

In this paper we address simple hypotheses about spatial variation in the surface abundance of newly metamorphosed toads over a 17 d period from first emergence from our study lake to the first significant snow accumulation. Our hypotheses focus on associations with lakeshore and stream habitats and how these associations changed over time. Specifically, we were interested in whether newly metamorphosed toads would be concentrated near lakeshore and stream habitats or more evenly distributed in both shore and terrestrial habitats. In addition, we hypothesized that the distribution of toads relative to water features would change as they dispersed to overwintering areas. The method leads to temporally and spatially smoothed estimates of local surface abundance and total surface abundance in terrestrial habitat that account for uncertain and variable probability of detection. We then relate body size, an important predictor of survival (Altwegg and Reyer 2003; Chelgren et al. 2006, 2008b), to the spatial distribution of toads. We describe the Bayesian estimation approach for line-transect distance sampling data adapted from existing models (Royle et al. 2004; Eguchi and Gerrodette 2009), and corroborate the model output with total surface abundance estimates made using a conventional design-based distance sampling estimator.

MATERIALS AND METHODS

Study area.—Tipsoo Lake is a shallow (average depth 1.8 m) palustrine wetland, approximately 1.45 ha in area at 1,617 m elevation located in the northeastern corner of Mount Rainier National Park, Washington, USA. This subalpine basin receives heavy winter snow leading to a short and variable snow-free season from late May or June to November. Roads and trails occur in high density surrounding the lake (Fig. 1), and the site receives up to 1,400 visitors on peak days. State highway 410 circumscribes three quarters of the lake's perimeter within 130 m of its shoreline and separates a secondary pool to the southeast, which is 13 m higher in elevation, from the main lake. To the west, within 35 m of a side pool of Tipsoo Lake, is a 0.4 ha parking area with nearby picnic facilities. The flow of water is from the southeast pool, through a perched culvert under the state highway into the south end of the main lake. Water then flows from the main lake into the west side-pool, and then exits the lake complex in a southwest direction, passing again under the highway in a second perched culvert located 30 m southeast of the main parking area. The lake was chosen for study because of its importance to the park as a toad breeding site and its potential vulnerability to human activities.

The terrestrial vegetation surrounding Tipsoo Lake is characterized by scattered stands of Subalpine Fir (*Abies lasiocarpa*) and Mountain Hemlock (*Tsuga mertensiana*)

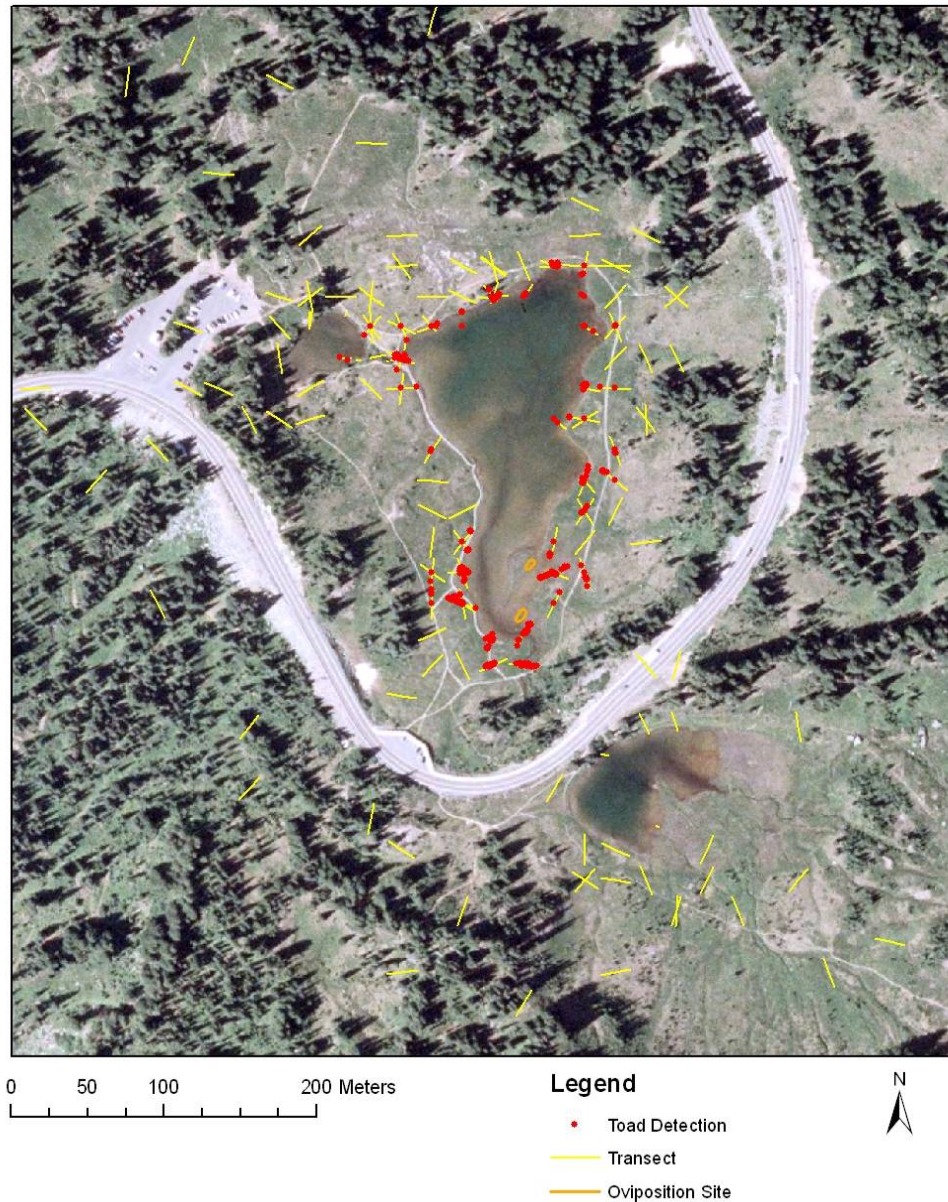


FIGURE 1. Tipsoo Lake in Mount Rainier National Park, Washington, USA, with transects (yellow lines) and locations (red polygons) of newly metamorphosed toads found from 15 September to 1 October 2009 during line-transects distance sampling. Oviposition sites are indicated with orange ellipses.

with little vegetative ground cover. Shrub cover is minimal in forest openings and is comprised of several species: Cascade Azalea (*Rhododendron albiflorum*), Rusty Menziesia (*Menziesia ferruginea*), Subalpine Spiraea (*Spiraea densiflora*), Sitka Mountain Ash (*Sorbus sitchensis*), and Grouseberry (*Vaccinium scoparium*). The herbaceous layer in forest openings, however, is dense, consisting of many forbs and grasses. The vertebrate community of the lake includes Cascade Frogs (*Rana cascadae*), Long-toed Salamanders (*Ambystoma macrodactylum*), and Northwestern Salamanders (*Ambystoma gracile*) coexisting with

introduced Rainbow Trout (*Oncorhynchus mykiss*).

Field methods.—We implemented a sampling design that was amenable to both the Bayesian and conventional distance sampling analytical methods and included features (stratification, spatially balanced random sampling, and inclusion of covariates) that were intended to improve the precision of abundance estimates and address our hypotheses. The study area surrounding Tipsoo Lake was limited to a 200 m radius from the lake shore to concentrate sampling yet still include plots on both sides of the state highway. We

partitioned the study area into 20 by 20 m (0.04 ha) contiguous plots as sample units. Plots that fell entirely within the lake were excluded from the sampling frame. We chose a plot size of 0.04 ha so that plots were large enough to reduce problems with error in navigation using aerial photographs and Global Positioning System (GPS) receivers, yet small enough to capture spatial variation in toad abundance that we expected to occur. We stratified the study area into three spatial strata (< 20 m, 20–50 m, and 50–200 m) based on the distance of plot centers from the lakeshore. While the strata boundaries were largely arbitrary, they permitted three levels of sampling intensity roughly proportional to abundance of toads observed anecdotally from trails in 2006. Within each stratum, we randomly selected a spatially balanced sample (Thompson 1992) of the 0.04 ha plots to be searched using line-transect distance sampling methods. The sample proportion was highest in the < 20 m stratum (74 transects), intermediate in the 20–50 m stratum (50 transects), and lowest in the 50–200 m stratum (30 transects). For each plot in the random sample, we randomly selected a compass bearing, and laid a 20 m measuring tape along the bearing such that the tape passed through the center of the plot. We avoided traversing the transect centerline during setup to minimize disturbance. We primarily used high-definition aerial photographs to locate plot centers, but used GPS receivers in forested areas (generally > 50 m from the lake).

Sampling occurred between 15 September and 1 October 2009. We defined three intervals of sampling as: week 1, September 15–18; week 2, September 22–25; and week 3, October 1. Random selection of plots and transects within plots was done each week so that individual plots were searched from zero to three times. We concentrated field sampling during mid-week to minimize conflicts with the majority of park visitors on weekends. The resulting temporally clustered sampling led to a practical weekly time-step for estimating temporal variation in total abundance and depicting change in the spatial distribution of toads. We searched for toads during daytime between 0900 and 1800 along the straight transect within the selected plots. Transects that intersected the lake were truncated and their surveyed lengths recorded. On hands and knees, we thoroughly searched the centerline, carefully turning and replacing cover objects on and near the centerline, and examining small mammal burrows, hoof prints and other depressions, duff, and vegetation cover. We proceeded along the transect attempting to avoid causing mortality to toads by carefully searching prior to moving, and minimizing our perpendicular movement, staying on the centerline.

At each toad sighting, we captured and held the individual in a plastic food-storage container to avoid double-counting and placed a pin flag at the location where the animal was first discovered. We recorded

numbers of individuals that we detected in clusters (defined by individuals touching one another) and recorded the cluster size on the pin flag. At the completion of the search, we then measured the perpendicular distance from the transect centerline to the location of each sighted animal or center of a cluster (hereafter labeled perpendicular distance). Because of the 50-m distance between plot centers, the rapid decline in detection with increasing distance from the centerline (maximum perpendicular distance after truncation = 1.38 m), and our perception of low vagility of toads, we believe there was a very small probability of double-counting individuals in more than one transect per week. We measured snout-vent length (SVL) of up to 20 individuals selected randomly from among those captured on each transect.

Analytical methods.—Distance-sampling is a method of estimating density or abundance of cryptic objects or wildlife that have less than certain detection. Provided that modeling assumptions are met, the method permits unbiased estimates while accounting for detection probability that decreases with increasing distance from the transect centerline or point location. Assumptions of basic line-transect distance-sampling are described by Buckland et al. (1993): detection on the transect centerline is certain; there is no movement of individuals in response to the observer; and the distances of individuals from the transect centerline are accurately measured. The area searched is generally assumed to be known, although in practice a truncation distance is often derived from the data (Buckland et al. 1993). In addition, the location of transects and the timing of sampling are such that the sampled area is a random sample of the total area and time-period, the observed distance data are independent of the total number of individuals, and detection of an object is independent of the spatial distribution of objects (Eguchi and Gerrodette 2009). The number of individuals detected during a survey is, in effect, adjusted by a correction factor that is derived from fitting a functional form to the decreasing frequency of detections with increasing distance from the observer (hereafter labeled detection function).

Two limitations of conventional distance sampling are that it is not possible to relate abundance to explanatory covariates, and fine-scale resolution in abundance is lost by pooling (Hedley et al. 2004; Royle et al. 2004). In the conventional framework, inference about spatial variation in abundance is limited to strata defined at the design stage (Hedley et al. 2004). Yet, the primary goals of our study were to address hypotheses related to the distance that toads moved into terrestrial habitat (distance as a continuous measure), and to produce fine-scale maps depicting spatial variation in abundance. Hedley et al. (1999), Hedley and Buckland (2004), and Royle et al. (2004) introduced methods to address these

shortcomings of conventional distance sampling. In the point-transect distance-sampling model of Royle et al. (2004) for binned radial distances, it is straightforward to relate explanatory covariates to the expectation of abundance at small spatial scales. Royle et al. (2004) provide a complete description of the model structure for binned (i.e., perpendicular distance data reduced to counts of observations falling within discrete distance categories), circular point-transects (Buckland et al. 1993). We describe the changes necessary for un-binned perpendicular distance data from line-transects in Appendix 1.

The distance-sampling model of Royle et al. (2004), which we have adapted for un-binned data from line-transects, permits linking explanatory variables to the expectation of abundance, much as in Poisson regression. This allows hypotheses to be directly assessed by examining the magnitude and significance of the coefficients of the explanatory variables. At the outset of the study, we defined four simple hypotheses about patterns of toad movement into terrestrial habitat following metamorphosis. First, we hypothesized that toads would initially be concentrated near the lake where they complete metamorphosis resulting in a negative effect of a covariate representing distance to lake. Next, American Toads (*Anaxyrus americanus*), and other anurans with rapid larval development, have depressed aerobic capacity and endurance immediately following metamorphosis, resulting in low mobility (Taigen and Pough 1981; Pough and Kamel 1984). Moreover, the wet bare mud and sand shoreline represents a unique habitat that may facilitate individuals maintaining consistent hydration when very small (Child et al. 2008a, b, 2009). Therefore, in our second hypothesis, we reasoned that abundance in shoreline plots would not follow the same continuous pattern with distance from the lake that we expected to observe in plots not directly adjacent the lake. We expected that an indicator variable (*Shore*) for shoreline plots (*Shore* = 1 for plots having some shoreline, otherwise *Shore* = 0) would be positive, reflecting low mobility of toads, and use of the moist lakeshore substrate immediately post-metamorphosis. Third, we hypothesized that distance to streams would be an additional factor affecting the distribution of toads because Western Toads may use streams (Young and Schmetterling 2009) and riparian habitats (Bull 2009) for dispersal. As a result, we expected a negative effect of a covariate representing distance to stream. Finally, we hypothesized that the relationships between toad abundance and spatial variables would change over time as toads transitioned to overwintering sites so we modeled change in abundance as a function of the spatial variables. While we originally hypothesized that roads could influence toad movement, the short distance toads moved from the lake precluded these hypotheses being addressed.

We used a geographic information system and aerial

photographs to acquire spatial explanatory variables. To model density D_{it} of newly metamorphosed toads in plot i during week t , we used the continuous variables *Lake* (distance of the plot center from the shore of the main lake, standardized to one standard deviation about the mean), and *Stream* (distance of the plot center to the nearest stream standardized to one standard deviation about the mean). Because there was little information available *a priori* regarding space use of newly metamorphosed Western Toads, we included random effect terms for plot by week w_{it} in the linear combinations to account for unexplained sources of variation in abundance. We modeled these random terms as spatially autocorrelated using the intrinsic Gaussian continuous autoregressive model of Besag et al. (1991) with week-specific variance parameters $\sigma^2_{w(t)}$. During weeks two and three, density was modeled as a function of density in the plot during the previous week. Along with the spatial random effects, this allowed plot- and week-specific estimates to be spatially and temporally smoothed.

Initially, examination of the estimated random effects revealed multi-modality. To correct for this poor model fit, we made two changes. First, we accounted for unexplained variation in numbers captured per transect by modeling the probability of capture, which is derived from the detection function, as over-dispersed using random effects P_{it} having variance σ^2_w (see Appendix 1). Second, we added an additional term *Ovip* to the linear combinations representing distance from the oviposition sites, standardized to one standard deviation about the mean:

$$D_{it} = \exp(\beta_{1,0} + \beta_{1,1}Lake_i + \beta_{1,2}Shore_i + \beta_{1,3}Stream_i + \beta_{1,4}Ovip_i + w_{it}) \quad (1)$$

$$D_{12} = D_{11} \exp(\beta_{2,0} + \beta_{2,1}Lake_i + \beta_{2,2}Shore_i + \beta_{2,3}Stream_i + \beta_{2,4}Ovip_i + w_{12}) \quad (2)$$

$$D_{13} = D_{12} \exp(\beta_{3,0} + \beta_{3,1}Lake_i + \beta_{3,2}Shore_i + \beta_{3,3}Stream_i + \beta_{3,4}Ovip_i + w_{13}) \quad (3)$$

The β s are intercepts and coefficients (fixed effects). To control for differences in transect length caused by intersection with the lake, abundance was scaled by the area sampled for each transect $a_{it} = 2WL_{it}$, where L_{it} is the transect surveyed length, and W is the effective half-width. The expectation of abundance λ_{it} for the Poisson model was then $\lambda_{it} = a_{it}D_{it}$. Truncation at the 90th percentile of perpendicular distance ($W = 1.38$ m) led to acceptable fit of the half-normal detection function based on the goodness of fit test procedure in program Distance (described below).

Finally, we attempted to improve the precision of abundance estimates by modeling detection probability as a function of a plot-scale covariate (Marques and Buckland 2004; Katsanevakis 2007). It was evident during anecdotal observations made in 2006 that newly metamorphosed toads on completely bare surfaces such as the mud and sand shoreline and groomed trails were

more visible than individuals that were dispersed among the densely vegetated ground cover. To take advantage of this observation, we modeled the effect of *Bare* (the proportion of the surveyed transect centerline that intersected completely bare habitats including shoreline, trail, and road surfaces) on the detection function using $\log(\sigma_{ii}) = \delta_0 + \delta_1 \text{Bare}_{ii}$ where σ_{ii}^2 is the variance of the half-normal detection function, and δ_0 and δ_1 are estimated intercept and coefficient parameters, respectively (Marques and Buckland 2004; Katsanevakis 2007).

To estimate model parameters, Royle et al. (2004) describe how the likelihood may be integrated, and inference based on the marginal model. However, in our case, because the spatial random effects preclude integration, we resorted to Bayesian Markov chain Monte-Carlo methods and averaged over the distribution of the random effects in the joint posterior. This was convenient in our application because it directly generated plot-specific estimates of local abundance. Response data for un-sampled plots were modeled as missing values, and total abundance was estimated by summing the plot-specific estimates over all plots within each of the three weeks. Prior distributions are described in Appendix 1. WinBUGS 1.4 (Gilks et al. 1994; available online <http://www.mrc-bsu.cam.ac.uk/bugs/>) code is provided in Appendix 2.

To corroborate the Bayesian spatial modeling, we analyzed the stratified data using the Distance 2.0 software (Thomas et al. 2010; available online <http://www.ruwpa.st-and.ac.uk/distance/>). We estimated stratum-specific abundance, although no estimate was possible for Stratum 3 (50–200 m from the lake shore), where no newly metamorphosed toads were encountered. We discarded the 10% of detections having the largest distance from the transect centerline to achieve model fit as was done in the Bayesian analysis. We used the half-normal detection function with parameters common to both strata. Based on Akaike Information Criterion (AIC), none of the cosine adjustments were included in the inferential model, nor was the effect of *Bare* included in the detection function.

Body size of newly metamorphosed anurans has been shown to relate to movement behavior (Beck and Congdon 2000; Chelgren et al. 2008b), physiological bases of movement such as hematocrit and hemoglobin concentrations (Pough and Kamel 1984) and aerobic scope (Taigen and Pough 1981), and habitat use (Chan-McLeod 2003), and can strongly impact survival (Altwegg and Reyer 2003; Chelgren et al. 2006; Chelgren et al. 2008a). We used standard multiple linear regression to examine the relationship between toad size ($n = 302$) and a measure of the distance of plot centers from the shore of the main lake. We related the natural log of snout-vent length $\ln SVL$ to $GTen$ (an indicator variable for plot centers located > 10 m from the main lake shore), using Day (number of days since 15

September) to control for growth and continued emergence of small late-metamorphosing toads:

$$\ln SVL \sim 1 + GTen + Day$$

We hypothesized that toads captured in entirely terrestrial plots would be larger than toads captured in plots adjacent the main lake. The 10 m cutoff ensured that no transect in the > 10 m set intersected the shore. We considered statistical significance at $\alpha = 0.05$ level with individual-parameter t-tests.

RESULTS

On 15 July 2009, we observed 21 adult Western Toads at Tipsoo Lake including three amplexed pairs. On the same day, at least four egg strings, including one being laid, were observed near the southern end of the lake (Fig. 1). Oviposition sites were in the shallow (5–10 cm) emergent zone among sparse sedge and mud. After 56 days (9 September), small numbers of newly metamorphosed toads were first observed near the shore of the main lake.

From 15 September to 1 October, when snow accumulation terminated our sampling, we completed 154 transect surveys totaling 2.2 km. We located 543 newly metamorphosed toads during the surveys (458 toads in 74 transects in the < 20 m stratum; 85 in 50 transects in the 20–50 m stratum; and 0 in 30 transects in the > 50 m stratum). Numbers observed per plot dropped quickly with increasing distance from the lakeshore (Fig. 1) and were greater near the southern end of the lake. The maximum distance from the lakeshore where we encountered a newly metamorphosed toad 38 m. The maximum perpendicular distance measured from a toad to the transect centerline was 4.18 m. Though many of the newly metamorphosed toads were detected on the wet bare sand and mud shoreline, individuals were also present but much more difficult to detect away from the shoreline in forb-dominated meadows (Fig. 2). Of the 543 toads found, only 48 were in clusters: eight clusters of two, four clusters of three, one cluster of four, and one cluster of 16 toads. Due to the small number of clusters, we ignored cluster size in the analysis and simply used, for each of the individuals separately, the measured perpendicular distance to the cluster center.

The surface abundance of newly metamorphosed toads peaked during 22–25 September, the second week of sampling, although abundance during weeks two and three were imprecisely estimated (Table 1). Posterior distributions of total weekly abundance derived from the Bayesian model were positively skewed (Fig. 3). As a result, the posterior medians (3,880, 12,150, and 6,015 toads, in weeks one through three, respectively) or modes (Fig. 3) were more representative point estimates of total abundance than the posterior means (Table 1).



FIGURE 2. Line-transect survey for newly metamorphosed Western Toads. Toad locations, indicated with orange flags, were typical of upland habitat used. (Photographed by Nathan Chelgren)

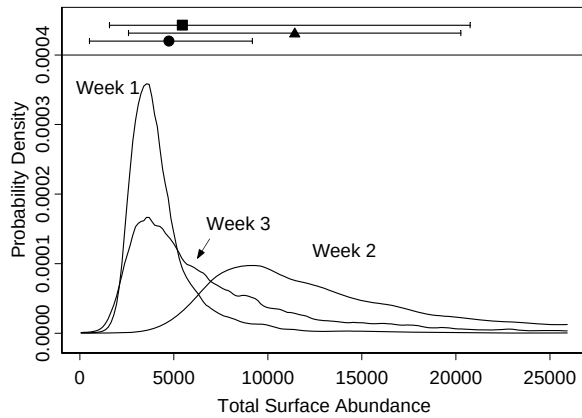


FIGURE 3. Posterior distributions of total surface abundance of toads by week (week 1, 15–18 September; week 2, 22–25 September; week 3, 1 October) from the Bayesian Spatiotemporal model. The point estimates with 95% confidence intervals at the top of the figure are the design-based estimates of total abundance from program Distance for week 1 (circle); week 2 (triangle); and week 3 (square). The y-axis is scaled so the area under each curve sums to one.

The Bayesian model corroborated well with the design-based approach. The design-based approach used in the Distance software produced estimates of total abundance that were 22% higher, 6% lower, and 9% lower than the posterior medians derived from the Bayesian analysis in weeks one, two, and three, respectively (Fig. 3).

As expected based on our first hypothesis, newly metamorphosed toads were initially concentrated near the shore of the main lake but there was no consistent spatial pattern of change in density between weeks. Toad surface density dropped off sharply as distance

from the main lake and from oviposition sites increased. These two variables (*Lake* and *Ovip*) were found to be important explanatory variables describing initial surface density, and had strong probabilistic support ($0.05 < \text{Pr}[\text{Parameter} < 0] < 0.95$; Table 1). Our second hypothesis that shoreline plots would have higher density than projected by the *Lake* effect was not supported (*Shore* effects; Table 1). Our third hypothesis that streams play an important role in dispersal was borne out by the fact that distance from the nearest stream (*Stream*) had the strongest probabilistic support in affecting change in density between weeks (Table 1). However, the effect of *Stream* was inconsistent between weeks, indicating a complex pattern of movements. There was no support for our hypothesis that change in density would relate to spatial variables other than the *Stream* effect. Based on the small magnitude of the spatial random effect standard deviations $\sigma_{w(t)}$ (Table 1), the explanatory variables accounted for the majority of spatial variation in toad surface density at the plot scale.

While the explanatory variables identified above captured the majority of variation in surface abundance between plots, the spatial random effects revealed a residual spatial pattern during week one. The residual spatial random effects estimated for week one w_{1i} (Fig. 4) indicated that initial toad surface density was lower to the west and higher to the east of the main lake relative to that predicted by the explanatory variables. The maximum (0.16) and minimum (-0.14) of the w_{1i} represent 17% higher and 13% lower density relative to that predicted by the explanatory variables. The very small values of $\sigma_{w(2)}$ and $\sigma_{w(3)}$ (Table 1) indicate that there was negligible residual spatial variation in weeks two and three, respectively. Cumulative probability of occurrence plots (Fig. 5) based on estimated surface abundance showed that the distribution of toads shifted in a consistent pattern, becoming more concentrated near the lake over time. Ninety-five percent of toads occurred within 20 m, 16 m, and 15 m of the shore during weeks one, two, and three, respectively. During sampling we observed that newly metamorphosed toads continued to emerge from the lake throughout the three weeks of sampling. We interpret the overall decrease in surface abundance and the shift toward proportionally greater numbers near the lake during weeks two and three to be the result of mortality and refuge or burrow use of dispersed individuals simultaneously with emergence from the lake of new individuals. The highest toad density (12.4 m^{-2}) occurred during week 2 near the southern end of the main lake in the vicinity of the inlet stream (Fig. 6).

TABLE 1. Summary of posterior distributions of model parameters and total abundance of toads by week ($N_{\text{week } t}$) from the Bayesian distance sampling model. Parameters δ_0 and δ_1 are the intercept and coefficient, respectively, for the effect of barren habitats on the detection function. Parameters $\beta_{t,r}$ from equations 1-3, are intercepts ($r = 0$) and coefficients for distance to lakeshore (*Lake*, $r = 1$), nearest stream (*Stream*, $r = 3$), and oviposition sites (*Ovip*, $r = 4$), and adjacency to lakeshore (*Shore*, $r = 2$) pertaining to toad density in week t . Spatial random effect standard deviations are $\sigma_{w(t)}$, and σ_p is the standard deviation for residual error. Parameters having strong probabilistic support ($0.05 < \text{Pr}[\text{Parameter} > 0] < 0.95$) are indicated with *. The summary $\text{Pr}(\text{Parameter} > 0)$ is not applicable (NA) for parameters bound in the positive range.

Parameter	Mean	Stdev	Lower 95%CI	Median	Upper 95%CI	Pr(Parameter > 0)
* δ_0	4.07	0.05	3.97	4.07	4.18	1.00
δ_1	-0.17	0.21	-0.55	-0.18	0.26	0.19
* $\beta_{1,0}$	-9.17	1.68	-13.33	-9.07	-6.34	0.00
* $\beta_{1,1}$	-5.54	1.74	-9.85	-5.50	-2.81	0.00
$\beta_{1,2}$	0.59	0.72	-0.95	0.60	1.89	0.76
$\beta_{1,3}$	-0.26	0.34	-1.05	-0.22	0.34	0.19
* $\beta_{1,4}$	-1.23	0.32	-1.91	-1.22	-0.61	0.00
$\beta_{2,0}$	-0.29	1.59	-3.54	-0.28	3.28	0.44
$\beta_{2,1}$	-1.22	1.53	-4.23	-1.17	2.30	0.20
$\beta_{2,2}$	0.04	0.61	-1.14	0.03	1.35	0.54
* $\beta_{2,3}$	-0.70	0.37	-1.44	-0.69	0.02	0.03
$\beta_{2,4}$	0.29	0.40	-0.49	0.30	1.07	0.78
$\beta_{3,0}$	-1.45	2.28	-5.95	-1.46	3.24	0.27
$\beta_{3,1}$	-0.51	2.05	-4.33	-0.60	3.88	0.40
$\beta_{3,2}$	0.69	0.83	-0.74	0.60	2.53	0.80
* $\beta_{3,3}$	0.97	0.54	-0.01	0.95	2.07	0.97
$\beta_{3,4}$	-0.15	0.53	-1.25	-0.11	0.78	0.41
$\sigma_{w(1)}$	0.37	0.35	0.01	0.29	1.21	NA
$\sigma_{w(2)}$	0.19	0.28	0.00	0.08	0.98	NA
$\sigma_{w(3)}$	0.21	0.37	0.00	0.07	1.22	NA
σ_p	0.69	0.09	0.51	0.69	0.87	NA
$N_{\text{week } 1}$	4861	6766	2235	3880	12600	NA
$N_{\text{week } 2}$	17360	35610	5543	12150	51670	NA
$N_{\text{week } 3}$	39990	790100	2095	6015	173600	NA

The covariate *Bare* did not explain variation in σ of the detection function (parameter δ_1 ; Table 1). This was consistent with the goodness of fit testing procedure in program Distance that did not support inclusion of a *Bare* effect on σ . There was, however, substantial variation associated with P_{it} (parameter σ_p ; Table 1). This represents residual (not spatially correlated) random

variation in numbers captured per transect, which may reflect true plot-level variation, or we suspect, fine-scale within-plot spatial variation that was not sampled adequately with the single transect per plot.

Snout-vent length was not strongly related to day and distance from shore (multiple $R^2 = 0.05$), though the effect of being greater than 10 m from shore (*GTen*) was significant ($t = 3.53$, $P = 0.0005$). Snout-vent length of toads was 5.27% (2.25%, 8.30% [95% confidence intervals]) greater in plots located > 10 m from the shore. The change in snout-vent length in the population over time (*Day*) was not significant at 0.17% (-0.05%, 0.39%) per day ($t = 1.55$, $P = 0.12$) over the three weeks of the study. Average snout-vent length was 12.25 mm (SE = 0.07).

DISCUSSION

Toad spatial ecology.—Newly metamorphosed Western Toads remained within 50 m of Tipsoo Lake in the three weeks between first emergence to first snow accumulation. Surface abundance became more concentrated close to the shoreline over time. Dispersed individuals were associated with the inlet stream of the main lake during the first two weeks following emergence and dissociated during the final week.

Other studies of the movements of newly metamorphosed toads (Sinsch 1997; Bull 2009) have documented that individuals move much greater distances from their natal ponds than we observed. Newly metamorphosed Western Toads have been observed at distances exceeding 2 km from their natal pond in northeastern Oregon within eight weeks of metamorphosis (Bull 2009). The maximum distance we observed toads was 38 m from the lake. However, the size of newly metamorphosed toads at Tipsoo Lake was small (12.25 mm) compared with other studies: Average SVL of newly metamorphosed Western Toads were 13.1 mm and 15 mm at two Colorado sites (Carey et al. 2005). Because size is positively related to physical and physiological bases of movement (Taigen and Pough 1981; Pough and Kamel 1984; Phillips et al. 2006), the small size of toads at Tipsoo Lake may have restricted the distances moved or delayed movements into terrestrial environments (Chelgren et al. 2008b). Indeed, toad size at Tipsoo Lake varied spatially, consistent with Child et al. (2009), with larger toads occurring further from the lakeshore. However, Sinsch (1997) observed that within weeks of metamorphosis, newly metamorphosed Natterjack Toads (*Epidalea calamita*) dispersed up to several hundred meters from their natal pond, despite even smaller size (6–11 mm SVL) than we observed.

While size can affect the magnitude of movements directly, small size is also linked with increased risk of desiccation (Child et al. 2008b), possibly limiting smaller toads to moist substrates. Recent work with newly metamorphosed Cane Toads (*Chaunus marinus*)

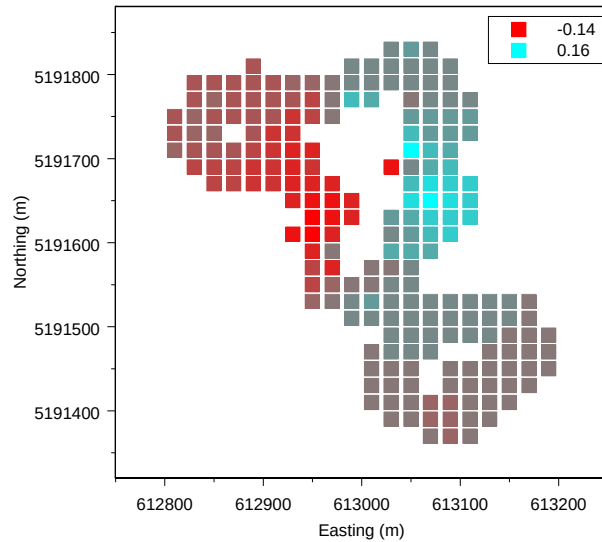


FIGURE 4. Spatially autocorrelated random effects depicting the spatial variation in log (density) that remained unexplained by independent variables during week one. Toad density was lower (bright red) than expected to the west and higher (bright blue) than expected to the east of the main lake (see Fig. 1 for sampling layout). Exponentiating the random effect estimates (i.e., $\exp[-0.14]$), which are posterior medians, yields the multiplicative effect on density relative to the value predicted by the fixed effects. Axes are Universal Transverse Mercator coordinates.

has shown that their movements are primarily driven by the need of individuals to hydrate on moist substrates (Child et al. 2009). Of toads that dispersed away from shoreline plots at Tipsoo Lake, there was evidence of their association with the lake inlet stream during weeks one and two, but this pattern was reversed in week three. This dissociation was not related to moisture, as the only precipitation fell between the week one and week two sampling episodes. Minimum temperature, however, plummeted to sub-freezing at the end of the week two sampling period. Child et al. (2009) described a diel “tidal” flow of juvenile Cane Toads away from and returning to the pond shore driven by desiccation risk; toads dispersed from the moist margins of the pond when moisture conditions permitted and retreated to the pond at midday. At Tipsoo Lake the difficulty of moving through dense terrestrial vegetation would seem to preclude this type of daily movement cycle, and we did not anecdotally observe regular movements away from and back to the lake shore during our sampling. The desiccation risk at our site was likely considerably lower than at the tropical Australian site studied by Child et al. (2009). Individuals using upland habitat surrounding Tipsoo Lake also may have retreated to the burrows of small mammals during critical periods for maintaining water balance, at least partially explaining the decrease in surface abundance during the third week of sampling. Burrow use is commonly reported among anurans and especially in the family Bufonidae (Campbell 1970; Moore

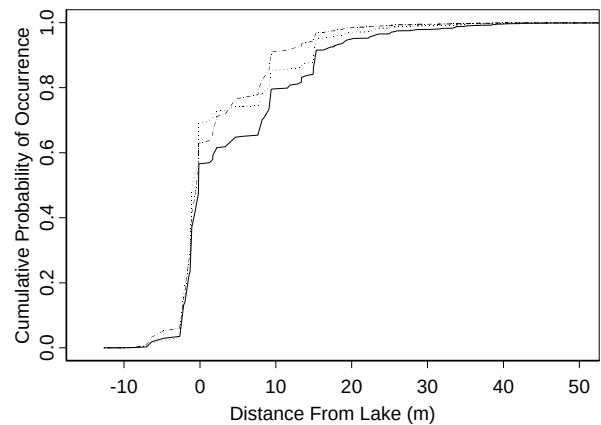


FIGURE 5. Cumulative probability of occurrence by distance of the plot center from the shore of the main lake and the week of sampling (week 1, 15–18 September, solid line; week 2, 22–25 September, dotted; week 3, 1 October, dot-dash). Plot centers in the negative distance range were located in the lake although the sampling was restricted to the upland (non-lake) portion of the transect.

and Moore 1980; Smits 1984, Browne and Paszkowski 2010). Mullally (1952) found adult Western Toads at 10 to 60 cm depth underground in over half of the Golden-Mantled Ground Squirrel (*Spermophilus lateralis*) burrows he excavated in October at Big Bear Lake in California, and adults were found crouching in surface depressions. Mullally (1953) also observed juvenile Yosemite Toads (*Anaxyrus canorus*) retreating to burrows in meadow areas surrounding breeding ponds in the Sierra Nevada. Our radio-telemetry work with Western Toads at Tipsoo Lake revealed that burrow use was the norm for adults during daytime (unpubl. data), and we regularly found newly metamorphosed individuals at the entrances of small mammal burrows and crouching in ungulate hoof prints and other depressions. The importance of subterranean retreats, which provide suitable stable temperatures for survival (Mullally 1952; Hossack et al. 2009), is underscored by Mullally (1952) who found that adult Western Toads that remained on the ground surface overnight were found dead and frozen solid at -2°C the next day. Roznik and Johnson (2009) observed that newly metamorphosed Gopher Frogs (*Rana capito*) that used burrows of other species survived at much higher rates than frogs that did not use burrows. At Tipsoo Lake, the only subterranean retreats available in the areas used by newly metamorphosed toads are the burrows of small mammals and we suspect these were the most likely microhabitats for overwintering. Temperatures reach freezing during the emergence period at montane sites, including Tipsoo Lake, thus we suspect that freezing may be a leading mortality factor for newly metamorphosed toads.

While desiccation risk was the primary factor affecting the spatial distribution of newly metamorphosed Cane Toads (Child et al. 2009), a secondary factor may be

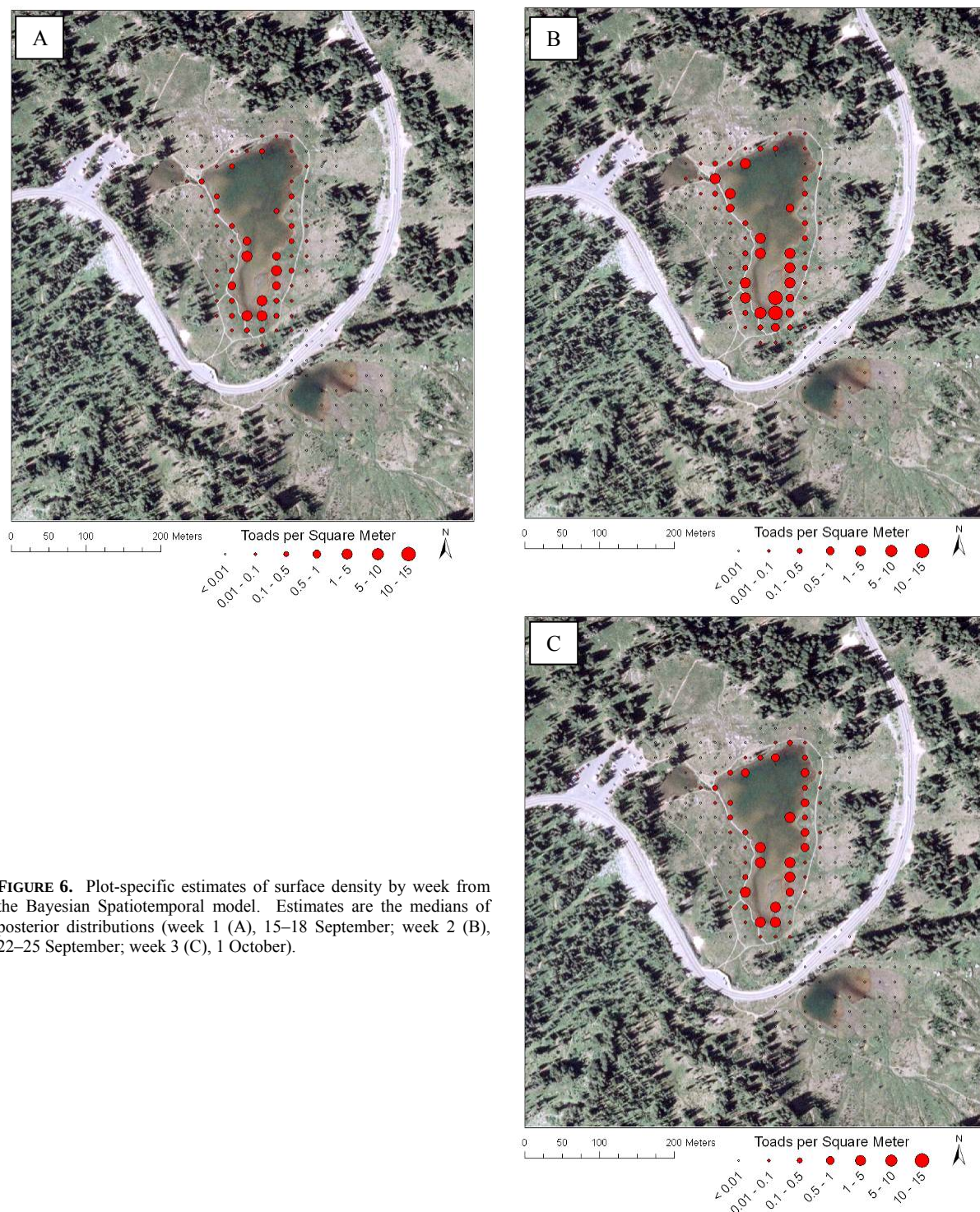


FIGURE 6. Plot-specific estimates of surface density by week from the Bayesian Spatiotemporal model. Estimates are the medians of posterior distributions (week 1 (A), 15–18 September; week 2 (B), 22–25 September; week 3 (C), 1 October).

avoidance of cannibalism from adults at the natal pond (Pizzatto et al. 2008; Child et al. 2009). The radio-telemetry portion of our study of adult Western Toads at Tipsoo Lake revealed that adults were distributed widely, hundreds of meters from the breeding site (unpubl. data). Cannibalism at Tipsoo Lake would therefore be minimal on newly metamorphosed toads

that remained near the lake. We did encounter adult anuran species during our distance sampling work that may prey on newly metamorphosed toads, but the numbers were small (one Western Toad, five Cascade Frogs, and one Coastal Tailed Frog [*Ascaphus truei*]). We more often observed flocks of American Robins (*Turdus migratorius*) apparently feeding on newly

metamorphosed toads, though we hypothesize that the overall risk from predation based on the numbers of predators observed was small in comparison to the risks of desiccation or freezing.

During our study, impacts from trail use appeared to be the only likely direct human impact to newly metamorphosed toads based on their spatial distribution up to the time that snow accumulated. Toads did not approach the nearby highway and we did not observe downstream dispersal as has been observed elsewhere (Young and Schmetterling 2009), possibly indicating avoidance of disturbance associated with the parking facilities. Child et al. (2008b) concluded from experimental work that the risk of mortality from predation strongly affected space use by newly metamorphosed Cane Toads. Disturbance may disrupt preferred habitat use and migration patterns or increase escape behavior (Garner et al. 2008), and these changes in behavior may also lead to greater exposure to desiccation or freezing conditions and higher energy expenditure. The pattern of spatial residuals during week one, where toads were less abundant to the west and more abundant to the east of the lake (Fig. 4), may support dissociation with the parking area and associated human disturbance. Alternatively, the same pattern may be explained by topography if toads are more likely to use flat meadow than the area with greatest slope to the west of the lake.

Distance sampling and estimation.—Estimates of total abundance compared reasonably well between the Bayesian model and the Distance software; however, measures of uncertainty were large using both approaches. The precision of our estimates of total abundance would be improved by increasing the spatial coverage of the distance sampling, especially near the lake and the inlet stream where abundance was greatest. A second important source of uncertainty in abundance estimates from the Bayesian model stemmed from the need to model variation in P_{it} , which represents the probability that an individual present within the terrestrial habitat of plot i at time t is within the effective area sampled $2 \times W \times L_{it}$. This was done to achieve model fit, but there was a cost in terms of precision. Poor sampling design within individual plots appeared to be the root of this problem. The single transect did not perform well in the face of fine-scale spatial variation in surface density within plots. A better practice would be spatially balanced random placement of multiple small transects (or point-sampling locations) rather than a single long transect per plot. Additional improvement to the precision of estimates might be made by stratifying by distance from streams, or by using adaptive distance sampling methods (Pollard and Buckland 2004).

The model-based Bayesian estimation approach has

three attractive benefits over the design-based approach of program Distance. First, it is straightforward to model local abundance relationships with continuous covariates or other explanatory variables. Second, fine-scale variation in abundance may be estimated, providing a means of characterizing abundance over any subset of the domain of sampling, and providing a means of producing fine-scale maps. A third advantage that we have not discussed is that model-based approaches alleviate the need for random transect placement (Hedley and Buckland 2004). It is this feature that allowed us to estimate abundance in the Bayesian model without taking account of the three different sampling intensities in the 0–20 m, 20–50 m and 50–200 m strata. There are also disadvantages of the model-based approach compared with the design-based approach. The model-based approach is computationally more intensive, and may be less robust to deviations from model fit than design-based approaches (Hedley and Buckland 2004).

Perhaps the most important assumption of distance-sampling methodology is that detection of animals on the transect centerline or point-transect center is certain (Buckland et al. 1993). Estimates of total toad abundance will be biased if a subset of the population is unavailable to be sampled, such as when toads are in burrows underground. Careful interpretation of results as surface abundance is technically correct, but may be inadequate for research and conservation needs. Lawton et al. (2006) presented estimates of abundance of burrowing seabirds using a combination of distance sampling and burrow-scoping. We suspect similar combined methods may be fruitful for separately estimating a below-ground component of total population size for Western Toads and other anurans that use subterranean terrestrial retreats. Alternatively, capture-recapture may be a more efficient method that can be made to account for numbers of individuals temporarily unexposed to the physical search methods (Kendall and Nichols 1995).

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Chelgren et al.—Space use of newly metamorphosed *Anaxyrus boreas*.



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APPENDIX 1

Royle et al. (2004) developed a distance sampling model wherein abundance may be modeled with covariates at small spatial scales. They describe the model likelihood function for binned circular point-transects. Here we first generalize the model to include temporal variation. We then show the changes in model structure that are made for un-binned line-transects. In the model of Royle et al. (2004), the likelihood for plot i at time t is the product of a multinomial term $m(\mathbf{y}_i | N_i, \theta)$ describing the number of individuals $\mathbf{y}_i = (y_{i1}, y_{i2}, \dots, y_{iK})$ detected within each distance class k , and a Poisson term $p(N_i | \lambda)$, that is a probability distribution for abundance N_i at the plot

$$L(N_i, \lambda, \theta | \mathbf{y}_i) = m(\mathbf{y}_i | N_i, \theta) p(N_i | \lambda). \quad (4)$$

The parameter θ characterizes the decreasing frequency of detections with increasing distance from the observer, and the parameter λ characterizes the expectation of abundance in the Poisson distribution. While the model described by Royle et al. (2004) is for data from binned, circular point-transect distance-sampling, Eguchi and Gerrodette (2009) describe the likelihood for a single plot with un-binned perpendicular distance data from line-transects such as our data.

Adapting the model of Royle et al. (2004) for un-binned line-transect surveys is straightforward. Assuming independence of the total number of detections n_i , and the perpendicular distance data $\mathbf{x}_i$, the multinomial term $m(\mathbf{y}_i | N_i, \theta)$ in equation (4) for counts is replaced with $b(n_i | N_i, \theta) f(\mathbf{x}_i | \theta)$ (Eguchi and Gerrodette 2009). The first component $b(n_i | N_i, \theta)$ describing the total number captured, is a binomial model

$$b(n_i | N_i, \theta) = \binom{N_i}{n_i} (\pi_a(\theta))^{n_i} (1 - \pi_a(\theta))^{N_i - n_i} \quad (5)$$

(Eguchi and Gerrodette 2009), since the total count is just a collapsing of the binned situation (multinomial) to a single distance bin (binomial), the outer distance limit of the binomial bin being referred to as the effective half-width W (Buckland et al. 1993). Next, for circular point-transect sampling as in Royle et al. (2004), the integrand that is necessary to compute the multinomial cell probabilities, in the case of binned counts, or binomial probability $\pi_a(\theta)$, in the case of un-binned but truncated distances, accounts for the area of the circle increasing non-linearly with the distance from the center-point. Eguchi and Gerrodette (2009) provide the probability of detecting an object within the rectangular sampled area for line-transects

$$\pi_a(\theta) = \frac{P_a}{W} \int_0^W g(y | \theta) dy \quad (6)$$

where $g(y | \theta)$ is the probability of detection as a function of perpendicular distance, and $g(y | \theta) \propto f(x | \theta)$. The proportion P_a , which we have inserted accounts for the spatial coverage bias (Buckland et al. 1993 [pg. 97]; Royle et al. 2007) that results from the effective area of the distance sampling in plot i at time t being only a fraction of the total area of upland habitat available in the plot. When there is adequate replication, extra-binomial variation in numbers captured per transect may be estimated using $P_a = (2WL_i / (\text{Plot Area}))^{\exp(e_i)}$, where e_i are normal random effects having variance σ_e^2 , and L_i is the transect length.

The model for the perpendicular distance data $f(x | \theta)$ can take many forms (Buckland et al. 1993). A convenient choice that we used, which was also used by Royle et al. (2004) and Eguchi and Gerrodette (2009), is the half-normal model with parameter σ^2 (i.e., $\theta = \sigma^2$)

$$f(x | \theta) = f(x | \sigma^2) = \frac{2}{\sigma\sqrt{2\pi}} \exp\left(-\frac{x^2}{2\sigma^2}\right). \quad (7)$$

This has computational advantages (Royle et al. 2004; Eguchi and Gerrodette 2009) and can be easily adapted to accommodate covariates

for the detection function by the substitution $\sigma_i = \exp(\delta_0 + \delta_i \text{Bare}_i)$ (Marques and Buckland 2004; Katsanevakis 2007). When distance data are truncated, which is often done to exclude outliers (Buckland et al. 1993), then a truncated normal distribution must replace (7) (Appendix 2). In the case of line-transect distance-sampling, whether distance data are truncated or not, the half-normal density function leads to

$$\pi_a(\theta)_i = \pi_a(\sigma^2)_i = \frac{P_a \sqrt{2\pi\sigma^2}}{W} \int_0^W \sqrt{\frac{1}{2\pi\sigma^2}} \exp\left(-\frac{x^2}{2\sigma^2}\right) dx \quad (8)$$

(Eguchi and Gerrodette 2009).

We used a Bayesian approach and the WinBUGS 1.4 software to simulate posterior distributions of model parameters. We used diffuse, non-informative, prior distributions for regression parameters and a hierarchical (two-level) prior arrangement for the random effect standard deviations. Regression coefficients $(\delta_1, \beta_{1,i}, \beta_{2,i}, \dots, \beta_{4,i})$ and intercept δ_0 were given independent Normal(0, 1.0e-4) priors, and the intercepts $\beta_{0,i}$ were given improper [flat()] priors (WinBUGS 1.4 Map Manual). We used the hierarchical half-t prior distribution recommended by Gelman (2006) for the random effect standard deviations $(\sigma_{w(1)}, \sigma_{w(2)}, \sigma_{w(3)}, \text{ and } \sigma_p)$ where the scale parameter controlling the extent of shrinkage was itself given a Uniform(0, 3) prior. Posterior distributions are based on 15,000 samples from the Markov chain taken every 500th iteration after an initial burn-in period required for the Markov chain to stabilize.

APPENDIX 2

The following code may be used in the WinBUGS 1.4 software to relate covariate data (Z) to animal density at site i using un-binned line-transect distance sampling data.

```
#-----Data-----
#nTran is the number of sites surveyed.
#nTranStar is the number of sites having at least one detection.
#Ensure that the first nTranStar records are those sites that have > 0
detections.
#The next (nTran - nTranStar) records should be those having 0
detections.
#n[i] is the number of individuals detected within distance W at site
i.
#y[i, j] is the perpendicular distance measured for individual j of site
i.
#Habitat[i] is the area of suitable habitat associated with site i.
#L[i] is the length of transect surveyed at site i.
#Z[i] is a covariate datum associated with site i.
#W is the transect effective half-width.
#T is the truncation distance. Commonly if data are truncated then
T=W.
#C is a positive constant necessary for ensuring p < 1 (see
"Specifying a new sampling
distribution" in "Advanced Use of the BUGS language" of the
WinBUGS user manual).
#pi is the mathematical constant.
#-----Parameters-----
#B[1] and B[2] are intercept and coefficient of covariate data Z.
#sigma is the square root of the variance of the normal distribution.
#N[i] is the latent abundance at site i. Initial values for N[i] must be
> 0.
#-----
model{
  for(i in 1:nTran){ #cycle through all transects,
    including those with no detections.
      #Next, relate the linear combination for density to the
      expectation of abundance lambda.
      lambda[i] <- Habitat[i]*exp(B[1] + B[2]*Z[i])
      N[i] ~ dpois(lambda[i]) #The number present at
                             site i is Poisson
                             distributed.
    }
  }
```

```
Pi[i] <- 2*W*L[i]/Habitat[i] #Pi[i] is the proportion
                              of the plot covered by
                              the effective # area.
Pn[i] <- Pa*Pi[i] #Account for the spatial
                  coverage bias.
n[i] ~ dbin(Pn[i],N[i]) #Model the number
                        captured given the
                        number present as a
                        # binomial outcome.
}
For (i in 1:nTranStar){ #cycle through only the sites having > 0
detections.
  for (j in 1:n[i]) { #for site i, cycle through all n[i] detections.
    #The following line is used when measured distances are
    not truncated.
    #Lik[i, j] <- 2/sigma * pow(2*pi,-0.5)*exp(-0.5*pow(y[i,
    j]/sigma,2))
    #The following line is used when measured distances are
    truncated at T.
    Lik[i, j] <- -1/sigma*pow(2*pi,-0.5)*exp(-
    0.5*pow(y[i,j]/sigma,2))/(phi(T/sigma)-0.5))
    #The following three lines are the 'ones trick' (see
    "Specifying a new sampling
    distribution" in "Advanced Use of the BUGS language" of
    the user manual).
    ones[i, j] <- 1
    p[i, j] <- Lik[i, j] / C
    ones[i, j] ~ dbern(p[i, j])
  }
}
#Next compute the probability of capture given an animal is within
the effective area of
#sampling.
Pa <- (1/W)*sqrt(2*pi/tau)*(phi(W*sqrt(tau))-0.5)
sigma ~ dunif(0,100) #Prior for the detection function
parameter.
tau <- pow(sigma,-2)
for(i in 1:2){
  B[i] ~ dnorm(0,1.0E-4) #Priors for the intercept and
coefficient related to density.
}
C <- 100000
pi <- 3.14159
}
```