Life history variation along an elevational gradient in *Plethodon montanus*: implications for conservation

Nicholas M. Caruso[1,2]

Leslie J. Rissler[1,3]

[1]Department of Biological Sciences, Box 870345 MHB Hall, University of Alabama, Tuscaloosa, Alabama 35487, USA

[2]Author for correspondence: carusonm@gmail.com

[3]Current address: Directorate for Biological Sciences, National Science Foundation, 4201 Wilson Blvd. Arlington, VA 22230, USA

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Abstract

Global amphibian populations are declining and evidence suggests that future changes in climate will have a negative effect on many populations, especially salamanders within the southern Appalachians. However, for many salamander species, the relationship between demographic vital rates (i.e., survival, growth, and reproduction) and climate is unknown, which limits predictive models. We, therefore, describe the life history variation of *Plethodon montanus* using capture-recapture data over a period of four years, at five sites along an elevational gradient and determined how vital rates vary with body size, elevation, sex, and season. We used a hierarchical model to estimate growth rate, asymptotic size, and the variance in periodic growth, while we used a spatial Cormack-Jolly-Seber model to estimate probability of capture and survival, as well as dispersal variance. Our results show that highest elevation population had a larger asymptotic size, slower growth, but also had higher survival compared to the lower elevation populations. Moreover, we found a disparity in seasonal survival among our elevations, at higher elevations, survival was higher during the inactive season (late fall, winter, early spring) compared to the active season, whereas the lower elevations showed either no difference in seasonal survival or had lower survival during the inactive season compare to the active season. Our results provide uncertainty in vital rates for this *P. montanus*, which can inform population models. Furthermore, given that survival is reduced in warmer habitats compared to cooler, the effect of future warming in the southern Appalachians and the ability of salamanders to adapt to these novel climates should be a focus of future research.

Introduction

Amphibians are one the most endangered vertebrate taxa (Hoffman et al., 2010; IUCN, 2016; McCallum, 2007; Sodhi et al., 2008; Stuart et al., 2004; Wake and Vredenburg, 2008) and face numerous threats including, but not limited to, emerging infectious diseases, habitat loss, invasive species, and climate change (Blaustein et al., 2011; Grant et al., 2016; Hoffman et al., 2010; Stuart et al., 2004). The status of global amphibian populations has deteriorated since the 1980s; currently, at least 41% of all species are considered threatened (Hoffman et al., 2010; IUCN, 2016; Stuart et al., 2004). Salamanders are likewise threatened, at least 50% of all salamander species are currently listed as “critically endangered”, “endangered”, or “vulnerable”, and nearly 54% of species within the most diverse family, *Plethodontidae*, are listed in these higher threat categories (IUCN, 2016). Trends in declining salamander populations have become ubiquitous; for example, occupancy of dusky salamanders (*Desmognathus fuscus fuscus*) has declined by 38% in Maine (Bank et al., 2006), while occupancy of salamanders surveyed throughout the United States has decreased by ~15% (Adams et al., 2013) and negative trends have been described for several other plethodontids in the eastern US (e.g., Caruso and Lips, 2013; Corser, 2001; Highton, 2005). These declines are especially concerning within the eastern United States and the Appalachian region because salamanders represent a significant portion of the total forest biomass and function as keystone predators (Burton and Likens, 1975; Milanovich and Peterman, 2016).

Given that many populations are already experiencing declines, future changes in climate, represent a compounding threat to amphibian populations (Caruso et al., *unpublished data* ; Milanovich et al., 2010; Sutton et al., 2015). Recent evidence suggests that contemporary changes in climate have already affected many Appalachian salamander communities. For example, Caruso et al. (2014) compared contemporary body size to historic collections for fifteen species across 102 sites finding that adult body sizes of six species have declined in areas that have become warmer and drier. In addition, we know that warmer conditions results in metabolic depression (Catenazzi, 2016) and slower growth rates of salamanders (Muñoz et al., 2016), which can negatively impact fitness in that smaller females typically produce fewer eggs (Petranka, 1998). Under future climate change, populations may become further isolated because montane salamanders are physiologically restricted to higher, cooler elevations which restricts their dispersal (Bernardo and Spotila, 2006; Bernardo et al., 2007; Gifford and Kozak, 2012; Lyons et al., 2016; Riddell and Sears, 2015). Current model predictions of how changes in climate may affect salamander populations are generally limited to correlative models (e.g., Caruso et al., *unpublished data* ; Milanovich et al., 2010; Sutton et al., 2015). These models, however, do not take into account metrics of demographic vital rates (i.e., survival, growth, and reproduction) as they are lacking for many salamander species. Therefore, current models likely underestimate the effects of future changes in climate (Buckley et al., 2010, Urban et al., 2016).

Demographic vital rates can vary across spatial gradients, and these rates are driven by the biotic (e.g., competition) and the abiotic (e.g., temperature) environment. Lower quality environmental conditions can limit a species’ distribution, while on the other hand, higher quality environmental conditions allow for persistence (Gaston, 2003; Hutchins, 1947). Whether these spatial gradients are predictable is up for debate (e.g., North-South Hypothesis, Cunningham et al., 2016), but in general, for many species, pole-ward range limits are thought to be set by abiotic factors and equator-ward limits by biotic interactions (Hairston, 1980; Lyons et al., 2016; Nishikawa, 1985; Schemske et al., 2009). Contrastingly, correlative niche models suggest that amphibian ranges may be more limited at the warmer range edges by the abiotic environment (Cunningham et al., 2016). Although data for montane salamander species are sparse, physiological constraints (Bernardo and Spotila, 2006; Gifford and Kozak, 2012; Lyons et al. 2016; Riddell and Sears, 2015) and results of reciprocal transplant experiments (Caruso et al., *submitted*) support this trend.

In natural populations, sampling biases such as unobservable ecological states, imperfect and variable detection, or measurement error can distort vital rate estimates (Eaton and Link, 2011; Kéry and Royle, 2016; Kéry and Schaub, 2012; Leberg et al., 1989; Royle and Dorazio, 2008; Schwarz and Runge, 2009). Capture-recapture (CR) methods offer a solution for accounting for these biases; observable ecological states and the transitions among these states can be tracked for individuals, while uncertainty in the unobservable states can be modeled by accounting for imperfect and variable detection of individuals through repeated surveys of a population (Kéry and Royle, 2016; Kéry and Schaub, 2012). Survival is often a focus of CR studies, as understanding survival, its variation (both temporal and spatial), and the abiotic and biotic factors that drive this variation, are necessary to understanding the underlying spatial and temporal variation in population growth (Lebreton et al., 1992; Saether and Bakke, 2000). However, using traditional CR models, true survival probabilities are often underestimated, as emigration from the study area and mortality are confounded (Lebreton et al., 1992; Schaub and Royle, 2014; Schaub et al., 2004). Recent advances in spatial CR models can alleviate these biases and produce more accurate survival estimates by accounting for dispersal behavior of individuals. Utilizing these models, the spatial location of individuals recorded during capture events and repeated captures is used to estimate dispersal (Schaub and Royle, 2014). Similarly, growth is useful for understanding population demographics since larger body size in many species, especially amphibians, is associated with higher survival and fecundity (Petranka, 1998). By estimating measurement error and variation within and among individuals, growth estimates can likewise be improved using CR methods (Eaton and Link, 2011; Link and Hesed, 2015).

As global climates continue to shift, baseline demographic vital rate estimates have become increasingly important to characterize the health of natural populations as well as critical data in the development of informed population models (Buckley et al., 2010; Caswell 2000; Coulson et al., 2005; Urban et al., 2016). Unfortunately, terrestrial plethodontids are fossorial and nocturnal, which means that vital rates, as well as other life history traits, are unknown for many species, adding further uncertainty to their potentially bleak future (e.g., Milanovich et al., 2010). Therefore, the objectives of our study were to 1) determine how demographic vital rates (growth, survival, reproduction) vary with body size, elevation, sex, and season, and 2) describe the elevational variation in life history characteristics (body size, movement, home range, and spatial distribution). This species is currently listed as Least Concern (IUCN, 2016) and is generally abundant within its range (Highton, 2005); however, future changes in climate will likely decrease suitable habitat throughout most of its range (Milanovich et al. 2010; Caruso et al. *unpublished data*). To develop predictions of population growth under future climate changes, the relationship between demography and climate is needed to inform models (McLean et al., 2016; Urban et al., 2016). Therefore, we collected four years of capture-recapture data for *Plethodon montanus* at five sites along an elevational gradient and used hierarchical models to test hypotheses about the demography of montane terrestrial salamanders. We hypothesized that *P. montanus* vital rates would be driven by climate, and that lower elevation populations will show reduced survival, growth, and reproduction compared to those at higher elevations.

Methods

We established five sites along an elevational gradient within the range of *P. montanus* in Pisgah National Forest in 2013 (Appendix 1): SPG (Spivey Gap; 996m), IMG (Iron Mountain Gap; 1,134m), HG, (Hughes Gap; 1,231m), BBT (Big Butt Trail; 1,300m), and CG (Carver's Gap; 1,464m). These sites were selected from a database of 192 historic collection localities made by Dr. Richard Highton and colleagues, and were chosen to minimize the differences among sites in leaf litter depth, slope-facing, canopy coverage, and amount of surface retreats while establishing an elevational gradient within known populations of *P. montanus*. Generally, lower elevation climates were marked by higher annual mean temperatures but also higher annual precipitation compared to higher elevation sites (Appendix 1).

Within each site, we delineated one-150 m^2 plot (10 x 15 m). Starting in 2014, we established a grid (25-2 x 3 m sections), within the plot to determine the location of each individual salamander within 0.5 m. In 2013 and 2014, we conducted diurnal and nocturnal surveys, while in 2015 and 2016 we only used nocturnal surveys. All areas of the plot were thoroughly searched and the starting corner of the plot was haphazardly chosen each survey. For diurnal surveys (n = 58; 31%), we generally searched plots just before dusk (median start times = 1900-1930; range of starting times = 1045-2005) and turned all available surface retreats within the study area. We used visual encounter surveys (n = 132; 69%) for nocturnal surveys, in which we started surveying after dusk (median start times = 2119-2120; range of starting times = 1900-2345) and captured salamanders that were active on the forest floor, and no retreats were turned. The majority of surveys (n = 164; 86%; 27-40 per site) were carried out by one surveyor, while two surveyors conducted 26 surveys (14%; 1-11 per site); the lead investigator was present at every survey to ensure consistency in sampling. Lastly, in approximately three-quarters of the 2015 surveys (n = 26/36) and all surveys during 2016 (n =20), we increased sampling effort by walking back through the plot. Salamanders were processed similarly regardless of survey type, amount of effort, or number of surveyors. Further details about sampling are available in Appendix 1.

Salamander Processing

We captured all salamanders by hand and placed each individual, separately, in a new plastic bag to facilitate measurements and reduce possible disease transmission between individuals; all salamanders were processed immediately after the plot had been searched. We determined sex based on presence of a mental gland and enlarged nasal labial grooves in males and large ova in females (visible through the ventral surface), and measured body size (tip of the snout to the posterior margin of the vent; SVL), tail length, and mass of each animal. For *P. montanus*, we marked individuals using Visual Implant Elastomer (VIE; Northwest Technology Inc., Shaw Island, Washington) tags. VIE tags have been shown to have minimal effects on salamander fitness and have low incidence of tag loss over time (Bailey, 2004; Davis and Ovaska, 2001). Individuals received 1-3 marks total at each of the five potential marking locations: left and right just posterior to the forelimbs, left and right just anterior to the hind limbs and immediately anterior to the anterior margin of the vent. We released all salamanders back to the original point of capture after all salamanders were processed.

Home Range Size, Movements, and Distribution of Captures

Because we determined the spatial location of each unique *P. montanus* individual we were also able to determine the distance moved between captures, home range size (for individuals with at least 5 collection localities), and the spatial distribution of captures. We estimated the distance moved between successive captures as Euclidian distance between capture locations and we determined home range size as the minimum convex polygon (MCP). We determined how site elevation, sex, and size (i.e., average SVL of individuals between successive captures) affects the distance moved using a linear mixed effects model, in which we included random intercepts for individual identity. To meet the assumption of normally distributed residuals, we log transformed the distance moved between successive captures plus one because many of the distances moved between successive captures were zero. We used a generalized linear model to determine how site elevation, sex, and size predicted home range size. Because home range sizes were bounded on the lower end by zero and were non-integers, we assumed a quasi-Poisson error distribution in our model. For both models, we included interactions between site elevation and size, and sex and size. We determined significance of fixed effects using a likelihood ratio test, and fit all models using maximum likelihood. Lastly, to determine if the spatial distribution of *P. montanus* at each site deviated from random, we compared the empirical cumulative distribution of observed nearest neighbor distances to the simulated spatial random distribution within the same observation window for each site.

Body Size, Maturation, and Reproduction

We determined the relationship between body size, site elevation, and the presence of mental glands and enlarged nasal labial grooves (males) or presence of eggs visible through the ventral surface (females) using a generalized linear mixed effects model with binomial error distribution. For both males and females, we only analyzed those individuals that were at least as large as the smallest individual that had a mental gland (males) or eggs (females) to ensure sampling of individuals that could at least potentially be sexually mature adults. To determine the relationship between the number of eggs per gravid female, and body size and site elevation, we used a generalized linear model with quasi-Poisson error distribution. For mixed models, individual identity was used as a random intercept since our dataset included multiple measurements for each individual.

Growth

We modeled growth using a hierarchical model (see Appendix 2) similar to those described by Eaton and Link (2011) and Link and Miller Hesed (2015). Briefly, our model assumes that growth of a given individual is a nondecreasing (i.e., ≥ 0) stochastic process, in which the true size of an individual at a given time is described by the size of the individual at a previous time and the amount of growth over the time interval. Each increment of growth is an independent gamma distributed random variable described by the difference in expected size (ΔES_{it}) over a given time interval and the variance in periodic growth for the population (λ).

$$Growth_{i\Delta t} \sim \Gamma(\lambda * \Delta ES_{it},\ \lambda) \quad \text{(Eq. 1)}$$

Where: ΔES_{it} is the difference in expected size for the *i*th individual at the *i*th measurement time. The expected size was estimated by the von Bertalanffy growth curve, parameterized for unknown ages (Fabens 1965; Eq. 2). Here, the expected size of an individual at time *t* (ES_{it}) is a function of its expected size at the previous measurement time (ES_{it-1}), the asymptotic size (*a*), the growth rate (*k*) scaled for 1000 day increments, and the interval between captures (Δt_i).

$$ES_{it} = ES_{it-1} + (a - ES_{it-1}) * (1 - e^{-k*\Delta t_i/1000}) \quad \text{(Eq. 2)}$$

Lastly, we estimated measurement error, in which our measurements of a given individual (y_{it}) are described by independent normal random variables with a mean of the true size (TS_{it}) and a variance of σ_ε^2

$$y_{it} \sim N(TS_{it}, \sigma_\varepsilon^2) \quad \text{(Eq. 3)}$$

Therefore, using this hierarchical model we were able to estimate growth rate (*k*), asymptotic size (*a*), variance in growth (λ), and measurement error (σ_ε^2) for each site. For all sites, we initially fit models with sex-specific values of *a*, *k*, and λ; however, we were unable to achieve convergence (i.e., $\hat{R}$ >> 1.1; Gelman et al., 2004) for either *a* (IMG, HG, CG) or λ (SPG, BBT) and assumed a single parameter value for both sexes at those sites (see Appendix 2).

Bayesian Growth Analysis

We assigned a vague normal (mean = 0; variance = 100,000) prior to the logarithm of parameters *k*, *a*, and λ and a vague Gamma prior (shape and rate = 0.001) to the parameter $1/\sigma_\varepsilon^2$. To assist with model convergence we set upper and lower limits on the priors for the logarithm of *a*, *k*, and λ indicating the assumed biological limits for this species. Because we were not able to observe the sex of all individuals without dissection, we modeled the sex of each individual with Bernoulli trials and assigned a 50% prior probability that animals were female. Dissection of *P. montanus* museum specimens, in which juveniles were sexed by visual inspection of gonads, supports this assumption of a 50:50 sex ratio (NMC *unpublished data*). We fit the model using Markov chain Monte Carlo using JAGS (Plummer, 2003), generating three chains, each with 70,000 iterations. We discarded 35,000 burn-in iterations, and used a thinning rate of ten, retaining 7,000 iterations to estimate posterior distributions. We examined trace plots of parameters for adequate mixing among chains and the $\hat{R}$ statistic (Gelman et al., 2004) to evaluate model convergence. We report posterior medians as point estimates, as well as 75% and 95% credible intervals (CRI) of all parameters.

Survival and Dispersal

In 2013 and 2014 we surveyed for three and four consecutive days (secondary periods), respectively, within each primary period. Using this design, we assume no change in ecological state of an individual (i.e., alive or dead) within a given primary period but populations are open between primary periods. In 2013, each primary period consisted of one diurnal surveys and two nocturnal surveys, while primary periods in 2014 consisted of two diurnal and two nocturnal surveys. Due to logistical constraints, we carried out one survey for each primary period (always nocturnal) during 2015 and 2016. Primary periods were separated by at least four days within a given year (range = 4-107). We used a spatial Cormack-Jolly-Seber (s-CJS) model (Schaub and Royle, 2014) to estimate salamander capture probability, movement, and survival (see Appendix 3 for code).

For each individual, we modeled survival to each primary period after its initial capture. Therefore, an individual's ecological state during the primary period where it is first captured and marked is known (i.e., equal to one). Thus, for subsequent primary periods, an individual's ecological state is described by a Bernoulli distribution where the probability of success (i.e., the individual is alive) is the product of the individual's probability of survival to that primary period ($\varphi_{i,t-1}$) and its previous ecological state ($z_{i,t-1}$).

$$z_{i,t} \sim B\ (\varphi_{i,t-1} * z_{i,t-1}) \qquad \text{(Eq. 4)}$$

Our observation process is likewise described by a Bernoulli distribution where the probability of success (i.e., finding the *i*th individual, at *t*th primary period, and *tt*th secondary period, given that it is alive) is the product of the capture probability ($p_{i,tt,t}$), ecological state ($z_{i,t}$), and its spatial state ($r_{i,tt,t}$).

$$y_{i,tt,t} \sim B\ (p_{i,tt,t} * z_{i,t} * r_{i,tt,t}) \qquad \text{(Eq. 5)}$$

To estimate true survival rather than apparent survival, which would include individuals who may still be alive but emigrated from the study area (Schaub and Royle, 2014), we included each individual's spatial location within each study site and estimated dispersal from subsequent recaptures. The spatial state ($r_{i,tt,t}$) of a the *i*th individual, at each *tt*th secondary period, and *t*th primary period, is given a value of one if the location ($Gx_{i,tt,t}$, $Gy_{i,tt,t}$) of the individual at that time is within the study area, while the spatial state receives a value of zero if the individual is outside the study area. Because we sampled secondary periods within primary periods (2013-

2014), we first describe the primary period center of activity ($Gx_{i,t}$). An individual's initial primary period center of activity is described by a uniform distribution, which is bounded by the lower and upper bounds of the plot area. An individual's center of activity at subsequent primary periods, therefore, is normally distributed where the mean is the individual's center of activity at a previous primary period ($Gx_{i,t-1}$, $Gy_{i,t-1}$) and estimated variance (σ^2_{Gxt}, σ^2_{Gyt}).

$$Gx_{ti,t} \sim N\ (Gx_{i,t-1}, \sigma^2_{Gxt}) \qquad \text{(Eq. 6)}$$

$$Gy_{i,t} \sim N\ (Gy_{i,t-1}, \sigma^2_{Gyt}) \qquad \text{(Eq. 7)}$$

Lastly, an individual's spatial location within a given primary period (i.e., during secondary periods) are also normally distributed, where the mean is the individual's primary period center of activity during the primary period ($Gx_{i,t}$, $Gy_{i,t}$) and the variance (σ^2_{Gxtt}, σ^2_{Gytt}) is estimated. We assigned uniform priors (min=0, max=10) to all spatial variance estimates. For capture probability, we included fixed covariates for survey type (diurnal or nocturnal), effort (1 or 2), number of people (1 or 2), linear and quadratic terms for Julian day, and random intercepts for individuals and primary period.

$$\text{logit}(p_{i,tt,t}) = \beta p_1[survey_{i,tt,t}] + \beta p_2[effort_{i,tt,t}] + \beta p_3[people_{i,tt,t}] +$$

$$\beta p_4 * jday_{i,tt,t} + \beta p_5 * jday^2_{i,tt,t} + \varepsilon_i + \gamma_t \qquad \text{(Eq. 8)}$$

As our initial study design included secondary sampling within primary periods, we modeled the logit of the capture probability ($p_{i,tt,t}$) for the *i*th individual, at the *t*th primary period, and *tt*th secondary period as a function of the five explanatory variables with estimated parameters (βp_1-βp_5) respectively, with random intercepts for primary period (γ_t) and individual (ε_i). Similarly, we described the logit of survival ($\varphi_{i,t}$) of an individual. Similarly, we modeled the logit of survival ($\varphi_{i,t}$) of the *i*th individual at the *t*th primary period as a function of four explanatory variables: sex (male or female), year (2013-2016), season (active or inactive season) and size (last SVL measurement). We estimate seven parameters ($\beta\varphi_1$ - $\beta\varphi_7$), allowing four parameters to correspond to categorical effects for each year:

$$\text{logit}(\varphi_{i,t}) = \beta\varphi_1[sex_i] + \beta\varphi_{2-5}[year_t] + \beta\varphi_6[season_t] + \beta\varphi_7 * size_i \qquad \text{(Eq. 9)}$$

While we initially fit the above-described model for all sites, for 4/5 sites we were unable to achieve convergence (i.e., $\hat{R} >> 1.1$; Gelman et al., 2004) for τ^{-2}_{Gxtt} (IMG, HG, BBT, CG) and therefore set $\tau^{-2}_{Gxtt} = \tau^{-2}_{Gxt}$. Additionally, for 2/5 sites (IMG, CG), we could not include the parameter $\beta\varphi_1[sex_i]$. For full model details, see Appendix 3.

Bayesian Survival Analysis

Numeric fixed covariates ($jday_{i,tt,t}$ and $size_i$) were centered and scaled prior to model fitting. We assumed vague normal priors (mean = 0; variance = 1,000) for all fixed parameters (βp_{1-5} and $\beta\varphi_{1-7}$), and random intercepts (γ_t and ε_i) were given normal priors. Fixed parameters were bounded between -10 and 10. Similar to the growth model, we modeled the sex of each individual with Bernoulli trials and assigned a 50% prior probability that animals were female (or male; i.e., we assumed a 50:50 sex ratio for each site). We fit the model using Markov chain Monte Carlo using JAGS (Plummer, 2003). For this model, we generated three chains, each with 100,000 iterations. We discarded 50,000 burn-in iterations, and used a thinning rate of ten (i.e., retained 15,000 iterations to estimate posterior distributions). As with the growth model, we examined trace plots of adequate mixing among chains and the $\hat{R}$ statistic (Gelman et al., 2004). We report posterior medians as point estimates, as well as 75% and 95% credible intervals (CRI) of all parameters.

All analyses were performed in program R version 3.3.1 (R Core Team, 2016). We used the *lme4* package (Bates et al., 2014) for fitting mixed effect models and determined significance of fixed effects using a likelihood ratio tests. We used the *adehabitatHR* package (Calenge, 2006) to determine MCPs and the *spatstat* package (Baddeley et al, 2015) to determine the observed spatial distributions and simulate the random distributions. Lastly, for all Bayesian analyses, we used the *R2jags* package (Su and Yajima, 2015) to call JAGS from Program R.

Results

We conducted a total of 190 diurnal (n = 58; 31%) and nocturnal (n = 132; 69%) surveys and captured 2,962 salamanders representing nine species (*P. montanus* = 2,413, 81%; non-target species = 549, 19%). For *P. montanus,* we marked a total of 1,343 individuals and recapture events constituted 1,070 (44%) of our total captures of this species; we recaptured 559 (42%) individuals at least once and recaptured individuals from a range of 1-15 times. For *P. montanus*, we found a range of body sizes from 15 – 68 mm, and the largest individuals were typically found at the highest elevation (see Appendix 4 for more details).

Movements, Home Range Size, and Distribution of Captures

For all sites, the distance moved between subsequent captures was typically low (mean = 1.784 m; SD = 1.875; range = 0 – 14.089 m) and home range sizes were small (mean = 1.306; SD = 1.176; range = 0 – 4.5 m^2). We found that males generally moved more and had larger home ranges than females and juveniles, and that the distance moved was positively related to the size of salamanders (Appendix 5). Lastly, we found that for 3/5 sites, salamanders exhibited a dispersed pattern, in which observed nearest neighbor distances were further apart than would be expected by chance (Appendix 5); both IMG and CG exhibited patterns no different from random.

Maturation and Reproduction

The smallest female with large visible eggs was 47.9 mm, while the smallest male showing secondary sex characteristics was 41.65 mm. Larger males and females had a higher probability of having mental glands and enlarged nasal labial grooves (χ^2 = 504.700; P < 0.001) and eggs ($\chi^2 = 57.971$; $P < 0.001$), respectively (Appendix 6). Moreover, we found that the size of reproductively mature males ($\chi^2 = 25.581$; $P < 0.001$) and females ($\chi^2 = 15.150$; $P = 0.004$) varied by site; at the highest elevations females reached reproductive maturity at larger sizes as compared to lower elevations (Appendix 6). However, for males, the probability of having a mental gland for a given body size was generally lower at the lower elevations (Appendix 6). Although, at the highest elevation, only large males (> 50 mm), showed presence of a mental gland, while smaller males at lower elevations displayed this secondary sex characteristic. However, for females we did not find a significant relationship between the number of eggs and body size ($\chi^2 = 6.378$; $P = 0.065$) or site ($\chi^2 = 5.714$; $P = 0.548$); gravid females had an average of 9.873 eggs (SD = 4.310).

Growth

Traceplots of growth parameters with the associated $\hat{R}$ statistic are show in Appendix 7. We used animals that were captured at least twice for all growth analyses, which included a range of total measurements of 54-529 per site (37-223 individuals; Appendix 4). We found variation in growth parameters (a, k, λ, and σ) between males and females and among our five sites (Figure 1). The three lowest elevation sites had similar asymptotic size (a) estimates (55.4-57.4mm), while BBT had the smallest asymptotic sizes (50.0-53.4mm), and our highest elevation site (CG) had the largest asymptotic size estimate (64.6mm); for both SPG and BBT, females had larger asymptotic sizes than males (Figure 1). The highest elevation site (CG) had the slowest estimated growth rates (k). While we found considerable overlap in growth rate estimates among our other four sites, females at our mid-elevation site (HG) had higher growth rates (Figure 1). Estimates of measurement error (σ) ranged from 0.632 to 1.183, while we found that our estimates of variance in growth (λ) had typically large and overlapping CRIs for all sites, though our lowest elevation site (SPG) showed lower estimates of λ (Figure 1).

Dispersal, Capture, and Survival

Traceplots of dispersal, capture, and survival parameters with their associated $\hat{R}$ statistic are show in Appendix 8. Dispersal variance estimates were similar for primary and secondary seasons, and across all sites (Figure 2) with values of approximately one in both directions, although the highest elevation site (CG) showed slightly lower values (Figure 2). Therefore, we would expect that 95% of an individual's movements in the x and y direction would be found within ~2m (range of all five sites = 1.721-2.397m) from their previous point of capture. Additionally, capture parameter estimates were similar, such that the direction of the parameters (i.e., positive or negative) was consistent across the elevational gradient; however, the magnitude for some parameters (i.e., βp_{JDay}, βp_{JDay^2}, and βp_{Survey}) varied. We found that the magnitude of the estimate of βp_{Survey} decreased (i.e., trended towards zero) with higher elevations. Probability of capture was higher during nocturnal surveys compared to diurnal surveys at all sites, but at higher elevations, the difference in capture probability between the two methods was reduced. Conversely, the magnitude of the parameters βp_{JDay} and βp_{JDay^2} generally increased (i.e., became more positive or more negative) with higher elevations (Figure 3). Capture probability was highest during early and mid July at the low and high elevation sites respectively and decreased towards both spring and fall seasons at all elevations.

For all five sites, we found that survival increased with increasing SVL, decreased for females compared to males, and showed opposing trends for seasonal survival along the elevational gradient. At higher elevations survival was higher during the inactive season compared to the active season, while at lower elevations survival was lower during the inactive season or was no different (Figure 4, 5). Moreover, we found that size-specific survival was similar for all sites during the active season; however, survival was consistently greater at the higher elevations compared to lower elevations during the inactive season (Figure 6).

Discussion

We present four years of capture-recapture data to provide a detailed account of the life history of *Plethodon montanus* along an elevational gradient, with a focus on growth and survival. We found that our high elevation populations had a larger asymptotic size, slower growth, and higher survival, especially during the inactive season, compared to lower elevation populations. Our results suggest that *P. montanus* exhibits variation in life history along this elevational gradient, likely resulting from the differences in abiotic environment experienced by those populations. Importantly, we provide baseline variation in vital rates for this species, and make recommendations for disentangling the environmental and genetic sources of variation in our observed differences in life history.

Movements, Home Range Size, and Distribution of Captures

Previous studies have found small home ranges, low dispersal, and territorial behavior in other species of terrestrial plethodontids (Kleeberger and Werner, 1982; Marvin, 1998; Mathis, 1991; Merchant, 1972; Muñoz et al., 2016; Petranka, 1998). Our observations for *P. montanus* are consistent with these patterns. Although we did not explicitly examine territoriality in these populations, spatial patterns of individuals were further apart than random, which is expected with territorial behavior (e.g., Mathis, 1991). Dispersal and subsequent immigration can buffer sink populations from declines even when climate negatively affects demographic vital rates and population growth (Brown and Kodric-Brown, 1977; Dias, 1996; Pulliam, 1988; Tavecchia et al., 2016). Unfortunately, montane salamanders, like *P. montanus*, are also physiologically restricted from warmer and drier valleys (Bernardo and Spotila, 2006). Therefore, tracking suitable climate would likely be limited through lower valleys and across latitudes, and may lead to population isolation and range contractions. The low dispersal observed for *P. montanus* and other terrestrial plethodontids (Cabe et al., 2007; Liebgold et al., 2011; Marsh et al., 2004; Ousterhout and Liebgold, 2010; Peterman and Semlitsch, 2013) further increases their risk of population decline under future climate change.

Reproduction, Survival, and Body Size

Larger body size in amphibians is advantageous; females tend to produce more eggs, larger males are more successful at mating than smaller males, and survival for larger individuals is greater than smaller individuals (Gibbons and McCarthy, 1986; Halliday and Verrell, 1988; Morrison and Hero, 2003; Semlitsch et al., 1988; Wells, 2007). Consistent with these findings, we found that larger females were more likely to be gravid and larger males were more likely to have enlarged mental glands. Additionally, we found that larger individuals had a higher probability of survival than smaller individuals for all five sites (Appendix 6; Figures 4, 5). Despite this, we did not find a significant relationship between the number of eggs and female body size. However, our methods were fairly crude because egg number had to be estimated in the field since animals were processed at the site of capture and immediately released, and, moreover, are likely overestimates, since clutch sizes are typically lower than counts of large follicles (Hairston, 1983). Unfortunately, for *P. montanus*, as well as other terrestrial plethodontids, clutch sizes are infrequently observed (Lannoo, 2005), making it difficult to estimate number of offspring per individual *in situ*.

Reproduction, Growth, Survival, and Elevation

Our results suggest that *P. montanus* employs variation in life history along an elevational gradient. At the highest elevation, individuals grew more slowly, took longer to mature, but had high and more constant survival across all sizes; at the lowest elevation, on the other hand, individuals exhibited slower growth, faster maturation, and lower survival (Figures 1, 4, and 5). While at our mid elevation site, survival estimates were typically similar to lower elevations (Figures 4 and 5), and females at the mid elevation site had the fastest growth rates (Figure 1). We hypothesize that this variation in life history is the result of the climatic differences along this elevational gradient, which has been previously documented in other amphibian species (e.g., Berven, 1982; Berven and Gill, 1983; Smith-Gill and Berven, 1979; reviewed in Morrison and Hero, 2003). Warmer temperatures can decrease survival through reducing surface activity and foraging time (Angilletta et al., 2004; Caruso et al., 2014; Muñoz et al., 2016; Ohlberger, 2013; Reading, 2007). Therefore, at the lower elevations earlier maturation and smaller size at first reproduction is favored. While at higher elevations, reduced physiological stress (Bernardo and Spotila, 2006; Bernardo et al., 2007; Catenazzi, 2016; Gifford and Kozak, 2012; Lyons et al., 2016; Riddell and Sears, 2015) leads to higher survival. Thus, delayed maturation is favored, which coincides with a larger size at first reproduction, and eventually a larger asymptotic size despite reduced growth rates (Morrison and Hero, 2003). These patterns are also consistent with the expectation that amphibians are limited at the southern or warmer edge by the abiotic environment (Bernardo and Spotila, 2006; Bernardo et al., 2007; Cunningham et al., 2016; Gifford and Kozak, 2012; Lyons et al., 2016). Though we are not able to distinguish if this life history variation is the result of local adaptation or a byproduct of phenotypic plasticity (Merilä and Hendry, 2014; Urban et al., 2014), elsewhere (Caruso et al., *unpublished data*) we show experimental evidence to support that abiotic-driven plasticity is a more likely explanation.

Alternatively, our observed elevational variation in life history characteristics could have also been affected by biotic interactions. We note that the number and abundance of other terrestrial salamander species varied among these sites (N.M.C. *unpublished data*), and these other species may function as competitors, predators, or even prey species for *P. montanus* (Petranka, 1998). Additionally, we were not able to measure total prey availability or the strength of predation on these populations to allow comparisons. However, when controlling for biotic variables, Caruso et al. (*unpublished data*) found similar patterns in demographic vital rates that we observed here, which indicates that the abiotic environment is the likely driver of this variation. Unfortunately, due to logistic constraints, abiotic and biotic variables are rarely experimentally manipulated in concert to understand species' range edges, especially in mobile vertebrates (but see Cunningham et al., 2009), and predictions of population persistence under future climate scenarios often focus only on the abiotic environment (e.g., Milanovich et al., 2010). Understanding how shifts in the distribution of one species (introduction or extirpation) can affect other species, and how these relationships change under different abiotic conditions, is a clear target for improving predictions under future changes in climate (Urban et al., 2016).

Seasonal Survival

Our results suggest a disparity in survival among elevations during the inactive season compared to the active season. At higher elevations, survival was much higher during the inactive season compared to the active season, whereas at the lower elevations survival was similar between the seasons or lower during the active compared to the inactive seasons (Figure 6). We posit that the differences in abiotic conditions (i.e., warmer temperatures and reduced snowpack) among our elevation gradient can, at least in part, explain our observed variation in survival among populations. Reductions in survival under warmer inactive season conditions have been found in other species. For example in mammals, species that hibernate typically have higher survival rates than similar-sized species that do not (Turbill et al., 2011), while for invertebrates, butterfly survival has been shown to decrease under warmer winter conditions (Stuhldreher et al., 2014). We suggest three possible scenarios to understand the mechanisms by which winter conditions at higher elevations could improve survival. First, salamanders that experience more consistent snowpack would have less surface activity, which would reduce the number of encounters with surface predators (e.g., birds), and mortality would likewise be reduced. Second, snow acts as a soil insulator (Pomeroy and Brun, 1990) and less snowpack can lead to more variable and colder soil temperatures (Brown and DeGaetano, 2011; Groffman et al., 2001; Henry, 2008). Therefore, underground salamanders in areas with more snowpack have a greater buffer from subzero temperatures (Decker et al., 2003). Lastly, salamanders that are active during warmer winter conditions may not be able to find the necessary food sources to compensate for this increased activity, leading to decreased body condition and lower survival (e.g., Catenazzi, 2016; Reading, 2007).

While space (e.g., an elevational gradient) may not always be an unbiased substitute for time (Krebs and Berteaux, 2006; Merilä and Hendry, 2014), our results also have implications for terrestrial plethodontids with respect to climate change. Warming is predicted to be unequal among seasons, winter months will likely see a greater increase in temperatures than the other seasons (Xia et al., 2014). Therefore, predictions of salamander population growth under future climate change that only account for responses to the active season conditions may underestimate losses. For logistic reasons, studies of terrestrial plethodontids have typically focused on the active season (i.e., when individuals are available for capture). However, determining the effect of winter conditions on salamander demography (e.g., survival) through the experimental manipulation of temperature or snowpack would improve mechanistic predictive population models (Sanders-DeMott and Templer, 2017).

Conclusions

Future warming is predicted to be a major challenge for Appalachian salamanders (Caruso et al., *unpublished data;* Catenazzi, 2016; Milanovich et al., 2010; Sutton et al., 2015). Yet mechanistic population growth models are lacking, due, in part, to the paucity of demographic data for many species. We provide estimates of the spatial variation in demographic vital rates, and their uncertainty, which are needed to model population growth and develop conservation strategies (Caswell, 2001; Easterling et al., 2000; Ellner and Rees, 2006; McLean et al., 2016; Urban et al., 2016). Furthermore, we recommend experiments, especially those manipulating the inactive season conditions, to reveal the abiotic mechanisms (e.g., temperature, snowpack) underlying the observed variation in vital rates. It is likely, however, that warming conditions will lead to decreases in survival for *P. montanus* and other terrestrial plethodontids, how this reduced survival, or changes in other demographic vital rates, affects population growth across the range, should therefore be a focus of future research.

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Figure 1: Growth model parameter (asymptotic size = a; growth rate = k; variance = λ; measurement error = σ) estimates for all five sites. Points represent median estimates, gray shaded bars show 75% CRI and black bar represents 95% CRI. Sites are arranged from lowest (SPG) to highest (CG) elevation.

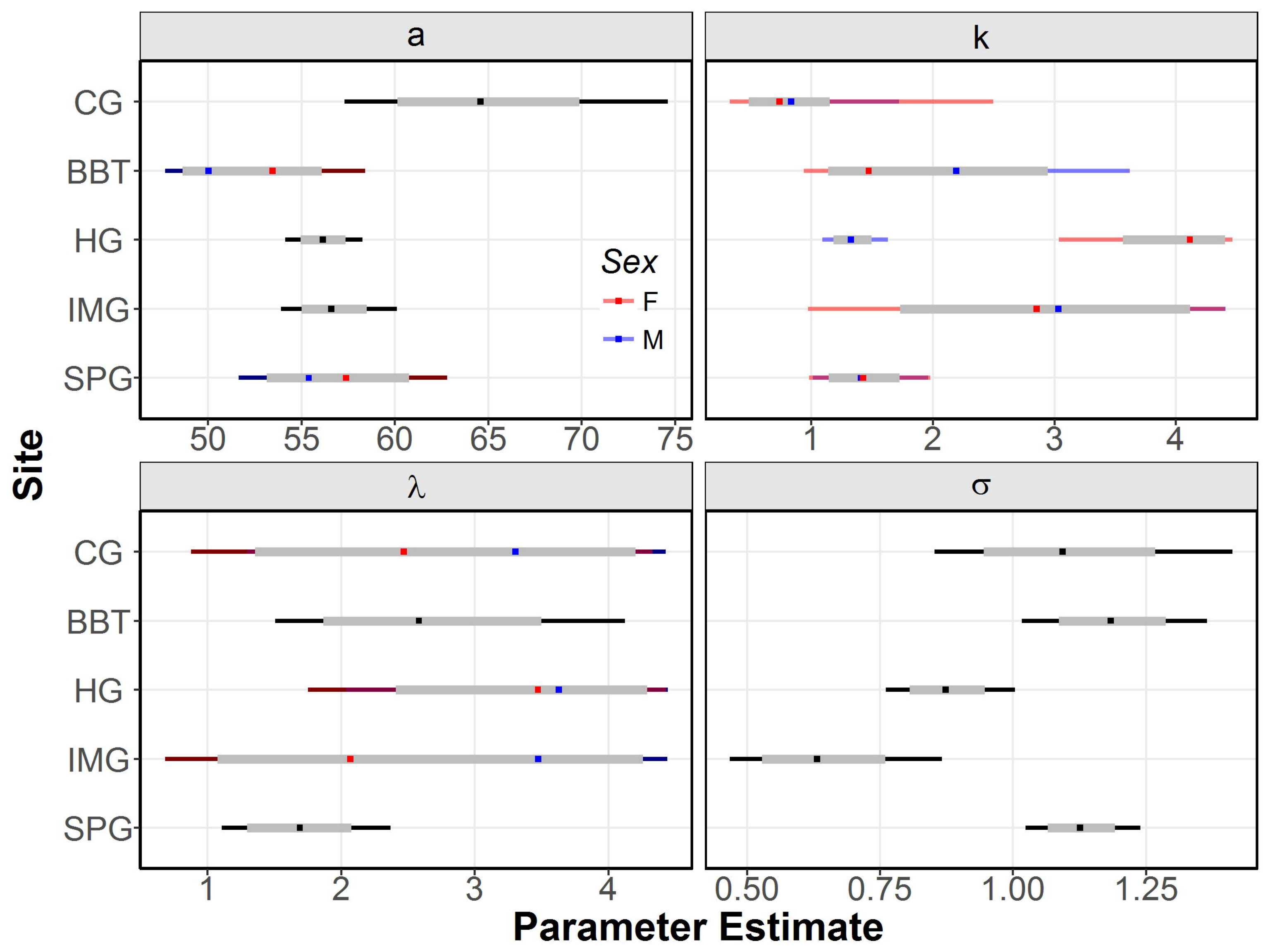
Figure 2: Spatial parameter ($\sigma^2_{Gxt}/\sigma^2_{Gyt}$ = primary period dispersal variance in x and y axis; $\sigma^2_{Gxtt}/\sigma^2_{Gytt}$ = secondary period dispersal variance in x and y axis) estimates for all five sites. Points represent median estimates, gray shaded bars show 75% CRI and black bar represent 95% CRI. Sites are arranged from lowest (SPG) to highest (CG) elevation.

Figure 3: Capture parameter estimates ($\tau_{\gamma}^{-2}/\ \tau_{\varepsilon}^{-2}$ = random intercept variance for primary period and individual respectively) for all five sites. Points represent median estimates, gray shaded bars show 75% CRI and black bar represent 95% CRI. Sites are arranged from lowest (SPG) to highest (CG) elevation.

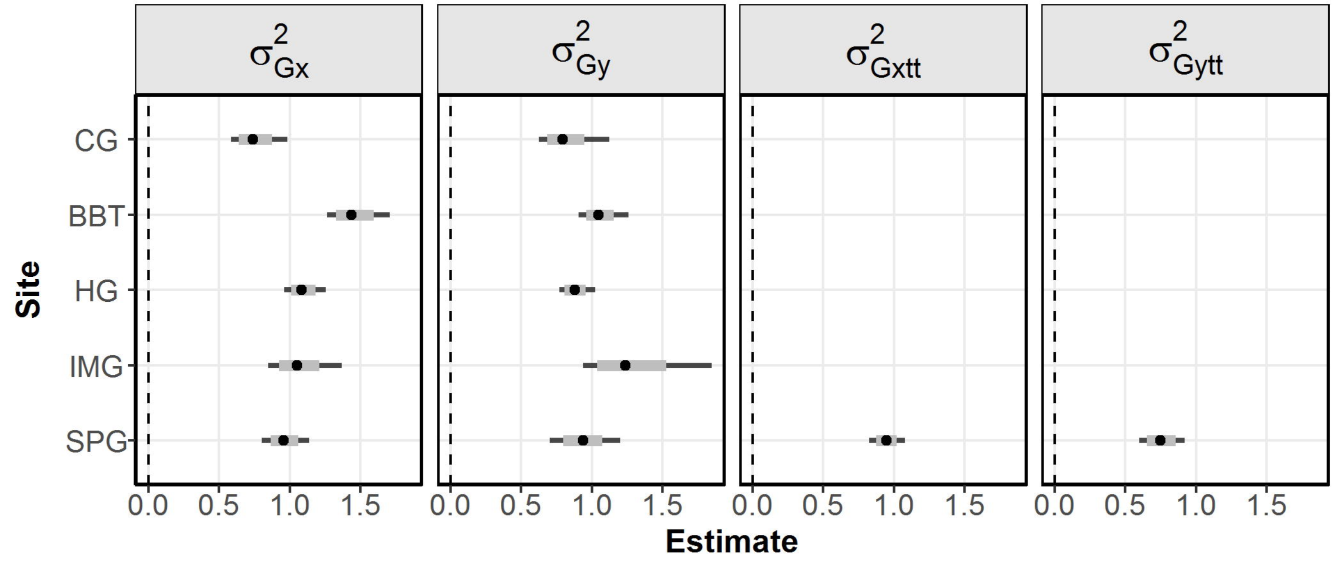
Figure 4: Survival parameter estimates for all five sites. Points represent median estimates, gray shaded bars show 75% CRI and black bar represent 95% CRI. Sites are arranged from lowest (SPG) to highest (CG) elevation.

Figure 5: Predicted survival probabilities (median estimates) for each year, season, sex, and size at each site. Sites are arranged from lowest (SPG) to highest (CG) elevation.

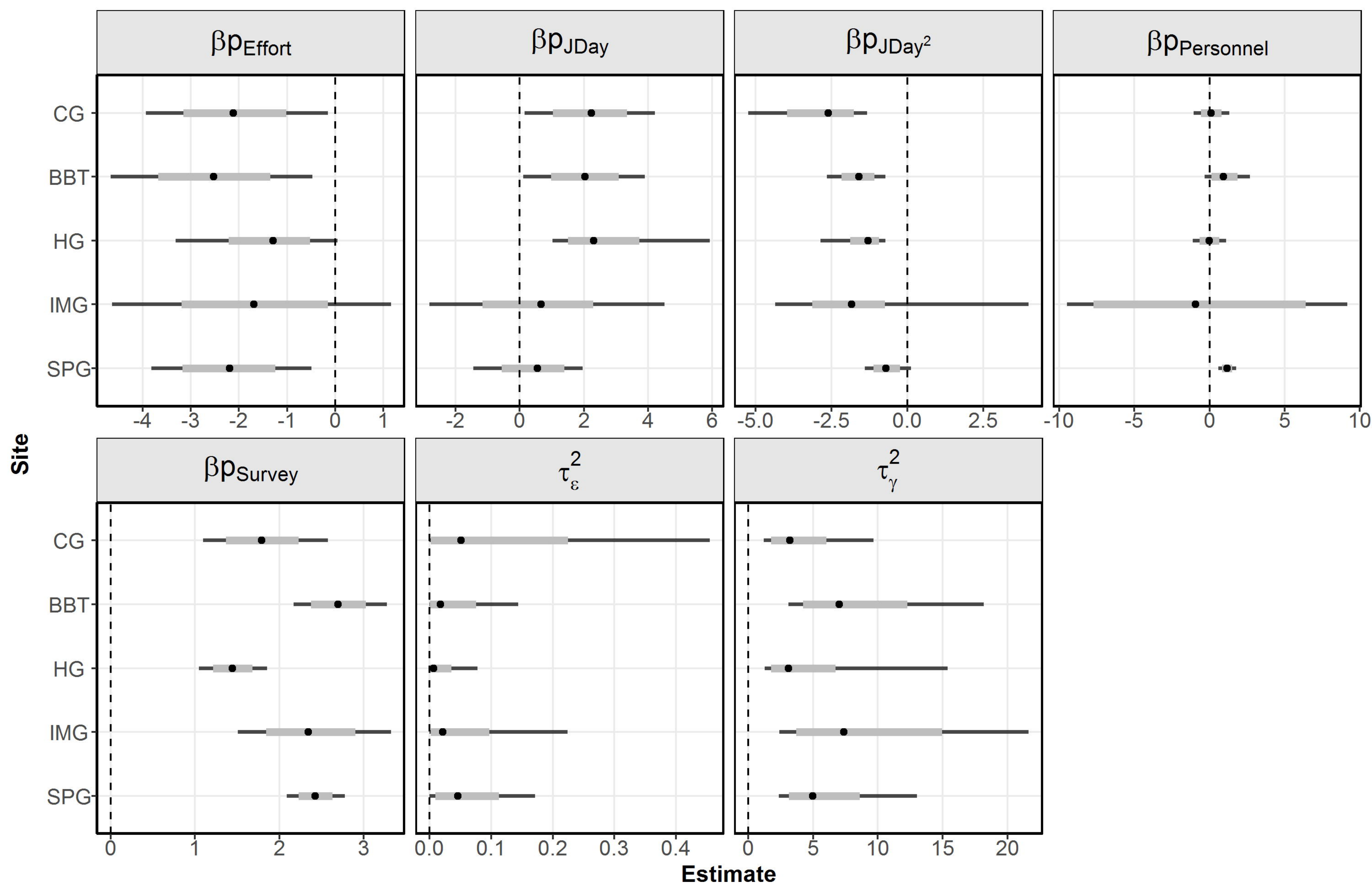
Figure 6: Median survival probabilities for a given size (20, 30, 40, 50, 60 mm SVL) showing the differences in predicted survival estimates between active and inactive seasons among sites. Sites are arranged from lowest (SPG) to highest (CG) elevation.



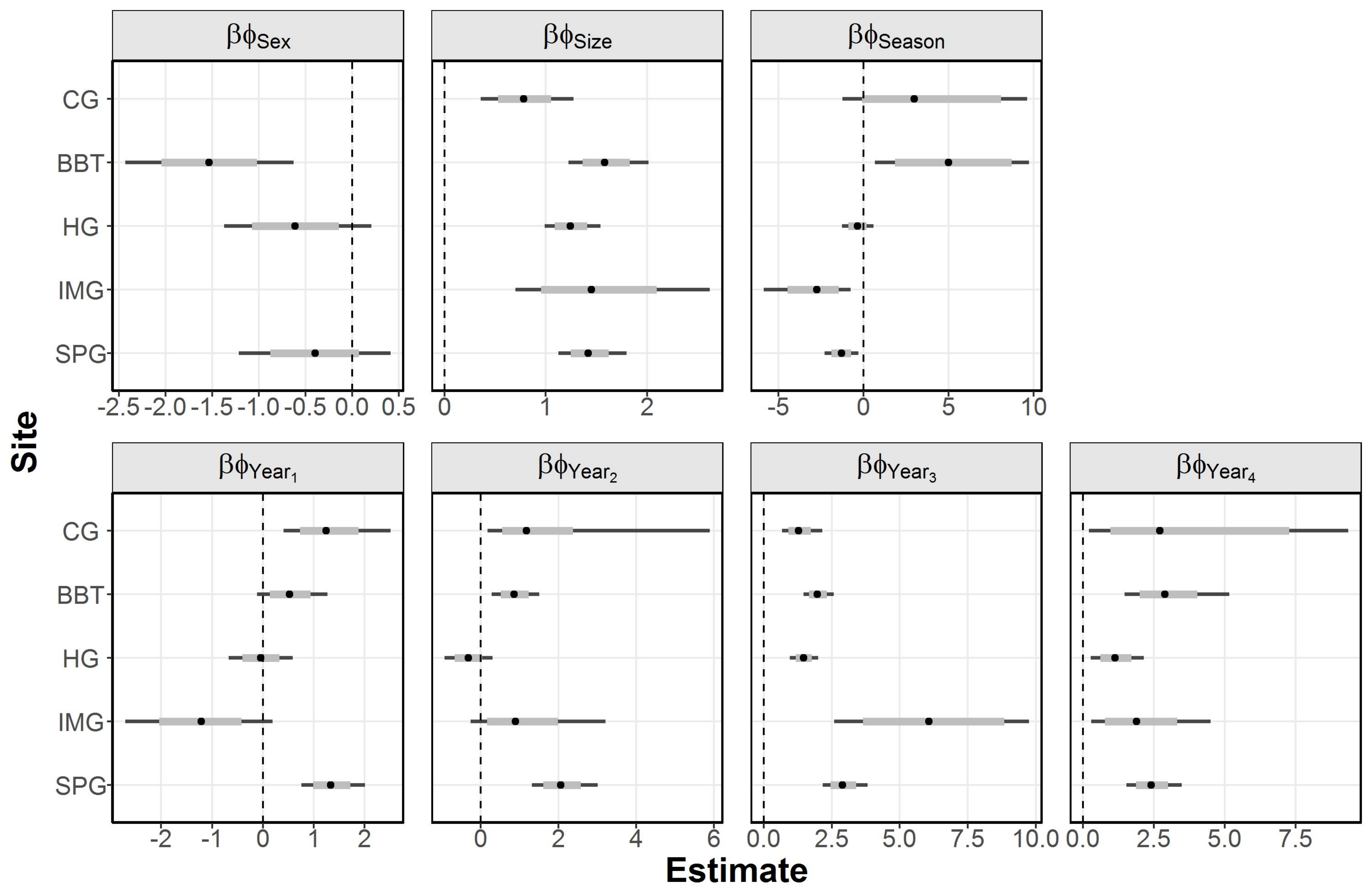
a
k
λ
σ
CG
BBT
HG
IMG
SPG
Sex
F
M
50
55
60
65
70
75
1
2
3
4
1
2
3
4
0.50
0.75
1.00
1.25
Site
Parameter Estimate



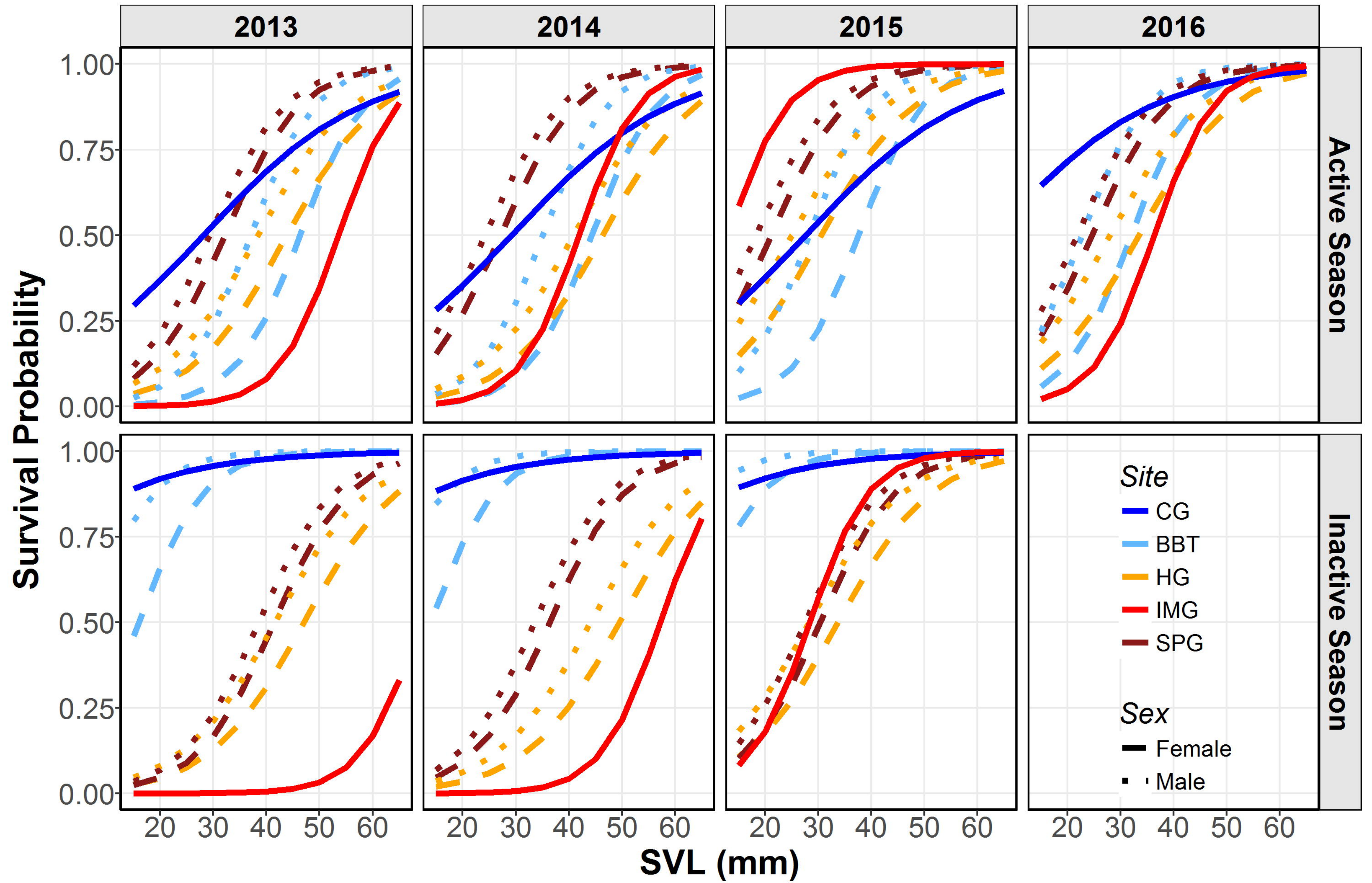
σ^2_{Gx}
σ^2_{Gy}
σ^2_{Gxtt}
σ^2_{Gytt}
Site
CG
BBT
HG
IMG
SPG
0.0
0.5
1.0
1.5
Estimate



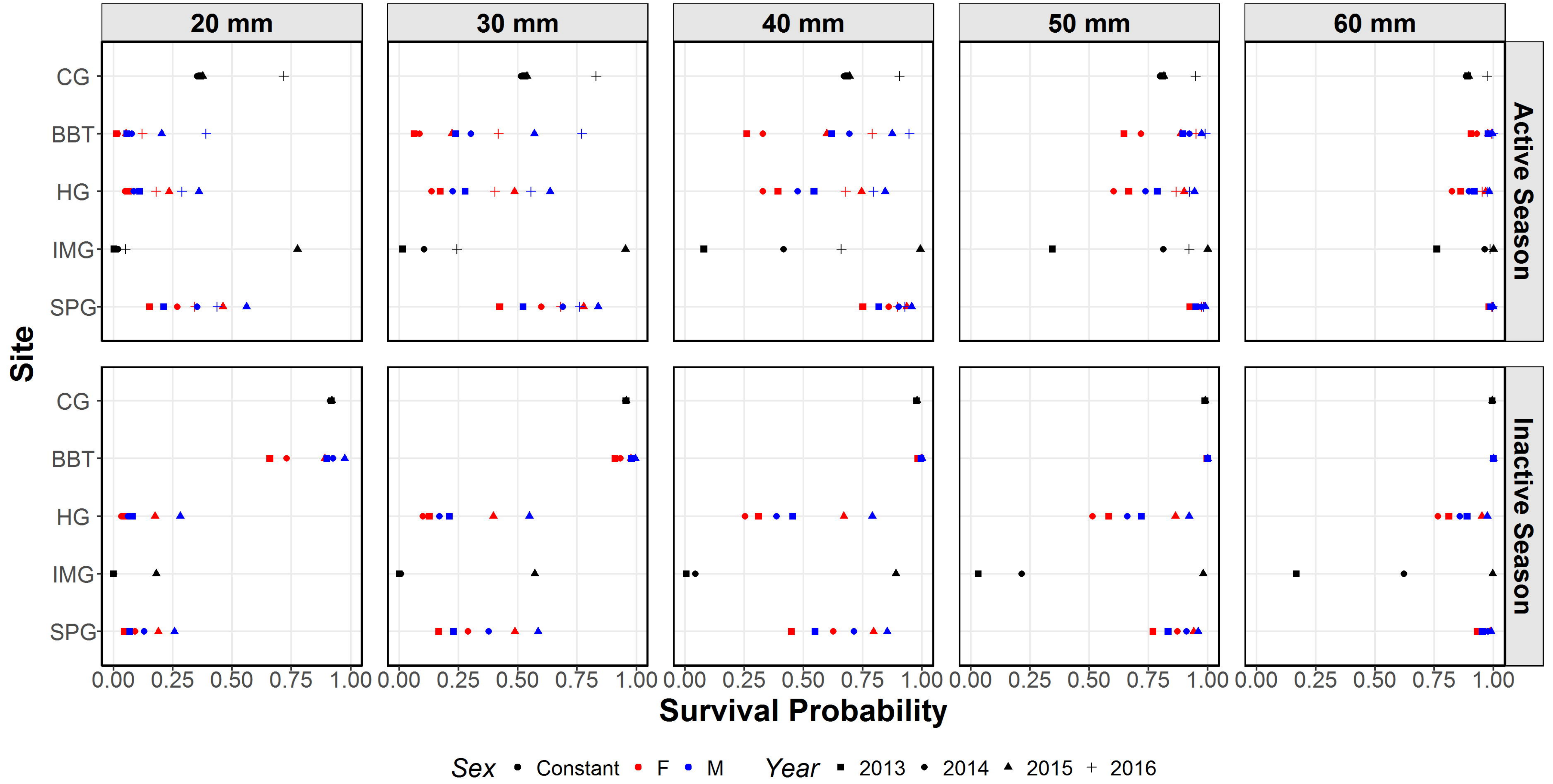
βp_Effort
βp_JDay
βp_JDay²
βp_Personnel
βp_Survey
τ_ε²
τ_γ²
CG
BBT
HG
IMG
SPG
-4 -3 -2 -1 0 1
-2 0 2 4 6
-5.0 -2.5 0.0 2.5
-10 -5 0 5 10
0 1 2 3
0.0 0.1 0.2 0.3 0.4
0 5 10 15 20
Site
Estimate



$\beta\phi_{Sex}$
$\beta\phi_{Size}$
$\beta\phi_{Season}$
$\beta\phi_{Year_1}$
$\beta\phi_{Year_2}$
$\beta\phi_{Year_3}$
$\beta\phi_{Year_4}$
CG
BBT
HG
IMG
SPG
Site
Estimate
-2.5 -2.0 -1.5 -1.0 -0.5 0.0 0.5
0 1 2
-5 0 5 10
-2 -1 0 1 2
0 2 4 6
0.0 2.5 5.0 7.5 10.0
0.0 2.5 5.0 7.5



2013
2014
2015
2016
Active Season
Inactive Season
Survival Probability
1.00
0.75
0.50
0.25
0.00
20
30
40
50
60
SVL (mm)
Site
CG
BBT
HG
IMG
SPG
Sex
Female
Male



20 mm
30 mm
40 mm
50 mm
60 mm
Active Season
Inactive Season
Site
CG
BBT
HG
IMG
SPG
0.00
0.25
0.50
0.75
1.00
Survival Probability
Sex
Constant
F
M
Year
2013
2014
2015
2016