

**Growth and Space-use of Eastern Red-backed Salamanders (*Plethodon cinereus*) in Mature and Regenerating Forests**

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**Abstract**

Movement and demographic rates are critical to the persistence of populations in space and time. Despite their importance, estimates of these processes are often derived from a limited number of populations spanning broad habitat or environmental gradients. With increasing appreciation of the role fine-scale environmental variation in microgeographic adaptation, there is need and value to assessing within-site variation in movement, growth, and demographic rates. In this study, we analyze three years of spatial capture-recapture data collected from a mixed-use deciduous forest site in central Ohio, USA. Study plots were situated in mature forest on a slope and in successional forest on a ridge but were separated by less than 100-m distance. Our data showed that the density of salamanders was less on ridges, which corresponded with greater distance between nearest neighbors, less overlap in core use areas, greater space-use, and greater

shifts in activity centers when compared to salamander occupying the slope habitat. However, these differences were moderate. In contrast, we estimated growth rates of salamanders occupying the ridge to be significantly greater than salamander on the slope. These differences result in ridge salamanders reaching maturity more than one year earlier than slope salamanders, increasing their lifetime fecundity by as much as 43%. The patterns we observed in space use and growth are likely the result of density-dependent processes, reflecting differences in resource availability or quality. Our study highlights how fine-scale, within-site, variation can shape population demographics. As research into the demographic and population consequences of climate change and habitat loss and alteration continue, future research should take care to acknowledge the role that fine-scale variation may play, especially for organisms with small home ranges or limited vagility.

**Keywords:** demography, lifetime fitness, fine-scale, salamander

## Introduction

Landscapes are a composition of biotic and abiotic features that are heterogeneous in at least one dimension at any assessed scale (Turner and Gardner, 2015). Species usually exist as populations adapted to their local landscapes (Urban et al., 2016); however, much of what we know about a given species is derived from a limited number of populations. Such generalizations may be particularly misleading for organisms who interact with their environment at fine-scales (i.e., tens of meters or less), such as plants, invertebrates, or amphibians. These organisms typically have limited dispersal and physiological and behavioral constraints that limit their ability to actively select habitat (De Bie et al., 2012). The result may be that populations of such species develop fine-scale variation based on their immediate surrounding environment (i.e., microgeographic adaptation; Richardson et al., 2014).

There is increasing evidence that microgeographic adaptation occurs in numerous taxa and ecosystems (Richardson et al., 2014), influencing species distribution and abundance and individual phenotype (Cicchino et al., 2021). For example, limpets (genus *Patella*) separated by less than 2 m experienced significantly different sun exposure and thermal stress depending on the side of the rock that they inhabit (Seabra et al., 2011). Chronic thermal stress can significantly impact growth, reproduction, and overall fitness (Dantzer et al., 2014; Wingfield and Romero, 2011), which likely results in heterogeneous fitness across limpet populations and individuals. Other species that are similarly limited in their habitat selection may also experience fitness variation across fine spatial scales that are heterogeneous in environmental conditions relevant to the species' ecology. Therefore, evaluating the demographics of multiple populations across fine-scales is important for developing comprehensive conservation and management goals of organisms with limited habitat selection capability.

Fine-scale information about space-use patterns of individuals within a population is necessary for fully understanding spatial population demographics. Space-use, or the amount and extent of a given area used by an individual, can be driven by numerous factors including spatial distribution and quality of resources, microclimate, and conspecific density (Gaillard et al., 2010; Morales et al., 2010). Conspecific density may be particularly influential to space-use and movement. For example, high density areas may indicate good quality habitats that can support more individuals and may offer cooperation with conspecifics (e.g., anti-predator grouping behavior, resource sharing, cooperative breeding), and consequently promote site philopatry and reduced movement and space-use. Conversely, high density areas may have higher competition for resources, mates, and more aggressive individuals thus promoting space-use and movement away from the site (Clobert et al., 2009). Similarly, population demographic rates such as growth rates can vary in density-dependent ways whereby higher densities result in lower growth rates, due to fewer resources available to each individual, and allocation of obtained resources towards other processes like aggressive interactions and competition (Getz, 1996). Animal movement and space-use often vary across the distribution of species (Boyle et al., 2009), and populations in close geographic proximity when habitats differ (Gonzales et al., 2020; Reeve et al., 2009). Yet, few studies have attempted to document life history and space-use variation at fine spatial scales whether because of increased cost, labor intensity, or methodological constraints.

Plethodontid salamanders provide a system particularly adept at evaluating questions of fine-scale variation in key demographic rates due to their high abundances and relative ease of capture. Terrestrial lungless salamanders in the genus *Plethodon* are the most abundant vertebrate animals in many North American forests, accounting for more vertebrate biomass than any other taxa in these ecosystems (Burton and Likens, 1975; Semlitsch et al., 2014). Terrestrial

salamanders of the genus *Plethodon* are highly philopatric and physiologically limited as a result of their lungless anatomy and requirement for cool and moist conditions to facilitate cutaneous respiration. Despite their ubiquity in temperate forests our understanding of fine-scale differences in space-use and demography is limited. One of the most abundant and widely distributed Plethodontid salamander species, *Plethodon cinereus*, can show genetic differentiation between populations separated by 200 m of forested habitat (Cabe et al., 2007). Such fine scale genetic differences suggest limited movement or dispersal, creating potential for spatial variation in demographic rates. However, this remains largely unknown. *Plethodon cinereus* is found across eastern North American forests but appear to be in higher abundances and density in forests with greater percent canopy cover, larger trees, and with high densities of well-decayed coarse woody debris (McKenny et al., 2006; Otto et al., 2014; Wilk et al., 2020). Forests with these attributes provide suitable cool and moist microhabitats and higher prey abundance for salamanders. Yet, within a given site, habitat heterogeneity exists and likely impacts demographic rates including survival, growth, and space-use of sub-populations (Peterman and Semlitsch, 2013).

Here, we use a multi-season spatial capture-mark-recapture study to evaluate fine-scale demographic rates of two sub-populations of *P. cinereus* separated by only 100 m but inhabiting different microhabitats. We predicted that salamanders occupying different habitats would exhibit meaningful differences in estimated parameters. Specifically, we expected that early successional forest habitat located on a ridge would be suboptimal to slope habitat with mature forests and would support fewer individual salamanders. As such, we predicted salamanders occupying early successional ridge habitat would have larger home ranges, more spatial overlap

with neighbors, and would have lower growth rates compared to salamanders occupying the slope habitat.

## **Methods**

### *Field Sampling*

We conducted this study in Galena, Ohio at a 36 ha site consisting of a mix of mature oak-hickory forest (*Quercus* and *Carya* spp.), early to mid- successional mesic hardwoods (*Acer* spp), white pine plantations (*Pinus strobus*), and open field habitats. The early successional forests are <40 years in age and are growing in what was previously pastureland used for grazing in the 1970s. The mature forests are found on the ravine slopes and bottomlands surrounding a rocky stream that flows through the property. The well-drained, relatively undisturbed upper slopes of this ravine (hereafter, ‘Slope’) are adjacent to the flat, poorly drained, early-successional upland forests which were previously grazed (hereafter, ‘Ridge’).

We established four cover board arrays each consisting of wooden boards measuring 30 x 30 x 2.5 cm. We set two arrays in Ridge habitat and two arrays on the adjacent Slope habitat. Each pair of arrays was at least 20 m apart and consisted of a 5 x 10-m array of 50 cover boards equally spaced 1 m apart. Ridge and Slope arrays were 60–100 m apart. We established all arrays during fall 2016 and began sampling in spring 2017.

*Plethodon cinereus* in Ohio are most active at the surface during spring and autumn and retreat into deeper soil to avoid desiccation and freezing during summer and winter, respectively (Pfingsten et al., 2013). Thus, we sampled for salamanders three times during both the spring (March 15<sup>th</sup> – May 15<sup>th</sup>) and fall (September 15<sup>th</sup> – October 15<sup>th</sup>) from 2017–2019. During each daytime sampling event, we searched for salamanders under all cover boards, captured animals

found underneath, and recorded the board and array of capture. We placed individual salamanders in zip-top bags for processing, which included uniquely marking individuals using a fluorescent subdermal visual elastomer implant (Northwest Marine Technologies, LLC); recorded snout-vent length (SVL), tail length (TL), and sex; identifying the marks of recaptured individuals using a UV flashlight; returning salamanders to their board of capture within 4-hours of initial capture.

During each sampling occasion, we measured weather covariates at each array including soil surface temperature, average leaf litter depth, and temperature. Additionally, we collected soil core samples at the center of each array to denote organic soil depth and obtain soil water content by measuring the difference in mass before and after air-drying soil samples. We also retrieved weather covariates for each sampling survey for our study site from the PRISM dataset. For each year, we designated spring and fall as the active seasons, with the remainder of the year as the inactive seasons. We estimated average temperature, precipitation, and days since rain using a 5-day moving window analysis for every day of active and non-active seasons. We calculated the coefficient of variation for 5-day average temperature and total precipitation by dividing the seasonal mean by the standard deviation.

#### *Statistical Analysis:*

SCR model — We investigated survival, space-use, and movement parameters using a robust-design spatial capture recapture (SCR) adapted from Ergon and Gardner (2013). The robust design describes a sampling structure that divides ‘primary’ seasons and ‘secondary’ sessions within each primary season. The robust design assumes that demographic processes are open between primary sessions but closed within a primary session (Pollock, 1982). In our study,

fall and spring sampling sessions serve as the primary sessions with 2–3 secondary sessions within each primary season. A SCR differs from a traditional Cormack-Jolly-Seber capture recapture model by explicitly incorporating spatial capture locations to account for individual movement or dispersal, allowing for a more accurate estimate of true survival (Schaub and Royle, 2014). Dispersal distance is an estimate of the difference between activity centers between seasons and activity centers were assumed to have a uniform distribution and dispersal only occurred between primary sessions. We included the aforementioned PRISM weather covariates in the survival sub-model of the SCR, however, null models were better supported and we subsequently only report results from those models.

Growth model — We estimated individual growth using Fabens capture-recapture growth model (Fabens 1965). The growth function for individual  $i$  at time  $t$  was defined as:

$$SVL_{i,t} = SVL_{i,t-1} + \left\{ L[SEX] - SVL_{i,t-1} \times \left[ 1 - \exp\left(-K_{i,t} \times \frac{I}{365}\right) \right] \right\}$$

where asymptotic size  $L$  was allowed to differ by sex and was estimated from a Normally distributed prior with a mean of 48 and precision of 0.01.  $SVL_{i,t}$  is the size at first capture and follows a Uniform distribution with a minimum of 10 and maximum of 60.  $K$  represents the individual growth rate, and  $I$  is the annual scaling interval between captures. We estimated  $K$  as a function of categorical plot position ( $POS$ ; Slope or Ridge) and  $SEX$  based on observed change in SVL of recaptured individuals across sampling periods.

$$K_{i,t} = \beta_0^{[K]} + \beta_1^{[K]} \times POS_i + \beta_2^{[K]} \times SEX_i$$

All  $\beta$  parameters were estimated from Normally distributed prior distributions with a mean of 0 and precision of 0.01. We evaluated the difference in  $K$  between Ridge and Slope by subtracting the two model coefficients, such that more positive values indicated larger growth



coefficients in Slope sub-populations. We treated the difference as significant if greater than 97.5% of the posterior density was on one side of zero. We ran the growth model on five MCMC chains for 200,000 iterations with a burn-in of 25,000 and a thinning rate of 5. We considered models to have fully converged if all parameters had Gelman-Ruben (Rhat) statistics below 1.05 and visual inspection of MCMC chains indicated clear and consistent mixing.

Space-use — Using parameters estimated from our fitted SCR model, we assessed space-use and overlap in salamanders occupying the Ridge and Slope habitats. Specifically, we plotted each individual's spatial location in coordinate space and then calculated the probability ( $p$ ) of each individual ( $i$ ) using adjacent spatial locations ( $j$ ) as a function of distance ( $d$ ) following a negative exponential function:

$$p_{ijk} = \exp\left(-\left(\frac{d_{ijk}}{\sigma_k}\right)^2\right).$$

The rate of probability decay in space is governed by  $\sigma$ , which was estimated during the fitting of the SCR model. Probability of use surfaces were created for each individual at 1,000 samples ( $k$ ) of the fitted posterior model distributions. Using the probability surfaces  $p_{ijk}$ , we distributed 1,000 hypothetical 'use' points on the landscape following a random multinomial process. We then calculated kernel density utilization distributions (UD) of these spatially referenced use points for each individual and posterior sample using the R package 'adehabitatHR' (Calenge, 2006). Finally, we calculated the probability that the core 50% of each individual  $i$ 's UD overlapped with all other core 50% UD <sub>$j$</sub>  calculated as the probability of home range overlap (Fieberg and Kochanny, 2005). We then determined the average number of individuals with overlapping core UD<sub>s</sub>, as well as the average probability of overlap.

### Population projection

— Using parameters from our fitted growth model and from the literature, we conducted population projection simulations to understand how differences in growth could impact lifetime fitness. We assume that all individuals are 13.5 mm SVL upon hatching, and that sexual maturity is first reached at 34 mm SVL (Pfingsten et al., 2013). However, following Lotter (1978) we assume that individuals between 34 and 43 mm SVL have 56% chance of being gravid, while 94% of females >43 mm SVL are likely to be gravid. Regional variation in reproduction has been documented (Lotter, 1978; Sayler, 1966; Werner, 1971), but our data are not sufficient to ascertain frequency of reproduction in our Ohio population. Similarly, we could not confidently determine the average number of eggs produced by each female, nor whether there was a size by fecundity interaction. As such, we fit a linear model with a normal distribution to the data reported in Lotter (1978) relating clutch size to SVL using the R package ‘brms’ (Bürkner, 2016). We found that the normally distributed model better fit the data than a generalized model with a Poisson or negative binomial distribution. Like previous demographic projection models of *P. cinereus* (Hernández-Pacheco et al., 2021; Homyack and Haas, 2009), we assume eggs have a 90% hatching rate.

We estimated growth and lifetime fecundity at each Slope and Ridge location using 100,000 samples from the posterior distributions of our fitted growth model and the clutch size model. Because the survival estimates from our spatial-capture-recapture data are unrealistically high (Table 2), we used the average of male and female annual survival estimates and uncertainty from Muñoz et al. (2016b). For each individual, at each time step (one year), we estimated survival as a random binomial process, with the annual probability of surviving being normally distributed with a mean of 0.836 and standard deviation of 0.07 (truncated to 0.4–1.0). The lifespan of wild *P. cinereus* is unknown; we projected our model out 20 years.

## Results

Ridge and Slope sites have very similar soil moisture, air temperature, soil temperature, and leaf litter depth across surveys (Table 1). Ridge sites tended to be  $\sim 1^{\circ}\text{C}$  warmer than the Slope, but with much greater variability; Slope sites tended to have more leaf litter, but with much greater variability. Across all plots and surveys, we captured 682 unique salamanders. Of these, we captured 390 salamanders in Slope plots (recaptured 114) and 292 salamanders in Ridge plots (recaptured 68). We observed 311 females, 217 males, and 154 juveniles across all plots (Table 1).

SCR Results — For most parameters estimated in our spatial capture-recapture model, Slope and Ridge plots had moderate differences (Table 2). Annual survival was estimated to be  $> 0.99$  for both Slope and Ridge plots. Activity centers of salamander in Ridge plots tended to shift slightly more between primary sample periods when compared to Slope plots (1.376 m vs. 1.241 m, respectively) and Ridge salamanders tended to move around more within a primary period (Ridge = 1.376 m, Slope = 1.241 m). The density of salamanders was significantly lower in Ridge plots, which also had significantly lower probability of detection (Table 2).

Growth Estimates and Time to Maturity — On average, initial salamander mean SVL was  $37.11 \pm 4.80$  mm, with little difference observed between males ( $38.00 \pm 3.61$  mm) and females ( $38.50 \pm 4.47$  mm). Similarly, there was no observed difference in the overall mean SVL between Slope ( $37.61 \pm 4.45$  mm) and Ridge ( $36.43 \pm 5.16$  mm) plots. However, there were significant differences in asymptotic growth and growth rates between males and females, and

significant differences in growth rates between the Slope and Ridge locations (Table 3; Fig. 1). This results in Ridge males reaching sexual maturity in 2.25 years and Slope males maturing in 2.75 years, while Ridge females mature in 3.30 years and Slope females mature in 4.30 years (Fig 2).

Space-use — Salamanders occupying Ridge habitat had substantially fewer individuals overlapping their core UD ( $35.8 \pm 12.1$ ) than salamanders occupying Slope habitat ( $43.8 \pm 13.3$ ; Table 4, Fig. 3). Despite the greater number of individuals potentially occupying the same space in the Slope habitat, the average probability of overlap was nearly identical between the two habitats (Table 4). However, the average distance to the nearest neighboring salamander tended to be less for salamanders occupying Slope habitat ( $0.40 \text{ m} \pm 0.06$ ) compared to salamanders occupying Ridge habitat ( $0.50 \text{ m} \pm 0.08$ ; Fig. 3).

Population projection — Given the annual survival rate estimated from Muñoz et al. (2016a), females are estimated to live an average of 5.87 years ( $\pm 4.90$  SD). Females in the Slope habitat are estimated to average 2.2 ( $\pm 3.7$ ) clutches in their lifetime, equating to a mean lifetime fecundity of 13.7 ( $\pm 27.3$ ). Because maturity is reached earlier in the Ridge habitat, Ridge females are estimated to average 2.8 ( $\pm 4.1$ ) clutches and produce a mean of 19.6 ( $\pm 33.5$ ) offspring in their lifetime, which is 43% more than Slope females (Table 4).

## Discussion

Demographic vital rates and movement and dispersal rates are driven by the abiotic and biotic environment experienced by an organism. While variation in these rates is often expected

266 across broad spatial scales (e.g., latitude, elevation), our study shows that variation can exist at  
267 fine spatial scales between animals occupying different microhabitats and separated by as a little  
268 as 100 m. In this study, we predicted that there would be differences in salamanders occupying  
269 the mature forest Slope plots and the successional Ridge plots. As expected, there was a lower  
270 density of salamanders occupying the successional Ridge habitat and these salamanders did tend  
271 to have greater space-use and to shift activity centers more than salamanders in Slope habitat.  
272 However, salamanders in Ridge habitat were estimated to be farther from their nearest neighbor  
273 and to have less core use overlap with conspecifics than Slope salamanders. Contrary to our  
274 predictions, these differences corresponded with Ridge salamanders growing more rapidly,  
275 reaching sexual maturity sooner, and subsequently having greater projected lifetime fitness.

276         We do not know the cause for the observed differences between Ridge and Slope  
277 salamanders. Despite being situated on different topographic positions on the landscape, the two  
278 sites were quite similar, but not identical, in measured habitat variables. However, site-level  
279 differences were substantial enough to result in meaningfully different population densities.  
280 *Plethodon cinereus* are known to have aggressive intraspecific interactions to maintain territories  
281 (Jaeger, 1979). We saw a higher density of animals with subsequently greater home range  
282 overlap and shorter distance between individuals on Slope plots. Although salamanders likely  
283 encounter each other more frequently at the Slope plots, they may not engage in territorial  
284 behaviors due to the energetic costs related to frequent aggressive interactions. *Plethodon*  
285 *cinereus* and related species are known to reduce agonistic interactions with familiar conspecifics  
286 (“dear enemy hypothesis”), especially in areas with high density (Dalton et al., 2020; Jaeger,  
287 1981; Jaeger and Peterson, 2002). Although we did not explicitly evaluate agonistic interactions,  
288 our home range analysis can suggest differential behaviors at fine scales. A similar study that

utilized the same sampling protocols as the present study found that home ranges are not limited by density and instead suggest that the seasonal changes in spatial distribution are driven by food and shelter (Hernández-Pacheco et al., 2019). Our study site has the highest observed density of salamanders per square meter compared to nine other sites in central Ohio, USA (Wilk et al., 2020), but the density estimates from the current study are moderate to low compared to spatial capture-recapture density estimates from other regions (Hernández-Pacheco et al., 2019). The high observed densities likely reflect habitat quality, as our study site has remained largely undisturbed relative to other central Ohio sites, and subsequent capacity to support a higher density of salamanders. However, there are limits to the number of individuals that can be supported before density-dependent effects emerge.

The most prominent effect observed in our study was the significant difference in growth rates between our plots (Fig. 2). Salamanders occupying Ridge plots grew faster and reached maturity >1 year earlier than Slope individuals. There are at least two possible mechanisms for the observed differences. First, given the reduced number of individuals with overlapping home ranges at the Ridge, competition for resources may have been reduced and thus more opportunities to forage and invest in growth. Second, or additionally, prey availability or quality may be greater in Ridge plots compared to the Slope, allowing a more acquired resources to be allocated to growth. Density dependence appears to be a likely driver of the observed differences in observed growth rates. Harper and Semlisch (2007) found that density had a negative effect on survival and growth in metamorphosed American toads (*Bufo americanaus*) and wood frogs (*Rana sylvatica*) and Berven (2009) confirmed these effects in a long-term data set of wood frogs. Numerous other studies have confirmed density dependence in demographic parameters in larval or aquatic urodeles (e.g., Bendik and Dries, 2018; Ousterhout and Semlitsch, 2016;

Semlitsch, 1987; Van Buskirk and Smith, 1991), but there is limited research into how density directly effects population demographic parameters of terrestrial Plethodontid salamanders. It is important to note, however, that we do not have any estimates of food availability or quality, which should be a focus of future work to better understand the role of density-dependent processes (Kuzmin, 1995).

Regardless of mechanism, the differences in growth rates between Slope and Ridge locations results in substantially greater lifetime fitness for females occupying the Ridge (Table 4). Interestingly, there was no difference in estimated survival, and only moderate differences in dispersal distance and space-use between locations. As such, there must be a greater rate of emigration off Ridge plots, otherwise we would expect more individuals and a higher density of salamanders. While not conclusive, our data allude to the potential for greater emigration as we had ~6% lower recapture rate on Ridge plots as compared to Slope plots. Spatial capture-recapture models fit to data collected under a robust design allow for the estimation of true rather than apparent survival (Ergon and Gardner, 2014; Gardner et al., 2010; Muñoz et al., 2016a), but permanent emigration remains an elusive parameter. Emigration in plethodontid salamanders can be particularly challenging as salamanders can temporarily migrate underground or can disperse over land to a new location. During any given survey, only a small fraction of the population is available to be sampled on the surface (Bailey et al., 2004a, 2004b).

Among processes affecting population persistence, demography is the most critical driver (Hanski and Gilpin, 1991). Low reproductive rates, slow maturation, and longer generation times all increase the susceptibility of a population to stochastic events and the potential for local extinction (McKinney, 1997). However, variation in life-history traits can buffer populations when environments change (Anderson et al., 2015). *Plethodon cinereus* has proven to be a

resilient and adaptable species with a distribution encompassing much of eastern North America and populations frequently persisting in highly altered or urbanized landscapes (Gibbs, 1998; Petranksa, 1998; Wilk et al., 2020). The ability to thrive and not just persist in altered or changing habitats may be critical to the species' broad distribution and persistence. We found *P. cinereus* occupying successional habitat to have greater growth rates, which are predicted to result in earlier maturation and greater lifetime fecundity. While observed differences in salamander growth rates and the subsequent demographic differences are likely driven by environmental variation and density-dependent processes, rather than adaptation and microevolutionary processes, our results reinforce the role that fine-scale variation can play in spatial-temporal population processes. Perhaps most notably, these differences occurred between sites less than 100 m apart, highlighting the importance of accounting for fine-scale, within-site variation when assessing demographic processes. As research into the demographic and population consequences of climate change and habitat loss and alteration continue, future research should take care to acknowledge the role that fine-scale variation may play, especially for organisms with small home ranges or limited mobility.

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procedures were approved by the Institutional Animal Care and Use Committee at The Ohio State University and permitted by the Ohio Division of Wildlife.

### **Data Accessibility**

We will deposit all data and code into the Dryad data repository upon acceptance.

### **Conflicts of Interests**

The authors do not have any competing interest

### **Author Contributions**

**Meaghan Gade** contributed to conceptualization, data curation, formal analysis, methodology, investigation, project administration, writing-original draft preparation, and writing-review and editing. **Philip Gould** contributed to conceptualization, data curation, formal analysis, methodology, investigation, visualization, writing-original draft preparation, and writing-review and editing. **Andrew Wilk** contributed to conceptualization, data curation, formal analysis, methodology, investigation, visualization, writing-original draft preparation, and writing-review and editing. **Kate Donlon** contributed to conceptualization, methodology, data curation, project administration, investigation, writing-review and editing. **Mackenzie Brown** contributed to data curation, investigation, and writing-review and editing. **Marnie Behan** contributed to data curation, investigation, and writing-review and editing. **Marissa Roseman** contributed to data curation, investigation, and writing-review and editing. **Annalee Tutterow** contributed to data curation, investigation, and writing-review and editing. **Evan Amber** contributed to data curation, investigation, formal analysis and writing-review and editing. **Ryan Wagner** contributed to data curation, investigation, and writing-review and editing. **Andrew Hoffman** contributed to data curation, investigation, writing-original draft, and writing-review and editing.

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381 **Peterman** contributed to conceptualization, data curation, formal analysis, funding acquisition,  
382 investigation, methodology, resources, supervision, visualization, writing-original draft  
383 preparation, and writing-review and editing.

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Table 1. Habitat characteristics and salamander capture summaries between the slope and ridge sites across sampling seasons. Presented habitat values are means ( $\pm$ SD) of measurements collected during each site survey.

<b>Habitat characteristic</b>	<b>Site</b>	
	<b>Slope</b>	<b>Ridge</b>
Soil Moisture (% water)	0.266 (0.087)	0.265 (0.094)
Air Temperature (C)	12.050 (6.259)	12.050 (6.220)
Surface Soil Temperature	10.198 (4.266)	11.169 (8.660)
Leaf Litter Depth (cm)	1.979 (4.162)	1.350 (0.818)
<b>Capture summary</b>		
Total Captures	390	292
Male / Female / Juvenile	131 / 179 / 80	86 / 132 / 74
Recapture Percentage	29.2	23.3
Average SVL (mm)	37.73	36.16

Table 2. Parameter estimates from fitted SCR model. Reported values are the mean  $\pm$  standard deviation with 95% Bayesian credible intervals in brackets. Dispersal represents the average shift in activity centers between seasons while space-use. The probability of the ridge parameter estimate being greater than the slope parameter estimate was determined by comparing posterior samples from the fitted model.

Parameter	Estimate		Probability
	Slope	Ridge	Ridge > Slope
Annual survival, $\Phi$	0.996 $\pm$ 0.002 [0.99, 0.999]	0.993 $\pm$ 0.004 [0.984, 0.999]	0.359
Mean dispersal (m)	1.241 $\pm$ 0.146 [0.961, 1.534]	1.376 $\pm$ 0.202 [0.995, 1.784]	0.708
Space-use, $\sigma$ (m)	3.496 $\pm$ 0.164 [3.189, 3.839]	3.823 $\pm$ 0.221 [3.419, 4.286]	0.885
Density (per m <sup>2</sup> )	0.613 $\pm$ 0.089 [0.558, 0.800]	0.432 $\pm$ 0.072 [0.380, 0.580]	0.050
Detection probability, $\lambda$	0.019 $\pm$ 0.002 [0.016, 0.023]	0.015 $\pm$ 0.002 [0.012, 0.019]	0.066

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Table 3. Parameter estimates from the fitted von Bertalanffy growth model. Reported values are the mean  $\pm$  standard deviation with 95% Bayesian credible intervals in brackets.

Parameter	Description	Estimate
<i>L</i> (male)	Asymptotic size (SVL) of males	43.569 $\pm$ 1.319 [41.721, 46.782]
<i>L</i> (female)	Asymptotic size (SVL) of females	52.164 $\pm$ 2.856 [47.958, 59.062]
<i>K</i> (slope, male)	Growth coefficient for males on the slope	0.671 $\pm$ 0.176 [0.36, 1.049]
<i>K</i> (slope, female)	Growth coefficient for females on the slope	0.237 $\pm$ 0.056 [0.137, 0.357]
<i>K</i> (ridge, male)	Growth coefficient for males on the ridge	0.97 $\pm$ 0.266 [0.506, 1.547]
<i>K</i> (ridge, female)	Growth coefficient for females on the ridge	0.339 $\pm$ 0.073 [0.205, 0.489]

Table 4. Summary table of space use statistics for salamanders occupying ridge and slope habitats. Probability of home range overlap (PHR) is reported as both the average for each individual (*i*) relative to all other individuals (*j*) within the same survey plot, as well as the maximum probability of core utilization distribution (UD) overlap. Overlap reports the average number of individuals with overlapping core UD and NN summarizes the average distance to the next closest salamander in the plot. All statistics are means ( $\pm$  standard deviation).

Parameter	Estimate	
	Slope	Ridge
Mean PHR <sub>ij</sub>	0.103 (0.014)	0.099 (0.017)
Max PHR <sub>ij</sub>	0.431 (0.042)	0.422 (0.047)
Overlap	43.8 (13.3)	35.8 (12.1)
NN (meters)	0.40 (0.06)	0.50 (0.08)
Average Clutches	2.2 (3.7)	2.8 (4.1)
Average Fecundity	13.7 (27.3)	19.6 (33.5)

Figure 1: Density plot showing the posterior distributions for asymptotic size for males and females (A) and posterior distributions for the growth coefficient for males and females occupying slopes and ridges (B). With greater than 99% probability, all contrasts indicate that males are smaller than females, males grow faster than females, and that males and females on the ridge growth faster than males and females on the slope.

Figure 2: Time to maturity plot, indicating the expected time it would take female (A) and male (B) salamanders to reach sexual maturity (34mm SVL), given their development in either slope or ridge habitats. Starting from a hatching SVL of 13mm, 50 % of juvenile female salamanders occupying ridge habitat are expected to reach the minimum size of sexual maturity after 3.30 years compared to 4.30 years for females occupying the slope (A). In contrast, 50% of males are expected to reach maturity in 2.25 years and 2.75 years in ridge and slope habitat, respectively (B).

Figure 3. Density plot showing the average number of individuals that had overlapping core (50% UD) home ranges with each salamander (A) and the average distance between salamander activity centers (B) in slope and ridge locations. Salamanders occupying slope habitat tended to have more individuals potentially occurring within their core home range than salamanders occupying ridge habitat, which coincided with less distance between slope salamanders.



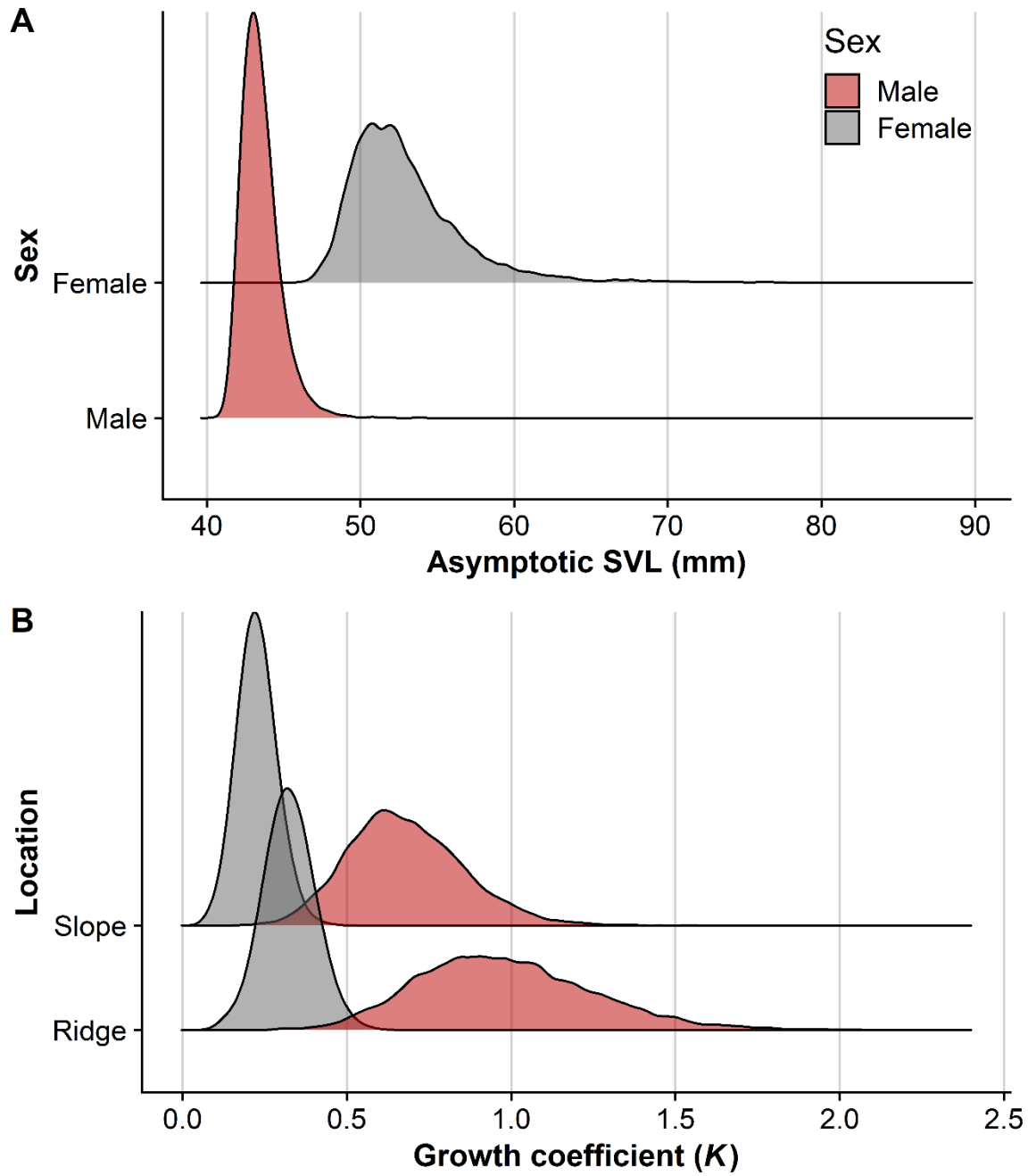


Figure 1

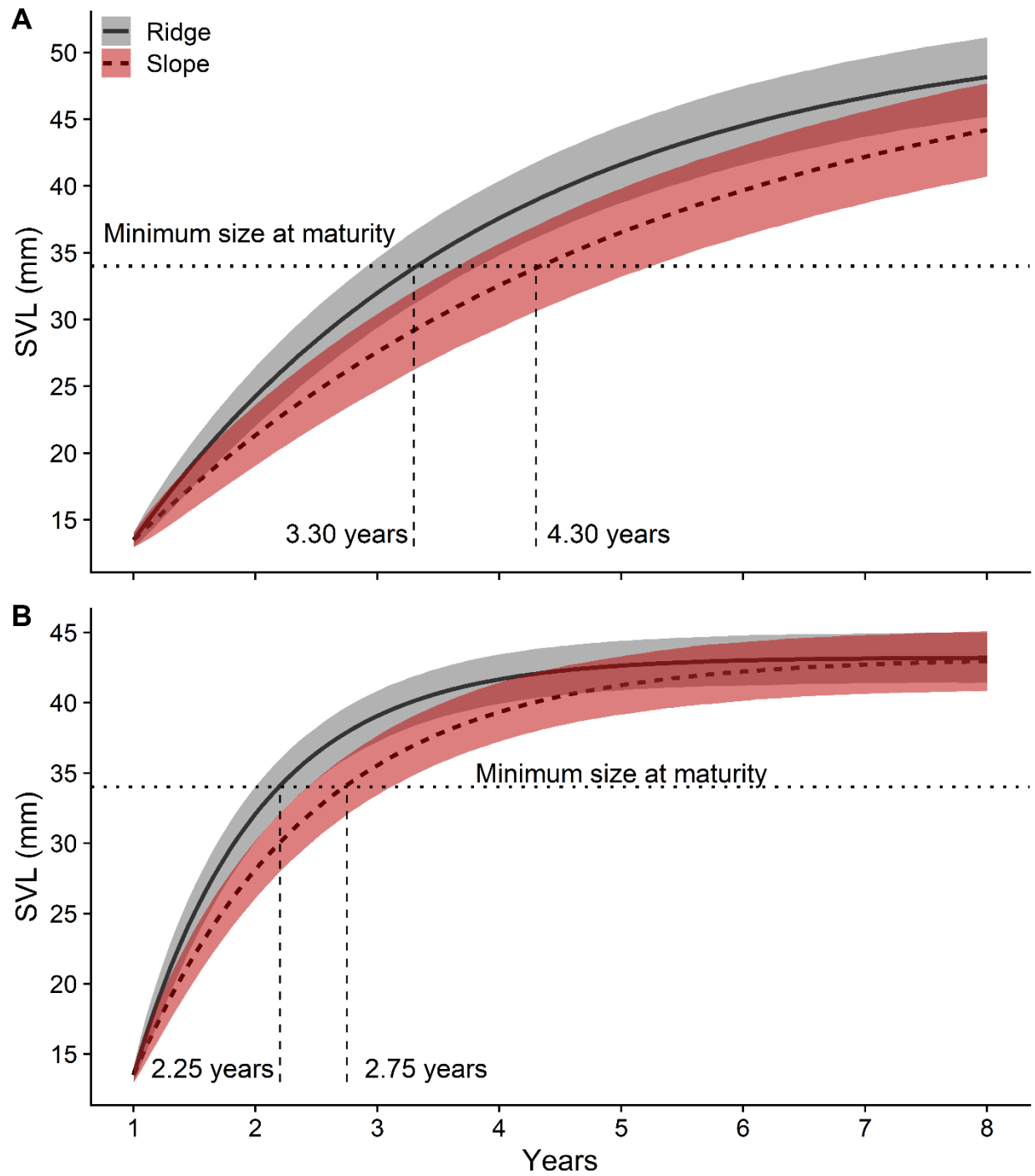


Figure 2

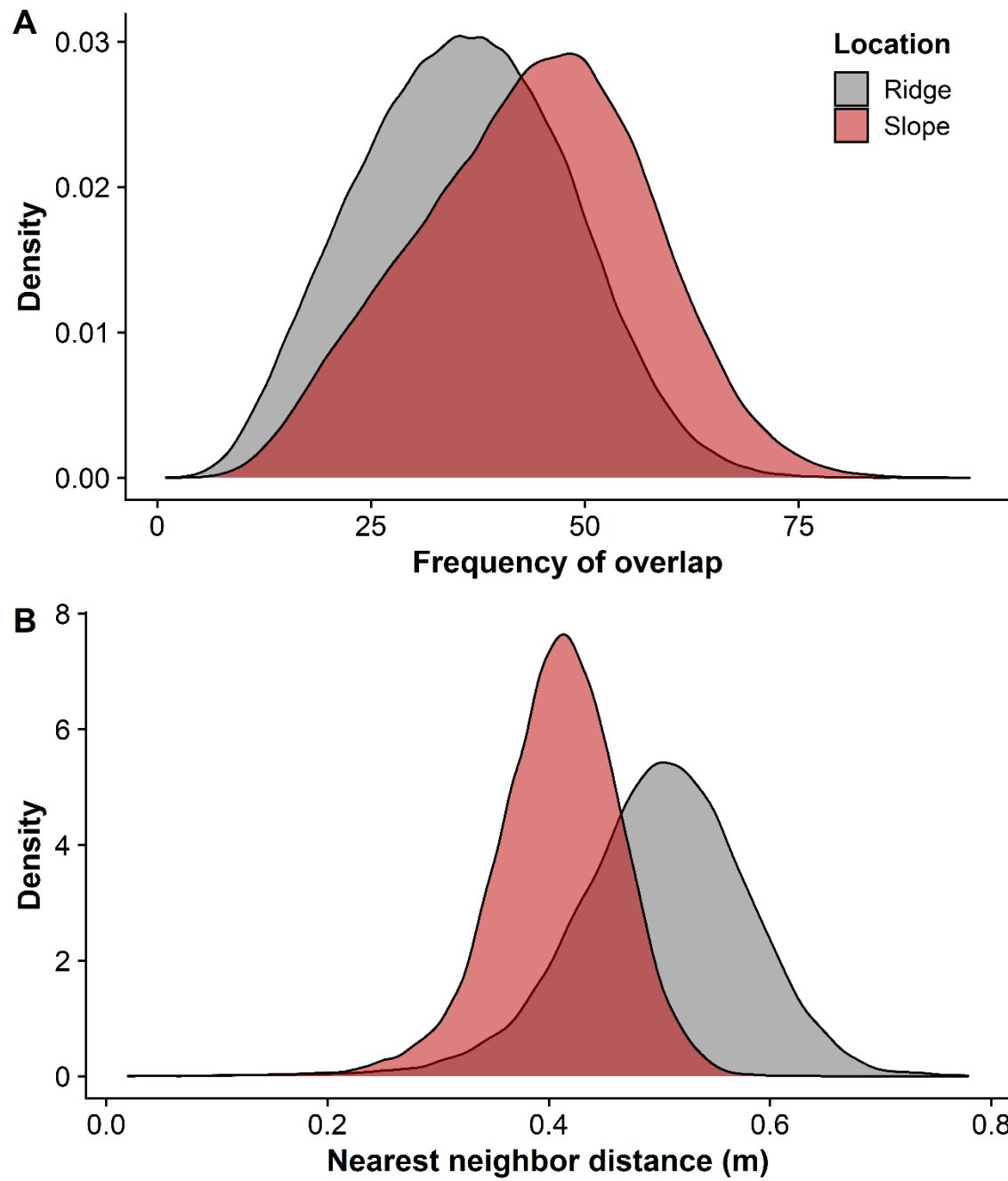


Figure 3