

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

3

4 Meaghan R. Gade<sup>1,2</sup>, Philip R. Gould<sup>1</sup>, Andrew J. Wilk<sup>1</sup>, Kate C. Donlon<sup>1</sup>, MacKenzie L.  
5 Brown<sup>1</sup>, Marnie L. Behan<sup>1</sup>, Marissa A. Roseman<sup>1</sup>, Annalee M. Tutterow<sup>1</sup>, Evan D. Amber<sup>1</sup>,  
6 Ryan B. Wagner<sup>1</sup>, Andrew S. Hoffman<sup>1</sup>, Jennifer M. Myers<sup>1</sup>, William E. Peterman<sup>1\*</sup>

7

8 <sup>1</sup> School of Environment and Natural Resources, The Ohio State University, 2021 Coffey Rd,  
9 Columbus, OH 43201

10 <sup>2</sup> Department of Ecology and Evolution, Yale University, New Haven, CT

11 \* Corresponding Author: Peterman.73@osu.edu

12

13 **Abstract**

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

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

35

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

37 **Introduction**

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

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

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

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

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

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

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

107

## 108 **Methods**

### 109 *Field Sampling*

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

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

123 *Plethodon cinereus* in Ohio are most active at the surface during spring and autumn and  
124 retreat into deeper soil to avoid desiccation and freezing during summer and winter, respectively  
125 (Pfungsten et al., 2013). Thus, we sampled for salamanders three times during both the spring  
126 (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  
127 daytime sampling event, we searched for salamanders under all cover boards, captured animals

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

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

144

145 *Statistical Analysis:*

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

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

160

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

$$163 \quad SVLO_{i,t} = SVLO_{i,t-1} + \left\{ L[SEX] - SVLO_{i,t-1} \times \left[ 1 - \exp\left(-K_{i,t} \times \frac{I}{365}\right) \right] \right\}$$

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

$$170 \quad K_{i,t} = \beta_0^{[K]} + \beta_1^{[K]} \times POS_i + \beta_2^{[K]} \times SEX_i$$

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

174 coefficients in Slope sub-populations. We treated the difference as significant if greater than  
175 97.5% of the posterior density was on one side of zero. We ran the growth model on five MCMC  
176 chains for 200,000 iterations with a burn-in of 25,000 and a thinning rate of 5. We considered  
177 models to have fully converged if all parameters had Gelman-Rubén (Rhat) statistics below 1.05  
178 and visual inspection of MCMC chains indicated clear and consistent mixing.

179

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

$$185 \quad p_{ijk} = \exp\left(-\left(\frac{d_{ijk}}{\sigma_k}\right)^2\right).$$

186 The rate of probability decay in space is governed by  $\sigma$ , which was estimated during the fitting  
187 of the SCR model. Probability of use surfaces were created for each individual at 1,000 samples  
188 ( $k$ ) of the fitted posterior model distributions. Using the probability surfaces  $p_{ijk}$ , we distributed  
189 1,000 hypothetical ‘use’ points on the landscape following a random multinomial process. We  
190 then calculated kernel density utilization distributions (UD) of these spatially referenced use  
191 points for each individual and posterior sample using the R package ‘adehabitatHR’ (Calenge,  
192 2006). Finally, we calculated the probability that the core 50% of each individual  $i$ ’s UD  
193 overlapped with all other core 50% UD $_j$  calculated as the probability of home range overlap  
194 (Fieberg and Kochanny, 2005). We then determined the average number of individuals with  
195 overlapping core UDs, as well as the average probability of overlap.

196

197            Population projection — Using parameters from our fitted growth model and from the  
198 literature, we conducted population projection simulations to understand how differences in  
199 growth could impact lifetime fitness. We assume that all individuals are 13.5 mm SVL upon  
200 hatching, and that sexual maturity is first reached at 34 mm SVL (Pfungsten et al., 2013).  
201 However, following Lotter (1978) we assume that individuals between 34 and 43 mm SVL have  
202 56% chance of being gravid, while 94% of females >43 mm SVL are likely to be gravid.  
203 Regional variation in reproduction has been documented (Lotter, 1978; Saylor, 1966; Werner,  
204 1971), but our data are not sufficient to ascertain frequency of reproduction in our Ohio  
205 population. Similarly, we could not confidently determine the average number of eggs produced  
206 by each female, nor whether there was a size by fecundity interaction. As such, we fit a linear  
207 model with a normal distribution to the data reported in Lotter (1978) relating clutch size to SVL  
208 using the R package ‘brms’ (Bürkner, 2016). We found that the normally distributed model  
209 better fit the data than a generalized model with a Poisson or negative binomial distribution. Like  
210 previous demographic projection models of *P. cinereus* (Hernández-Pacheco et al., 2021;  
211 Homyack and Haas, 2009), we assume eggs have a 90% hatching rate.

212            We estimated growth and lifetime fecundity at each Slope and Ridge location using  
213 100,000 samples from the posterior distributions of our fitted growth model and the clutch size  
214 model. Because the survival estimates from our spatial-capture-recapture data are unrealistically  
215 high (Table 2), we used the average of male and female annual survival estimates and  
216 uncertainty from Muñoz et al. (2016b). For each individual, at each time step (one year), we  
217 estimated survival as a random binomial process, with the annual probability of surviving being  
218 normally distributed with a mean of 0.836 and standard deviation of 0.07 (truncated to 0.4–1.0).  
219 The lifespan of wild *P. cinereus* is unknown; we projected our model out 20 years.

220

## 221 **Results**

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

229

230 SCR Results — For most parameters estimated in our spatial capture-recapture model,  
231 Slope and Ridge plots had moderate differences (Table 2). Annual survival was estimated to be  $>$   
232 0.99 for both Slope and Ridge plots. Activity centers of salamander in Ridge plots tended to shift  
233 slightly more between primary sample periods when compared to Slope plots (1.376 m vs. 1.241  
234 m, respectively) and Ridge salamanders tended to move around more within a primary period  
235 (Ridge = 1.376 m, Slope = 1.241 m). The density of salamanders was significantly lower in  
236 Ridge plots, which also had significantly lower probability of detection (Table 2).

237

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

243 significant differences in growth rates between the Slope and Ridge locations (Table 3; Fig. 1).  
244 This results in Ridge males reaching sexual maturity in 2.25 years and Slope males maturing in  
245 2.75 years, while Ridge females mature in 3.30 years and Slope females mature in 4.30 years  
246 (Fig 2).

247  
248 Space-use — Salamanders occupying Ridge habitat had substantially fewer individuals  
249 overlapping their core UD ( $35.8 \pm 12.1$ ) than salamanders occupying Slope habitat ( $43.8 \pm 13.3$ ;  
250 Table 4, Fig. 3). Despite the greater number of individuals potentially occupying the same space  
251 in the Slope habitat, the average probability of overlap was nearly identical between the two  
252 habitats (Table 4). However, the average distance to the nearest neighboring salamander tended  
253 to be less for salamanders occupying Slope habitat ( $0.40 \text{ m} \pm 0.06$ ) compared to salamanders  
254 occupying Ridge habitat ( $0.50 \text{ m} \pm 0.08$ ; Fig. 3).

255  
256 Population projection — Given the annual survival rate estimated from Muñoz et al.  
257 (2016a), females are estimated to live an average of 5.87 years ( $\pm 4.90$  SD). Females in the Slope  
258 habitat are estimated to average 2.2 ( $\pm 3.7$ ) clutches in their lifetime, equating to a mean lifetime  
259 fecundity of 13.7 ( $\pm 27.3$ ). Because maturity is reached earlier in the Ridge habitat, Ridge females  
260 are estimated to average 2.8 ( $\pm 4.1$ ) clutches and produce a mean of 19.6 ( $\pm 33.5$ ) offspring in  
261 their lifetime, which is 43% more than Slope females (Table 4).

## 262 263 **Discussion**

264 Demographic vital rates and movement and dispersal rates are driven by the abiotic and  
265 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

289 utilized the same sampling protocols as the present study found that home ranges are not limited  
290 by density and instead suggest that the seasonal changes in spatial distribution are driven by food  
291 and shelter (Hernández-Pacheco et al., 2019). Our study site has the highest observed density of  
292 salamanders per square meter compared to nine other sites in central Ohio, USA (Wilk et al.,  
293 2020), but the density estimates from the current study are moderate to low compared to spatial  
294 capture-recapture density estimates from other regions (Hernández-Pacheco et al., 2019). The  
295 high observed densities likely reflect habitat quality, as our study site has remained largely  
296 undisturbed relative to other central Ohio sites, and subsequent capacity to support a higher  
297 density of salamanders. However, there are limits to the number of individuals that can be  
298 supported before density-dependent effects emerge.

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

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

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

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

335 resilient and adaptable species with a distribution encompassing much of eastern North America  
336 and populations frequently persisting in highly altered or urbanized landscapes (Gibbs, 1998;  
337 Petranka, 1998; Wilk et al., 2020). The ability to thrive and not just persist in altered or changing  
338 habitats may be critical to the species' broad distribution and persistence. We found *P. cinereus*  
339 occupying successional habitat to have greater growth rates, which are predicted to result in  
340 earlier maturation and greater lifetime fecundity. While observed differences in salamander  
341 growth rates and the subsequent demographic differences are likely driven by environmental  
342 variation and density-dependent processes, rather than adaptation and microevolutionary  
343 processes, our results reinforce the role that fine-scale variation can play in spatial-temporal  
344 population processes. Perhaps most notably, these differences occurred between sites less than  
345 100 m apart, highlighting the importance of accounting for fine-scale, within-site variation when  
346 assessing demographic processes. As research into the demographic and population  
347 consequences of climate change and habitat loss and alteration continue, future research should  
348 take care to acknowledge the role that fine-scale variation may play, especially for organisms  
349 with small home ranges or limited mobility.

350

### 351 **Acknowledgements**

352 We would like to thank the many people who aided in the field data collection including Eric  
353 Gangloff, Alyssa Baxter, Christy Kunkle, Kasey Foley, Amelia Gray, Renna Wittum, and Aaron  
354 D'Amore. We also thank Harlan Bockbrader, the Overbrook Presbyterian Church, and John  
355 Beltz Retreat Center for property access and support of this research. This research is part of and  
356 stemmed from the Salamander Population Adaptation Research Collaboration Network  
357 (SPARCnet). We are especially grateful to David Muñoz for advice on statistical analyses. All

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

### 360 **Data Accessibility**

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

### 362 **Conflicts of Interests**

363 The authors do not have any competing interest

### 364 **Author Contributions**

365 **Meaghan Gade** contributed to conceptualization, data curation, formal analysis, methodology,  
366 investigation, project administration, writing-original draft preparation, and writing-review and  
367 editing. **Philip Gould** contributed to conceptualization, data curation, formal analysis,  
368 methodology, investigation, visualization, writing-original draft preparation, and writing-review  
369 and editing. **Andrew Wilk** contributed to conceptualization, data curation, formal analysis,  
370 methodology, investigation, visualization, writing-original draft preparation, and writing-review  
371 and editing. **Kate Donlon** contributed to conceptualization, methodology, data curation, project  
372 administration, investigation, writing-review and editing. **Mackenzie Brown** contributed to data  
373 curation, investigation, and writing-review and editing. **Marnie Behan** contributed to data  
374 curation, investigation, and writing-review and editing. **Marissa Roseman** contributed to data  
375 curation, investigation, and writing-review and editing. **Annalee Tutterow** contributed to data  
376 curation, investigation, and writing-review and editing. **Evan Amber** contributed to data  
377 curation, investigation, formal analysis and writing-review and editing. **Ryan Wagner**  
378 contributed to data curation, investigation, and writing-review and editing. **Andrew Hoffman**  
379 contributed to data curation, investigation, writing-original draft, and writing-review and editing.

380 Jen Myers contributed to data curation, investigation, and writing-review and editing. **William**  
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.

384 **Literature Cited**

- 385 Anderson, T., Ousterhout, B., Peterman, W.E., Drake, D., Semlitsch, R.D., 2015. Life history  
386 differences influence the impacts of drought on two pond-breeding salamanders.  
387 Ecological Applications 25, 1896–1910.
- 388 Bailey, L.L., Simons, T.R., Pollock, K.H., 2004a. Estimating site occupancy and species  
389 detection probability parameters for terrestrial salamanders. Ecol. Appl. 14, 692–702.
- 390 Bailey, L.L., Simons, T.R., Pollock, K.H., 2004b. Spatial and temporal variation in detection  
391 probability of *Plethodon* salamanders using the robust capture-recapture design. J. Wildl.  
392 Manage. 68, 14–24.
- 393 Bendik, N.F., Dries, L.A., 2018. Density-dependent and density-independent drivers of  
394 population change in Barton Springs salamanders. Ecology and Evolution 8, 5912–5923.  
395 <https://doi.org/10.1002/ece3.4130>
- 396 Berven, K.A., 2009. Density dependence in the terrestrial stage of wood frogs: Evidence from a  
397 21-year population study. Copeia 2009, 328–338. <https://doi.org/10.1643/CH-08-052>
- 398 Boyle, S.A., Lourenço, W.C., Silva, L.R. da, Smith, A.T., 2009. Home range estimates vary with  
399 sample size and methods. FPR 80, 33–42. <https://doi.org/10.1159/000201092>
- 400 Bürkner, P.-C., 2016. brms: An R package for Bayesian multilevel models using Stan. Journal of  
401 Statistical Software 80, 1–28.
- 402 Burton, T.M., Likens, G.E., 1975. Salamander populations and biomass in the Hubbard Brook  
403 Experimental Forest, New Hampshire. Copeia 1975, 541–546.
- 404 Cabe, P.R., Page, R.B., Hanlon, T.J., Aldrich, M.E., Connors, L., Marsh, D.M., 2007. Fine-scale  
405 population differentiation and gene flow in a terrestrial salamander (*Plethodon cinereus*)  
406 living in continuous habitat. Heredity 98, 53–60.

407 Calenge, C., 2006. The package “adehabitat” for the R software: A tool for the analysis of space  
408 and habitat use by animals. *Ecol. Model.* 197, 516–519.  
409 <https://doi.org/10.1016/j.ecolmodel.2006.03.017>

410 Caruso, N.M., Rissler, L.J., 2019. Demographic consequences of climate variation along an  
411 elevational gradient for a montane terrestrial salamander. *Popul. Ecol.* 61, 171–182.  
412 <https://doi.org/10.1002/1438-390x.1005>

413 Caruso, N.M., Rissler, L.J., 2018. Life history variation along an elevational gradient in  
414 *Plethodon montanus*: implications for conservation. *bioRxiv*.  
415 <https://doi.org/10.1101/130922>

416 Cicchino, A.S., Martinez, C.M., Funk, W.C., Forester, B.R., 2021. An integrative eco-evo-devo  
417 framework identifies complex drivers of oral morphology in tailed frog (*Ascaphus* spp.)  
418 tadpoles. *bioRxiv* 2020.04.06.027664. <https://doi.org/10.1101/2020.04.06.027664>

419 Clobert, J., Le Galliard, J.-F., Cote, J., Meylan, S., Massot, M., 2009. Informed dispersal,  
420 heterogeneity in animal dispersal syndromes and the dynamics of spatially structured  
421 populations. *Ecol. Lett.* 12, 197–209. <https://doi.org/10.1111/j.1461-0248.2008.01267.x>

422 Connette, G.M., Semlitsch, R.D., 2013. Life history as a predictor of salamander recovery rate  
423 from timber harvest in southern Appalachian Forests, U.S.A. *Conserv. Biol.* 27, 1399–  
424 1409. <https://doi.org/10.1111/cobi.12113>

425 Dalton, B., Settle, R., Medley, K., Mathis, A., 2020. When neighbors cheat: a test of the dear  
426 enemy phenomenon in southern red-backed salamanders. *Behav Ecol Sociobiol* 74, 56.  
427 <https://doi.org/10.1007/s00265-020-02838-9>

428 Dantzer, B., Fletcher, Q.E., Boonstra, R., Sheriff, M.J., 2014. Measures of physiological stress: a  
429 transparent or opaque window into the status, management and conservation of species?  
430 Conservation Physiology 2, 1–18. <https://doi.org/10.1093/conphys/cou023>

431 De Bie, T., De Meester, L., Brendonck, L., Martens, K., Goddeeris, B., Ercken, D., Hampel, H.,  
432 Denys, L., Vanhecke, L., Van der Gucht, K., Van Wichelen, J., Vyverman, W., Declerck,  
433 S.A.J., 2012. Body size and dispersal mode as key traits determining metacommunity  
434 structure of aquatic organisms. Ecol. Lett. 15, 740–747. [https://doi.org/10.1111/j.1461-](https://doi.org/10.1111/j.1461-0248.2012.01794.x)  
435 [0248.2012.01794.x](https://doi.org/10.1111/j.1461-0248.2012.01794.x)

436 Ergon, T., Gardner, B., 2014. Separating mortality and emigration: modelling space use,  
437 dispersal and survival with robust-design spatial capture–recapture data. Methods in  
438 Ecology and Evolution 5, 1327–1336. <https://doi.org/10.1111/2041-210X.12133>

439 Fieberg, J., Kochanny, C.O., 2005. Quantifying home-range overlap: The importance of the  
440 utilization distribution. The Journal of Wildlife Management 69, 1346–1359.  
441 [https://doi.org/10.2193/0022-541x\(2005\)69\[1346:Qhotio\]2.0.Co;2](https://doi.org/10.2193/0022-541x(2005)69[1346:Qhotio]2.0.Co;2)

442 Gade, M.R., 2021. Spatial variation in the abundance, demography, and physiology of the  
443 montane endemic salamander, *Plethodon shermani*, and the consequences of climate  
444 change (Dissertation). The Ohio State University, Columbus, OH, USA.

445 Gade, M.R., Peterman, W.E., 2019. Multiple environmental gradients influence the distribution  
446 and abundance of a key forest-health indicator species in the Southern Appalachian  
447 Mountains, USA. Landscape Ecol. 34, 569–582. [https://doi.org/10.1007/s10980-019-](https://doi.org/10.1007/s10980-019-00792-0)  
448 [00792-0](https://doi.org/10.1007/s10980-019-00792-0)

449 Gaillard, J.-M., Hebblewhite, M., Loison, A., Fuller, M., Powell, R., Basille, M., Van Moorter,  
450 B., 2010. Habitat–performance relationships: finding the right metric at a given spatial

451 scale. *Philosophical Transactions of the Royal Society B: Biological Sciences* 365, 2255–  
452 2265. <https://doi.org/10.1098/rstb.2010.0085>

453 Gardner, B., Royle, J.A., Wegan, M.T., Rainbolt, R.E., Curtis, P.D., 2010. Estimating black bear  
454 density using DNA data from hair snares. *J. Wildl. Manage.* 74, 318–325.  
455 <https://doi.org/10.2193/2009-101>

456 Getz, W.M., 1996. A hypothesis regarding the abruptness of density dependence and the growth  
457 rate of populations. *Ecology* 77, 2014–2026. <https://doi.org/10.2307/2265697>

458 Gibbs, J.P., 1998. Distribution of woodland amphibians along a forest fragmentation gradient.  
459 *Landscape Ecol.* 13, 263–268.

460 Gonzales, S., Crowell, H., Harmel, M., Maier, P., Nhu, T., Nolan, J., Whelan, J., Taylor, E.,  
461 2020. Variation in rattlesnake spatial ecology among individuals and populations.  
462 *Herpetological Review* 51, 680–685.

463 Hanski, I., Gilpin, M., 1991. Metapopulation dynamics: brief history and conceptual domain.  
464 *Biol. J. Linn. Soc.* 42, 3–16. <https://doi.org/10.1111/j.1095-8312.1991.tb00548.x>

465 Harper, E.B., Semlitsch, R.D., 2007. Density dependence in the terrestrial life history stage of  
466 two anurans. *Oecologia* 153, 879–889.

467 Hernández-Pacheco, R., Plard, F., Grayson, K.L., Steiner, U.K., 2021. Demographic  
468 consequences of changing body size in a terrestrial salamander. *Ecology and Evolution*  
469 11, 174–185. <https://doi.org/10.1002/ece3.6988>

470 Hernández-Pacheco, R., Sutherland, C., Thompson Lily, M., Grayson Kristine, L., 2019.  
471 Unexpected spatial population ecology of a widespread terrestrial salamander near its  
472 southern range edge. *Royal Society Open Science* 6, 182192.  
473 <https://doi.org/10.1098/rsos.182192>

474 Homyack, J.A., Haas, C.A., 2009. Long-term effects of experimental forest harvesting on  
475 abundance and reproductive demography of terrestrial salamanders. *Biol. Conserv.* 142,  
476 110–121.

477 Jaeger, R.G., 1981. Dear enemy recognition and the costs of aggression between salamanders.  
478 *The American Naturalist* 117, 962–974. <https://doi.org/10.1086/283780>

479 Jaeger, R.G., 1979. Seasonal spatial distributions of the terrestrial salamander *Plethodon*  
480 *cinereus*. *Herpetologica* 35, 90–93.

481 Jaeger, R.G., Peterson, M.G., 2002. Familiarity affects agonistic interactions between female  
482 red-backed salamanders. *Copeia* 2002, 865–869. [https://doi.org/10.1643/0045-](https://doi.org/10.1643/0045-8511(2002)002[0865:FAAIBF]2.0.CO;2)  
483 [8511\(2002\)002\[0865:FAAIBF\]2.0.CO;2](https://doi.org/10.1643/0045-8511(2002)002[0865:FAAIBF]2.0.CO;2)

484 Kleeberger, S.R., Werner, J.K., 1982. Home range and homing behavior of *Plethodon cinereus*  
485 in northern Michigan. *Copeia* 1982, 409–415. <https://doi.org/10.2307/1444622>

486 Kuzmin, S.L., 1995. The problem of food competition in amphibians. *Herpetological Journal* 5,  
487 252–252.

488 Liebgold, E.B., Brodie, E.D., Cabe, P.R., 2011. Female philopatry and male-biased dispersal in a  
489 direct-developing salamander, *Plethodon cinereus*. *Mol. Ecol.* 20, 249–257.  
490 <https://doi.org/10.1111/j.1365-294X.2010.04946.x>

491 Lotter, F., 1978. Reproductive ecology of the salamander *Plethodon cinereus* (Amphibia,  
492 Urodela, Plethodontidae) in Connecticut. *J. Herpetol.* 12, 231–236.  
493 <https://doi.org/10.2307/1563411>

494 Marsh, D.M., Page, R.B., Hanlon, T.J., Corritone, R., Little, E.C., Seifert, D.E., Cabe, P.R.,  
495 2008. Effects of roads on patterns of genetic differentiation in red-backed salamanders,  
496 *Plethodon cinereus*. *Conserv. Genet.* 9, 603–613.

497 McKenny, H.C., Keeton, W.S., Donovan, T.M., 2006. Effects of structural complexity  
498 enhancement on eastern red-backed salamander (*Plethodon cinereus*) populations in  
499 northern hardwood forests. *For. Ecol. Manage.* 230, 186–196. [https://doi.org/DOI:](https://doi.org/DOI:10.1016/j.foreco.2006.04.034)  
500 10.1016/j.foreco.2006.04.034

501 McKinney, M.L., 1997. Extinction vulnerability and selectivity: Combining ecological and  
502 paleontological views. *Annu. Rev. Ecol. Syst.* 28, 495–516.  
503 <https://doi.org/10.1146/annurev.ecolsys.28.1.495>

504 Morales, J.M., Moorcroft, P.R., Matthiopoulos, J., Frair, J.L., Kie, J.G., Powell, R.A., Merrill,  
505 E.H., Haydon, D.T., 2010. Building the bridge between animal movement and population  
506 dynamics. *Philosophical Transactions of the Royal Society B: Biological Sciences* 365,  
507 2289–2301. <https://doi.org/10.1098/rstb.2010.0082>

508 Muñoz, D.J., Miller, D.A.W., Sutherland, C., Campbell Grant, E.H., 2016a. Using spatial  
509 capture–recapture to elucidate population processes and space-use in herpetological  
510 studies. *J. Herpetol.* 50, 570–581. <https://doi.org/10.1670/15-166>

511 Muñoz, D.J., Miller Hesed, K., Campbell Grant, E.H., Miller, D.A.W., 2016b. Evaluating  
512 within-population variability in behavior and demography for the adaptive potential of a  
513 dispersal-limited species to climate change. *Ecology and Evolution.*  
514 <https://doi.org/10.1002/ece3.2573>

515 Otto, C.R.V., Roloff, G.J., Thames, R.E., 2014. Comparing population patterns to processes:  
516 Abundance and survival of a forest salamander following habitat degradation. *PLoS ONE*  
517 9, e93859. <https://doi.org/10.1371/journal.pone.0093859>

518 Ousterhout, B.H., Semlitsch, R.D., 2016. Non-additive response of larval ringed salamanders to  
519 intraspecific density. *Oecologia* 180, 1137–1145. <https://doi.org/10.1007/s00442-015->  
520 3516-y

521 Peterman, W.E., Connette, G.M., Semlitsch, R.D., Eggert, L.S., 2014. Ecological resistance  
522 surfaces predict fine-scale genetic differentiation in a terrestrial woodland salamander.  
523 *Mol. Ecol.* 23, 2402–2413. <https://doi.org/10.1111/mec.12747>

524 Peterman, W.E., Semlitsch, R.D., 2013. Fine-scale habitat associations of a terrestrial  
525 salamander: the role of environmental gradients and implications for population  
526 dynamics. *PLoS ONE* 8, e62184. <https://doi.org/10.1371/journal.pone.0062184>

527 Petranka, J.W., 1998. *Salamanders of the United States and Canada*. Smithsonian Institution  
528 Press, Washington D. C.

529 Pfungsten, R.A., Davis, J.G., Matson, T.O., Lipps, G.J., Wynn, D.E., Armitage, B.J., 2013.  
530 *Amphibians of Ohio*, Ohio Biological Survey Bulletin New Series. Columbus, OH.

531 Pollock, K.H., 1982. A capture-recapture design robust to unequal probability of capture. *The*  
532 *Journal of Wildlife Management* 46, 752–757. <https://doi.org/10.2307/3808568>

533 Reeve, J.D., Strom, B.L., Rieske, L.K., Ayres, B.D., Costa, A., 2009. Geographic variation in  
534 prey preference in bark beetle predators. *Ecological Entomology* 34, 183–192.  
535 <https://doi.org/10.1111/j.1365-2311.2008.01055.x>

536 Richardson, J.L., Urban, M.C., Bolnick, D.I., Skelly, D.K., 2014. Microgeographic adaptation  
537 and the spatial scale of evolution. *Trends in Ecology and Evolution* 29, 165–176.  
538 <https://doi.org/10.1016/j.tree.2014.01.002>

539 Saylor, A., 1966. The reproductive ecology of the red-backed salamander, *Plethodon cinereus*, in  
540 Maryland. *Copeia* 1966, 183–193. <https://doi.org/10.2307/1441125>

541 Schaub, M., Royle, J.A., 2014. Estimating true instead of apparent survival using spatial  
542 Cormack–Jolly–Seber models. *Methods in Ecology and Evolution* 5, 1316–1326.  
543 <https://doi.org/10.1111/2041-210X.12134>

544 Seabra, R., Wethey, D.S., Santos, A.M., Lima, F.P., 2011. Side matters: Microhabitat influence  
545 on intertidal heat stress over a large geographical scale. *Journal of Experimental Marine*  
546 *Biology and Ecology, Global change in marine ecosystems* 400, 200–208.  
547 <https://doi.org/10.1016/j.jembe.2011.02.010>

548 Semlitsch, R.D., 1987. Density-dependent growth and fecundity in the paedomorphic salamander  
549 *Ambystoma talpoideum*. *Ecology* 68, 1003–1008. <https://doi.org/10.2307/1938371>

550 Semlitsch, R.D., O’Donnell, K.M., Thompson, F.R., 2014. Abundance, biomass production,  
551 nutrient content, and the possible role of terrestrial salamanders in Missouri Ozark forest  
552 ecosystems. *Can. J. Zool.* 997–1004. <https://doi.org/10.1139/cjz-2014-0141>

553 Turner, M.G., Gardner, R.H., 2015. *Landscape Ecology in Theory and Practice: Pattern and*  
554 *Process*, 2nd ed. Springer New York, New York, NY.

555 Urban, M.C., Bocedi, G., Hendry, A.P., Mihoub, J.-B., Pe’er, G., Singer, A., Bridle, J.R.,  
556 Crozier, L.G., De Meester, L., Godsoe, W., Gonzalez, A., Hellmann, J.J., Holt, R.D.,  
557 Huth, A., Johst, K., Krug, C.B., Leadley, P.W., Palmer, S.C.F., Pantel, J.H., Schmitz, A.,  
558 Zollner, P.A., Travis, J.M.J., 2016. Improving the forecast for biodiversity under climate  
559 change. *Science* 353, aad8466. <https://doi.org/10.1126/science.aad8466>

560 Van Buskirk, J., Smith, D.C., 1991. Density-dependent population regulation in a salamander.  
561 *Ecology* 72, 1747–1756. <https://doi.org/10.2307/1940973>

562 Werner, J.K., 1971. Notes on the reproductive cycle of *Plethodon cinereus* in Michigan. *Copeia*  
563 1971, 161–162.

564 Wilk, A.J., Donlon, K.C., Peterman, W.E., 2020. Effects of habitat fragment size and isolation  
565 on the density and genetics of urban red-backed salamanders (*Plethodon cinereus*). Urban  
566 Ecosyst 23, 761–773. <https://doi.org/10.1007/s11252-020-00958-8>

567 Wingfield, J.C., Romero, L.M., 2011. Adrenocortical Responses to Stress and Their Modulation  
568 in Free-Living Vertebrates, in: Comprehensive Physiology. American Cancer Society,  
569 pp. 211–234. <https://doi.org/10.1002/cphy.cp070411>

570

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

1

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

<b>Parameter</b>	<b>Description</b>	<b>Estimate</b>
<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]

4

5

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

12

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)

13

14

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

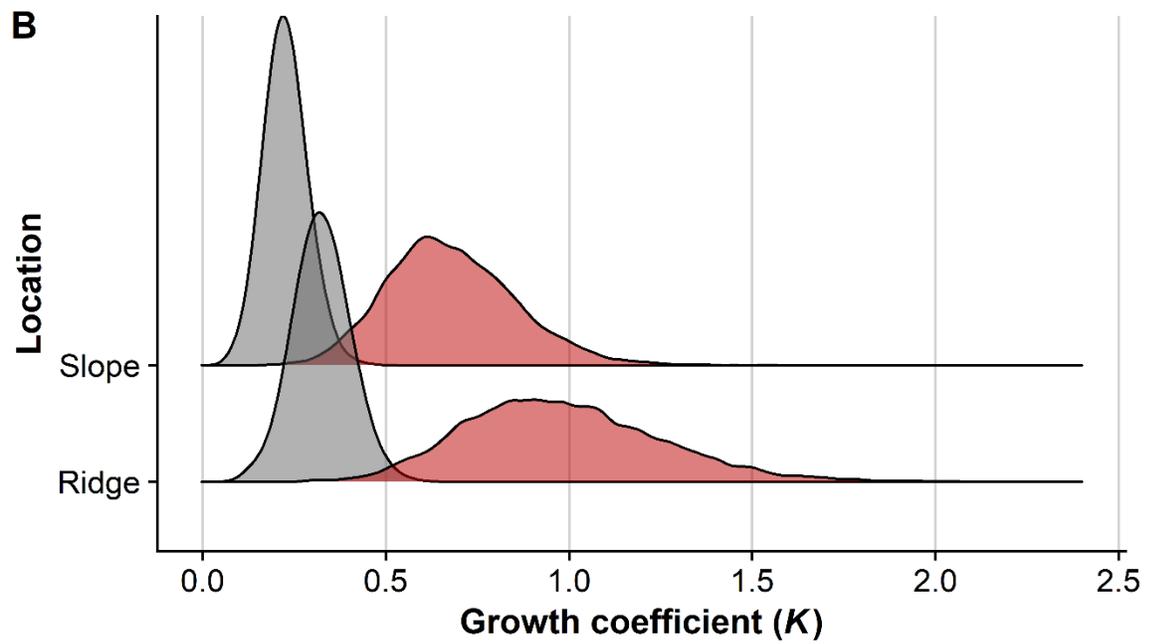
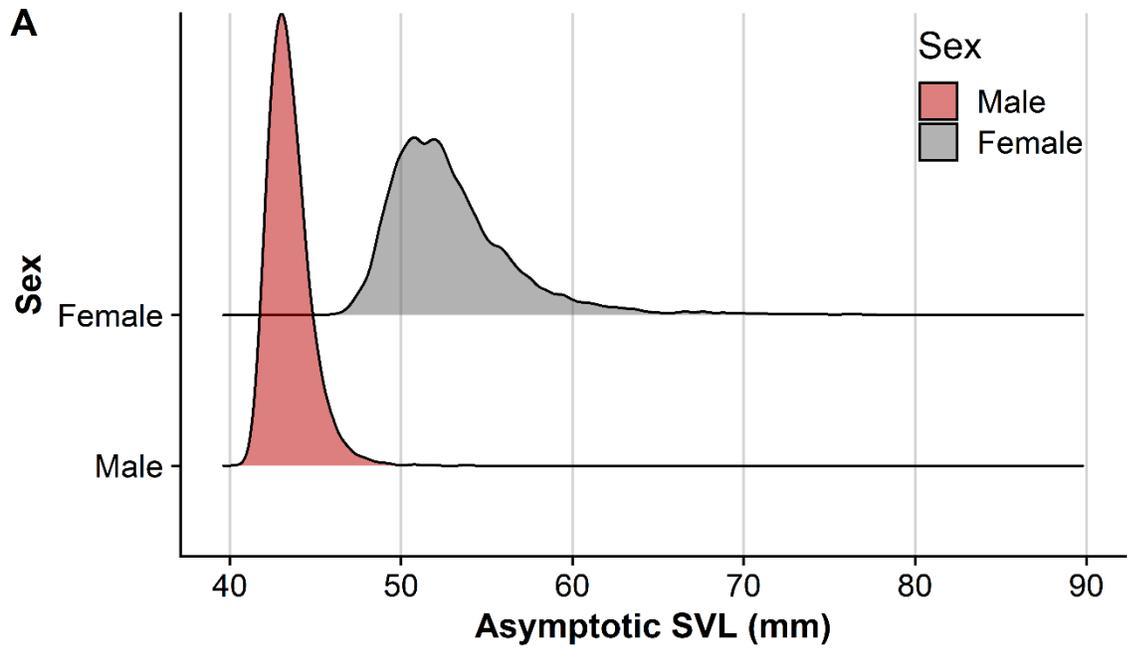
20

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

28

29 Figure 3. Density plot showing the average number of individuals that had overlapping core  
30 (50% UD) home ranges with each salamander (A) and the average distance between  
31 salamander activity centers (B) in slope and ridge locations. Salamanders occupying slope  
32 habitat tended to have more individuals potentially occurring within their core home range  
33 than salamanders occupying ridge habitat, which coincided with less distance between slope  
34 salamanders.

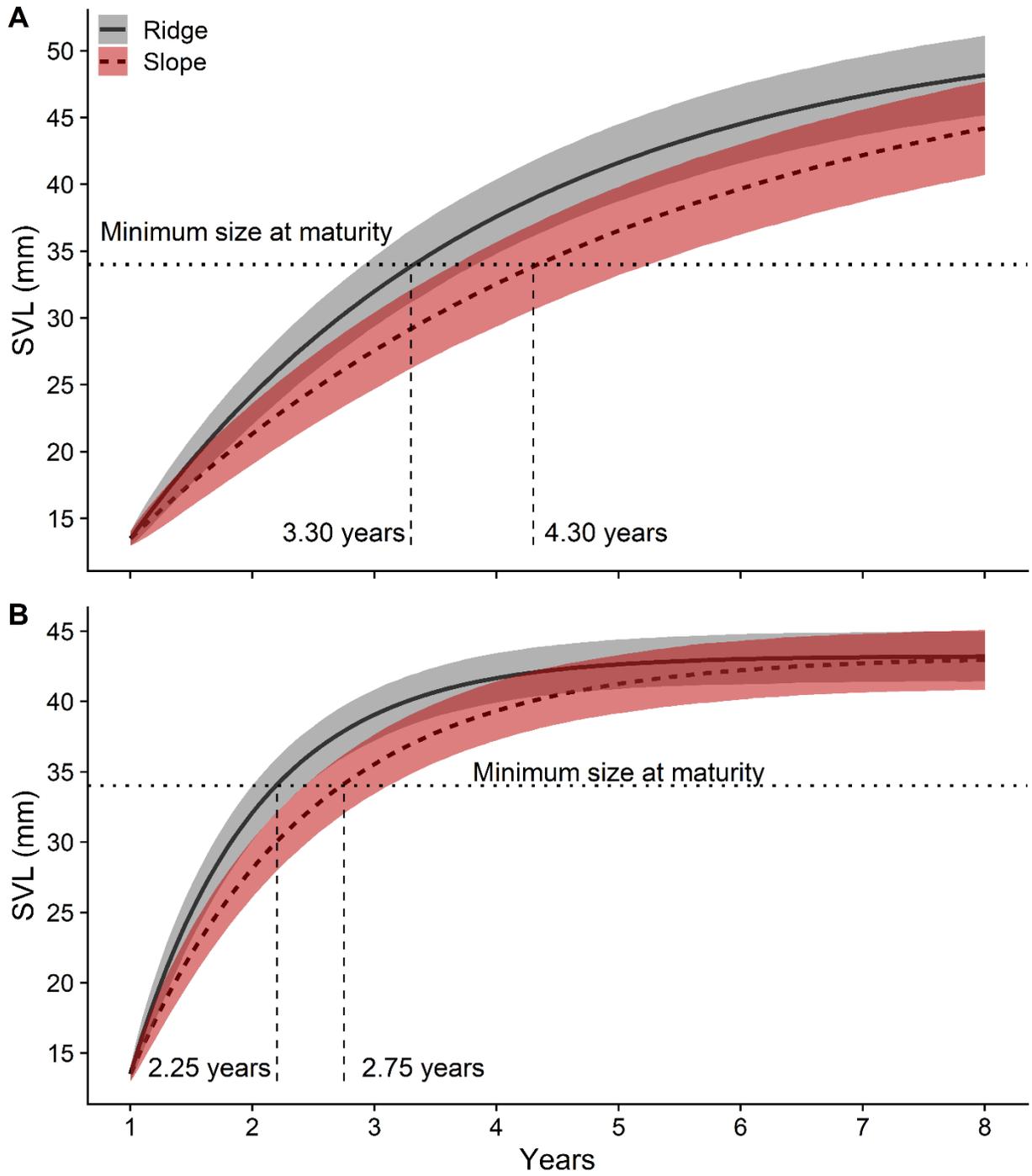
35



36

37 Figure 1

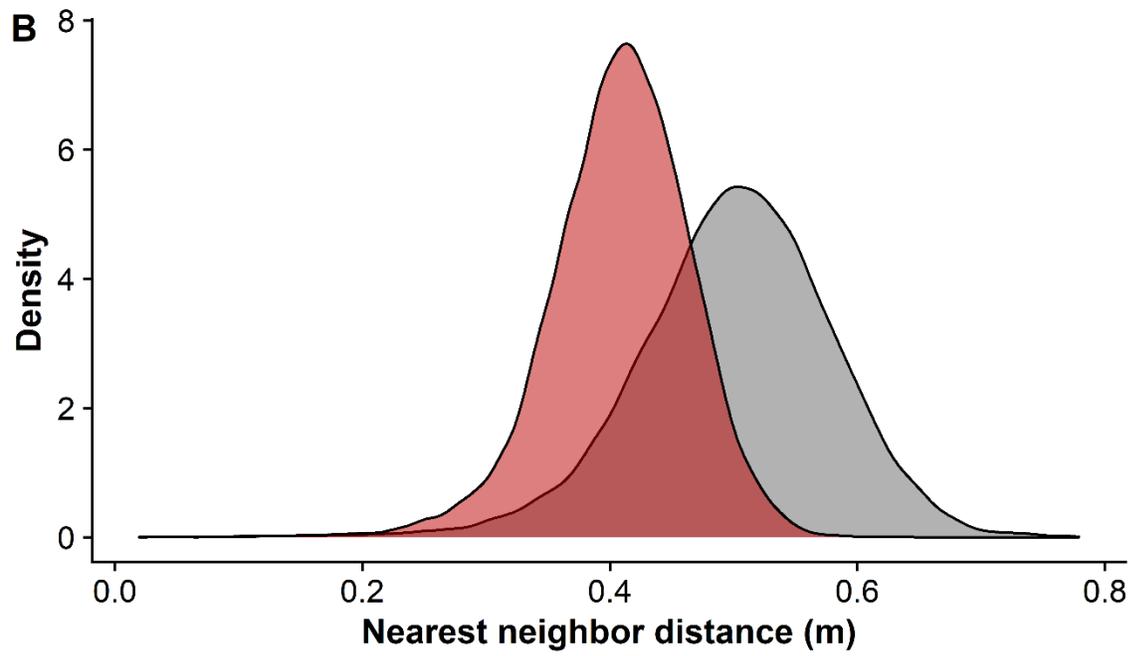
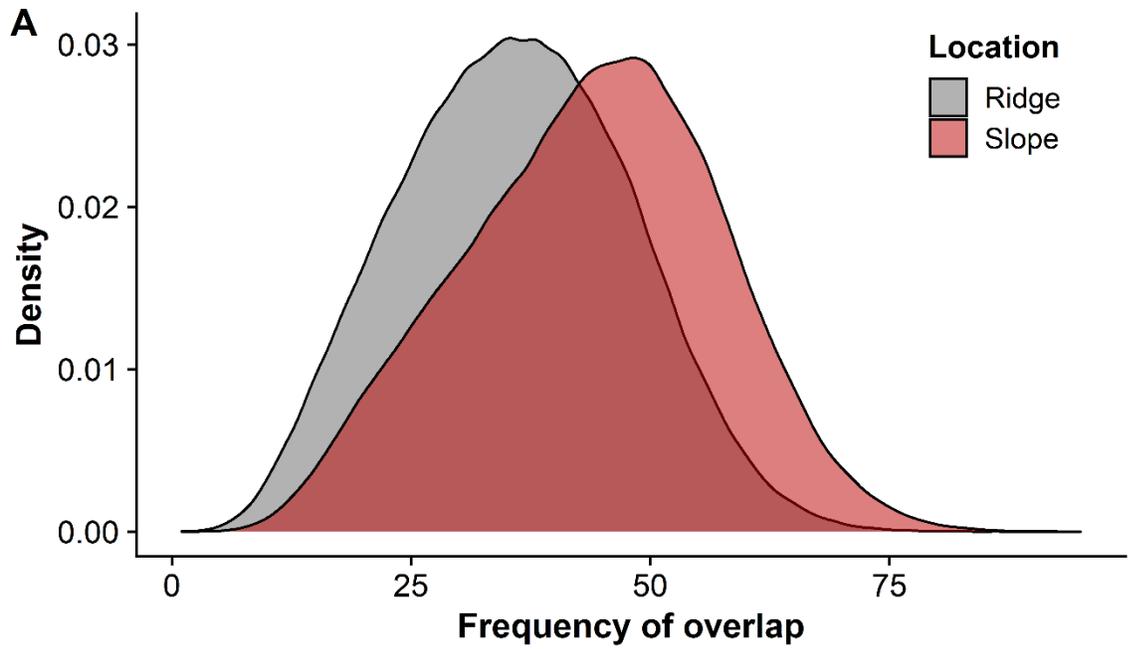
38



39

40 Figure 2

41



42

43 Figure 3

44