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NATURAL HISTORY OF THE VALLEY AND RIDGE SALAMANDER (*PLETHODON HOFFMANI*): DEMOGRAPHY, MOVEMENT, MICROHABITATS, AND ABUNDANCE

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Abstract.—Understanding the natural history of a species is critical for conservation, yet basic information about the ecology of many amphibian species is lacking. The biology of the Valley and Ridge Salamander (*Plethodon hoffmani*) is poorly known. We expanded upon this knowledge by conducting a 2-y mark-recapture study of *P. hoffmani* in central Pennsylvania, USA. We estimated a population density of 281 salamanders/ha, among the lowest reported densities for *Plethodon* salamanders. When recaptured, *P. hoffmani* were usually near a previous capture site (median movement distance = 0.4 m), though movement across larger distances occurred (up to 90 m). In general, *P. hoffmani* did not select cover objects based on temperature. However, they were more abundant under cover objects when the temperature was moderate (about 12–16° C), corresponding with peaks in abundance during the spring and autumn. This contrasted with sympatric Northern Slimy Salamander (*P. glutinosus*), which were similarly abundant across temperatures. We also found that *P. hoffmani* did not select microhabitats that differed from sympatric Red-backed Salamander (*P. cinereus*), in contrast to hypotheses presented in the literature. Altogether, our work augments our understanding of this species with information that will be important for understanding and predicting its response to environmental change.

Key Words.—Northern Slimy Salamander; *Plethodon cinereus*; *Plethodon glutinosus*; Plethodontidae; population density; Red-backed Salamander; site fidelity

INTRODUCTION

Natural history descriptions of wildlife are the fuel for conceptual evolutionary and ecological analyses. These studies also permit informed conservation practices, enabling scientists to accurately predict species-specific responses to environmental change and develop mitigation strategies focused on important aspects of the niche of a species (Greene 1994; Bury 2006). Given the current biodiversity crisis and phenomenon of global amphibian declines (Stuart et al. 2004), studies documenting aspects of the natural history of amphibian species, even common species, are especially valuable. In short, we agree with the call by Lannoo (2005) for studies that contribute to our understanding of the natural history of amphibian species.

The salamander genus *Plethodon* is a speciose component of the North American herpetofauna (Kozak et al. 2006) and is abundant and ecologically important in many forest ecosystems (Davic and Welsh 2004). Numerous studies of the natural history of *Plethodon* spp. have made possible theory-driven studies of topics such as life-history evolution (e.g., Chippindale et al. 2004), behavioral ecology (e.g., Gibbons et al. 2005), and intra- and interspecific competition (e.g., Jaeger 1981; Adams 2004). Some species of *Plethodon* are also of conservation concern. Large population declines have been documented for many species (Highton 2005). Declines may be caused by habitat destruction or alteration (Petranka et al. 1993; Knapp et al. 2003), climate change (Milanovich et al. 2010), invasive species (Maerz et al. 2009), and disease (Vazquez et al. 2009). These factors can be exacerbated by limited dispersal capability (Smith and Green 2005) and small distributions (Bernardo and Spotila 2006). The volume of natural history data and the number of species in this genus have made this group valuable for testing evolutionary and ecological hypotheses, and knowledge of *Plethodon* natural history will be crucial to understanding and managing threats to their populations. However, aspects of the ecology of some *Plethodon* species remain undocumented, and although certain features of their ecology and behavior appear to be highly conserved, others are more variable, necessitating additional investigations.

The Valley and Ridge Salamander, *Plethodon hoffmani*, is a small, elongate salamander (Fig. 1) primarily distributed in the Ridge and Valley (or Valley

FIGURE 1. Examples of Valley and Ridge Salamanders (*Plethodon hoffmani*) encountered during this study. Photographs taken at Tussey Mountain, Centre County, Pennsylvania, USA. (Photographed by Bradley E. Carlson).

and Ridge) physiographic province of the northern Appalachians from Pennsylvania through Virginia (Petranka 1998; Highton 1999). Although it is currently considered common in this region and has stable populations (Highton 2005), its global distribution is relatively small, suggesting that current or future threats to this species could lead to its imperilment. Aspects of *P. hoffmani* life history and reproduction (Angle 1969), activity patterns (Fraser 1976a, b), diet (Fraser 1976a, b; Adams and Rohlf 2000), predation (Adams 1999), and intra- and interspecific competitive interactions (Fraser 1976a, b; Thurow 1976; Adams and Rohlf 2000; Jaeger et al. 2002) have received attention; however, additional questions about its natural history remain. For example, population density estimates for *P. hoffmani* have not been reported (Beamer and Lannoo 2005). Although *P. hoffmani* does not appear to exhibit territorial behavior (Thurow 1976; Jaeger et al. 2002), it remains to be demonstrated whether this species occupies small home ranges and exhibits high site fidelity, as does the Red-backed Salamander, *P. cinereus* (Kleeberger and Werner 1982). Knowledge of these basic aspects of population biology will be valuable for managing *P. hoffmani* populations and potentially have use in comparative studies of demography and behavior.

Additionally, analyses of interspecific interactions between *P. hoffmani* and *P. cinereus* found evidence for competition, resource partitioning, and character displacement between the two species, but no evidence of interference competition (Fraser 1976b; Adams and Rohlf 2000; Jaeger et al. 2002). As such, other mechanisms may explain the largely allopatric distribution of these species, and how they reduce competition when in syntopy. For example, it has been suggested anecdotally that the two species appear to select microhabitats with different abiotic features, in particular, soil moisture (Hulse et al. 2001), a view supported by experimental studies documenting greater ability to recover from dehydration via water uptake in *P. hoffmani* than *P. cinereus* (Brown et al. 1977). However, few data exist on the impact of abiotic factors such as moisture and temperature on *P. hoffmani* to

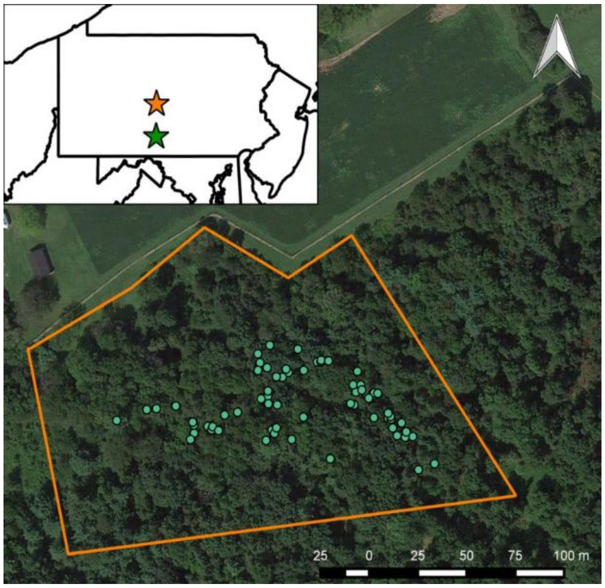

FIGURE 2. Map of Site 1 showing outline of surveyed location (orange line) and locations of cover objects (green symbols). Inset shows locations of Site 1 at Tussey Mountain, Centre County, Pennsylvania, USA, (orange) and Site 2 at Little Aughwick Creek, Fulton County, Pennsylvania, USA (dark green). (Satellite imagery data ©2015 Google).

permit evaluation of these ideas. Differences in abiotic aspects of the niche may also occur between *P. hoffmani* and other plethodontid salamanders, but this has not yet been evaluated. Such information will inform our understanding of species diversity in this group and support the ability to predict responses to future changes in climate.

In this study we document aspects of the natural history and ecology of *P. hoffmani* in the northern portion of its geographic range in central and south-central Pennsylvania, with the specific goal of filling information gaps for this species relative to other small *Plethodon* species. We initiate a mark-recapture study and collect natural history data to address the following questions: (1) What are basic demographic features of *P. hoffmani* (sex ratio, size distribution, and population density)? (2) Does *P. hoffmani* exhibit site fidelity and small home ranges as in related congeners? (3) How do temperature and moisture, important abiotic features for plethodontids (Spotila 1972), influence abundance in *P. hoffmani* compared to sympatric Northern Slimy Salamanders (*P. glutinosus*)? Additionally, we collect data on retreat site temperature and humidity at a second site to evaluate whether there is evidence that syntopic *P. hoffmani* and *P. cinereus* segregate by retreat site microclimate, as suggested (Hulse et al. 2001).

MATERIALS AND METHODS

We studied populations of *Plethodon hoffmani* at two field sites: our primary mark-recapture site in central Pennsylvania (Tussey Mountain; Centre County, USA; hereafter, Site 1; Fig. 2) at which *P. glutinosus* were also regularly observed, and a secondary site in south-central Pennsylvania (Little Aughwick Creek, Fulton County, USA; hereafter, Site 2) with abundant *P. cinereus*. Site 2 was used previously for studies that examined interspecific interactions between *P. hoffmani* and *P. cinereus* (Adams and Rohlf 2000) and is a second growth hardwood forest of varying maturity and slope aspects. Site 1 was a mixed conifer-hardwood forest along the north-facing slope of Tussey Mountain, adjacent to farm fields (portions of the study area ranged from approximately 30–110 m from the forest edge), and subdivided by a small stream.

We conducted mark-recapture studies at Site 1 during a two-year period, from October 2011 to November 2013. We sampled salamanders once every two weeks during the active season (March to June, September to October). We sampled only once per month during the winter (November to February) and summer (July to August) because *P. hoffmani* are not generally surface-active in Pennsylvania during these seasons (Hulse et al. 2001; also see Results). During exploratory visits, we delineated our study site (2.48 ha), using areas inhospitable for or resistant to dispersal by woodland salamanders (e.g., streams, saturated soils, and agricultural fields) as boundaries (Fig. 2). We also identified suitable microhabitat for *P. hoffmani*, and formed a transect (about 360 m) that passed through these areas. During each site visit, we walked along this transect searching beneath rocks and logs within sight distance (about 5 m in this habitat) looking for individuals of *P. hoffmani* and *P. glutinosus* and marking cover objects (COs) under which *P. hoffmani* had been found with labeled flags. During the surveys conducted from October 2011 to March 2012, we located salamanders by examining COs with a level of effort (the number of COs overturned) that varied between sampling events and was not recorded, which was appropriate for data on retreat sites and mark-recapture data. Beginning April 2012, we standardized and documented our collecting efforts to also estimate relative abundance, searching beneath all previously marked COs to evaluate site fidelity, and an additional 100 randomly selected, unmarked objects to locate additional salamanders and those that had moved from a previous site of capture. We conducted most of our surveys during the daylight hours (approximately 0900–1600). However, we surveyed once after sunset and surveyed once 2 d after a scheduled survey. We excluded data collected from these latter two surveys, and from the pre-April 2012 surveys for relative

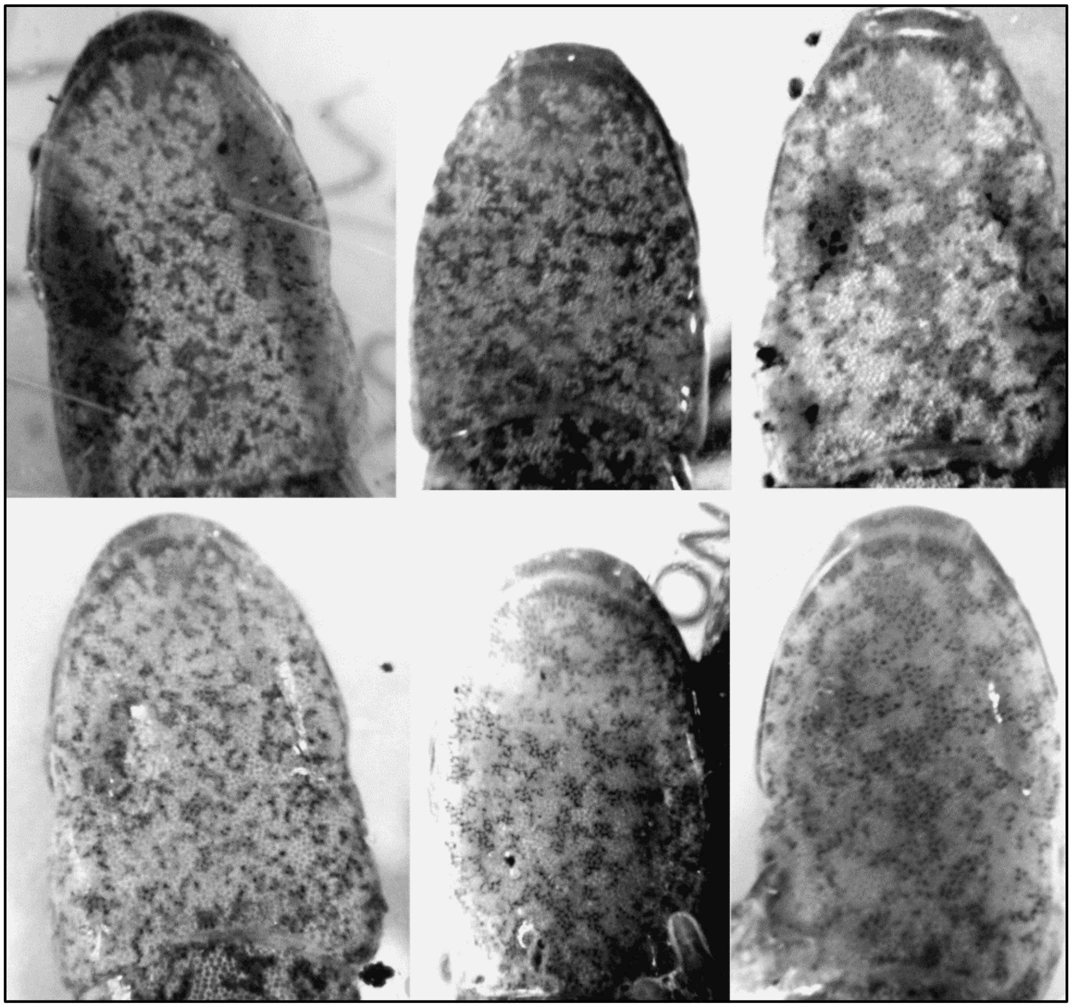

FIGURE 3. Examples of matching chin photographs from recaptured Valley and Ridge Salamanders (*Plethodon hoffmani*). Photographs of initial captures of an individual salamander appear on the top and photographs from recaptures appear beneath them. The saturation, brightness, and contrast of the images have been adjusted to facilitate comparison. (Photographed by Bradley E. Carlson and Christopher J. Thawley).

abundance estimates (estimates were only comparable on days with captures standardized by sampling effort). However, we did use data collected during all surveys to estimate population size (the mark-recapture data for which the location and individual identity of salamanders were the only variables of interest).

We captured *P. hoffmani* by hand and temporarily restrained them in a clear acrylic sheet squeeze box or a disposable plastic bag, and we took photographs of their venter with a Pentax Optio W90 digital camera (Pentax Imaging Company, Golden, Colorado, USA) with a centimeter rule for scale. We used ImageJ software (Schneider et al. 2012) to measure individual snout-vent-lengths (SVL) and to match venter pigment patterns for identification of individual salamanders. For pattern matching, we visually analyzed the mottling of the ventral surface of the chin of the salamanders (Fig. 3). Individual *P. hoffmani* were identified from these photographs by comparing each capture to all previous captures. Pigmentation patterns have been used successfully to identify individuals in other salamander species (Doody 1995; Davis and Ovaska 2001; Bailey 2004; Bendik et al. 2013). Nevertheless, pigmentation patterns can change as a salamander ages (Waye 2013), at least in some individuals, which potentially reduces our apparent recapture rate and hence overestimates population density. We also weighed each salamander to the nearest 0.1 g with a spring scale (Pesola AG, Baar, Switzerland) and determined their sex, if possible, on the basis of visible eggs in the abdomen and the presence/absence of cirri (a male characteristic) beneath the nostrils. When both characters were absent, we noted them as juvenile (if < 0.9 g), unknown sex (if sexually dimorphic features were not distinct), or non-gravid female (if of similar size to other reproductive individuals and lacking cirri). We did not collect any data on *P. glutinosus* beyond recording the number encountered during sampling.

We measured temperature under COs with a Raytek MT-6 infrared thermometer (Raytek Corporation, Santa Cruz, California, USA) accurate to ± 0.2° C, targeting the approximate location where the salamander was observed. We recorded CO temperatures once per month when salamanders were active during 2011 and 2012; during 2013, we recorded CO temperatures during every survey. Because of logistical constraints, we occasionally recorded temperatures on different days than salamander surveys. These temperature data were used for examining temperature stability of individual COs, but not for evaluating relationships between CO temperature and occupancy by salamanders on particular days (see Statistical analysis below). During most surveys, we recorded temperatures for all COs that had been flagged as being previously occupied by *P. hoffmani* up to that time in the study, and 10 additional, randomly selected, unoccupied objects. During September and October 2012, we recorded temperatures only under 10 randomly selected, unoccupied COs and COs that were occupied at the time of sampling. We also used data from a nearby weather station (approximately 680 m from the study site, in an open field) to calculate the mean air temperature (° C), mean relative humidity (%), and total rainfall (mm) during a three day period ending the day that COs were surveyed. Although the weather conditions at the station almost certainly were consistently different from that in the forest, because of the close proximity to the study site, we assumed they correlated well with fluctuations in forest weather conditions. To that end, CO temperatures and mean air temperatures at the weather station were strongly correlated ($r = 0.79$).

We used a GPS unit with sub-2 m precision to record the coordinates for each flagged (salamander-occupied) CO. A Google Earth map was generated from these points and straight-line distances between objects were used to measure one long distance movement (90 m) of a recaptured salamander. We used a tape measure to determine distances between COs used by other recaptured salamanders.

At Site 2, we collected data 7 October 2012. We specifically used this site to evaluate whether differences in microhabitat selection existed between sympatric *P. hoffmani* and *P. cinereus*, as the latter was absent from Site 1. Our search methods were as described above for Site 1, and we captured 20 *P. hoffmani* and 26 *P. cinereus*. For each individual encountered, we recorded the temperature and percent humidity of their retreat under the COs using a digital temperature/humidity reader (Traceable model 7004, Control Company, Friendswood, Texas, USA).

***Statistical analysis*.—**Given our sampling design, comparatively low number of captures, and recapture rate, we could not effectively employ more modern, powerful methods that estimate both abundance and detectability (e.g., O'Donnell and Semlitsch 2015). As such, we chose to calculate a simple Lincoln Index estimate of population size (Adams 1951), which has been used in other studies of salamander densities (Huheey and Brandon 1973; Burton and Likens 1975). We designated two sampling periods, all captures in 2012 and all captures in 2013, as two periods of similar sampling intensity and seasonal variation in salamander activity. The Lincoln Index relies on several assumptions, including a closed population and marked animals having the same mortality as unmarked animals (Adams 1951). We controlled for some of these factors by removing individuals likely to be young-of-the-year (Angle 1969) from our 2013 data. Emigration and immigration were likely low as long distance movements in *P. hoffmani* were likely to be rare (as in other small *Plethodon* species, Jewell 1991; Ousterhout and Liebgold 2010). Indeed, all movements observed by individuals in this study were ≤ 4 m except for one long-distance movement (90 m; see Results). Given that *P. hoffmani* did not seem to engage in frequent long-distance movements, and that the study site is bounded by habitat inhospitable for plethodontid salamanders on most sides, the assumption of a closed population was strong. As we used naturally occurring patterns to identify individuals, it is unlikely that marked individuals experienced higher mortality than unmarked ones.

At Site 1, we tested whether *P. hoffmani* showed microhabitat selection based on temperature by comparing temperatures under occupied and unoccupied COs. We first analyzed whether all measured COs that were occupied on a given day were different in temperature from objects that were unoccupied that day (using only dates on which *P. hoffmani* were found). We hypothesized that during cooler weather (i.e., early spring and late fall), *P. hoffmani* would prefer COs that were warmer than average; whereas, they would prefer colder retreats during warm conditions. We therefore fit a linear mixed model (LMM) with temperature as the dependent variable and the following fixed effects as predictors: whether a CO was occupied (to test for differences between occupied and unoccupied COs), recent air temperature measured at the weather station, and an interaction between CO occupancy and air temperature (to test whether the temperature difference between occupied and unoccupied COs depended on overall weather conditions). Minimum and maximum air temperatures (over three days) had qualitatively similar effects as average air temperature, so average air temperature alone was used in the final analysis. We included a random intercept for sampling date to account

TABLE 1. Summary of data on Valley and Ridge Salamanders (*Plethodon hoffmani*) collected at Site 1 (Tussey Mountain, Centre County, Pennsylvania, USA) from 2011 to 2013. Sample sizes (n) for mass and snout-vent length (SVL) reflect the number of measurements, not the number of individual salamanders encountered. Some individuals did not have mass and/or SVL measured. The mean value for an individual salamander was used in the case of recaptures, except for comparing gravid and nongravid mass and length. The asterisks (*) refer to the total number of captured females that were gravid or non-gravid rather than the total number of individuals. This was done to characterize the proportion of encountered female salamanders of each reproductive status and because individual females were captured in both states.

Group	n	Mass n	Mean mass ± 1 SD (g)	SVL n	Mean SVL ± 1 SD (mm)
Females: total	34	29	1.56 ± 0.38	34	46.1 ± 5.5
Females: gravid	11*	10*	1.83 ± 0.40	11*	49.6 ± 5.7
Females: non-gravid	32*	26*	1.47 ± 0.35	32*	45.4 ± 5.5
Male	32	30	1.39 ± 0.29	32	45.1 ± 4.4
Juvenile	19	15	0.61 ± 0.13	19	35.2 ± 5.7
Unknown	22	21	1.37 ± 0.48	22	45.5 ± 6.5

for the non-independence of sampling many COs on the same date, and a random slope to permit the relationship between CO occupancy and CO temperatures to vary because of unmeasured factors. Residuals were not normally distributed initially; these were corrected by log-transforming both measures of temperature and eliminating observations associated with the upper and lower 1% of residuals. We fit models with the package lme4 in R and evaluated significance of fixed effects with F tests using the Kenward-Roger approximation of the denominator degrees of freedom, as implemented in the package lmerTest (Bolker et al. 2009).

We also tested whether thermal characteristics of repeatedly measured (flagged) COs predicted how often they were occupied by *P. hoffmani*. We expected that frequently occupied COs might be more thermally stable (less prone to temperature fluctuations) than other COs, and might also tend to be cooler or warmer on average. For each CO, we calculated the amount of variation in temperature (standard deviation of the measured temperatures). We also calculated mean relative temperature of each CO (CO temperature minus mean temperature from all other COs each day), for which positive values would indicate being warmer on average than other COs. We then used these variables as predictors in two logistic regression models, with the proportion of times *P. hoffmani* was encountered as a binomially distributed outcome. Logistic regressions were weighted by the number of observations per CO, such that COs first measured at an earlier date (and thus more times total) were weighted more heavily in the model. However, we also included the total number of observations on each CO as a covariate, correcting for an inherent tendency for COs with fewer observations to have both lower variance in temperature and higher occupancy frequency (because they were only flagged after having been occupied).

At Site 1, we tested the influence of weather conditions on the abundance of both *P. hoffmani* and *P. glutinosus* under COs. For each species, we fit a generalized linear model (GLM) with either a quasi-Poisson distribution (for *P. hoffmani,* accounting for over-dispersion of residuals; Ver Hoef and Boveng 2007) or Poisson distribution (for *P. glutinosus*) and a log-link. The response was the number of salamanders collected, and an offset for the log-transformed number of COs overturned was used to control for sampling effort. (Dividing the number of captures by COs to create a catch-per-unit-effort for evaluation in a linear regression was explored but yielded heteroscedastic residuals.) As predictor variables, we used the mean air temperature, total rainfall, and mean relative humidity for three consecutive days. To allow nonlinear (quadratic) relationships, we also initially included the squared value of each predictor; non-significant quadratic terms were dropped from final models reported.

Using data from Site 2, we jointly tested for differences in the humidity and temperature under COs used by *P. hoffmani* and *P. cinereus* using a multivariate analysis of variance (MANOVA) model with species as a factor. We also used Welch's *t*-test (which accounts for unequal variances) for individually examining differences in humidity and temperature between the COs of the two species. We conducted all analyses in R (version 2.15.0; R Development Core Team 2013) at the $\alpha = 0.05$ significance level.

RESULTS

We captured 107 individuals of *P. hoffmani* (Table 1). Based on individuals for which we are confident of their sex, there was an equal sex ratio (1.06:1, females:males; $\chi^2 = 0.06$, df = 1, $P = 0.806$). Approximately 18% of the salamanders were juveniles. The mean snout-vent length (SVL) of all salamanders was 43.7 mm (± 6.72 mm, Fig. 4). SVL did not differ between males and females (Welch two-sample *t*-test: $t = 0.833$, df = 62.4, $P = 0.408$). Using the recapture data, we estimated a total population of 697 *P. hoffmani* at our site, which equates to a density of 281 salamanders/ha. Of the COs occupied by *P. hoffmani*, 3.3% were cohabited by two salamanders and 0.8% by three. Cohabitated COs included male-female pairs, adult-juvenile pairs, female-

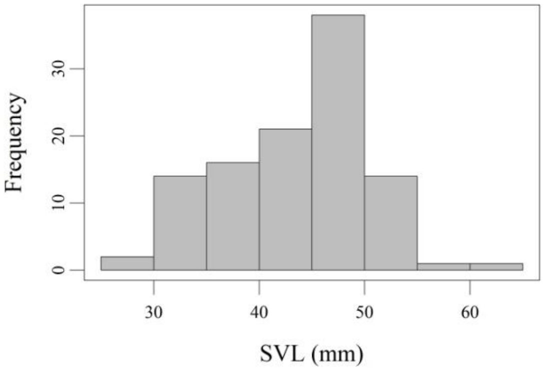

FIGURE 4. Distribution of snout-vent lengths (SVL) of sampled Valley and Ridge Salamanders (*Plethodon hoffmani*).

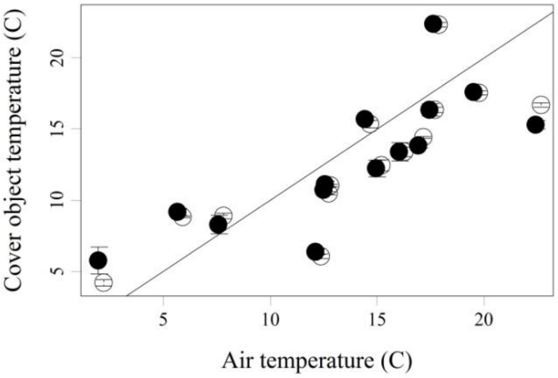

Figure 5. Temperatures under Valley and Ridge Salamander (*Plethodon hoffmani*)-occupied (filled circles) and -unoccupied cover objects (unfilled circles) versus mean air temperatures over the previous 72 h. The diagonal line represents a slope of 1.0 and is presented for reference, indicating identical temperatures measured under COs and in the air. Bars represent ± 1 standard error.

female pairs, and pairings involving unknown sexes. Furthermore, we found cohabited COs only from 31 March to 8 April and 22 October to 5 November. This timing coincides not only with the period during which *P. hoffmani* are reproductively active (Angle 1969), but also with peaks in surface activity in this study.

We recaptured 14 salamanders once, and none multiple times. The pigmentation patterns on the identified recaptured salamanders were consistent over time. Elapsed time between captures ranged from 2 to 528 d (mean = 163 ± 159 d). We found one-half of these salamanders under the same CO both times, with as many as 195 d between captures. The other seven salamanders moved from 0.73–90 m (mean = 14.7 ± 33.1 m). Overall, the median distance moved between recaptures (which is the measure least biased by rare long distance movements) was 0.4 m. There was no significant variation among males, females, and juveniles in the probability an individual would be captured twice vs. once ($\chi^2 = 4.13$, df = 2, $P = 0.127$).

The temperature under COs was significantly related to an interaction between salamander occupancy and the air temperature (LMM: $F_{1,\ 24.5} = 9.81$, $P = 0.004$). Graphical examination revealed that this interaction occurred because the occupied COs were warmer than unoccupied COs when the air temperature was lower and cooler than unoccupied COs when the temperature was higher (Fig. 5). One date (5 April 2013, the coolest day on which *P. hoffmani* was found) appeared to be highly influential in this finding, so we performed the same analysis without this date. Accordingly, we found no interaction between salamander occupancy and air temperature in association with CO temperatures ($F_{1,\ 12.9} = 1.12$, $P = 0.309$), nor did occupied COs differ in general from unoccupied COs ($F_{1,\ 12.4} = 1.13$, $P = 0.308$).

COs that varied more in temperature had significantly lower rates of occupancy compared to COs with more stable temperatures ($\chi^2 = 4.31$, df = 1, $P = 0.038$). However, this finding may be spurious: the number of times a CO was observed was strongly correlated with the SD of its temperature ($r = 0.68$, $t = 8.02$, df = 76, $P < 0.001$). We included the number of observations as a covariate to account for this, but the collinearity between these variables may have inflated the apparent effect of thermal variation. Whether a specific CO was warmer or cooler on average than other COs did not influence the proportion of times it was found occupied ($\chi^2 = 0.97$, df = 1, $P = 0.326$).

Controlling for sampling effort, the surface abundance of *P. hoffmani* under COs was significantly and non-linearly associated with air temperature but not with humidity or rainfall (Table 2). Abundance of *P. hoffmani* was highest at intermediate temperatures of about 12–16° C, and they were rarely encountered above 20° C or below 5° C (Fig. 6a). In contrast, none of the weather variables were associated with *P. glutinosus* abundance (Table 2). However, there was a positive but non-significant tendency towards greater *P. glutinosus* abundance at higher temperatures ($\chi^2 = 2.28$, df = 1, $P = 0.131$; Table 2, Fig. 6b). At Site 2, there were no significant microhabitat differences between *P. hoffmani* and *P. cinereus* (overall: Pillai trace = 0.06, $F_{2,\ 30} = 1.00$, $P = 0.380$; temperature: $t = 1.09$, df = 20.6, $P = 0.288$; humidity: $t = 0.74$, df = 30.8, $P = 0.463$).

DISCUSSION

We found that the population of *P. hoffmani* at Site 1 had a sex ratio that did not differ from unity, a common feature of many species of *Plethodon*, including *P. cinereus* (Marvin 1996; Petranka 1998; Riedel et al. 2012). Our estimate of 281 salamanders/ha at this site is

TABLE 2. Parameters from final models testing associations between weather variables and the abundance of Valley and Ridge Salamanders (*Plethodon hoffmani*) and Northern Slimy Salamanders (*Plethodon glutinosus*). Models were generalized linear models with quasi-Poisson (a) or Poisson (b) distributions and log links. Non-significant squared terms representing quadratic (rather than linear) effects were dropped from an initial model.

Term	Estimated β coefficient	Test statistic and df	*P*
a) *Plethodon hoffmani*			
Average temp. (°C)	0.55	$t_{12} = 3.60$	0.004
Average temp.^{2}	-0.02	$t_{12} = -3.92$	0.002
Relative humidity (%)	-0.01	$t_{12} = -0.80$	0.438
Total rainfall (mm)	0.002	$t_{12} = 0.10$	0.926
b) *Plethodon glutinosus*			
Average temp. (° C)	0.06	$\chi^2_1 = 2.28$	0.131
Relative humidity (%)	0.03	$\chi^2_1 = 1.25$	0.264
Total rainfall (mm)	-0.04	$\chi^2_1 = 1.45$	0.229

a minimum estimate of density as more traditional methods of estimating terrestrial salamander population sizes, including estimates based on the Lincoln Index, are likely to underestimate the true population size (O'Donnell and Semlitsch 2015). Nonetheless, this estimate is approximately an order of magnitude lower than those calculated for a congener, *P. cinereus*, using similar methods (2,118/ha; Klein 1960). Other estimates of densities for populations of *P. cinereus* generated via surface sampling or mark-recapture techniques ranged from 1,650‒32,000 individuals/ha (Heatwole 1962; Burton and Likens 1975; Mathis 1991; Kniowski and Reichenbach 2009). Our estimated density of *P. hoffmani* also sharply contrasted with densities estimated for other congeners: *P. glutinosus* (690–8,440/ha; Semlitsch 1980; Petranka and Murray 2001), *P. hubrichti* (21,000‒45,000/ha; Kramer et al. 1993; Kniowski and Reichenbach 2009), *P. jordani* (1,300–8,611/ha; Merchant 1972; Smith and Petranka 2000), *P. kentucki* (about 5,000/ha; Marvin 1996), *P. punctatus* (3,600–6,700/ha; Flint and Harris 2005), *P. werhlei* (1,000/ha; Hall and Stafford 1972), and *P. yonahlossee* (430/ha; Petranka and Murray 2001). Because our data represent a single site that may have unusual characteristics, we cannot conclude that *P. hoffmani* exhibits invariably low population densities relative to other *Plethodon* species. Notably, this study was conducted near the northern extent of the distribution of *P. hoffmani*, and the low population density we observed may be a consequence of this. Nevertheless, the notably lower population density of *P. hoffmani* warrants further investigation. Does population size regulation differ in this species from congeners? Is *P. hoffmani* potentially more susceptible to population declines? Detailed examination of additional populations using more robust sampling protocols should illuminate these questions.

Less than 5% of occupied COs had more than one *P. hoffmani* under them. The congener *P. cinereus* is generally considered aggressively territorial (Jaeger et al. 1982), but co-occupancy rates of *P. cinereus* under cover objects can range from 16.5% to 25%, depending on the season (Jaeger 1979; Quinn and Graves 1999). Possible explanations for this difference between *P. hoffmani* and *P. cinereus* include higher levels of territoriality in *P. hoffmani* (but see Jaeger et al. 2002), lower levels of surface activity in *P. hoffmani*, lower population densities, or that COs are not a limiting resource (resulting in more COs per capita) in *P. hoffmani*.

The distances moved between subsequent captures of individual *P. hoffmani* reveal a tendency towards site fidelity, with a median movement distance of only 0.4 m. This is similar to the median distances moved by adult (0.9 m) and juvenile (1.2 m) *P. cinereus* (Ousterhout and Liebgold 2010). Similarly, *P. hubrichti* moved a median distance of about 1 m (Kramer et al. 1993), *P. kentucki* moved a mean distance of 1.5 m (Marvin 2001), and *P. punctatus* moved a mean of about 1‒2 m (Flint and Harris 2005). Notably, one individual in our study (a small adult female) moved 90 m. Similar movement distances have been noted in *P. glutinosus* (Wells and Wells 1976), and *P. cinereus* can move as far as 143 m (Sterrett et al. 2015), though it does not appear that such movement distances are typical for *P. cinereus* (Taub 1961; Ousterhout and Liebgold 2010). Altogether, these comparisons suggest that the movement behavior of *P. hoffmani* was typical of the genus.

The temperature of a cover object did not appear to generally influence its use by *P. hoffmani*. However, an exception was that the salamanders appeared to favor warmer COs on the coldest day they were active (average air temp = 1.9° C); however, this suggestion, while intuitive, is driven by a datum from a single date. Similarly, the average temperature or variation (SD) of a particular CO was not meaningfully associated with how frequently it was occupied by *P. hoffmani*. This finding contrasts with expectations based on another study in which large COs, which were found to be preferred territories for *P. cinereus*, maintained significantly cooler temperatures during the hottest part of the year (Mathis 1990). The apparent avoidance of surface activity by *P. hoffmani* during particularly cool or warm weather may minimize the significance of CO temperature (as the salamanders would only be occupying COs under a restricted range of temperatures), or the COs at our study site may not vary meaningfully in temperature.

The abundance of *P. hoffmani* under cover objects is not affected by humidity and rainfall. In contrast, *P. cinereus* increases its use of COs (vs. leaf litter) under

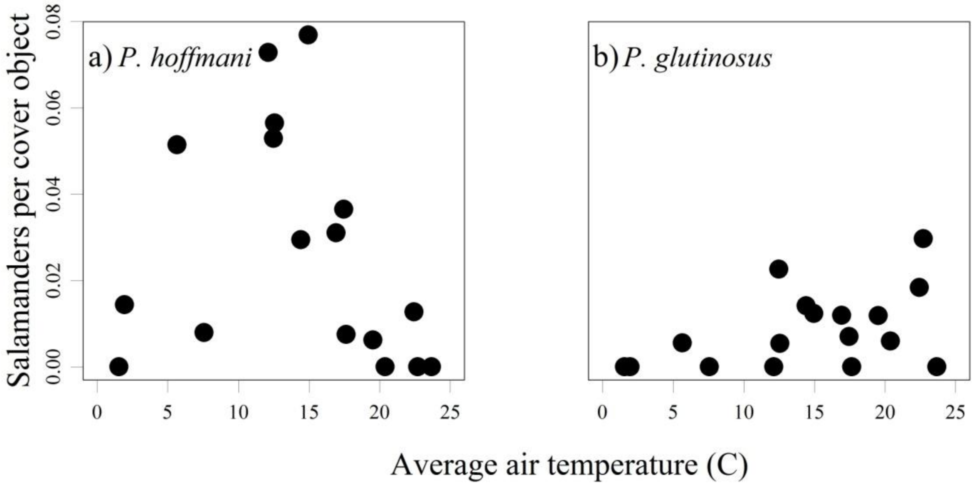

Figure 6. Relative abundance of a) Valley and Ridge Salamanders (*Plethodon hoffmani*) and b) Northern Slimy Salamanders (*Plethodon glutinosus*) under cover objects in relation to mean air temperature measured over the previous 72 h.

drier conditions (Jaeger 1980). *Plethodon serratus* similarly shifts its surface-active time to COs as rainfall declines, but becomes less surface active overall under drier conditions (Semlitsch et al. 2014). Because we did not conduct leaf litter searches, we cannot assess the extent to which *P. hoffmani* may have shifted its habitat use between leaf litter and COs. Instead, we can only conclude that their absolute abundance under COs was unaffected by our two measures of moisture. Conceivably, as in *P. serratus* (Semlitsch et al. 2014), *P. hoffmani* became less surface active overall, with those that are active at the surface preferentially occupying COs, resulting in little observable change in CO occupancy. Temperature, however, had a non-linear impact on *P. hoffmani* abundance under COs, with abundance peaking at intermediate temperatures of 10–15° C. This is consistent with the seasonally bimodal activity pattern observed here and in other studies in which *P. hoffmani* are most active during the spring and autumn (Angle 1969; Fraser 1976b). Similar patterns of activity have been observed in *P. cinereus* (Williams and Berkson 2004) and other *Plethodon* species (e.g. Ovaska and Gregory 1989). This suggests that, although *P. hoffmani* may cope with drier conditions (Brown et al. 1977), they do not tolerate temperature extremes, and this may have important consequences as temperature regimes shift with a changing climate.

In contrast, *P. glutinosus* abundance was not influenced by temperature, humidity, or rainfall. This is consistent with previous work on this species (Crawford et al. 2015) as well as work on other large *Plethodon* species (Petranka and Murray 2001). However, others have reported that *P. glutinosus* surface activity declines under drought conditions (Wells and Wells 1976; Hulse et al. 2001). *Plethodon hoffmani* can tolerate drier conditions (Brown et al. 1977), but this ability may not serve to partition microhabitats between *P. hoffmani* and *P. cinereus* in free-living populations, as the microhabitats of the two species did not differ in this study. Under at least some conditions, *P. hoffmani* and *P. cinereus* appeared to occupy similar microhabitats. However, our data at this site were collected in a single day making it difficult for us to generalize without further, more extensive sampling. Further research could reveal that microhabitat usage changes under periods of drought or temperature extremes or in areas near the edges of their respective geographic ranges.

In conclusion, *P. hoffmani* at a site in Pennsylvania was found to have demographic and life-history features that were similar to those of other *Plethodon*, including *P. cinereus*. *Plethodon hoffmani* has a sex ratio close to 1:1, exhibits site fidelity, and rarely undertakes long distance movements. *Plethodon hoffmani* is most active at intermediate temperatures and, when syntopic with *P. cinereus*, occupies similar microhabitats. However, its population densities are much lower than those of other congeners, and a large portion of the population may remain underground and unobserved, even when surface conditions are favorable (Fraser 1976b). Low population densities result in lower encounter and recapture rates despite low movement rates, making mark-recapture studies difficult. Given the diversity of *Plethodon* species, including many that are difficult to study due to restricted ranges or conservation concerns, researchers tend to use information from related species, especially the well-studied *P. cinereus*, to make best-guess conclusions about the life histories of less studied species (Petranka 1998). Our work shows that this may be a valuable approach for many life-history characters, but also provides evidence that understudied *Plethodon* can be divergent in aspects of their life histories. In the light of concerning population declines in many species of *Plethodon* (Highton 2005) and the ongoing threat of anthropogenic environmental change, we encourage future research into the life histories of this diverse group to support the conservation and preservation of its diversity.

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