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Eastern Red-Backed Salamanders: A Comprehensive Review of an Undervalued Model in Evolution, Ecology, and Behavior

M. Caitlin Fisher-Reid[1,6], Kristine L. Grayson[2], Sara R. Grouleff[3], Madelyn A. Hair[2],
Tanya J. Hawley Matlaga[4], Angelina K. Ireland[3], Louise S. Mead[5], Alyssa St John[1], Meigan Starr[5],
Sean C. Sterrett[3], and Kody N. Streeter[4]

[1] Bridgewater State University, Bridgewater, MA 02325, USA
[2] University of Richmond, Richmond, VA 23173, USA
[3] Monmouth University, West Long Branch, NJ 07764, USA
[4] Susquehanna University, Selinsgrove, PA 17870, USA
[5] Michigan State University, East Lansing, MI 48824, USA

Abstract: What makes a model organism? Identifying the qualities of a model organism has been given a great deal of attention in the biomolecular sciences, but less so in the fields of evolution, ecology, and behavior (EEB). In contrast to the biomolecular sciences, within EEB, biotic and abiotic variation are features to understand, not bugs to get rid of, and EEB scientists often select organisms to study which best suit the scientific question at hand. Successful EEB model organisms can be studied at multiple biological scales and often have a wealth of accumulated knowledge on which current research programs build. A recent call within EEB communities to invest in the development of diverse model systems led us to evaluate the standing of a widespread, abundant, terrestrial salamander in this review: the Eastern Red-backed Salamander (*Plethodon cinereus*). We first look at salamanders as EEB models more generally and determine where *P. cinereus* fits in this broader context. The core of our monograph reviews over 400 recent studies on *P. cinereus* and highlights inconsistencies, gaps in our knowledge, and future directions in the context of our findings and those of three prior comprehensive reviews: two comprehensive reviews published in 1998 and 2013, and a book published in 2016 focused on the behavioral ecology of *P. cinereus*. After completing our review, we conclude by evaluating the current status of *P. cinereus* as a model organism in EEB and describe how a collaborative research network, SPARCnet, can serve as a starting point for improving the range-wide understanding of *P. cinereus* ecology, evolution, and behavior. More generally, we argue that collaborative research networks can and should be applied to other EEB model systems, so that future EEB research may benefit from model systems that accurately represent, in Darwin's words, "endless forms most beautiful and most wonderful."

Key words: Amphibians; Model organism; *Plethodon cinereus*; Plethodontidae

What defines a model organism for a particular biological field? Although this idea has captured much discussion in biomolecular literature (e.g., Müller and Grossniklaus 2010; Ankeny and Leonelli 2011; Leonelli and Ankeny 2013; Russell et al. 2017), the fields of evolution, ecology, and behavior (hereafter, EEB) have historically focused more on studying the systems suited to answer the scientific question at hand. Yet, even without a broader community discussion, particular research systems in EEB stand out for their body of knowledge and contributions to unifying principles, and researchers often invoke their study species as being excellent models for "robust inference" (sensu Travis 2006). Duffy et al. (2021) laid out a broad framework for defining, developing, and nurturing model organisms and model systems in EEB, including describing important contrasts with the biomolecular sciences, which we briefly summarize in the following section. Similarly, Edwards (2021) discussed the value of a model clade to EEB and systematic biology in particular. In this monograph, we argue that one of the most common vertebrates in northeastern North American forests, the Eastern Red-backed Salamander (*Plethodon cinereus*), deserves recognition and further development as an EEB model organism.

We make this argument based on several factors, including (1) the depth of knowledge published on this species that highlights the tractability and potential of *P. cinereus* both in the laboratory and field for answering EEB questions (Petranka 1998; Anthony and Pfingsten 2013; Jaeger et al. 2016; studies reviewed herein), (2) the critical niche position of woodland salamanders in forest ecosystems (Davic and Welsh 2004), (3) the accessibility of this species as easy to find, human-tolerant, and locally abundant across a large geographic and climatic range (Fig. 1; Petranka 1998), and (4) the potential for transferable methods and knowledge to a wide range of salamander species given the extensive diversity, abundance, and well-studied systematics of family Plethodontidae (e.g., Adams et al. 2009; Kozak and Wiens 2010; Pyron and Wiens 2011; Jaramillo et al. 2020). In making our argument, we review recent gains in knowledge of this species and discuss the next steps in investment and infrastructure needed for model organisms like *P. cinereus* to continue furthering our scientific understanding (Ankeny and Leonelli 2011; Leonelli and Ankeny 2013; Duffy et al. 2021; Wale and Duffy 2021).

Our monograph has four overarching goals and is organized as follows. First, we briefly discuss the definition and use of model organisms in EEB, highlighting salamanders more generally as good candidates for model clade status. Second, we determine the current level of EEB knowledge on *P. cinereus* compared to other well-studied salamander species. Third, we share the results of a comprehensive literature review of the EEB research on *P. cinereus* which focuses on literature published since Petranka (1998) and is written in the context of two more recent reviews (Anthony and Pfingsten 2013; Jaeger et al. 2016). Finally, we discuss the challenges of advancing *P. cinereus* and similarly well-studied species into the next stage of model organism status. We suggest that a collaborative ecological research network structure offers an opportunity for the continued development of *P. cinereus* as a model system in EEB.

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[6] Correspondence: e-mail, mfisherreid@bridgew.edu

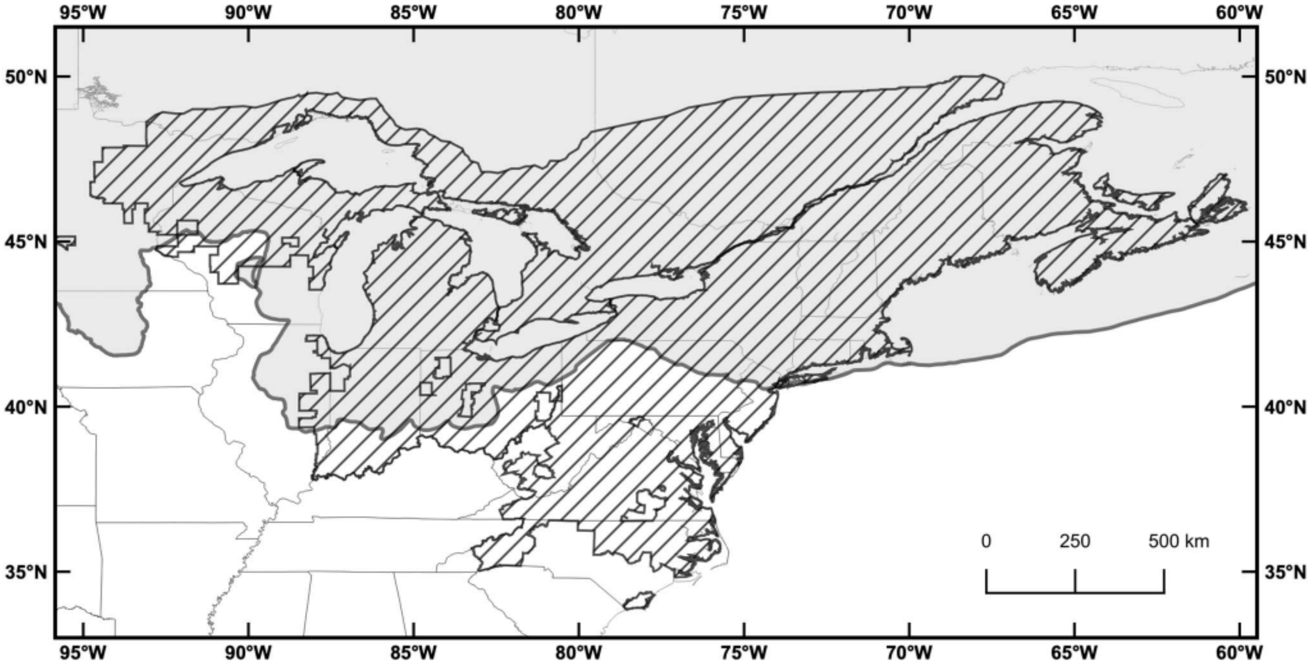

FIG. 1.—Top: Geographic range of *Plethodon cinereus* shown as diagonal lines is 1.89 million km^2 (IUCN 2020). The gray shaded area represents the extent of the Wisconsin ice sheet at the last glacial maximum (CRC 2014). Bottom: The three most common color phenotypes of *P. cinereus* are the striped morph (A), the unstriped morph (B), and the erythristic morph (C). All photos used with permission from photographers (A and B by T. Pierson, C by T. Leenders).

Model Systems in Evolution, Ecology, and Behavior

As part of defining what EEB model organisms are, Duffy et al. (2021) summarized the considerations for using model organisms in cellular, molecular, and developmental biology (hereafter collectively referred to as the biomolecular sciences, e.g., Müller and Grossniklaus 2010; Ankeny and Leonelli 2011; Leonelli and Ankeny 2013; Russell et al. 2017), aptly noting that these fields tend to neglect the ecology and evolution of their models. For example, Russell et al. (2017) profile 14 "non-model model organisms" and focus on fundamental phenomena (i.e., the key processes and general principles of interest to a discipline; Ankeny and Leonelli 2011; Leonelli and Ankeny 2013; Wale and Duffy 2021) at the scale of molecules, genes, or cells with little regard for fundamental phenomena at the scale of populations, communities, or ecosystems. There is some discussion of how non-model model organisms have been used to study major evolutionary events (e.g., the origins of multicellularity with *Volvox*; Russell et al. 2017), but the fields of EEB are not well represented in the model organism literature. However, the EEB scientific community values many of these same organisms (e.g., *Escherichia coli, Drosophila melanogaster, Arabidopsis thaliana*), often for many of the same reasons (e.g., short generation time, lab tractability). Despite these overlaps in utility for both fields, Duffy et al. (2021: 55) argue that there are several challenges in applying the biomolecular definition of a model organism to EEB research. Instead, they propose the following definition for a model system in EEB:

> . . . a species, taxon, community, or ecosystem that has been studied from multiple angles with a goal of developing a deep understanding of that organism (or taxon, community, or ecosystem), in a manner that enables comparisons with other systems to illuminate general ecological, evolutionary, and/or behavioral principles; achieving this will require that the system has been studied long enough for a substantive body of knowledge to have been generated.

In thinking about qualities that model systems in EEB share, the authors identify three axes which define the use of a given model system for a particular research question: lab tractability, field tractability, and the range of biological scales which can be addressed (see Duffy et al. 2021: fig. 1). It is important to highlight that their approach defines model *systems*—not always just a single species—which more accurately reflects how EEB scientists generally approach science from the perspective of larger biological scales compared to the biomolecular sciences. We add to Duffy et al. (2021) that model systems in EEB often benefit from encompassing taxa that are locally abundant and/or span relatively large geographic ranges. Local abundance and large geographic ranges both contribute to the accessibility of a model system and the potential for lessons learned from the model to have broader applicability to other species.

The exemplary taxa in EEB textbooks and research programs often take the form of model systems or clades: groups of closely related, ecologically diverse species, found in relatively well-defined geographic regions (e.g., *Anolis* lizards, Darwin's Finches, *Heliconius* butterflies), which lend themselves to addressing a variety of broader EEB research questions. Instead of using common ancestry and evolutionarily conserved traits to declare EEB model systems representative of other species, as is done in the biomolecular sciences, EEB tries to conceptually unify the natural world. As Duffy et al. (2021: 55) state, EEB scientists "aim to see the forest *and* the trees" (their emphasis).

Important to the goals of this monograph, model systems in EEB must contribute to robust inference across the fundamental phenomena of the field (Travis 2006). Both Travis (2006) and Duffy et al. (2021) argue that an organism or system must generate a great body of knowledge to support continued study of EEB fundamental phenomena. In this monograph, we demonstrate that *P. cinereus* has well surpassed the bar of knowledge, but requires further development of infrastructure, community ethos, and funding investment to facilitate continued robust inference on woodland salamanders within their ecological communities.

Salamanders and the Plethodontidae as Model Organisms in EEB

Amphibians are represented in biomolecular model species by the Axolotl (*Ambystoma mexicanum*; Russell et al. 2017) and the African Clawed Frog (*Xenopus laevis*; Müller and Grossniklaus 2010). In EEB, pond-breeding amphibians have long played a major role in studies of metamorphosis and complex life cycles (Wilbur 1980), and salamanders have been the focus of a great number of studies on broad questions within ecology and evolutionary biology (e.g., Wake and Larson 1987; Bruce 2008; Wake 2009). Despite pond-breeding salamanders being more commonly recognized, the salamander family Plethodontidae represents nearly two-thirds of all salamander species (516 of 817; AmphibiaWeb 2024), and its members occupy a wide range of aquatic and terrestrial microhabitats, often with distinctly different life histories from pond-breeding amphibians (Wake and Lynch 1976; Petranka 1998; Blankers et al. 2012). Plethodontidae is the only salamander family to have radiated extensively in the tropics (tropical bolitoglossines; Wake 1970; Wake and Lynch 1976; Wiens 2007; Rovito et al. 2012, 2015; Jaramillo et al. 2020), and the only family of salamanders with species that have direct development (i.e., no aquatic larval stage; Wake and Hanken 2004). In fact, because Plethodontidae is the largest salamander family, direct development is the most common mode of reproduction in salamanders as a whole and was likely a key innovation involved in the diversification of Plethodontidae (Schluter 2000; Wake and Hanken 2004; Bonett et al. 2022). In terms of conservation status, species of Plethodontidae run the gamut from least concern to endangered or data deficient (see Supplemental Material S1; Supplemental Table S1, available online; IUCN 2020).

As amphibians and ectotherms, salamanders are generally sensitive to their environment (Duellman and Trueb 1986). Ecologically, salamanders are often mid-level consumers who play a critical role in nutrient cycling and other ecosystem processes throughout the aquatic and/or terrestrial ecosystems where they live (Davic and Welsh 2004). Plethodontid salamanders are particularly sensitive to climate, as these species are all lungless: all respiration is cutaneous, which requires moist skin. Climates and seasons that are too hot, too cold, or too dry are inhospitable to plethodontids. In part because of this environmental sensitivity, several studies have already made a case for the use of plethodontid salamanders as indicator species in biodiversity and ecosystem monitoring (Welsh and Ollivier 1998; Welsh and Droege 2001; Best and Welsh 2014; Farallo and Miles 2016; Fleming et al. 2020); however, others have argued for caution when using amphibians as "canaries in a coal mine" for anthropogenic change (e.g., Kerby et al. 2010).

The genus *Plethodon* includes 58 terrestrial woodland species found in North America; most of these species (49) form a clade of eastern *Plethodon*, and the remaining 9 species form a clade of western *Plethodon*, which are primarily found in the Pacific Northwest (Wiens et al. 2006; Kozak et al. 2009; Fisher-Reid and Wiens 2015; AmphibiaWeb 2024). Eastern *Plethodon* are further broken down into three well-supported clades: *cinereus* group, *wehrlei-welleri* group, and *glutinosus* group (Wiens et al. 2006; Kozak et al. 2009; Fisher-Reid and Wiens 2015). Phylogenetically, *P. cinereus* is a member of *cinereus* group, which is sister to the rest of eastern *Plethodon* (Wiens et al. 2006; Fisher-Reid and Wiens 2015). *Plethodon cinereus* is the sister species to the vulnerable *P. shenandoah* (IUCN 2020), which, although locally abundant where found, is geographically restricted to three mountaintops in Virginia, USA (Petranka 1998; Sites et al. 2004). *Plethodon cinereus* is a wide-ranging species found in temperate forest habitats along the eastern seaboard of North America from southern Canada to North Carolina, USA, and west to Minnesota, USA, in the north, and to the Appalachians in the south (Fig. 1). Within its range, *P. cinereus* is often locally abundant, with surface density estimates regularly ranging from 0.05 to 3.4 salamanders/m^2 (Petranka 1998; Anthony and Pfingsten 2013; Semlitsch et al. 2014; Grant et al. 2024), and some locations reporting even larger outlier surface densities. For example, Jung et al. (2000a) reported densities as high as 18.5 salamanders/m^2 in Shenandoah National Park, Virginia, and Hernández-Pacheco et al. (2019) reported densities of 2.5–6.3 salamanders/m^2 in urban Richmond, Virginia.

As the most common and most widely distributed species in the genus *Plethodon*, we argue that *P. cinereus* is an ideal candidate for an EEB model species and endeavor to provide an updated, range-wide review of knowledge on this salamander. There is a wealth of natural history, evolutionary, ecological, and behavioral research that has been done on *P. cinereus* over the decades; however, the most accessible and cited range-wide review was conducted over 20 yr ago as part of a book detailing the natural history of all North American salamanders (Petranka 1998). In the early 2000s, some authors wrote additional broad overviews of amphibian biology which included species-specific knowledge (Casper 2005; Wells 2007), but these compendiums largely rely on the details found in Petranka (1998), with minimal updates. In 2013, Anthony and Pfingsten (2013) wrote a detailed species account of *P. cinereus* for the book "Amphibians of Ohio" (Pfingsten et al. 2013). This review more than doubled the number of citations provided by Petranka (1998) and included Ohio-based updates, including several tables and figures of new data from Ohio populations and a detailed discussion as to how these data fit with the broader literature covering the rest of the geographic range of *P. cinereus*. We have therefore incorporated information first summarized by Anthony and Pfingsten (2013) in relevant sections. Finally, 50 yr of behavioral research on *P. cinereus* was recently reviewed in Jaeger et al. (2016), in which the authors highlight both Petranka (1998) and Anthony and Pfingsten (2013) as the authoritative accounts for *P. cinereus* life history and ecology (Jaeger et al. 2016: 3). Our review aims to synthesize these prior reviews with the entire EEB literature that has been published on *P. cinereus* since 1998.

In order to quantify the body of knowledge on *P. cinereus* for EEB fields in comparison to other well-studied salamanders, we conducted several rigorous literature searches. From these searches, we used the resulting studies on *P. cinereus* to comprehensively review the post-Petranka (1998) literature, and then make the argument for *P. cinereus* to be elevated to an EEB model organism.

MATERIALS AND METHODS

As a first step for establishing a species of woodland salamander (*P. cinereus*) as a model organism in EEB, we investigated its prevalence in the literature relative to other well-studied salamanders. We conducted three sets of taxonomically progressive Web of Science topic searches using the Web of Science All Databases for All Years (1864–present). All searches were conducted on 18 June 2020. The goal of our search strategy was to restrict our focused efforts to the most well-studied salamanders, first by identifying the most well-studied families, then genera within those families, and finally species within those genera. Full details of our search methods, including search terms and database settings, as well as summary tables of the results (Supplemental Material S1; Supplemental Tables S1–S4, available online) can be found in Supplemental Material S2 (Supplemental Data S1), although raw results can be found in Supplemental Materials S2-S15 (Supplemental Data S1–S14, available online). Supplemental Material S2 (Supplemental Data S1) also contains detailed methods for our estimation of geographic range size and inclusion of sources in the comprehensive literature review which were not recovered by our Web of Science searches.

RESULTS

Literature Searches

Results for the family-level and genus-level searches are shown in Supplemental Material S1 (Tables S2 and S3), respectively, and the full results for all 50 genera are in Supplemental Material S2 (Supplemental Data S1), and for all 179 species in Supplemental Material S3 (Supplemental Data S2). In the species-level search (Supplemental Material S1; Table S4), in terms of raw numbers of articles in EEB-related fields compared to non-EEB related fields, *P. cinereus* ranks fifth, behind two salamandrids from Europe (*Triturus cristatus* and *Salamandra salamandra*) and two ambystomatids from North America (*Ambystoma tigrinum* and *A. maculatum*). Like *P. cinereus*, all four of these species have large ranges and are locally abundant (Lannoo 2005; Wells 2007; IUCN 2020). Unlike *P. cinereus*, they are all largely pond-breeding species with an aquatic larval stage, the exception being *Salamandra salamandra*, for which some populations have a fully terrestrial, viviparous reproductive mode (e.g., Velo-Antón et al. 2012). *Plethodon cinereus* is the only representative of Plethodontidae among the top eight most well-studied salamander species, which is surprising, given that Plethodontidae is the largest family of salamanders (AmphibiaWeb 2024), and the only salamander family with a direct developing reproductive mode (Wake and Hanken 2004). However, the vast majority of salamander reproductive and developmental biology has been studied in species with an aquatic larval stage (e.g., see non-EEB sources for *A. mexicanum*, Supplemental Material S5; Supplemental Data S4).

Estimation of Geographic Range Size

Among all salamanders for which geographic range data were available ($n = 607$; IUCN 2020), *P. cinereus* has the 11th largest geographic range (Supplemental Material S13; Supplemental Data S12). Among the top eight most well-studied salamander species (Supplemental Material S1; Table S4), five have geographic range sizes larger than *P. cinereus*, supporting the idea that well-studied species often have large ranges. Among plethodontids, *P. cinereus* has the second largest range overall (1.89 million km^2; Supplemental Material S13; Supplemental Data S12; IUCN 2020), and the largest range of North American plethodontids. The tropical South American plethodontid *Bolitoglossa altamazonica* is reported to have the largest plethodontid range at 1.97 million km^2 (Supplemental Material S13; Supplemental Data S12; IUCN 2020). However, recent molecular and morphological analyses of *B. altamazonica* and *B. peruviana* (Cusi et al. 2020; Jaramillo et al. 2020) suggest *B. altamazonica* has previously been used as a catchall taxon for any specimens from Venezuela south to Bolivia and from Ecuador east to Brazil, and that instead *B. altamazonica* is a microendemic species restricted to forests in northern Peru, between the rivers Nanay in the north, Tigre and Marañón in the south, and Amazon in the west. Therefore, it is likely that *P. cinereus* has the largest range of the plethodontids.

Comprehensive Literature Review of *P. cinereus*

The following sections summarize the results of our comprehensive literature review of *P. cinereus* research since Petranka (1998) and published prior to our search date in June 2020. Additional sources published after our search date but suggested by anonymous reviewers during peer review have also been incorporated (see Supplemental Material S2; Supplemental Data S1).

We use the same section headers as Petranka (1998), but we have added subheaders for larger topics. We follow Petranka's (1998) organization of topics closely. We have taken special care to note when more recent research 1) supports what is written in Petranka (1998), 2) fills in a gap in understanding which Petranka (1998) identified, or 3) contradicts what is written in Petranka (1998). In Supplemental Material S3 (Supplemental Data S2), we include our categorization and key results summaries of these sources, which we used to organize this review (Supplemental Material S12; Supplemental Data S11). We also include the full list of sources returned by Web of Science on *P. cinereus* (Supplemental Material S9; Supplemental Data S8) and as well as the full list of sources cited by Petranka (1998) and Anthony and Pfingsten (2013) for completeness (Supplemental Material S14; Supplemental Data S13).

Identification.— Petranka (1998) describes the two predominant color phenotypes (striped morph or red-back and unstriped morph or lead-back) as well as the erythristic or all-red morph (Fig. 1). Since Petranka (1998), documentation of other color phenotype anomalies (e.g., leucistic) from throughout the geographic range have been published regularly, often in the *Herpetological Review* Natural History Notes section (e.g., Mendyk et al. 2010; Sawyers and Novick 2011; Jongsma 2012a,b). Recently, Moore and Ouellet (2014) reviewed color phenotypes in *P. cinereus,* summarizing eight diagnosable color phenotypes with photographs. Moore and Ouellet (2014) provided a dichotomous key for identifying the color phenotypes and established and maintain an open-access database of photographs, providing an email address for photograph submissions. The authors also provide a table documenting each state or province in which different morphs have been found, noting that the unstriped morph is absent at range edge populations in Minnesota, Kentucky, and Tennessee. Moore and Ouellet (2014) argue that the striped, unstriped, and erythristic morphs (Fig. 1) should be considered the primary color phenotypes of *P. cinereus*, as they are the most abundant and occur most widely through the geographic range. The remaining five color phenotypes (iridistic, albino, leucistic, amelanistic, melanistic) are somewhat rare anomalies, possibly simply teratological mutations, with patchy observations throughout the range. It is not known if any of these anomalous color phenotypes persist in any population long-term.

Additional work on color phenotypes since Petranka (1998) includes studies on the expression of different color phenotypes over time and during development. Over time, Kraemer et al. (2012) observed decreasing brightness of dorsal and lateral pigmentation and increasing ventral reflectance in both striped and erythristic morphs kept in a laboratory. The authors hypothesized that the changes in brightness were due to upregulation of dermal pigments (Kraemer et al. 2012) but noted that little is known about the cellular mechanisms of dermal pigmentation in this species. Kraemer et al. (2012) also caution that their study suggests laboratory quantification of coloration may not be representative of similar measurements recorded in natural settings.

Over the course of development, Evans et al. (2020) found that temperature may play a role in the expression of the color phenotype. The authors reared eggs at different temperatures and found a higher proportion of unstriped individuals hatch at higher temperatures. The authors note, however, that it is difficult to know if this is true phenotypic plasticity in color phenotypes (i.e., high temperatures induce expression of unstriped morph) or simply differential mortality based on temperature (i.e., eggs containing unstriped individuals are more likely to survive rearing at high temperatures compared to eggs containing striped individuals; Evans et al. 2020). Further work is needed to tease apart these hypotheses.

Recent research has revealed an additional interesting trait related to skin phenotypes, one that is likely sexually dimorphic (see Anthony et al. 2023). Muñoz (2018) described natural green fluorescence under a blacklight on the ventral side of tails for 45 salamanders (33 males and 12 females) in Pennsylvania during the autumn (September to November) 2014 season. In Massachusetts, one of us documented the same ventral fluorescence in 60 individual salamanders using a 395-nm blacklight during the autumn 2019 season (M. C. Fisher-Reid, personal observation), as well as in a handful of individuals in the autumn seasons of 2017 and 2018 (prior to intentionally recording these observations; Supplemental Material S16; Supplemental Material Fig. S1, available online). In 2019, we observed a strong male bias in fluorescence ($n = 53/87$ individual males (60.9%), 3/83 individual females (3.6%), 4/93 individual unknowns (4.3%); M. C. Fisher-Reid [personal observation]). We further observed that fluorescence persists for several weeks, as 15 individual males were recaptured 2–4 times (mean = 2.6) during the same season and exhibited fluorescence each time they were caught (sample dates are generally ≥7 d apart; M. C. Fisher-Reid [personal observation]). Muñoz (2018) speculates that the fluorescence may aid in night vision but acknowledges that our lack of knowledge on how the fluorescent compounds are generated and on the natural light conditions under which they fluoresce makes it difficult to hypothesize as to their ecological or evolutionary importance.

Anthony et al. (2023) was the first study to characterize tail fluorescence formally. The authors sampled more than 300 salamanders over 12 mo from a single population in Ohio plus more than 100 salamanders from additional populations in Indiana, Pennsylvania, northern Ohio, and southern Ohio, all during the month of October. Anthony et al. (2023) confirmed the fluorescence occurs in Serous 1 (S1) glands (Simons et al. 1999; Hecker et al. 2003; see Terrestrial Ecology: Territories and Home Range Size), the trait is more commonly observed in males than females, more commonly observed in autumn than spring, and only observed in adults. These patterns hold across the different geographic locations, which include three of the six phylogeographic clades of *P. cinereus* (Radomski et al. 2020). In their discussion, Anthony et al. (2023) provided an excellent starting point for further characterization of the trait and future tests of its hypothesized function.

More broadly, Petranka (1998) summarizes few sexually dimorphic traits in *P. cinereus*, with sexually active males showing swollen nasolabial glands, hedonic glands on the tail, and a mental gland. Two additional studies describe noninvasive methods for sexing adult salamanders. Quinn and Graves (1999a) report on sexual dimorphism in the internares distance (distance between nares and snout tip). They show that males had significantly larger internares distances than females, for salamanders whose sex was confirmed by dissection. Although this trait is extremely useful for sexing preserved specimens without dissection, it is more difficult to use with live animals. Measuring internares distance on a live animal requires that the animal be cooled on ice prior to measuring; thus this method is unlikely to be practical in the field (Quinn and Graves 1999a). Gillette and Peterson (2001) describe a candling method for determining sex non-invasively, which is used commonly today in both laboratory and field settings (e.g., Cabe et al. 2007; Novarro et al. 2018). One can determine sex by shining a light through the dorsal side of the salamander and looking at the ventral body wall for shadows of testes and vas deferens (if male) or eggs (if female). Gillette and Peterson (2001) also note that sexually active males have a whitish, enlarged area lateral to the cloaca, and gravid females have easily visible eggs once eggs are >2 mm. Gravid females can have their eggs counted by pressing gently on the body wall to make the individual eggs visible through the ventral skin. Distinguishing between subadult females with no eggs and subadult males with un- or underdeveloped testes is difficult with candling; however, in our experience, candling works well on adult salamanders (i.e., salamanders that are approximately 35 mm snout–vent length [SVL]; see Petranka [1998] for a summary of the geographic variation and sexual dimorphism in SVL at sexual maturity).

Systematics and geographic variation.— Genetic and bioinformatic tools for understanding the systematics and geographic variation of *P. cinereus* were only just becoming inexpensive and commonplace in 1998. The studies Petranka (1998) cites on this topic rely exclusively on allozyme data to distinguish species-level and population-level genetic variation (e.g., Highton and Webster 1976; Highton and Larson 1979). However, the early inferences made from these data have largely held up under the scrutiny of both Sanger and next-generation sequencing methods combined with more robust modern computational phylogenetic methods (e.g., Wiens et al. 2006; Fisher-Reid and Wiens 2011; Radomski et al. 2020). Today, we are confident that *P. cinereus* is genetically distinct from both its sister species *P. shenandoah* (Highton 1999; Sites et al. 2004; Wiens et al. 2006; Highton et al. 2012) and the phenotypically similar Southern Red-backed Salamander (*P. serratus*, Wiens et al. 2006; Highton et al. 2012). There is limited evidence of hybridization between *P. cinereus* and *P. shenandoah* (see summary in the discussion of Carpenter et al. 2001), no evidence for hybridization between *P. cinereus* and either *P. sherando* or *P. serratus* (Bayer et al. 2012), and limited evidence of hybridization between *P. cinereus* and *P. electromorphus* in Ohio (Kuchta et al. 2022; which reexamined data from Lehtinen et al. 2016).

The systematics of plethodontid salamanders has been one of the most active areas of research, both prior to Petranka (1998), and since. Because Plethodontidae is the largest family of salamanders, and the only group of salamanders to radiate in the tropics (Wake and Lynch 1976; Wiens 2007), there has been much interest using them to study evolutionary questions in a phylogenetic context. From a systematics perspective, recent research supports the earlier conclusions of Highton and colleagues that *P. cinereus* appears to be a single evolutionary species, that is, individuals from across the range form a single phylogenetic lineage (Highton and Webster 1976; Highton 1999; Wiens et al. 2006; Fisher-Reid and Wiens 2011). A recent study has identified six phylogeographic clades within *P. cinereus*, based on both mitochondrial and nuclear genes (Radomski et al. 2020). Waldron et al. (2019) found a clinal transition between two of these clades in Ohio, detectable in the mitochondrial cytochrome *b* gene, but not in the 10 nuclear microsatellite markers used. Waldron et al. (2019) suggest two scenarios to explain the discordance between mitochondrial and nuclear data: first the cline could be an artifact of genetic drift or lineage merger, and second, that there may yet be a nuclear cline that is outside their sampling transect. The authors note that a genomic study with wider sampling is needed to fully understand the discordance between mitochondrial and nuclear genomes in *P. cinereus.* For additional work in this particular geographic region see our discussion of Hantak et al. (2019).

At the population level, Petranka (1998) notes that *P. cinereus* populations in formerly glaciated regions are less genetically variable than southern populations that were never glaciated (see Fig. 1 for glacial extent). This observation supports a hypothesis of postglaciation range expansion from southern refugia, which has been further supported by more recent studies using either microsatellites (e.g., Cameron et al. 2017) or a combination of mitochondrial and nuclear genes (Radomski et al. 2020). Molecular ecology studies using microsatellites have been an area of active research since Petranka (1998). Connors and Cabe (2003) published the first set of microsatellite markers for *P. cinereus* using individuals from Mountain Lake Biological Station (MLBS). These markers have since been widely used by researchers to test hypotheses of: isolation by distance (Cabe et al. 2007); the strength of natural and human-made barriers to dispersal (Marsh et al. 2007, 2008); impacts of habitat fragmentation on urban populations (Noël et al. 2007; Noël and Lapointe 2010; Wilk et al. 2020); multiple paternity of clutches (Liebgold et al. 2006); kin discrimination (Liebgold and Cabe 2008); influence of historical landscape change on population structure (Jordan et al. 2008); and color-biased dispersal (Grant and Liebgold 2017). The results of these studies are discussed in detail in the appropriate sections. Here, we note that Cabe et al. (2007) found low-level but detectable population structure over 2 km of continuous habitat in Virginia (but see Cameron et al. 2019 for conflicting results in Ohio), consistent with an isolation-by-distance model, and no evidence for sex-biased dispersal. In Maryland, Grant and Liebgold (2017) also found no evidence for sex-biased dispersal but did find evidence for color-biased dispersal: striped salamanders showed evidence of philopatry, whereas unstriped salamanders showed evidence of dispersal. It remains to be seen if this pattern exists in other populations. For further discussion on sex-biased dispersal, and dispersal more generally, see the section on Terrestrial Ecology: Seasonal Activity and Dispersal.

Additional microsatellite marker sets were developed from populations on Long Island, New York (Fisher-Reid et al. 2013), and from populations in Virginia, Ohio, and Pennsylvania (Cameron et al. 2017). Combined, these three marker sets cover five of the six phylogeographic clades identified by Radomski et al. (2020), all except the “North Carolina” clade at the southwestern range limit. Population-level comparisons between the phylogeographic clades have been hampered by low variation in the formerly glaciated regions (e.g., Fisher-Reid et al. 2013; Radomski et al. 2020) and difficulty amplifying markers outside of the populations in which they were developed in (e.g., Cameron et al. 2017).

Petranka (1998) focuses his discussion of geographic variation on ratios of color phenotypes across the range, hypotheses as to the persistence of color polymorphism, and why the color phenotype frequencies vary. Like the population genetic studies, this has been an extremely active area of research in the decades since Petranka (1998), and it has proven to be a complex puzzle. Generally speaking, we have ample evidence that the color phenotype frequencies observed prior to 1998 are stable 3–5 decades later (e.g., King et al. 1997; Fisher-Reid et al. 2013; Hantak et al. 2015; Evans et al. 2018; although, see our discussion of Grant et al. 2018). Less clear are the hypothesized relationships between color phenotypes and their physiology or climatic preferences. At the time Petranka (1998) wrote his chapter on *P. cinereus*, he summarized studies that provided evidence that striped morphs were more common in cooler climates (i.e., higher latitudes) and that unstriped morphs had a physiology consistent with being more tolerant of warmer conditions than striped morphs. However, more recent studies have identified exceptions to these general patterns and contradictory results that suggest high levels of local variation in both color phenotype frequency (e.g., Hantak et al. 2019) and color phenotype physiologies (e.g., Petruzzi et al. 2006). For example, Petruzzi et al. (2006) found that the patterns of physiological differences between color phenotypes first detected by Moreno (1989) in New Jersey were inconsistent and variable across several populations in Ohio. Additionally, Smith et al. (2015) found that, although both morphs were equally able to resist water loss, striped morphs recovered from dehydration more successfully than unstriped morphs, particularly in autumn.

Gibbs and Karraker (2006) show that frequencies of the unstriped morph have increased with sampling year alongside increasing global temperatures, supporting the patterns cited by Petranka (1998) and implying that the unstriped morph may become more common as global temperatures increase because of climate change. However, Moore and Ouellet (2015), Cosentino et al. (2017), and Evans et al. (2018) show no relationship between color phenotype frequency and sampling year. Cosentino et al. (2017) combined the Gibbs and Karraker (2006) and Moore and Ouellet (2015) data sets and found evidence that color phenotype frequency is related to an interaction between land use and temperature: The proportion of striped individuals was positively correlated with forest cover in warmer regions; however, this relationship weakened and disappeared as regional temperatures decreased with increasing latitude. This study suggests that forest cover may buffer natural selection on *P. cinereus* color phenotypes in warmer regions because of global climate change (Cosentino et al. 2017).

Recently, Hantak et al. (2021) looked at changes in morph frequency and body size (as measured by SVL) over time using specimens from Highton's National Museum of Natural History (NMNH) collection. These specimens cover 37 geolocations (in New York, Maryland, and Virginia) and 43 yr (1956–1999). Hantak et al. (2021) found the frequency of striped morphs increased with increasing temperatures, increasing elevation, and through time, but decreased with increasing precipitation, contrary to previous studies (e.g., Lotter and Scott 1977; Gibbs and Karraker 2006; Fisher-Reid et al. 2013). Both morphs show decreases in body size with increases in temperature and increases in body size with increased elevation; however, these relationships show different strengths between morphs. Striped morph body size is more sensitive to temperature than unstriped morph body size, and unstriped morph body size is more sensitive to elevation than striped morph body size (Hantak et al. 2021). Over time, the body size of unstriped morphs is increasing, while the body size of striped morphs is decreasing. These complex patterns lead the authors to suggest that *P. cinereus* color morphs have a suite of co-adapted traits that are responding to multiple climate and geographic drivers over time (Hantak et al. 2021).

Cosentino et al. (2017) noted in their discussion that the many studies that examine trait differences between color phenotypes (e.g., Petruzzi et al. 2006; Anthony et al. 2008; Davis and Milanovich 2010; Fisher-Reid et al. 2013; Smith et al. 2015; Muñoz et al. 2016a; Cosentino and Droney 2016) suffer from being limited to a single population or geographic region. Related discussion of the pros and cons of single-population studies can be found in Hantak et al. (2019, 2020). In order to visualize the limitations in geographic scope, we recorded the geographic location (state) for 410 of the studies we reviewed in depth (Supplemental Material S15; Supplemental Data S14). Studies with data from multiple states were counted once for each state (see Supplemental Material S2; Supplemental Data S1 and Supplemental Material S3; Supplemental Data S2), resulting in 448 total state-level locations. Excluding range-wide studies and those with unknown locations, we found that just over half (52.2%, $n = 234/448$) of the locations where research has been conducted on *P. cinereus* since Petranka (1998) are in just three states in the center/southern part of the range: Virginia (29.5%, $n = 132/448$), Ohio (13.2%, $n = 59/448$), and Pennsylvania (9.6%, $n = 43/448$). Nearly one-third of the Virginia studies are from MLBS (9.2%, $n = 41/448$), a field station in southwestern Virginia, at elevation (~1,100–1,200 m). MLBS has an atypical pattern of color phenotype frequencies for a high-elevation population (Angleberger and Chinnici 1975) and likely belongs to a geographically restricted clade (the Southern clade; sensu Radomski et al. 2020). Phylogeographically, these three states do include 5/6 clades (the North Carolina clade is not present); however, the most widespread Northern clade is not well represented by these three states (Radomski et al. 2020). This geographic bias in focal study populations indicates that, when trying to address geographic variation over large spatial scales, future work should be intentional in selection of new, unstudied site locations and take into consideration which of the six phylogeographic clades identified by Radomski et al. (2020) are under study.

Fisher-Reid and Wiens (2015) looked at the maintenance of color polymorphism throughout the genus *Plethodon* in relation to climate. Striped/unstriped polymorphism is observed in at least 8 other species of *Plethodon*, and another 14 species are fixed for either the striped or unstriped morph (7 species each). All of the polymorphic and monomorphic species are in the three most basal clades of *Plethodon*, suggesting color polymorphism existed within the ancestor of all *Plethodon*, and has been maintained in the genus for over 40 million years (Fisher-Reid and Wiens 2015). Interestingly, there is a strong relationship between color phenotype and climate among species which is similar, but not identical to that observed in *P. cinereus*, but there are only two significant within-species climate-morphology relationships among the eight polymorphic species (Fisher-Reid and Wiens 2015). Only *P. cinereus* and a western species, *P. vehiculum,* show significant climate-morphology relationships, and they are not identical (Fisher-Reid and Wiens 2015).

Several studies since Petranka (1998) have explored the variation of *Plethodon* color phenotypes for reasons other than climate, most using *P. cinereus*. Three of these focus on selection imposed by predators using clay models (Fitzpatrick et al. 2009; Kraemer et al. 2016; Grant et al. 2018), while two more focus on genetic structure and landscape heterogeneity (Fisher-Reid et al. 2013; Hantak et al. 2019). Fitzpatrick et al. (2009) used striped and unstriped clay models within the geographic range of polymorphic *P. ventralis.* The authors found that avian predators will attack the more common morph when presented with striped and unstriped clay models at varying frequencies, suggesting that negative frequency-dependent selection could be acting to maintain color polymorphism within *Plethodon* species. However, given the wide variation in morph frequencies in the literature (Petranka 1998; Cosentino et al. 2017), it is likely that other mechanisms are contributing to the proportion of different color morphs in a population.

Kraemer et al. (2016) used a clay model approach to test for predation selection on *P. cinereus* color phenotypes (striped, unstriped, and erythristic) imposed by mammals. In this study, the authors found complex results driving mammalian predator attacks on the clay models, including both directional selection favoring inconspicuous salamanders and, more strongly, negative frequency-dependent selection which favors novel (i.e., rare) salamander coloration. The latter pattern matches the findings of Fitzpatrick et al. (2009), which focused on avian predators. Kraemer et al. (2016) argue that the complexity of how mammals prey on salamanders is strongly influenced by local conditions and is only one piece of the complex puzzle of morph frequency variation throughout the range of *P. cinereus*.

Grant et al. (2018) combined the clay model approach with demographic data from 3 yr of *P. cinereus* mark–recapture at a Maryland population on the Delmarva Peninsula (i.e., the peninsula which includes portions of Deleware, Maryland, and Virginia) to explore morph-specific differences in survival. Delmarva is another location with atypical color phenotype frequencies (Highton 1977; Petranka 1998). Delmarva has a gradient in morph frequency, from majority striped in the north, to majority unstriped in the south (Highton 1977). Grant et al. (2018) found that there was a greater proportion of striped juveniles compared to the proportion of striped adults, suggesting differential survival of the two color phenotypes, with fewer striped individuals reaching adulthood. The authors also found that survival was only explained by the combination of color and age in spring, but not in autumn. Birds were more likely to attack the striped clay models, providing a potential mechanism for the differential survival, whereas mammals showed no differential predation by color phenotype (Grant et al. 2018). Interestingly, Grant et al. (2018) documented color phenotype frequencies that are opposite to what Highton (1977) found. In 1977, Highton recorded a color frequency of ~70–80% striped at the sample locations closest to where Grant et al. (2018) conducted their study. Grant et al. (2018), on the other hand, recorded a color frequency of just 29% striped over their 3 yr of mark–recapture. This suggests that, unlike other locations which have been sampled repeatedly over time, the color phenotype frequencies on the Delmarva peninsula may not have been stable over 40 yr. It would be interesting to completely resurvey Highton's (1977) localities and follow the modeling methods of Cosentino et al. (2017) to determine if the same covariates explain the change in color phenotype frequency over time.

Fisher-Reid et al. (2013) and Hantak et al. (2019) are two of several recent studies mentioned briefly above which have tried to leverage the technological advances in genetics since Petranka (1998) to understand variation in color phenotype frequencies in *P. cinereus*. Williams et al. (1968) were the first to note that the most common color morph ratio (70:30 striped: unstriped) is not observed on Long Island, New York: western Long Island is 100% striped, southeastern Long Island is 100% unstriped, and the center and northeastern parts of Long Island are roughly 50:50 striped:unstriped (Williams et al. 1968; Fisher-Reid et al. 2013). Using microsatellite markers, Fisher-Reid et al. (2013) found that the 100% unstriped populations are genetically isolated from the rest of the Long Island *P. cinereus* populations (as measured by F_{ST}), and show significant differences in morphology. Additionally, localities across Long Island show significant differences in microclimate and macroclimate when salamanders are active. Fisher-Reid et al. (2013) documented a soil moisture gradient on Long Island that correlated with the change in morph frequency, suggesting selection may have played a role in driving the less-fit morph extinct at the gradient extremes.

Anthony and Pfingsten (2013: Fig. 18-4) documented a similar correlation between a precipitation gradient and morph frequencies in Ohio. Much like on Long Island, their work shows that unstriped morph frequency increases in drier regions of Ohio. Further work in northern Ohio by Hantak et al. (2019) focused on the population genetics from 28 localities which span a range of color phenotype frequencies from 100% striped in eastern Ohio to nearly 100% unstriped in western Ohio. Using microsatellite markers, they found a complex interaction between gene flow, genetic drift, and natural selection working together to explain morph frequencies. Thus, both Hantak et al. (2019), at the genetic level, and Kraemer et al. (2016; see the foregoing), at the predator–prey interaction level, find evidence for complex evolutionary dynamics driving morph frequencies (see also Hantak et al. 2021). Using ecological niche modeling, Hantak et al. (2019) further found waterways were the most important factor in explaining morph frequency variation, likely, as the authors suggest, because waterways are strong dispersal barriers for a terrestrial salamander.

Our search recovered two additional studies that explored geographic variation not related to color phenotypes: one focused on skin microbial communities (Muletz-Wolz et al. 2017) and the other on phylogeographic patterns of pheromone profiles (Kunkel et al. 2019). Muletz-Wolz et al. (2017) is discussed in more detail in our section Additional Topics: Microbiota. In the context of geographic variation, Muletz-Wolz et al. (2017) sampled the skin microbial communities of 37 *P. cinereus* individuals across three localities in the central Appalachians, with one locality encompassing an elevation gradient. As other microbial studies have found (see Additional Topics: Microbiota), the authors report high levels of microbial diversity, and little overlap from one location to another, suggesting high taxonomic turnover of microbial communities across the landscape (Muletz-Wolz et al. 2017). Kunkel et al. (2019) compared the pheromone profiles of striped males from the Ohio clade to striped males from the Pennsylvania clade (Radomski et al. 2020) across a gradient in northern Ohio (overlapping the study area of Hantak et al. 2019). They found that, while pheromone profiles differed between populations, they did not differ between phylogeographic clades (Kunkel et al. 2019). These results suggest that the Ohio and Pennsylvania clades are not yet reproductively isolated from each other.

Taken together, the many studies focused on geographic variation in color morphology in *P. cinereus* make a strong case for complex interactions between macroclimate, microclimate, forest type, and predators on variation in color phenotype in *P. cinereus*. We refer the reader to the detailed discussion of Hantak et al. (2019) on the complex maintenance of color polymorphism in *P. cinereus* for additional thoughts on the complexity of color polymorphism in *P. cinereus.* Further, we discuss several studies that address the maintenance of the color polymorphism through other mechanisms (e.g., sexual selection, diet, territoriality) in greater detail in the Terrestrial Ecology section. We also note that there has been very little work on the genetic determination of color morphology in *P. cinereus* since Highton (1975) first documented that color is a polygenic trait. The genetics of color morphology in *P. cinereus* would benefit greatly from use of modern genetic tools to understand links between genes and color polymorphism better. Finally, our review of the literature clearly demonstrates a

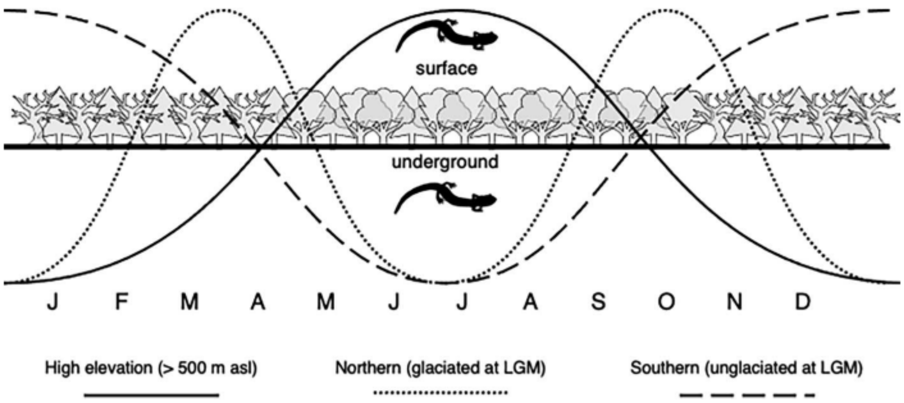

FIG. 2.—Three regional phenologies of *P. cinereus* surface activity throughout their large range. Biogeographic break points between the three phenologies are approximate based on our experience working with this species and five studies (Leclair et al. 2008; Becker et al. 2013; Anthony and Pfingsten 2013; Meshaka and Wright 2017; Hernández-Pacheco et al. 2019). Within a region, there is local variation, and we generally find *P. cinereus* to be opportunistic about surface activity during otherwise stressful seasons (winter and summer): if the abiotic conditions (soil moisture and temperature) are suitable, some salamanders will be surface active. Salamander silhouette from PhyloPic. LGM = last glacial maximum; asl = above sea level.

need for studies which focus on geographic variation in traits other than color morphology.

Distribution and adult habitat.— Petranka (1998) gives a brief description of the geographic range of *P. cinereus,* as well as the preferred habitat of adult salamanders. He noted that *P. cinereus* adults can be found in deciduous, northern conifer, and mixed deciduous–conifer habitats throughout their range, but he cited research that finds *P. cinereus* reach their greatest densities in well-drained, mature forests with deep soils. Petranka (1998) also cited evidence showing that populations are absent or at low densities in highly acidic soils, perennially wet soils, and shallow, rocky soils.

In compiling the more recent literature on the distribution and adult habitats of *P. cinereus* we noted more than 20 sources that simply document that *P. cinereus* was present at a given study site and categorized these as Regional Herpetofaunal Lists (Supplemental Material S12; Supplemental Data S11). In reviewing these sources, it is clear that the geographic distribution of *P. cinereus* has remained stable over the decades of intensive study, and if anything, it is underestimated by the most commonly cited range maps. That said, we found three sources explicitly documenting new records of *P. cinereus.* The first, Placyk et al. (2002), documented *P. cinereus* from two islands in Lake Michigan that had not been previously inventoried. Island populations of *P. cinereus* are common, particularly in areas that were formerly glaciated (e.g., Long Island, Martha's Vineyard, Maine coastal islands, Canadian provincial islands; VertNet 2021). The second source recorded a new, high-latitude, high-elevation record for *P. cinereus*, found on Mount Katahdin at 1,173 m in central Maine, in what is considered subalpine habitat (Willey and Jones 2010). Finally, Baxter-Gilbert et al. (2022) documented a newly introduced population of *P. cinereus* on the island of Newfoundland, Canada, ~530 km east of the nearest known native population on Nova Scotia.

Three studies noted fewer than expected (Silva et al. 2003; Meshaka et al. 2019) or no (Hartzell 2019) *P. cinereus* in suitable habitat; however, all of these studies focused their sampling during the summer months, when the heat drives the vast majority of *P. cinereus* underground (Fig. 2); thus we doubt these three studies represent true absences or declines in density at these locations (e.g., for evidence of true declines, see Highton 2005). Silva et al. (2003) were working at the northern edge of the geographic range of *P. cinereus*, where summer sampling is typically warranted (Fig. 2). They sampled from the start of May through the end of September and noted that prior work has shown *P. cinereus* is generally rare on Prince Edward Island (PEI), Canada. Their study suggests *P. cinereus* is even rarer than previously thought (Silva et al. 2003). That said, because island insulation likely means PEI forest climates are still suitable for *P. cinereus* in April and October, a survey that starts earlier in spring or continues later into autumn may provide a clearer picture of the actual abundance of *P. cinereus* on PEI. In general, the autumn season, particularly October, has the highest detection rates (e.g., Leclair et al. 2008; Anthony and Pfingsten 2013; McGhee 2013; Sutherland et al. 2016), and in the far southern part of the range, salamanders are surface active from autumn through the winter months into spring (Becker et al. 2013; Hernández-Pacheco et al. 2019; Fig. 2).

Much of the recent work on distribution and habitat has focused on the microhabitat preferences of both adult and juvenile salamanders, particularly with regards to refining sampling methods using natural or artificial cover objects (NCOs and ACOs, respectively). We categorized more than 50 studies as focusing on adult and/or juvenile habitat, as well as an additional 19 studies that test a variety of sampling methods based on presumed habitat preferences. Of those latter 19 studies, 18 are focused on ACO survey design, ACO survey performance compared to NCO and leaf litter surveys, and ACO best practices. Generally speaking, ACOs are a well-vetted method for standardized sampling of *P. cinereus*. Indeed, Hesed (2012) argues that ACO methodology has been optimized for *P. cinereus* over other woodland salamander species. Among our reviewed studies, at least one found ACOs are more efficient than leaf litter surveys (e.g., Otto and Roloff 2011) and several found ACO surveys are comparable to NCO surveys (e.g., Monti et al. 2000; Grover 2006; Moore 2009; Ciul et al. 2010).

In terms of best practices, wood boards (MacNeil and Williams 2013a; Hesed 2012), resting directly on the ground (Carfioli et al. 2000; Hickerson et al. 2012), and sampled no more frequently than once per week (Marsh and Goicochea 2003; Otto et al. 2013) have the highest encounter rates. Generally, ACOs are colonized by salamanders within 2 mo of installation (Bonin and Bachand 1997); however, other studies have documented faster colonization rates (e.g., 2 wk in Hickerson et al. 2012, which used ceramic floor tiles placed directly on the soil). There does not seem to be much impact on occupancy under ACOs based on the type of wood used (Bennett et al. 2003; Moore 2005) or the age of the ACO (Monti et al. 2000; Carlson and Szuch 2007). However, more recent work has shown ACO age may be important, with older, more weathered boards capturing more salamanders than younger, less weathered boards (Hedrick et al. 2021). In Virginia, one study found ACOs may be biased toward attracting adult salamanders and exclude juveniles compared to NCOs (Marsh and Goicochea 2003), but other studies from Maine and Québec found no age/size differences between ACO and NCOs (Monti et al. 2000; Moore 2009). When true density was estimated from removal, Siddig et al. (2015) found that ACO surveys overestimate the true density of salamanders, and NCO surveys underestimate the true density. However, the sampling in Siddig et al. (2015) was done in July in Massachusetts, when surface densities are at or approaching their lowest (see Terrestrial Ecology: Seasonal Activity and Dispersal and Fig. 2), and so should be repeated during the autumn or spring surface-active seasons for accuracy. Recent modeling using *P. cinereus* density estimates based on a mark–recapture data set has suggested that model-derived estimates of individual space use and detectability are both sensitive to the spacing of ACOs (0.5, 1, or 2 m apart) and the extent of an ACO array (total area occupied; Fleming et al. 2021). In contrast, model-derived estimates of population density are robust to variation in both ACO spacing and array extent (Fleming et al. 2021).

Beyond comparisons of ACOs to NCOs, several studies note that, although you can find *P. cinereus* in the leaf litter, they are more likely to be encountered under cover objects (Moore et al. 2001; Otto and Roloff 2011; McGhee 2013). Preference for woody NCOs vs rocky NCOs varies by study location. In one Ohio study, woody NCOs were preferred (Iverson and Smith 2010), whereas in Vermont (Richmond and Trombulak 2009) and Ohio more broadly (Anthony and Pfingsten 2013), rocky NCOs were preferred. Positive correlations between cover-object size (diameter or area) and salamander size (mass or snout–vent length) are inconsistent in those studies that have explored the relationship. Some studies found these correlations (e.g., Moore et al. 2001; Hickerson et al. 2004; Strojny and Hunter 2010a; Walton 2013), while others found no relationship between cover-object size and salamander size (e.g., Faragher and Jaeger 1997; Moore 2005, 2009). The inconsistencies may in part be because of different goals of these studies, and whether the study was designed to focus on adults, juveniles, or both age groups.

A study in Vermont by McKenny et al. (2006) suggests that structural complexity of the forest floor is important, finding *P. cinereus* to be more abundant when there was well-decayed coarse woody debris compared to less-well-decayed coarse woody debris. Strojny and Hunter (2010a) suggest that large coarse woody debris is important based on their study in Maine, which found salamanders to be more abundant under logs of larger diameter in canopy gaps after timber harvest. Using salamanders and substrate from the same population in Ohio, leaf litter preferences are inconsistent across a field-situated mesocosm experiment (Iverson and Smith 2010) and in a laboratory-based choice experiment (Renaldo et al. 2011). This result suggests that individual preferences are highly variable over time. Iverson and Smith (2010) found *P. cinereus* had no preference for deciduous vs. pine leaf litter, whereas Renaldo et al. (2011) found a preference for deciduous over pine, and the strongest preference for a combination of deciduous and pine litter.

Several studies directly contradict Petranka's (1998) note that *P. cinereus* is uncommonly found on perennially wet or highly acidic soils: Chalmers and Loftin (2010) regularly observed *P. cinereus* in wetland habitats in Maine, and several studies have found *P. cinereus* in riparian environments (e.g., Moore et al. 2000, 2001 in Pennsylvania; Anderson et al. 2013 in West Virginia; McGhee 2013 in Virginia). In particular, Anderson et al. (2013) and McGhee (2013) both found equal encounter rates for *P. cinereus* between riparian and upland habitats. Moore and Wyman (2010) found a seemingly healthy population of *P. cinereus* in an extremely acidic forest in Québec, Canada. The pH under coverboards ranged from 3.1 to 5.2, and 82% of captures over 5 y were from coverboards with a soil pH $\leq$3.8 (Moore and Wyman 2010). This Québec population also had larger salamanders (both in SVL and mass; Moore and Wyman 2010) compared to other studies, directly contradicting an earlier laboratory experiment that found that *P. cinereus* living on low pH substrates experienced a significant loss of body mass and other potentially negative osmoregulatory effects (Frisbie and Wyman 1991). Similarly, Bondi et al. (2016) found *P. cinereus* to occupy a wider range of soil pH than earlier studies, 5 of their 34 sites in northern New York, Vermont, and New Hampshire had pH $<$3.0 and seemingly healthy *P. cinereus* populations. They found no evidence that *P. cinereus* was selecting microhabitats preferentially by pH (Bondi et al. 2016). Although these low pH values may be tolerable to *P. cinereus*, at least one recent study suggests they prefer more neutral soil pH. In Ontario, Gorgolewski et al. (2016) added wood ash to forest floors to raise the pH from $\sim$5 to $\sim$6.5 and found that the abundance of *P. cinereus* increased under coverboards with ash compared to those without ash. In contrast to Gorgolewski et al. (2016), Cameron et al. (2016) studied the effects of long-term soil liming (which increases soil pH) in an Ohio population and found no effect of liming on salamander body condition, population demographics, or surface density.

Three additional sources found *P. cinereus* in novel environments. Hughes et al. (1999) found one salamander dead inside a pitcher plant (*Sarracenia purpurea*) in two different locations: West Virginia and Pennsylvania. Both sites were the typical bog habitat of *S. purpurea*, which is an unusual place to find woodland salamanders. Hughes et al. (1999) hypothesize these two individuals were foraging when they died, given their stomach contents and the abundance of arthropod prey in the bog. Roble (1999) found an unstriped individual under driftwood on the sandy bank of the Potomac River in Virginia. Finally, LeGros (2018) found an individual hiding under the lid of a backcountry privy in Ontario, possibly feeding on the flies attracted to the privy. LeGros (2018) displaced the individual from the privy, and it returned within 9 h. Individual identification was confirmed using photographs of the spotting pattern on the head and tail (LeGros 2018). Such novel environment observations as those just cited are likely underreported in the literature. In our own field experience and those of our colleagues, *P. cinereus* is regularly found under anthropogenic objects (i.e., trash) within or near suitable forest habitats, including in suburban environments (e.g., Meshaka and Wright 2017). These observations are potentially important for understanding the dispersal and notably fast habitat colonization behavior of *P. cinereus* (e.g., see discussion in Williams et al. (1968) on colonization of formerly glaciated regions by *P. cinereus*).

Many studies attempt to characterize the preferred microhabitat of *P. cinereus*, either by measuring covariates in the field where salamanders are present or by doing behavioral choice trials of different habitats in a laboratory setting. In Virginia, Mitchell et al. (1997) found deep soils to be important in predicting *P. cinereus* presence in four out of five forest stands. Anthony and Pfingsten (2013) reviewed the maximum soil depths at which *P. cinereus* has been found, and noted that several pre-Petranka studies report finding salamanders at depths approaching 1 m. In the laboratory, individuals from an Ohio population preferred high pH, shaded habitat with medium-high moisture (Sugalski and Claussen 1997). The authors were able to show that pH was most influential in preferences, and that the combination of acceptable soil pH and moisture levels made a wider range of light intensities acceptable. In Pennsylvania, Brenner et al. (2005) found the presence of *P. cinereus* was correlated with soil moisture and temperature, and indirectly correlated with litter depth. Not surprisingly, given *P. cinereus* is fully terrestrial, they also found that salamander presence was not related to either distance or direction from vernal pools (Brenner et al. 2005).

Farallo and Miles (2016) compared the microhabitat characteristics of *P. cinereus* to two microendemic species, *P. sherando* and *P. hubrichti* in Virginia. They found evidence that all species seek their preferred habitats, as measured by temperature and moisture levels of the air and soil. There is additional evidence of microclimatic niche differentiation among all three species, suggesting character displacement when *P. cinereus* is sympatric with the microendemic species (Farallo and Miles 2016). A follow-up study on the same three species by Marsh et al. (2019) found that peak activity temperatures for *P. cinereus* were similar to *P. sherando* and cooler than *P. hubrichti*. There were no significant moisture patterns detected. As expected, the wide-ranging *P. cinereus* had a much larger range of active temperatures compared to *P. hubrichti*, but not when compared to *P. sherando* (Marsh et al. 2019). Yu et al. (1998) found that *P. cinereus* from Pennsylvania had high levels of constitutive heat shock protein 70; these levels did not change with acclimation to different temperatures in the laboratory. They compared *P. cinereus* to southern congener, *P. jordani*, and found that *P. jordani* was not as tolerant of heat shock as *P. cinereus* (Yu et al. 1998). In Ontario, Luymes and Chow-Fraser (2019) found populations to have stable abundances over an 18-y sample period with an average temperature of 12°C during the spring and autumn active seasons. The authors suggest that monitoring programs should plan on sampling for at least a decade to estimate occupancy more accurately (Luymes and Chow-Fraser 2019).

Kolozsvary and Swihart (1999) explored the relationship between patch size and *P. cinereus* occurrence in Indiana, finding a strong positive relationship as forest size increased from 1 ha to 1000 ha. McGhee and Killian (2012) found pH variability to be important in detecting *P. cinereus* using a regression model based on presence/absence data from a location in northern Virginia. They suggest salamanders actively select good microhabitat patches within less desirable patches. However, their sample size for their presence data was very low compared to their absence data ($n = 42$ salamanders over 2 y; presence detected on 29% of transects). McGhee and Killian (2012) argue that at their location, soil pH may be more important in determining which habitats salamanders avoid (low pH with low variability in pH). In Ontario, Brown et al. (2020) found that a suite of understory characteristics better predicted presence of *P. cinereus* than more macroscale variables like climate, disturbance, canopy cover, or landscape.

Finally, a handful of studies have explored how social hierarchies may be involved in habitat choices in *P. cinereus*. Forester and Anders (2000) found that hatchlings are more likely to associate with substrates marked by their mother than they are with substrates that are just wet or marked by a nonrelative conspecific female. Hurst and Smith (2006) found that females will avoid areas with cues from five or more conspecifics, whereas males do not discriminate. These two studies, as well as much of the work reviewed in Jaeger et al. (2016), imply that *P. cinereus* can not only recognize kin vs nonkin (but see Gibbons et al. 2003), and conceptualize the number of individuals in an area, but use this information to inform movement decisions. In West Virginia, Riedel et al. (2012) found that juveniles may actively avoid or be unable to compete for limited cover in nonforested habitats (e.g., meadows, pastures) that adults appear to live in without issue.

Future studies that try to understand the distribution and habitat of *P. cinereus* should first determine the phenology (Fig. 2) of their study sites, and then plan to sample during peak surface-active seasons. This will allow for more accurate presence, abundance, and density estimates, as well as increased sample sizes for characterizing microhabitat. Field methods for sampling *P. cinereus* during surface-active seasons are well developed and flexible, depending on the resources and personnel available. Well-designed choice experiments that offer *P. cinereus* different abiotic microhabitats or different cover objects are needed to characterize how salamanders perceive and select their habitat further. Once these abiotic requirements are met, there is ample evidence that social interactions are likely to shape habitat preferences further (Jaeger et al. 2016), and so these should be considered when designing experiments. Finally, and not surprisingly given the logistical difficulties of studying underground behavior, little is known about the underground activity of *P. cinereus*, and much of what is known about underground activity was largely documented pre-1998 (e.g., the depth that salamanders retreat to [Anthony and Pfingsten 2013]; see also the Terrestrial Ecology: Seasonal Activity and Dispersal section). Revisiting the methods of those earlier studies combined with creative solutions using modern radio-frequency tags (e.g., passive integrated transponders [PIT], tags; Sterrett et al. [2022]) provide an excellent starting point for further investigation of the underground activity of *P. cinereus*.

Breeding and courtship.— Petranka (1998) splits *P. cinereus* reproductive biology into two sections: Breeding and Courtship, which details all male and female behavior prior to insemination, and Reproductive Strategy, which focuses solely on female behavior after insemination. We follow a similar structure here. Petranka (1998) first describes the remarkably long mating season in *P. cinereus* based on studies that document the presence of sperm in female cloacae from autumn through winter to early spring. Mating is believed to occur primarily in the autumn. Breeding frequency is annual for males, whereas females breed biennially in most populations, particularly in more northern portions of the range, where the active season is shorter. That said, there is some evidence that larger females can breed annually even in more northern populations

(>44 mm SVL in Connecticut; Lotter 1978). The courtship behaviors of *P. cinereus* are highly stereotyped, as they are for the entire plethodontid family, and therefore have been evolutionary stable for 50–100 million years (Houck and Arnold 2003). Detailed accounts of courtship behavior in *P. cinereus* have been well described elsewhere (Petranka 1998; Anthony and Pfingsten 2013; Jaeger et al. 2016). Although these descriptions are detailed, they are based on just two studies, one field study (Gergits and Jaeger 1990) and one lab study (Dyal 2006), both using salamanders from high-elevation Virginia populations. Additional observations of courtship throughout the range are needed. Briefly, *P. cinereus* courtship includes pheromone signaling, male abrasion of females with enlarged premaxillary teeth, nose tapping, and a coordinated tail-straddle walk, during which males deposit a spermatophore on the ground which females pick up by walking over it (Arnold 1977). Prior to 1998, sources cited by Petranka (1998) had observed that intruder males could disrupt courtship by biting the courting male. Lastly, Petranka (1998) summarizes two studies that support fecal pellet squashing behavior by gravid females as a mechanism for selecting mates with higher diet quality. Much of the related behavioral work on *P. cinereus* breeding and courtship has been thoroughly reviewed in Jaeger et al. (2016). Therefore, we focus this section of our review on recent studies that either (1) focus on nonbehavioral aspects of breeding and courtship (e.g., those focused on glandular physiology or life history timing) or (2) behavioral work independent of the R. G. Jaeger research program.

Since Petranka (1998), extensive work has been done to characterize the sexually dimorphic glands and the male pheromone proteins used in courtship by *P. cinereus* and other plethodontids. Sever (1997) and Sever and Siegel (2006, 2015) have characterized the sexually dimorphic glands using males and females from a single population of *P. cinereus* in Indiana. Sever (1997) observed that females usually store sperm for 3 to 4 mo, and up to 9 mo if mating occurred right before the winter hibernation period; however, contrary to other locations reviewed by Petranka (1998), autumn mating was rare in this population. A follow-up study described the complex spermatheca of females, where sperm clusters occurred in parallel arrays (Sever and Siegel 2006), and confirmed the predominance of spring mating in their population based on absence of sperm in females collected in October compared to those collected in April. Sever and Siegel (2015) found seasonal differences in the size and secretory activity of caudal courtship glands in males, with the greatest gland size and secretory activity occurring in April and October. Mental glands, found on the chins of mature males and used to produce and deliver pheromones to the female during courtship, show similar seasonal changes in size and secretory activity (Sever 2017). Related to these patterns, Church and Okazaki (2002) found that plasma testosterone levels and testes mass both vary seasonally in males from Virginia. Testosterone levels peak in the autumn in early October and reach their lowest point at the end of the spring in May. Peak testes mass is offset from testosterone, peaking in midsummer (July), and reaching its lowest point in the winter hibernation season (November–March). Additional details on the glands used for scent marking and territoriality can be found in the Terrestrial Ecology section.

Plethodon cinereus individuals from MLBS have been used to characterize both the evolution and function of courtship pheromones at the species, genus, and family level (e.g., Watts et al. 2004; Palmer et al. 2005, 2007, 2010; Wilburn et al. 2014). Here, we will focus on summarizing the pheromone protein research as it relates to courtship in *P. cinereus*, but we refer the reader to the extensive work of L. D. Houck and colleagues for greater detail on the evolution of plethodontid pheromones and courtship behaviors. To date, three pheromone proteins have been identified in Plethodontidae: the more recently evolved plethodontid receptivity factor (PRF), which is found only in eastern *Plethodon* (Palmer et al. 2005, 2007), and two ancestral proteins, plethodontid modulating factor (PMF) and sodefrin precursor-like factor (SPF), both of which were likely present in the ancestor of all plethodontids (Palmer et al. 2007, 2010). PRF and PMF are both expressed in the mental glands of sexually mature male *P. cinereus* (Wilburn et al. 2014), and there is evidence that rapidly evolving PRF has replaced the more ancestral SPF protein in *P. cinereus* (Palmer et al. 2007; Wilburn et al. 2014). PRF acts to increase female receptivity (Watts et al. 2004; Palmer et al. 2005), but much work remains to be done on the functional morphology and evolution of female receptors. As noted previously, Kunkel et al. (2019) did find population-level differences in pheromone chemistry, but these differences were not enough to prevent gene flow across two phylogeographic clades. Given the rapid evolution of these proteins (Palmer et al. 2005, 2007, 2010) and their importance in courtship success, further work on pheromone chemistry across the range of *P. cinereus* is warranted.

At the northern range limit, Leclair et al. (2006, 2008) document a much more delayed reproductive phenology in *P. cinereus,* particularly in females. In a Québec population, males become sexually mature between 3 and 5 y old and reproduce annually, whereas females were mostly unable to reproduce until 4–6 y old (Leclair et al. 2008), much later than results from studies conducted in more southern populations suggest (see sources cited by Petranka 1998). The decreased growth rate in northern populations is possibly due to colder temperatures and more limited opportunities for growth (Leclair et al. 2008). Both studies aged individuals using skeletochronology and found that these northern females typically only live 8 y, and it takes 3 y for a clutch of eggs to mature (Leclair et al. 2006, 2008). Therefore, most female *P. cinereus* in this population only reproduce once in their lifetime. Leclair et al. (2008) also found the juvenile sex ratio in this Canadian population was female-biased, likely because of the delayed female maturity and rare subsequent reproduction.

Male–female pairs are often observed sharing cover objects in *P. cinereus* populations, especially during the courtship season, whereas female–female pairs were uncommon and male–male pairs were very rare or nonexistent (Peterson et al. 2000; Anthony et al. 2008). Peterson et al. (2000) hypothesizes same-sex pairs occur coincidentally because of limited territory space. Meche and Jaeger (2002) argue that tail loss in females may impact the number of eggs that can be laid, as an individual female's energy allocation for reproduction might shift towards tail regeneration. From this premise, the authors hypothesized that males would prefer tail-intact females over those who have recently lost their tails, with males using tail status of potential mates as a proxy for energy available for reproduction. However, males showed no preference for females based on tail status in laboratory experiments. This result is particularly interesting in the context of two studies discussed in detail in Reproductive Strategy: Madison et al. (1999a), which found tails were critically important for females to assume the posture needed to properly suspend a clutch of eggs, and Yurewicz and Wilbur (2004), who observed that tailless females did produce fewer ova.

In Ohio, Anthony et al. (2008) and Acord et al. (2013) both observed that male–female pairs found in the field are usually of the same color phenotype, suggesting positive assortative mating by color. However, a follow-up study by Jaworski et al. (2018) found that, in the laboratory, striped males cannot differentiate between female color phenotypes and thus showed no preference for either striped or unstriped females. These males did show a preference for larger females, presumably because female body size positively correlates with fecundity (Jaworski et al. 2018; see sources cited in Petranka 1998). There is some evidence that *P. cinereus* follow social monogamy for a mating strategy, and the male often aids the female in brooding eggs (e.g., Liebgold et al. 2006; see sources cited by Petranka 1998). Several articles from Jaeger and colleagues support the hypothesis of social monogamy (e.g., Guffey et al. 1998; Gillette et al. 2000; Jaeger et al. 2001; Jaeger et al. 2002a), noting that males and females exposed to unfamiliar individuals (and their scents) behave more aggressively than when exposed to familiar or partner individuals. Males and females were observed to be more aggressive towards polygamous partners than monogamous partners or strangers (Jaeger et al. 2016). Using this evidence, Jaeger et al. (2002a) hypothesized that *P. cinereus* uses sexual coercion against polygamous partners. For a thorough review of the behavioral work on *P. cinereus*, as it pertains to the courtship season and territoriality, we recommend Jaeger et al. (2016).

Atypical courtship behaviors have been observed in *P. cinereus*, although their relevance to the breeding and courtship of this species is unclear. In Virginia, Dyal (2006) observed a female-first tail straddle walk in *P. cinereus* that was not observed in two other plethodontid species studied. However, the data suggested that this behavior did not lead to successful spermatophore deposition in *P. cinereus*, and therefore Dyal's (2006) hypothesis, that females have a larger role in courtship than previously thought, is difficult to evaluate. Courtship behaviors in plethodontids more generally were recently reviewed by Staub et al. (2020). They specifically describe a more active role for females in courtship than historical studies would suggest, a pattern of omission not unique to salamanders, as EEB fields strive to achieve greater gender parity in both scientists and their science (Staub et al. 2020).

Finally, a small number of recent studies have further investigated fecal pellet squashing behavior, which Petranka (1998) briefly summarizes at the end of his Breeding and Courtship section. To date, this behavior, a modification of nose tapping substrate to detect chemical cues, has only been observed in females and is thought to be involved in female choice of mates (e.g., Karuzas et al. 2004; Chouinard 2012; Jaeger et al. 2016). In laboratory settings, females have been observed squashing fecal pellets with their snouts, and experimental trials suggest they are detecting chemical cues about male diet and male health, which are then used to assess male territory quality and/or mate quality (Jaeger et al. 2016). Karuzas et al. (2004) found that while all females investigated male-marked substrates more than female ones, females on poor diets were especially likely to participate in the pellet-squashing behavior. Karuzas et al. (2004) agree with Petranka's (1998) suggestion that the behavior is likely used to assess the diets of conspecifics; however, they suggest that the behavior is not limited to the context of mate selection. Instead, females could be using pellet-squashing to assess prey availability in the environment (Karuzas et al. 2004). Chouinard (2012) suggests that fecal pellets may not be the only method females have for assessing diet quality of potential mates. In a laboratory setting, Chouinard (2012) observed that males on high-quality diets had more protein in the mental gland compared to males on low quality diets. Females responded more quickly to and spent more time with males fed high quality diets (Chouinard 2012).

We still do not know what influences paternity, but females are known to be able to store multiple spermatophores and frequently lay clutches with multiple sires (Liebgold et al. 2006). We also do not know how the sperm from different males interact. There are additional gaps in our knowledge surrounding how or why males and females may occupy and co-defend (e.g., Mathis 1989) the same cover object, and if there is any geographic variation in mating behavior, as almost all of the research surrounding mating strategies has been done with individuals from MLBS. Morph-specific variation in mate quality has been documented at one population in Ohio: striped males cohabitate with larger, heavier females relative to those females cohabitating with unstriped males (Anthony et al. 2008). Given the variation in other morph-specific differences across populations (see above), this pattern should be explored at other sites. Related to this, more field research including capture–mark–recapture methods should be performed to determine if long-term pairing of males and females over multiple seasons occurs. Further research should also focus on mate selection in *P. cinereus*, specifically identifying the role of visual stimuli. Finally, we are unsure of the specific function of courtship pheromones, especially PRF and PMF, because previous research assumes they perform similar roles in *P. cinereus* as in other tested plethodontids.

Reproductive strategy.— In this section, Petranka (1998) summarizes what was known at the time about *P. cinereus* oviposition, parental care, and basic development. Generally, females oviposit in late spring or early summer, although observations of oviposition were reported as late as August in northern Michigan. Nests are made in cavities or crevices that females, and sometimes males, attend while brooding. Females aggressively defend eggs from conspecifics and predators, and Petranka (1998) cited evidence for reduced survivorship of abandoned clutches. During brooding, females have limited opportunities to feed, and grow significantly less, a pattern which is exacerbated in the presence of another female (Petranka 1998). However, females frequently cannibalize their own eggs when induced to oviposit in a lab and eat the eggs of abandoned clutches in both laboratory and field observations. Northern or high-elevation females tend to oviposit in cavities within decaying logs or beneath rocks and logs, whereas oviposition in southern populations was typically observed in subsurface retreats created by other animals. Petranka (1998) describes the gross anatomy of eggs and their arrangement in the clutch: Generally, clutches are suspended from the roof of the cavity in a grape-like cluster. Petranka (1998) further summarizes reports of clutch sizes and ovarian egg counts from several locations, with an average clutch size between six and nine eggs. In three populations where it was explored, the number of mature eggs was correlated with female SVL (Connecticut, Lotter 1978; Tennessee, Nagel 1977) or female body mass (New York, Fraser 1980). Egg incubation lasts for approximately 6 wk, and Petranka (1998) summarized studies of several populations where hatching occurs in August or September. In 1998, very little was known about the development of embryos, but mature embryos had been observed with three gills on either side of the head that are lost around the time of hatching.

Because *P. cinereus* has not yet been documented to oviposit naturally in the lab (published laboratory oviposition is induced via hormone injection, typically with agonists of luteinizing hormone-releasing hormone [LHRH], e.g., Evans et al. 2020), and their nests are often difficult to locate underground, studies on their reproductive strategy since Petranka (1998) have been limited. There have been several important studies, however, which document key oviposition and care behaviors and further characterize the development of *P. cinereus* eggs and embryos. Oviposition dates, when reported, generally match those reported in sources cited by Petranka (1998), occurring frequently around June, although, more recently, a nest in Virginia was found as early as April (Orr and Ernst 2005).

Madison et al. (1999a) described the exact ovipositing behavior of females induced to lay eggs in the lab. Females assume an upside-down S-shape to lay eggs, using their tail to brace themselves, and were in this position for over 6 h. From this position, females suspended their eggs from the base of a log and adjusted the positioning of the eggs after oviposition with her snout. Madison et al. (1999a) hypothesized that this behavior would place tailless females at a disadvantage for ovipositing, and more recent work has observed tailless females to produce fewer ova, indicating that reproductive success is inhibited by tail loss (Yurewicz and Wilbur 2004). Madison et al. (1999a) also hypothesized an evolutionary advantage for egg suspension, since unsuspended eggs were cannibalized 100% of the time, while suspended eggs were only cannibalized 50% of the time.

Controlled laboratory breeding of *P. cinereus*, for example, crosses of specific males and females as would be needed for selection experiments or quantitative trait loci (QTL) analysis, is not documented to date, and generally considered not possible in this species (Petranka 1998). Females do store sperm, and so can be induced to lay fertilized eggs in the lab (e.g., Madison et al. 1999a; Evans et al. 2020), thus cross-fostering experiments are possible once females produce clutches. Crespi and Lessig (2004) successfully cross-fostered 15 clutches, with 10 control clutches (eggs removed from mother's care and then replaced). This study showed the presence of maternal effects, likely driven by differences in brooding behavior: There was a positive correlation between a foster mother's SVL and hatchling's body length. Behaviorally, larger mothers did not move their eggs as often and spent more time in direct contact with their eggs (Crespi and Lessig 2004).

Brooding females were more likely to abandon clutches in low-resource conditions (Yurewicz and Wilbur 2004). The authors found that smaller clutch sizes were not correlated with larger eggs, making clutch size an appropriate proxy for reproductive investment. Yurewicz and Wilbur (2004) also found that females were less likely to abandon or cannibalize larger clutches (about eight eggs), indicating that the high energetic cost of brooding outweighs the fitness value of smaller clutches (about five eggs). However, another study showed that brooding females defended large (10 eggs) and small (4 eggs) clutches with equal aggressiveness (Tornick 2010). These results seem contradictory, regarding the ability of females to differentiate between clutch sizes and make energetic investment decisions accordingly, but the discrepancy may be because Tornick (2010) did not investigate female behavior with clutches of fewer than four ova. Females were more aggressive when defending more mature clutches, indicating that the developmental stage of eggs influences investment decisions by brooding female *P. cinereus* (Tornick 2010). Ovarian egg counts were also used to determine the average clutch size of some populations, as these observations are typically more accessible and noninvasive. However, no studies have yet determined the relationship between ovarian egg counts and actual clutch size. Because *P. cinereus* are known to reabsorb eggs (Ng and Wilbur 1995), is it unclear how reliable this method is for predicting clutch size.

Kerney (2011) created a complete larval staging table for *P. cinereus*, showing the development of embryos over 72 d until hatching. Despite being a direct-developing species, *P. cinereus* embryos were found to have many characteristics indicative of a metamorphosing species, including hyobranchial skeleton development and the temporary presence of certain cartilages, gill clefts, and Leydig cells (Kerney 2011; Kerney et al. 2012). This is relevant to the loss and re-evolution of the larval stage by plethodontid species in the genus *Desmognathus*, as this shows that the development of key larval traits was not fully lost in direct-developing plethodontids (Kerney et al. 2012). Recent work by Lewis et al. (2022) has fully characterized the developmental basis of lung loss in Plethodontidae using *P. cinereus*, *Desmognathus fuscus*, and *Hemidactylium scutatum*. Interestingly, plethodontid embryos do begin to develop lungs, but these lung primordia regress via apoptosis prior to hatching (Lewis et al. 2022).

Future research on the reproductive strategy of *P. cinereus* females should be cognizant of potential behavioral changes due to laboratory settings (e.g., inducing oviposition increases oophagy; Petranka 1998; Madison et al. 1999a). More field-based studies and observations of reproduction and brooding are necessary for confidence in the results from laboratory studies. No study published since 1975 has used Highton's (1975) method of burying jars with gravid females inside. Highton (1975) later collected the jars which contained both the brooding female and her clutch. This method provides an alternative to hormone injections for studies that require females and clutches and could possibly be refined for laboratory use. Future studies should also determine the accuracy of using ovarian egg counts to predict clutch size, as gravid females are much easier to capture and assess than nesting females. We still do not know what factors influence reabsorption of eggs, nor what factors induce females to cannibalize their own eggs. Finally, although reproductive timing and clutch size have been shown to be influenced by latitude, there have not been any recent studies investigating reproductive trends in populations at the southern range limit and our knowledge of patterns at the northern range limit is from a single population (Leclair et al. 2006, 2008). Those southern populations that have been studied are at elevation (i.e., at MLBS; Crespi and Lessig 2004; Yurewicz and Wilbur 2004) and have their own local phenology distinct from both southern and northern low elevation populations (Fig. 2), suggesting their results may not be generalizable to those regions.

Terrestrial ecology: Introduction.— The terrestrial ecology section is the lengthiest section of Petranka (1998). When categorizing studies, we found it useful to use a finer-scale breakdown of topics within terrestrial ecology, and these are represented by our subheaders in this section. There are some topics that overlap with other sections of this review, and are discussed in those other sections (e.g., juvenile habitat is summarized in Distribution and Adult Habitat), and some topics we have opted to combine (e.g., diet and feeding behaviors). Finally, we end this section with a catchall section on studies of general behavior and experimental methods not directly related to any of the preexisting categories in this or other sections.

Terrestrial ecology: Diet and feeding behavior.— Petranka (1998) described the diet of *P. cinereus* as any palatable metazoan prey an individual can capture. He also noted that diet is variable, but the literature Petranka (1998) reviews suggests there are no noticeable shifts in dietary preferences as individuals grow. Prior observations indicated that adults can be cannibalistic, consuming eggs and juveniles in both the lab, and on rare occasions, in the field. It was thought that *P. cinereus* fed primarily on the forest floor, but individuals have been observed to climb vegetation to forage. Petranka (1998) cited limited evidence for winter feeding in underground retreats from a population in Indiana, based on the stomach contents of specimens dug out of abandoned ant mounds. Adult *P. cinereus* are known to use both visual and olfactory cues to find prey. Individuals have been observed selecting higher-quality (i.e., higher caloric value) prey over low-quality prey when prey density is high, but eating all available prey when prey density was low (summarized in Petranka 1998).

At least 35 recent studies have focused on the diet and/or feeding behaviors of *P. cinereus* since Petranka (1998). Diet was assessed directly by examining stomach contents (via dissection or flushing) in 15 studies. As might be expected, prey items vary by location, but ants, mites, annelid worms, and springtails (Collembola) are the most common prey items across the range (Bellocq et al. 2000; Rooney et al. 2000; Adams and Rohlf 2000; Maerz and Karuzas 2003; Maerz et al. 2005, 2006; Arif et al. 2007; Anthony et al. 2008; Ivanov et al. 2011; Bondi et al. 2015, 2019; Paluh et al. 2015; Stuczka et al. 2016; Hantak et al. 2016, 2020). Interestingly, one study based in Delaware found an abundance of Collembola in the field, but none in salamander stomachs, although the sample size of individual stomach contents was small compared to other studies listed above ($n = 12$; Rooney et al. 2000). Three studies explored relationships between *P. cinereus* and nonnative prey, finding evidence that nonnative invertebrates can either serve as an added resource consumed alongside native prey (Maerz et al. 2005; Ivanov et al. 2011) or are ignored if deemed unpalatable (Ducey et al. 1999). Although by no means the first study to use the method, Bondi et al. (2015) tested the efficacy of the gastric lavage method (i.e., stomach flushing) as a technique for nonlethal sampling of salamander stomach contents. The authors find it to be reliable; 95% of salamanders regurgitated some or all of their stomach contents. Large prey (land snails, adult Coleoptera) were the least likely to be recovered through gastric lavage, and often these instances were singular items left behind while all smaller prey were recovered (Bondi et al. 2015). Finally, there were two studies that provide additional confirmation of cannibalism in the field (Maerz and Karuzas 2003; Gade et al. 2017).

Several studies have explored head morphology in *P. cinereus* and other congeners (e.g., Adams and Rohlf 2000; Maerz et al. 2006; Arif et al. 2007; Adams 2011), focusing on questions of character displacement in sympatry with congeners and relationships between head shape and prey size. These are all discussed in more detail in the Community Ecology: Other Salamanders and *P. cinereus* Interactions section. Here, we note that Adams (2011) explored the heritability and quantitative genetics of head shape variation in hatchling *P. cinereus* and *P. nettingi*. The heritability of head shape was generally high ($h^2 > 0.65$); however, Adams (2011) also found evidence that these two species would evolve differently in response to the same selection pressure on head shape, suggesting head shape as a potential trait axis by which diversification in salamanders occurs. Foraging-associated behaviors, such as territorial defense of prey-rich space, have also been studied in detail, and are summarized in the section Terrestrial Ecology: Territories and Home Range Size.

Anthony et al. (2008, 2017) explored the relationship between diet and color phenotype of a single population in Ohio. In autumn, Anthony et al. (2008) found that striped morphs eat more diverse and more profitable (i.e., easier to digest) prey than unstriped individuals, whereas the follow-up study found that striped morphs resided on territories with a greater abundance of available prey items (Anthony et al. 2017). At the same population, with regular sampling across 13 mo, Stuczka et al. (2016) found the opposite pattern to Anthony et al. (2008): The diet of unstriped morphs was more diverse than that of striped morphs; however, they also found that the diet differences observed between morphs were greatest during seasons with the greatest surface activity of salamanders (spring and autumn), that is, when competition among individuals is highest. Together with a related study from the same population on morph-specific aggression by Reiter et al. (2014), these four studies suggest that striped morphs may competitively exclude unstriped morphs from territories with larger quantities of more energetically profitable prey.

Two recent studies by Hantak et al. (2016, 2020) suggest that these documented diet differences between morphs are likely population specific and highly variable across both time and space. At one location in Ohio, Hantak et al. (2016) found no significant differences between the diets of sympatric striped ($n = 29$) and erythristic ($n = 25$) morphs. Hantak et al. (2020) looked at stomach contents for salamanders at six Ohio populations: two monomorphic striped, two polymorphic, and two nearly monomorphic (>99%) unstriped. One of the polymorphic populations was the same population sampled by Anthony et al. (2008, 2017), Reiter et al. (2014), and Stuczka et al. (2016). Hantak et al. (2020) also looked at temporal differences in diet, by sampling in both the spring and autumn seasons. Contrary to earlier studies discussed previously, they found high levels of diet overlap between morphs, both within a population, across populations, and across seasons. The polymorphic population sampled by both Hantak et al. (2020) and the studies cited above only showed morph-specific differences in diet in autumn. The other polymorphic population showed no significant morph-specific differences in diet (Hantak et al. 2020). The dietary breadth of both morphs did not change between monomorphic and polymorphic populations, and diet composition varied across seasons.

Hantak et al. (2020) noted in their discussion that the sample sizes in their study were much lower than the earlier studies: for the same polymorphic population, the sample size for Hantak et al. (2020) was $n = 40$, and for Stuczka et al. (2016) was $n = 256$. Thus, although Hantak et al. (2020) and other multipopulation studies (e.g., Petruzzi et al. 2006) suggest that many of previously documented differences between morphs may be highly localized, Hantak et al. (2020) particularly call attention to the logistical challenges of balancing sample size and effect size in multipopulation studies for a geographically wide-ranging species like *P. cinereus.* These challenges make detection of subtle differences between morphs difficult without large sample sizes; however, the challenges may be surmountable with a networked research approach by multiple research teams across the range of *P. cinereus*. Finally, Hantak et al. (2020) make a strong case for reanalysis of morph-specific trait complexes within a geographic context. As noted earlier, consideration of the phylogeographic clade to which a population belongs (Radomski et al. 2020) will help in this endeavor.

More generally, recent work confirms that *P. cinereus* forage at all times of day, although night foraging is likely the predominant mode (Placyk and Graves 2001a; Liebgold and Dibble 2011). Night-active salamanders had higher mass, and there was lower prey abundance in their field enclosures, compared to enclosures with fewer night-active salamanders (Liebgold and Dibble 2011). At night, olfactory cues are thought to be most important, as evidenced by increased nose tapping in the dark (Placyk and Graves 2001a), and decreased predation efficiency when the vomeronasal system is impaired (Placyk and Graves 2002). Telfer and Laberge (2013) found that salamanders were more likely to find and investigate soluble olfactory cues over volatile cues. The reliance on soluble olfactory cues is also supported by Maerz et al. (2001), which found that the foraging activity of individuals was reduced when exposed to water soiled by Common Garter Snakes (*Thamnophis sirtalis*). Social hierarchies also appear to influence foraging activity. Liebgold and Dibble (2011) found that both adults and juveniles foraged more actively when enclosed with familiar individuals of the opposite age class compared to when enclosed with unfamiliar individuals of the opposite age class.

Wise and Buchanan (2006) summarize three previously unpublished studies from their research group which explore how different levels of ambient light at night impact foraging. In all three studies, there is evidence that foraging is aided by increasing ambient light levels, especially if prey chemical cues are blocked. In the first two studies, when prey chemical cues are available, there is no change in foraging behavior under different light treatments (Wise and Buchanan 2006). However, when prey chemical cues are not available, salamanders are faster to orient to and attempt capture of prey in treatments that include either rapid shifts from total darkness ($\leq 10^{-5}$ lux) to bright light (3.8 or 12 lux) or by increases in natural levels of ambient light (e.g., twilight, moonlight, starlight; treatments ranging from 10^{-1}–10^{-5} lux; Wise and Buchanan 2006). In the third study summarized by Wise and Buchanan (2006), salamanders were significantly more active in twilight (10^{-1} lux) and day (photophase; 1 lux; equivalent to dim daylight under a forest canopy) treatments than under the night treatment (scotophase; 10^{-3} lux; equivalent to moonlight in the forest). However, the observed increases in activity did not change the amounts of prey consumed across treatments (Wise and Buchanan 2006).

Gibbons et al. (2005) found that although there is a genetic component to foraging efficiency, learning and exposure to prey can improve foraging efficiency over time. Sources cited by Petranka (1998) suggested that climbing behavior was likely a foraging tactic, and the results of Cote et al. (2016) support this. They found that salamanders exposed to dowels with prey scent trails climbed higher and for longer than on control (unscented) dowels. Individuals experimentally infected with the fungal pathogen *Batrachochytrium dendrobatidis* (*Bd*) appear to compensate for this infection by foraging more in a laboratory setting (Hess et al. 2015). The authors found minimal fitness effects of *Bd* infections compared to uninfected controls, suggesting that the extra foraging did help those individuals fight infection.

Physiologically, temperature seems to play a critical role in the efficiency of feeding. Diversity in the gut microbiome of *P. cinereus* begins to decline at 20°C, and digestion efficiency was the greatest at 15°C (Fontaine et al. 2018). Two studies have explored the use of stable isotope analysis to study diet and other factors (e.g., ecosystem-level nutrient cycling, Milanovich and Maerz 2012, 2013). These studies are discussed in more detail in the Additional Topics: Ecosystem Ecology section.

Gastric lavage has proven to be an invaluable method for nonlethal investigations into the diet of *P. cinereus* (e.g., Bondi et al. 2015). Future characterization of the diet of *P. cinereus* may be further improved by application of modern molecular methods, such as DNA metabarcoding (e.g., Harms-Tuohy et al. 2016), to stomach contents and fecal material. As with many topics reviewed here, and exemplified by the more spatially and temporally extensive work of Hantak et al. (2020), there is much to learn on the geographic variation and social context for both diet and foraging behaviors, including field observations of foraging behavior to complement lab studies.

Terrestrial ecology: Relative abundance and density.—Relative abundance and density were only briefly discussed by Petranka (1998). At that time, several studies had independently suggested that most of the *P. cinereus* population was below the soil surface on any given day (see also discussion of this topic in Anthony and Pfingsten 2013). Therefore, Petranka (1998) concluded, counts of salamanders on the surface and mark–recapture methods likely underestimate the true population size. Indeed, as part of a predator-removal experiment, Hickerson et al. (2017) removed all surface-active salamanders from under 144 ACOs during 98 visits across 4 y and estimated that this only depressed the salamander population density by 28%. Sources cited by Petranka (1998) estimated salamander density ranged from 0.21 salamanders/m^2 in Pennsylvania to 2.8 salamanders/m^2 in Virginia.

Both Semlitsch et al. (2014) and Grant et al. (2024) summarize previously published density estimates for *P. cinereus*. Both summaries report density estimates ranging from 0.05 to 3.3 salamanders/m^2 (Semlitsch et al. 2014; table 4; Grant et al. 2024: table 1). Grant et al. (2024) additionally present new data from a networked spatial capture–recapture project conducted in 18 study areas across the range of *P. cinereus.* Using these new data, Grant et al. (2024) estimated the range of average densities to be 0.195–3.43 salamanders/m^2, with a network-wide average density of 1.16 salamanders/m^2. In Virginia, additional outlier populations with even higher average densities have been recorded: first, in Shenandoah National Park, Virginia, Jung et al. (2000a) estimated density as high as 18.5 salamanders/m^2 and second, at the southern range edge in urban Richmond, Virginia, Hernández-Pacheco et al. (2019) estimated densities from 2.49 to 6.26 salamanders/m^2 per plot surveyed over 2 yr (Supplemental Material S16; Supplemental Fig. S2, available online; this population is also included in Grant et al. 2024).

More recent research focuses on how salamander abundance is impacted by human activities. These are discussed in more detail in the Conservation Biology and Additional Topics: Management sections to follow, but here we briefly describe the impact of roads, forest–farm edges, and prescribed fire on counts of surface-active salamanders. *Plethodon cinereus* has been observed to occupy forested locations along an urban to rural gradient (Gibbs 1998a). However, salamander counts are reduced near gravel roads, and this is likely due to a reduction in soil moisture near roads (Marsh and Beckman 2004). Dry conditions at forest-farm edges also lead to reduced counts of salamanders in these ecotones (Young and Yahner 2003). An experimental study corroborates these observations, with adults and juveniles found to be more abundant in plots with added moisture and more active in plots with more cover objects (Grover 1998). Increased abundance of cover objects near maintained recreational trails may be responsible for increased salamander counts near trails (Fleming et al. 2011). Prescribed fire did not impact capture rates of *P. cinereus* in Virginia (Keyser et al. 2004).

Seburn and Mallon (2017) highlight some of the challenges of using community science data to detect changes in abundance and occupancy. As a cryptic species, *P. cinereus* may not be well represented in community science data because of its low detection probability and therefore, may appear as if it is declining. When investigating potential declines of *P. cinereus* in Ontario, Canada over a 20-y period, Seburn and Mallon (2017) used natural cover searches and found that 84% of areas designated as unoccupied by community science data were actually occupied. From these findings, they suggest that at least 30 cover objects needed to be searched to attain 50% detection probability. The results of this study parallel other suggestions that accounting for detection is critical for determining the status (e.g., abundance or occupancy) of *P. cinereus* populations (e.g., Sutherland et al. 2016).

Terrestrial ecology: Seasonal activity and dispersal.—Petranka (1998) describes how little we know about the activity of salamanders underground and how these patterns vary geographically. Many of the studies cited by Petranka (1998) indicated that there is a seasonal pattern to vertical movement, with suitable soil moisture levels and temperatures driving movement to the surface during the spring and autumn in most locations (northern in Fig. 2). Petranka (1998) summarizes one study that found *P. cinereus* as deep as 1 m in winter and another study which demonstrated that *P. cinereus* not only relies on the burrows and tunnels made by other fossorial species to retreat underground, but is likely incapable of doing much more than enlarging existing burrows. Recent work by Cáceres-Charneco and Ransom (2010) confirms that *P. cinereus* uses earthworm burrows. Petranka (1998) did not mention any studies on natural dispersal or migration but he did summarize research documenting how *P. cinereus* can return to its original location after a 90-m displacement.

Based on Petranka's (1998) summary, our own field experience with this species throughout its range, and the five recent supporting studies described here, we depict the surface activity phenology of *P. cinereus* in Fig. 2. There are at least three regional phenologies of surface activity that depend on latitude (north vs. south) and elevation (high vs. low). We hypothesize the latitudinal break between the northern and southern phenologies (Fig. 2) is at or near the extent of the Wisconsin ice sheet at the last glacial maximum (LGM; Fig. 1). In support of this hypothesis, Meshaka and Wright (2017) studied a southern Pennsylvania population of *P. cinereus* approximately 150–200 km south of the LGM ice edge and found individuals to have life history traits more similar to southern populations compared to northern ones (e.g., 75.9% of females at that site breed annually). Anthony and Pfingsten (2013: fig. 18-8) present data on the phenology of a single northeastern Ohio population using 6000+ observations collected over 4 yr. Their data closely match the northern phenology we suggest in Fig. 2 (Anthony and Pfingsten 2013). Leclair et al. (2008) examined a population near the northern range edge in Québec, showing a slight spring peak and a strong autumn peak in activity. This population also has a notably delayed life history (see foregoing discussion in Breeding and Courtship; Leclair et al. 2008). Finally, both Becker et al. (2013) and Hernández-Pacheco et al. (2019) have documented the southern phenology of continuous winter activity (Fig. 2) in Cary, North Carolina and Richmond, Virginia, respectively. Several sources and the references cited therein (e.g., Petranka 1998; Anthony and Pfingsten 2013; Stuczka et al. 2016) plus our own field experience suggest that *P. cinereus* is opportunistic about surface activity: If temperature and moisture conditions at the surface permit activity, some salamanders will be active, even in winter or summer. There is much to learn on this topic: We do not know how *P. cinereus* determines surface conditions from underground, what cues prompt vertical movement, or even how deep individuals can or will go during stressful seasons.

There is evidence that daily changes in ambient illumination play a role in cuing nightly emergence from leaf litter or cover object refugia. Wise and Buchanan (2006) summarize two of their previously unpublished field studies that conducted night censuses to determine the relationships between surface activity and ambient light. The first study found that surface activity of *P. cinereus* greatly increased 1–2 h after sunset, and was more strongly related to changes in ambient lighting than changes in temperature. In this study, the total duration of surface activity was positively related to humidity or moisture. The second study focuses more on the potential impacts of artificial night lighting on salamander activity. Wise and Buchanan (2006) describe an experiment that surveyed field transects with artificial light (10^{-2} lux at leaf litter surface) and without artificial light (10^{-4} lux at leaf litter surface). Unlit transects had significantly more active salamanders during the first 1–2 h after dark, but later in the evening there were no significant differences between unlit and lit transects in the abundance of active salamanders. This suggests that increased artificial lighting delayed the onset of surface activity. Wise and Buchanan (2006) note that this delay in nightly emergence time could have several negative downstream effects, including reductions in: total foraging time, overall food intake, growth rates, reproduction, and survival during hibernation.

Additional studies that have examined natural and induced movements via displacement and homing to original locations have given some insight into movement patterns of *P. cinereus*. Seasonal movements of adults up a rocky hillside in autumn and down in spring were reported in New York (Woolbright and Martin 2014). The authors suggest that this movement is in response to increased availability of crevices in rocks uphill, allowing for more activity during winter months. A study using drift fences with pitfall traps found that the abundance of salamanders captured was not influenced by proximity to forest edges or streams, but roads likely acted as a barrier to dispersal (Gibbs 1998b). This is more rigorously supported by Marsh et al. (2005), who found that salamanders displaced across gravel and paved roads have reduced return rates to their original location in comparison to those returning across the same distance within continuous forest habitat. Similarly, small streams also reduce return rates of salamanders after displacement (Marsh et al. 2007; Snyder et al. 2022), and both roads and streams limit gene flow, suggesting these landscape features act as dispersal barriers for *P. cinereus* (Marsh et al. 2007, 2008; see also Hantak et al. 2019).

We still know relatively little about natural dispersal distances of *P. cinereus*. Petranka (1998), Williams et al. (1968), and Radomski et al. (2020) all speculate that *P. cinereus* is capable of moving great distances, since it presumably expanded from southern refugia to its current geographic extent in southern Canada (Fig. 1) during the last 10–15,000 yr after the Wisconsin glacier receded: a distance of at least 1000 km, suggesting dispersal rates are between 67 and 100 m (0.067–0.1 km) per year. Mark–recapture studies (e.g., Marsh et al. 2004, 2005, 2007) and studies of population genetic structure over relatively short distances in continuous forest or in habitat fragments separated by known dispersal barriers (Cabe et al. 2007; Marsh et al. 2007, 2008; Fisher-Reid et al. 2013; Cameron et al. 2019; Hantak et al. 2019) suggest that, although individuals generally do not disperse far, they are capable of longer movements across open fields, roads, or streams to return to familiar territory when displaced (25–55 m in Marsh et al. 2004, 2005, 2007; Snyder et al. 2022) or to colonize new habitat (5–25 m in Marsh et al. 2004). A recent observation increased the maximum distance that a single *P. cinereus* individual is known to have traveled, up to 143 m (Sterrett et al. 2015). Dispersing individuals are likely "floaters"—defined as adults without territories who readily colonize available habitat (Mathis 1991). Marsh et al. (2004) found that artificial habitat islands installed on an abandoned golf course (i.e., watered areas covered with shade cloth, supplemented with ACOs and leaf litter) were colonized within 1 yr of installation by young adult (based on SVL) *P. cinereus* in Virginia. Additionally, Snyder et al. (2022) found that displaced adults returned to their original location with greater frequency than did juvenile individuals.

The low lifetime dispersal distances of individuals likely helps *P. cinereus* persist in small forest fragments where other amphibians with greater dispersal distances have been extirpated (Gibbs 1998a). It is unclear if *P. cinereus* engages in sex-biased dispersal. Two studies, both conducted at MLBS in Virginia had conflicting results. Cabe et al. (2007) found no evidence of sex-biased dispersal using population genetic assignment indices. Liebgold et al. (2011) found evidence of females being more philopatric than males, confirmed through both lack of genetic structure at short distances in males and greater overall dispersal distances of males compared to females. A more recent study at a Maryland population using similar methods to Liebgold et al. (2011) did not find any evidence for sex-biased dispersal (Grant and Liebgold 2017). In an experiment exploring the movement behavior of individuals in unfamiliar environments, Cosentino and Droney (2016) found that individual movement behavior is highly repeatable and varies by forest age. In unfamiliar environments, individuals from older forest stands moved more than those from younger stands, and edge vs interior individuals within a stand did not show any movement differences. Individuals showed consistent movement patterns across time, suggesting movement personalities and heritable genetic variation for movement behavior (Cosentino and Droney 2016).

Our review of the literature on seasonal activity and dispersal shows that we now have a well-supported understanding of at least three surface-activity phenologies throughout the range of *P. cinereus* (Fig. 2). Awareness of the local phenology is important for appropriate scheduling of field sampling and experiments. Further studies show that *P. cinereus* can move substantial distances across the forest floor, but unless deliberately displaced, it seems that the majority of individuals do not move much within and between seasons (see also the Terrestrial Ecology: Territories and Home Range Size section). We do not know what abiotic cues drive movement—either vertically to/from underground and the soil surface, or horizontally during the surface-active seasons—although one study found changes in ambient light to be a potential cue for horizontal movement (Wise and Buchanan 2006). Methods discussed previously and in the following sections, such as tracking individuals with PIT tags (e.g., Sterrett et al. 2022) or fluorescent powder trails (e.g., Orlofske et al. 2009), may prove useful to investigate the abiotic cues and movement patterns more generally. Additional laboratory experiments following the methodological example of Cosentino and Droney (2016) could also further address these topics.

Terrestrial ecology: Territories and home range size.—Petranka (1998) devoted several pages to summarizing research on territoriality in both sexes and age classes of *P. cinereus*, noting that *P. cinereus* is a model organism for studying the ecology and evolution of territorial behaviors. Much of the work he cites, and that which has been done since, has previously been thoroughly reviewed in Jaeger et al. (2016). To avoid duplication of effort, we focus this section of our review on recent studies that were either (1) independent of the R. G. Jaeger research program, (2) published after Jaeger et al. (2016), or (3) from non-MLBS locations. Reference information for all studies on this topic returned by our literature search are included in Supplemental Material S12 (Supplemental Data S11). We encourage those interested in territoriality, aggression, and related topics (e.g., chemical communication) in *P. cinereus*, to read Jaeger et al. (2016).

Briefly, there is ample evidence that both males and females defend territory, and that territorial behaviors (e.g., aggression, scent marking, avoidance of residents) vary both seasonally and by local abiotic (temperature, moisture) and biotic (food availability) conditions (Petranka 1998; Jaeger et al. 2016). At the time Petranka (1998) was published, estimates of home range sizes varied by study location. The average home range area in a Virginia population (MLBS) was estimated to be 0.16–0.33 m^2 with no significant differences between males, females, or juveniles (Mathis 1991), whereas the average home range area in a Michigan population was estimated to be 13 m^2 for males and juveniles and 24 m^2 for females (Kleeberger and Werner 1982). The latter study also reported daily movement of surface-active individuals (average = 0.43 m), with increases reported during and after precipitation events, and found that displaced individuals home at distances of 30–90 m (with declining success at longer distances; Kleeberger and Werner 1982). Petranka (1998) notes that the reason *P. cinereus* holds territories is unknown, but it is hypothesized that territories may be used to defend food, defend or attract mates, and/or defend suitable microhabitats. Petranka (1998) also acknowledges that a large proportion of individuals are floaters that do not hold territories (Mathis 1991; see also the Terrestrial Ecology: Seasonal Activity and Dispersal section). Larger individuals can successfully defend their territories from smaller individuals, and males who hold higher-quality territories are more likely to attract females. To mark their territories, *P. cinereus* use both fecal pellets and glandular secretions, and they are known to threaten and attack each other during territorial disputes (Petranka 1998; Jaeger et al. 2016). Interestingly, adult males are less aggressive to juveniles, and they are more tolerant of familiar intruders, which suggests the potential for kin recognition and/or a "dear enemy effect," in which individuals tolerate near neighbors to reduce energy expended by acts of aggression (Petranka 1998; Jaeger et al. 2016).

Maerz and Madison (2000) offer a field-based study of territorial behavior from three non-Virginia populations, and specifically explore the relationship between territorial behavior and food availability. At a site in Pennsylvania with lower food density (as determined by total volume of prey in salamander stomachs), males and females were more territorial, exhibiting higher site fidelity, lower same-sex home area overlap, and body size and foraging success were positively correlated. At two sites in New York with higher food density there was lower site fidelity and more same-sex cohabitation of cover among females. Males in the high food environment still defended spaces, likely to attract mates (Maerz and Madison 2000).

Like many traits, there is geographic variation in territorial behavior; however, the scope and general patterns of that geographic variation are understudied (Jaeger et al. 2016). In the laboratory, Wise and Jaeger (2016) explored geographic variation in male aggression in *P. cinereus* using salamanders from eight populations from the center and southern parts of the range (Indiana, Maryland, Virginia, and West Virginia). They deliberately selected populations that were previously associated with two documented allozyme clades (Hass 1985), which now likely belong to at least three mitochondrial clades (see discussion in Radomski et al. 2020). Wise and Jaeger (2016) found significant variation in aggressive and submissive behaviors among males from different genetic groups and in individuals from different elevations. Individuals of one genetic group were more submissive than the other genetic group. The variation in territorial behaviors due to elevation was more complex, showing a significant negative correlation between submissive behavior and elevation, and a significant resident advantage (i.e., intruders are more submissive) that was independent of elevation. Anthony and Pfingsten (2013: table 18-3) summarize the variation in aggressive behavior in laboratory experiments across several Ohio populations as compared to one New York and one MLBS population. Interestingly, Ohio (central to the range) shows some of the longest average bouts of aggressive posture, whereas results from New York and MLBS are both shorter than Ohio and very similar to each other.

There is ample evidence from field studies that supports widespread expression of territorial behavior in *P. cinereus*. For example, field studies from across the geographic range show positive relationships between cover-object size and SVL (e.g., Moore et al. 2001; Hickerson et al. 2004); majority singleton observations under cover objects over opposite or same-sex pairs (e.g., Anthony et al. 2008); site fidelity (e.g., Gillette 2003; Reiter et al. 2014; see below); homing behavior to cover objects (e.g., Marsh et al. 2005; Ousterhout and Liebgold 2010; Martin and Hantak 2011); and invasion of experimentally vacated cover objects by smaller individuals (e.g., Marsh et al. 2004; Anthony and Pfingsten 2013). All of these studies are discussed in more detail in other sections of this review.

In addition to the comparisons of Ohio territorial behavior to New York and MLBS by Anthony and Pfingsten (2013), there are a handful of observations that suggest that expression of territorial behaviors in *P. cinereus* may be reduced in northern populations. One study (Quinn and Graves 1999b) and one observation (Placyk et al. 2000), both from the upper peninsula of Michigan, have reported large aggregations of *P. cinereus* under a single cover object throughout the active season (May through September). The observation by Placyk et al. (2000) is difficult to interpret in the context of territoriality, because sizes and sexes of the aggregating individuals are not reported. In Ontario, Rollinson and Hackett (2015), found male salamanders to be moderately aggressive in laboratory trials, but contrary to predictions from territoriality theory, resident salamanders were not more aggressive than intruders. However, intruding salamanders did exhibit more escape behavior than did residents, as expected from a territorial species. In the field, the authors did not observe any aggregations under cover objects and found a random spatial distribution of adults in 16 out of 17 visits between May and July, suggesting weak to no territoriality (Rollinson and Hackett 2015). Rollinson and Hackett (2015) hypothesize that the reduction in territoriality might be caused by less restricted daily foraging activity in northern populations compared to southern populations; however, this hypothesis has not yet been explicitly tested.

One of us (K.L. Grayson) has seen multiple large aggregations ($n \geq 7$) of adult *P. cinereus* (>34 mm SVL) under a single coverboard at a low-elevation southern site (Richmond, Virginia; Supplemental Material S16; Supplemental Fig. S2). Aggregations are common throughout the active season (October to March; Fig. 2). This location also has some of the highest reported densities for this species (Hernández-Pacheco et al. 2019). Thus, it is not clear that latitude alone explains why Michigan and Ontario salamanders appear to be less territorial than Ohio and high-elevation Virginia salamanders. As Wise and Jaeger (2016) found, there is probably a genetic component to territoriality: the less territorial populations observed in Michigan, Ontario, and Richmond, Virginia, are likely all members of the Northern clade (Radomski et al. 2020). Additional work in both the field and laboratory is needed to both document and understand the causes of variation in expression of territorial behavior across the range of *P. cinereus*.

Chemical communication is thought to be very important in territory establishment and retention, identification of individuals, and even determination of potential predation risk (see the Predators and Defense section). In Virginia, Simons et al. (1999) identified and described several mucous and serous glands in both the shoulder and postcloacal region of *P. cinereus*. Importantly, the authors compared the glands in the two regions, hypothesizing that the postcloacal region would show differences if those glands were important for scent marking and communication, as earlier studies had suggested. The shoulder and postcloacal glands had notable differences in both morphology and physiological status over time (full, empty, renewing) in response to individuals being placed on novel substrates. Simons et al. (1999) present evidence to support the hypothesis that the shoulder glands show morphology and physiological status consistent with the proposed ancestral function of serous glands in amphibians (predator defense), whereas the postcloacal glands have morphology and physiological status consistent with territorial scent marking. Simons et al. (1999) was followed by Hecker et al. (2003) in New York, who focused on the postcloacal mucous and two types of serous glands (S1 and S2). Hecker et al. (2003) hypothesized that the S1 serous glands are for scent marking, and the S2 serous glands are used in nutrient storage and defense.

Duhaime-Ross et al. (2013) tested both visual and chemical communication in adults and juveniles from Ontario, and found complex interactions between social context, cue type, and age class, suggesting multimodal communication is common. Wise and Buchanan (2006) summarize a previously unpublished study by Buchanan that measures territorial behavior under different lighting conditions: moonlight (10^{-2} lux), starlight (10^{-4} lux), and total darkness (10^{-5} lux). Buchanan found that residents increased their use of visual displays with increasing ambient light (Wise and Buchanan 2006). Dawley et al. (2000, 2006) studied the cellular physiology of the olfactory and vomeronasal systems across seasons in a Pennsylvania population. Both studies found an increase of vomeronasal cellular proliferation in May and June, and Dawley et al. (2006) found a subsequent increase of vomeronasal apoptotic activity in July, suggesting the importance of these cells during the nonbreeding early summer months, when territorial behavior is believed to be strongest (Jaeger et al. 2016). Additional studies focused specifically on *P. cinereus* interpreting and responding to chemical cues from predators are summarized in the Predators and Defense: Defensive Behaviors section.

Site fidelity has been explored in Michigan, Ohio, and Virginia. In Michigan, Placyk and Graves (2001b) found the same individual under the same cover object 1 yr apart. In Ohio, Martin and Hantak (2011) document a low level of homing behavior (~16% return, similar to reports in Jaeger et al. 2016) in both striped and erythristic individuals displaced 5 m from their original cover object. Larger individuals are more successful at homing in Virginia (Ousterhout and Liebgold 2010). This study also found low levels of between-year movements (0.85–1.22 m/yr), suggesting high site fidelity (Ousterhout and Liebgold 2010). Gillette (2003) found year-to-year site fidelity in Virginia, as did Reiter et al. (2014) in Ohio. Reiter et al. (2014) found individual residency (number of days between first and last capture under the same cover object) to range from 10 to 1281 d, with 46 individuals showing residencies longer than 700 d (four active seasons). To this we add that we have all seen some level of site fidelity across both seasons and years in our long-term research plots in Massachusetts, Virginia, Michigan, Pennsylvania, and New Jersey (M. C. Fisher-Reid, K. L. Grayson, L. S. Mead, T. H. J. Matlaga, and S. C. Sterrett, respectively, personal observations), but we have not yet quantified these patterns. Anecdotally, we expect formal analyses of our data will yield patterns similar to Reiter et al. (2014).

Recently, with the introduction of visual implant elastomer (VIE) marking methods (Heemeyer et al. 2007), studies have explored field-based space use in *P. cinereus*. In Virginia, Schieltz et al. (2010) found that adults often use more than one cover object, regardless of spacing between cover objects, with males never occupying adjacent cover objects. Muñoz et al. (2016b) used spatial capture–recapture (SCR) to understand space use, dispersal patterns, and density in Pennsylvania. This study found mean densities of 0.423–0.473 salamanders/m^2. Contrary to what is reported in Petranka (1998), Muñoz et al. (2016b) found males to use larger areas than females, regardless of season. Dispersal distances between seasons averaged <1 m, again suggesting high levels of site fidelity (Muñoz et al. 2016b). As described above, young adult floaters will quickly take over new habitat when it becomes available (Marsh et al. 2004; Anthony and Pfingsten 2013).

In Ohio, two studies explored territoriality differences between color morphs, and a third studied differences between sympatric *P. cinereus* and *P. electromorphus*. Reiter et al. (2014) found that striped morphs were more aggressive and held on to their territories for longer periods of time than unstriped morph, with both laboratory and field support for these patterns. A follow-up field study by Anthony et al. (2017) found that striped morph territories had 32% higher quantity of prey than unstriped morph territories. Other work in this population suggests that these differences in territories and territorial behavior between color morphs may play a role in mate choice (e.g., Anthony et al. 2008; Acord et al. 2013). Deitloff et al. (2009) explored the territorial behavior of sympatric and allopatric *P. cinereus* and *P. electromorphus* in response to heterospecific intruders in Ohio. Residents did not change behavior based on the source of their intruder; however, residents from sympatric populations of both species showed increased aggression toward heterospecific intruders than residents from allopatric populations.

In reviewing the territoriality literature on this species, it is clear that much of what we know stems from a small portion of the very large geographic range, 60% of the initial batch of studies we categorized into this topic are from MLBS or other Virginia locations ($n = 21/35$; Supplemental Material S12; Supplemental Data S11, Supplemental Material S15; Supplemental Data S14). Future work that tests previously documented patterns at other locations is imperative to first, fully understand the social behavior of *P. cinereus* across its range and second, tease apart abiotic and biotic factors that influence the expression of social behavior. We also have much to learn about the details of chemical communication, from the compounds and glands involved to the types of information *P. cinereus* regularly communicates about and with whom, and the geographic consistency of these patterns. Both Anthony and Pfingsten (2013) and Jaeger et al. (2016) provide excellent starting points for what we do know about chemical communication in *P. cinereus*, especially as it relates to territoriality, kinship, and mate choice.

Terrestrial ecology: Miscellaneous experimental methods and behavior.— In the course of our review, we found several studies that we initially classified as belonging to the primary category "other," with further comments that these studies related to physiology, behavior, other methods, or sensory ecology. Those studies that remained difficult to place in other sections of our review are summarized here. Generally, these sources focus on experimental methods not directly related to field sampling salamanders and behavior that is not directly related to breeding and courtship, foraging, territoriality (all discussed above), or antipredator tactics (discussed in the next section).

Three studies documented specific methods or approaches that may be useful for those designing experiments with *P. cinereus*. First, using salamanders from a Michigan population, Placyk and Graves (2001c) tested the ability of *P. cinereus* to detect and respond to different wavelengths of light. Because the majority of *P. cinereus* behavior is nocturnal, the authors hoped to find a wavelength under which humans could observe salamanders behaving, but which could not be perceived by the salamander, to better simulate night conditions in experiments. When presented with a visual stimulus under broad spectrum fluorescent (400–700 nm) or black (4–400 nm) light, salamanders spent significantly less time looking at the stimulus under black light. Placyk and Graves (2001c) therefore suggest black light conditions will effectively simulate night conditions for future experiments.

Second, Wise and Buchanan (2006) reviewed the literature on salamander responses to artificial light. As part of this review, they criticize the experimental design of Placyk and Graves (2001c) and argue the results are difficult to interpret because (1) light treatment acclimation times that were too short, (2) bright light treatments had unrealistically high illuminations, and (3) there was missing information on the illumination and spectral properties of all treatments. The critiques of Placyk and Graves (2001c) by Wise and Buchanan (2006) apply to many of the studies the latter reviewed, and thus the authors make methodological suggestions for those wishing to conduct experiments on the impacts of light on salamander behavior: (1) use realistic, and thus ecologically relevant, artificial light levels that would be experienced by wild populations; (2) ensure full reporting of the intensity and spectral properties of their treatments. Wise and Buchanan (2006) conclude their chapter by noting that the physiological and behavioral responses of salamanders to artificial night lighting is understudied, particularly on longer time scales in both the field and the lab.

Third, using salamanders from MLBS, Novarro et al. (2017) expand upon earlier work by Lowe (2004) to determine what concentration of tricaine methanesulfonate (MS-222) works best for short-term anesthesia of *P. cinereus*. Lowe (2004) had found that, of five plethodontids tested, *P. cinereus* had the longest times to anesthetization, often 2–3× longer than the next longest, *P. elongatus*, and suggested higher concentrations might be needed for efficient anesthetization of *P. cinereus*. Novarro et al. (2017) determined the optimal MS-222 concentrations for rapid anesthetization (i.e., induction) time and a range of initial and full recovery times. In addition to publishing details of these concentrations and timings in their Table 1, Novarro et al. (2017) also explored the relationship between several morphological traits and induction time. Both tail length and mass significantly and positively affected induction time and should be factored into experiments requiring short-term anesthetization of *P. cinereus*.

Other studies that were difficult to categorize focused on the physiology of *P. cinereus*. Davis et al. (2009a) found that the roundness of red-blood cells is strongly positively correlated with body condition and body size. The authors suggest that taking blood samples might be a useful nondestructive method of tracking population health over time (Davis et al. 2009a). Fluorescent powder pigment has been used with success to track amphibian, reptile, and small mammal movement over short durations (e.g., Lemen and Freeman 1985; Graeter et al. 2008; Roberts and Liebgold 2008). Orlofske et al. (2009) was the first study to test explicitly how the fluorescent powders affect respiration and metabolism in a lungless amphibian using *P. cinereus*. They found that there was no impact on either oxygen consumption or standard metabolic rate (SMR). Instead, it appeared that the stress of being handled was greater than the stress of being temporarily covered in powder (Orlofske et al. 2009). Homyack et al. (2010a) found that SMR increased with both body mass and temperature. Novarro et al. (2018) complements this result by assaying corticosterone (CORT) of salamanders living at different temperatures. Salamanders housed at 25°C had higher CORT, levels indicating higher levels of stress, compared to those housed at 15°C. Additionally, salamanders housed at the warmer temperature ate more food than salamanders housed at the cooler temperature (Novarro et al. 2018). Takahashi and Pauley (2010) observed altitudinal differences in resource allocation. Salamanders from higher elevations (i.e., cooler climates) allocated more energy to storage than growth or reproduction compared to salamanders from lower elevations. Biddle et al. (2017) looked at factors that impact growth, using mark–recapture methods to track individuals over multiple years and seasons. Color morph had no effect on growth, but they did find an effect based on both initial size and environmental fluctuations. Small juvenile salamanders who experienced milder winters showed the greatest growth (Biddle et al. 2017).

From a purely behavioral perspective, at the end of Jaeger et al. (2016), the authors note the new work being done on salamander cognition and cognitive ecology. One of the first studies to explore this topic is Uller et al. (2003), which documents rudimentary numerical discrimination in *P. cinereus*. In choice trials containing one, two, three, four, or six food items, salamanders regularly opted for the larger quantity of food in one vs two and two vs three forced-choice tests, but could not distinguish between three vs four or four vs six. Kight et al. (2005) explored learning in *P. cinereus* using classical conditioning. Individuals from New Jersey were successfully conditioned to low-frequency sound and vibration, but not to visual or chemical stimuli. As Jaeger et al. (2016) note, cognition and cognitive ecology is an area of *P. cinereus* research that is particularly wide open for new questions and experiments.

The last two behavioral studies that were difficult to categorize both explored the social context of juvenile salamander behavior. Liebgold and Cabe (2008) explored if juvenile growth rates were affected by familiarity or relatedness of the adults nearby at MLBS. The results varied by year: in the first year, familiarity had a strong effect on mass and size, but not the following year. The authors hypothesize that temperatures may have played a role in the different familiarity results, as the first year was significantly cooler than the second year. Additionally, there was no evidence that familiarity or spatial proximity were indicative of relatedness, or that relatedness to nearby adults affected juvenile growth rates (Liebgold and Cabe 2008). Liebgold (2014) followed up on this by testing the effect of the presence of territorial adults on juvenile behavior using salamanders from Michigan (presumably nonterritorial) and Virginia (presumably territorial, see the Terrestrial Ecology: Territories and Home Range Size section). Michigan juveniles were more strongly affected by being housed with territorial adults. In juvenile–juvenile interactions, Michigan juveniles showed increased investigatory and escape behaviors compared to juveniles housed with nonterritorial adults.

In sum, much like in 1998, terrestrial ecology of *P. cinereus* remains a large and prominent focus of recent research. In nearly all instances, the topics summarized here are only just scratching the surface of our understanding of the ecology of this species, and offer many excellent starting points of background knowledge, useful methodology, and testable hypotheses for continued research to resolve some of the more challenging or elusive questions. Important to future study of terrestrial ecology topics will be expansion of research programs to investigate geographic and phylogeographic variation in terrestrial ecology, and experiments to determine the relative roles of phenotypic plasticity and local adaptation.

Predators and defense: Introduction.— Petranka's (1998) section on predators and defense in *P. cinereus* was brief, and there has been much work exploring these topics since. Petranka (1998) focused on describing general predators of *P. cinereus* (i.e., birds, snakes, spiders), with an emphasis on snakes, and summarized the experimental studies that have focused primarily on snake predators (Garter Snakes, *Thamnophis* spp., and Ringneck Snakes, *Diadophis punctatus*). Petranka (1998) describes the results of one study that suggests that Ringneck Snakes may be able to distinguish the scent of *P. cinereus* from nonedible prey and even distinguish particular parts of the body (i.e., tail vs. body; Lancaster and Wise 1996). In response to a predator, *P. cinereus* individuals generally change their behavior (i.e., staying motionless or coiling) or autotomize their tails (Petranka 1998). A measurable proportion of *P. cinereus* populations appear to have broken or regenerating tails, although it is not clear if this indicates predation rates, rates of intraspecific conflict, or, most likely, some combination of both (Jaeger et al. 2016). Anthony and Pfingsten (2013) concur in their review that crypsis in the form of immobility and tail autotomy are both primary defense strategies but add that noxious skin secretions (e.g., Brodie et al. 1979) may be another primary defensive trait for *P. cinereus*. In the following sections, we first discuss new knowledge on the predators and parasites of *P. cinereus*. Next, we discuss a handful of studies which have explored differential predation of color phenotypes of *P. cinereus*. Finally, we discuss the many studies which have explored *P. cinereus* defensive behaviors. There are many studies relating to skin and gut microbial communities, particularly how they are involved in defense against the amphibian fungal pathogen *Bd*. These have been summarized in their own subsection, Additional Topics: Microbiota.

Predators and defense: Predators and parasites.— Since Petranka (1998), a small number of studies have documented unusual predators for *P. cinereus*. Jung et al. (2000b) observed a Rove Beetle (*Platydracus vidatus*) preying upon live *P. cinereus* under a cover board in Maryland. The Creek Chub (*Semotilus atromaculatus*) was observed preying on *P. cinereus*, likely after the salamander was washed into the creek during a flash flood (Sharp et al. 2005). As noted earlier, Hughes et al. (1999) found two salamanders dead inside Pitcher Plants (*Sarracenia purpurea*) in bogs in West Virginia and Pennsylvania. These observations are incidental, but there are likely many species that find *P. cinereus* palatable, particularly woodland snakes and ground-foraging birds. Anthony and Pfingsten (2013) have a detailed summary of known instances of specific predators consuming *P. cinereus*. Most studies of antipredator responses use chemical cues from *T. sirtalis* fed a diet of *P. cinereus*, other salamander species, or earthworms. These are summarized in the next two subsections.

There are conflicting reports as to whether Northern Dusky Salamanders (*D. fuscus*) eat *P. cinereus*. Jaeger et al. (1998) found evidence to suggest that *D. fuscus* does eat *P. cinereus*, and that *P. cinereus* actively avoids encounters with *D. fuscus*. However, a follow up study by Ransom and Jaeger (2006) found no evidence of either predation or tail loss caused by *D. fuscus*, although *P. cinereus* still seemed to avoid *D. fuscus* in mesocosms. Other large salamanders likely to prey on *P. cinereus* where their ranges overlap include *D. quadrimaculatus*, *Gyrinophilus porphyriticus*, and *Pseudotriton ruber* (Petranka 1998).

Anthony and Pfingsten (2013) also reference and summarize Casper's (2005) summary of parasites reported to infect *P. cinereus*, and indeed, there has been more work done on the parasites of *P. cinereus* since Petranka (1998). Muzzall et al. (1997) and Bolek and Coggins (1998) document several species of trematode, nematode, and protozoan parasites on *P. cinereus*. Most salamanders sampled in Muzzall et al. (1997) hosted at least one parasite, and a trematode (*Brachycoelium* spp.) was the most common parasite in *P. cinereus* from New Hampshire. In Wisconsin, Bolek and Coggins (1998) found lower overall rates of infection than Muzzall et al. (1997), but a nematode species (*Rhabdias* spp.) was the most common parasite on *P. cinereus*. In Michigan, Gillilland and Muzzall (2002) again found high rates of helminth infection, but no evidence that these parasites caused limb deformities. Most studies that have tested wild populations have found low prevalence of the amphibian pathogens *Ranavirus* or *Bd* on the skin of *P. cinereus* (e.g., Harris et al. 2009; Gratwicke et al. 2011; Wunder et al. 2012; Muletz et al. 2012, 2014; Augustine and Neff 2016), except Jongsma et al. (2019), which found much higher than typical (but still low overall) rates of *Bd* infection in *P. cinereus* from New Brunswick, Canada.

Rickettsial intracellular pathogens may also influence *P. cinereus* ecology and health. A rickettsial intraerythrocytic pathogen of the family Anaplasmatacea was found in 16.7% of 102 *P. cinereus* individuals tested from Pennsylvania, New York, and Virginia (Davis et al. 2009b). Infected salamanders had significantly larger snout–vent length and more circulating white blood cells than uninfected salamanders. Males in these populations were more likely to be infected than females. The authors hypothesize that the trombiculid mite, *Hannemania dunni*, a common amphibian ectoparasite, is the likely vector of the rickettsial pathogen, as these mites are the only ectoparasite which has been observed parasitizing plethodontid salamanders (Davis et al. 2009b). The male bias in infections also suggests a trombiculid mite, as they were previously documented parasitizing plethodontid salamanders differentially by sex (Anthony et al. 1994).

A follow-up study by Davis and Cecala (2010) focused on *Desmognathus ocoee* and found an obligate intracellular *Rickettsia* spp. at a much higher prevalence (35%) in *D. ocoee* compared to previous data on *P. cinereus* (8%–17%). Morphologically, the parasite infecting *D. ocoee* appeared to be a different type of *Rickettsia* spp. than the one found in *P. cinereus* by Davis et al. (2009b). The difference in average prevalence between *Desmognathus* spp. (30%) and *Plethodon* spp. (8%; see Table 2 in Davis and Cecala 2010) was significant, and the authors suggest that this difference is probably due to the difference in the habitat use of the two genera. *Plethodon* are completely terrestrial, whereas *Desmognathus* are semiaquatic; therefore these species are likely exposed to and contract different species of *Rickettsia*, which have different vectors and life cycles (Davis and Cecala 2010).

Predators and defense: Differential predation risk by color.— Predation risk for *P. cinereus* may be influenced by color phenotype, although patterns across the range of *P. cinereus* are complex and variable. There is some evidence that the color morphs respond differently to predators. In Ohio, Venesky and Anthony (2007) found that striped salamanders spend more time in the "all-trunk-raised" defensive posture in the presence of neonate *T. sirtalis* than unstriped salamanders, and unstriped salamanders were more mobile than striped salamanders. A concurrent look at museum specimens showed that unstriped morphs more frequently showed evidence of tail autotomy than striped morphs (Venesky and Anthony 2007). These differences in behavior and tail autotomy suggest that the two morphs experience different rates of predation, with the authors hypothesizing that unstriped morphs experience greater predation by *T. sirtalis* (Venesky and Anthony 2007). After simulated predation (i.e., a tail clip), Otaibi et al. (2017) found that the autotomized tails of striped morphs move longer and faster than those of unstriped morphs.

Although differential predation by color is well documented, which morph gets predated on more often seems to depend on the population and the predator (see additional discussion in the foregoing Systematics and Geographic Variation section). In the range of polymorphic *P. ventralis* in Tennessee, Fitzpatrick et al. (2009) found that the rare morph was attacked less than the common morph, arguing for negative frequency-dependent selection on color phenotype. This was further supported in a Massachusetts population of *P. cinereus* by Kraemer et al. (2016; see Systematics and Geographic Variation section). In Maryland, Grant et al. (2018) found positive frequency-dependent selection to favor the more common unstriped morph. In this population, the rarer striped morph individuals were attacked more often by avian predators and had lower survival rates over 3 yr compared to the more common unstriped morphs. However, there was no observed difference in survival between color phenotypes when mammalian predators were present (Grant et al. 2018). In Pennsylvania, Davis and Milanovich (2010) observed higher levels of hematological stress markers in unstriped individuals compared to striped, which may be explained by unstriped morphs being exposed to predator attacks more often. In Ohio, Hantak and Kuchta (2018) found that the striped morph had overall better camouflage, based on reflectance measurements taken in the field, but there was variation in camouflage by season, population, and body region.

Finally, there has been some work exploring the potential Batesian mimicry of the red eft stage of the Eastern Red-spotted Newt (*Notophthalmus viridescens*) by erythristic *P. cinereus* (Fig. 1C; Kraemer and Adams 2014; Kraemer et al. 2015a,b). In Pennsylvania, high frequencies of the erythristic morph (range = 21%–43.3%) have been found in populations that are syntopic with the eft stage of *N. viridescens* (Cassell and Jones 2005), supporting the possibility of selection for Batesian mimicry. Kraemer et al. (2015a) tested for four general patterns expected if a Batesian mimicry co-evolutionary dynamic existed between *N. viridescens* and erythristic *P. cinereus.* All four of these were supported, and additional studies by Kraemer and colleagues investigated specific details of the mimicry system. Kraemer and Adams (2014) suggest that mimicry by erythristic *P. cinereus* may be due to differences in color, not brightness. Using a visual model of predator spectral sensitivities and of the colors of newts, striped, and erythristic *P. cinereus*, Kraemer and Adams (2014) found that only birds could possibly discriminate between newts and striped *P. cinereus* based upon color, not snakes or mammals. Importantly, the visual model suggested that birds would not be able to differentiate between newts and erythristic morphs, suggesting bird predation would be the primary source of selection in a Batesian mimicry scenario. Kraemer et al. (2015b) found that there was no relationship between the toxicity of the local *N. viridescens* population and the frequency or presence of erythristic *P. cinereus*.

Predators and defense: Defensive behaviors.— A number of predator-related cues, both simulated and natural, have been documented to alter behavior in *P. cinereus*, and presumably reduce the frequency of predation in nature. In Michigan, Mathis and Lancaster (1998) demonstrated that exposure to water that previously held stressed conspecifics led to *P. cinereus* spending more time trying to escape the study chamber relative to individuals exposed to control water. Another Michigan study followed up on this by showing that *P. cinereus* avoided the skin secretions of stressed conspecifics for up to 2 mins after the alarm pheromone had been collected (Graves and Quinn 2000). Sullivan et al. (2003) found that *P. cinereus* from New York avoid chemical cues from injured salamanders (both conspecific and heterospecific), but do not avoid chemical cues from noninjured salamanders. Earthworms share common vertebrate predators with salamanders (woodland snakes and birds), and thus could be a source of information on general presence of predators; however, salamanders did not respond to chemical cues from either injured or noninjured earthworms (Sullivan et al. 2003). More recently, also in New York, Sullivan and Jensen (2013) found that after exposure to different concentrations of damage-released conspecific cues, *P. cinereus* significantly decreased their activity compared to a control, but did not discriminate between the differing concentrations of the cue. After simulated predation by tail clips, Roberts and Liebgold (2008) found that individuals climbed higher than those without simulated predation in the field, especially male individuals.

Most defensive behaviors in *P. cinereus* have been induced using Garter Snake (*Thamnophis* spp.) chemical cues (Petranka 1998; Jaeger et al. 2016). Murray and Jenkins (1999) tested how *P. cinereus* responded to cues from *T. sirtalis* fed different diets in the lab. Using salamanders from Massachusetts, they showed that salamanders avoided the chemical cues of *T. sirtalis* compared to a control, regardless of what prey (*P. cinereus* or earthworms) the snakes had been fed prior to collecting the cue; however, they avoided the *P. cinereus*–fed snake cues more strongly than the earthworm-fed snake cues. Using salamanders from New York, Madison et al. (1999b) found the avoidance behavior of *P. cinereus* in response to chemical cues from *T. sirtalis* to be quite complex. Salamanders generally avoided substrates that smelled like *T. sirtalis*; however, their response varied by what the snake had eaten (conspecifics, earthworms, or nothing) and the time of day (night, day). During the day, when *T. sirtalis* is more active, salamanders avoided snake-scented substrates in all diet treatments. At night, when *T. sirtalis* are less active, salamanders only avoided the snake-scented substrates of those snakes who were fed conspecifics. The impact of time of day was not due to ambient lighting, suggesting circadian regulation is involved, in addition to detecting predator cues that are further modulated by predator diet (Madison et al. 1999b).

Studies that examine salamander responses to Common Garter Snake cues have mostly been done using *P. cinereus* individuals from upstate New York. Following up on Madison et al. (1999b), Madison et al. (2002), found similarly complex interactions between the time of day, and the combination of cues from snakes fed different diets and stressed or undisturbed conspecifics. Maerz et al. (2001) found that foraging activity decreased with exposure to chemical cues from *T. sirtalis*. Sullivan et al. (2002) found that *P. cinereus* hid out in refugia when exposed to chemical cues from *T. sirtalis* fed *P. cinereus* in both the lab and field; however, time spent in the refugia was significantly shorter in the field than in the lab. This study also speculated that presence of other individual salamanders under a cover object may provide additional protection by keeping salamanders under cover objects when predatory cues are present (Sullivan et al. 2002). A follow-up study supports this speculation by showing that *P. cinereus* avoided chemical cues from Common Garter Snakes fed *Eurycea bislineata* (Sullivan et al. 2004). The authors suggest that closely related prey species have similar antipredator behaviors and thus *P. cinereus* can avoid the cues of predators who have recently eaten either conspecifics or closely related species (Sullivan et al. 2004). Sullivan et al. (2005) further describe how the ability of *P. cinereus* to avoid chemical cues of predators is dependent upon both genetic and ecological relatedness of the prey which was consumed.

As noted by Petranka (1998) and in multiple studies already discussed, *P. cinereus* are known to autotomize their tail in the presence of a threat, and since then, researchers have learned more about the frequency, timing, and effects of this behavior. Wise and Jaeger (1998) found that in territorial contexts, a salamander's personal tail loss did not have a large influence on either a resident or intruder's behavior, but they are both more aggressive when facing an opponent without a tail. Meche and Jaeger (2002; see Breeding and Courtship section) found that males did not distinguish between tailed or tailless females in the lab; however, in the field, they found males associated with tailless females more often. Meche and Jaeger (2002) offer two hypotheses to explain this result (after rejecting male preference based on their lab results): that females without tails prefer to associate with males, or that male aggression from the courtship process itself results in lost tails for females.

Yurewicz and Wilbur (2004) found that tail loss is energetically costly to females; those with lost or regenerating tails made fewer ova. Meshaka and Wright (2017) found that males and juveniles had a higher incidence of broken or regrown tails than females in a collection of museum specimens from south central Pennsylvania. Given that Madison et al. (1999a) documented the importance of having a tail for proper clutch suspension, it is likely that females are under stronger selection to retain their tails than either males or juveniles. This could mean that they are more behaviorally cautious, avoid risky situations, or are less likely to autotomize their tails than males or juveniles. As noted previously, Otaibi et al. (2017) found that the autotomized tails of striped morphs move longer and faster than those of unstriped morphs, suggesting striped morph tails may be more effective at distracting predators than unstriped morphs. Hessel et al. (2017) found no significant difference in jumping or mobility between individuals with and without tails.

Although the sources cited above indicate regular investigations of tail autotomy, there has been very little study on tail regeneration in *P. cinereus* (e.g., timing, physiological mechanisms, role of external factors on regrowth). Wise et al. (2022) tested the impacts of different levels of artificial light at night (ALAN) on tail regeneration, and found a complex, nonmonotonic pattern. Using four light treatments (10^{-4}, 10^{-2}, 1, and 100 lux), they found that tail regeneration was significantly faster for salamanders exposed to 10^{-4} and 1 lux treatments compared to the 10^{-2} and 100 lux treatments. These authors also explored the potential interaction of differences in prey consumption under different light treatments on tail regeneration; however, they did not find any significant differences in the amount of prey eaten between treatments, suggesting the impacts of ALAN on tail regeneration are independent of prey consumption effects on tail regeneration (Wise et al. 2022).

Finally, Liebgold (2019) documented one case of a female with a bifurcated tail at MLBS in Virginia. Both tail ends had regenerating tips, which indicated that autonomy and regrowth can occur in both the main and supernumerary tails. Two of us (T. J. H. Matlaga and K. N. Streeter) have also seen tail bifurcation during our own field work in Pennsylvania (Supplemental Material S16; Supplemental Fig. S3, available online). Additional work on the context of tail loss and regeneration across the range of *P. cinereus* is needed, specifically whether tail loss occurs primarily due to predation or intraspecific conflict. Research directions to fill the gaps in our comprehensive understanding of tail loss and regeneration in *P. cinereus* can be grouped into four main areas: (1) the selective pressures acting on tail loss and retention; (2) the behavior of autotomized tails; (3) the physiological and genetic mechanisms of tail regeneration; and (4) any morph, age, or sex-specific differences in tail autotomy or regeneration.

In reviewing the broader literature on predation of *P. cinereus*, it is clear that we have very few direct, nonincidental observations of predation on *P. cinereus*. The observations we do have are often single studies by scientists focused on the predator, not the prey, and most of these observations predate Petranka (1998), often by several decades (see summary in Anthony and Pfingsten 2013). The paucity of observations is likely, in part, because of the nocturnal nature of *P. cinereus*, but creative approaches should be able to address this challenge. For instance, collaboration with those who study the presumed vertebrate predators (birds, snakes, mammals, and larger salamanders) to complete targeted sampling of predator stomach contents during seasons of peak *P. cinereus* surface activity (Fig. 2) would help confirm the general palatability of *P. cinereus*, as well as contribute to our understanding of what proportion of predator diets are represented by *P. cinereus*. As we suggested earlier for refining our understanding of the diet of *P. cinereus,* the use of molecular methods, such as DNA metabarcoding (e.g., Harms-Tuohy et al. 2016), on predator stomach contents or predator fecal matter could greatly expand our ability to identify *P. cinereus* as a prey item as well as give us a relative idea of its prevalence in predator diets. We also need to expand our consideration of likely predators beyond vertebrates to include large arthropods (Anthony and Pfingsten 2013), and it is likely that DNA metabarcoding of arthropod gut contents and feces will also be an effective way to identify the invertebrates who are eating *P. cinereus* (e.g., Sint et al. 2015).

Our lack of knowledge of who specifically eats *P. cinereus* makes it difficult to draw conclusions about differential predation on and observed antipredator behaviors of color morphs. Many studies on this topic assume visual predators who can differentiate between the two color morphs in much the same way humans do. Kraemer and Adams (2014) show that only birds are likely to have this visual perception, not snakes or mammals. Because we have ample evidence that *P. cinereus* can detect chemical cues from predators, it would be interesting to test predators for chemical discrimination of salamander prey items more thoroughly, and for possible chemical discrimination of striped and unstriped morphs. Preliminary work in this area has been done with ringneck snakes (Lancaster and Wise 1996). Methods for these types of experiments with snakes are well established; for example, in the work of Brodie, Brodie, and colleagues on the predator–prey relationships of garter snakes (*Thamnophis* spp.) and newt species that produce tetrodotoxin (e.g., Avila et al. 2012). These studies often use the tongue-flick attack score method (reviewed by Cooper and Burghardt 1990).

It is also clear that our knowledge of *P. cinereus* parasites and pathogens is, at best, preliminary. Much of the work in this field has focused exclusively on testing for *Bd* or Ranaviruses. Surveillance testing for these pathogens has clear value for conservation of herpetofauna generally, but there are either no data on the impact or incidence of these pathogens on *P. cinereus* populations (e.g., Winzeler et al. 2014) or evidence of extremely low incidence of these pathogens within *P. cinereus* populations (e.g., Muletz et al. 2014; Augustine and Neff 2016; see discussion of *Bd* resistance in Additional topics: Microbiota). It will be important for future studies to follow up on the limited information we do have on the ecto- and endoparasites of *P. cinereus* to determine prevalence, transmission routes, natural susceptibility and symptomology, and natural resistance levels. Even from these few sources, we already have evidence suggesting a case of sex-biased vector transmission of a pathogen (Anthony et al. 1994; Davis et al. 2009b) and that there may be latitudinal (and thus likely climatic) differences in infection rates (Jongsma et al. 2019).

Community ecology: Introduction.— Petranka's (1998) section on community ecology is limited to the interactions of *P. cinereus* with other salamanders, particularly congeners most closely related to it. The section primarily summarizes interactions (or lack thereof) with its sister species, *Plethodon shenandoah*, work largely done by Jaeger in the 1970s (Jaeger 1970, 1971a,b, 1972, 1974). According to Petranka's (1998) summary of Jaeger's work, *P. shenandoah* and *P. cinereus* are strongly segregated on the three Virginian mountain tops that *P. shenandoah* occupies, with *P. shenandoah* restricted to the talus habitat, and *P. cinereus* found in every other terrestrial habitat available on the mountains. It was thought that there was coexistence in the talus of Hawksbill Mountain; however, Petranka (1998) recounts Jaeger (1970), which suggests that this is only apparently true, as Jaeger (1970) found strong microspatial segregation between these two species. Jaeger (1970) found *P. shenandoah* existing in five talus isolates surrounded by continuous nontalus habitat occupied solely by *P. cinereus*. Jaeger (1970) notes that these are not actually cases of coexistence, as within the isolated talus, there is only *P. shenandoah*, and outside of the talus, there is only *P. cinereus*. Petranka (1998) goes on to review what we know about competitive behaviors between these species, and notes that the field and laboratory studies are often contradictory, making it difficult to determine what is happening. Petranka (1998) offers Jaeger's (1972) hypothesis that perhaps adult *P. cinereus* exclude juvenile *P. shenandoah*. The remainder of this section of Petranka (1998) briefly discusses three additional interactions *P. cinereus* may (or may not) have with other salamander species: (1) potential for food competition between *P. cinereus* and either *P. hoffmani* or *P. wehrlei,* but lack of support when studied; (2) documented aggressive interactions between *P. cinereus* and both juvenile *P. glutinosus* and adult *Desmognathus ochrophaeus;* and (3) laboratory predation on *P. cinereus* by *Ambystoma maculatum* in 9% of staged encounters.

There has been much additional work on the community ecology of *P. cinereus* since Petranka (1998); importantly, these studies now regularly include interactions with nonsalamander species. In this section, we start by reviewing the more recent research on *P. shenandoah* and *P. cinereus*, continue by reviewing studies on interactions between *P. cinereus* and other salamander species, and finally, we review those studies focused on how *P. cinereus* interacts with nonsalamander species.

Community ecology: *P. shenandoah* and *P. cinereus* interactions.— The same year that Petranka's book was published, Griffis and Jaeger (1998) found further evidence supporting interspecific territoriality in *P. cinereus* but were unable to document any behavioral differences between these two species in biting, threat posture, or submissive posture. Evidence supporting the interspecific territoriality of *P. cinereus* came from a competitive release experiment, which removed *P. cinereus* residents from rocks close to a *P. shenandoah* isolate (experimental treatment) or left the *P. cinereus* residents in place (control treatment) and tracked how often and how quickly *P. shenandoah* were able to invade the experimental vs control rocks. Experimental rocks were invaded more quickly and more frequently by *P. shenandoah* than control rocks, suggesting active defense by *P. cinereus* against *P. shenandoah* (Griffis and Jaeger 1998).

Additional recent research further strengthens Jaeger's (1972) argument that *P. cinereus* adults may exclude *P. shenandoah* juveniles. Myers and Adams (2008) observed phenotypic shifts between allopatric and sympatric populations of *P. cinereus* and *P. shenandoah* but no evidence of character displacement between sympatric populations. This observation suggests competitive exclusion is driving the segregation, restricting *P. shenandoah* to talus, an environment uninhabitable by *P. cinereus* because of its susceptibility to desiccation (Petranka 1998; Myers and Adams 2008). As noted earlier in Systematics and Geographic Variation, early morphological and genetics work on *P. cinereus* and *P. shenandoah* found limited evidence of introgression or hybridization (see summary in Carpenter et al. 2001).

Additional investigation into competitive interactions between the species found that, under current climate conditions, *P. shenandoah* lost more mass during competition than *P. cinereus*, indicating *P. cinereus* is competitively superior to *P. shenandoah* (Dallalio et al. 2017). Predicted future climate warming conditions suggest a more costly outcome for *P. cinereus*, though, as average mass loss was comparable for the two species under presumed future (warmer) temperatures. However, during intraspecific trials, *P. cinereus* experienced no difference in mass loss between current and future conditions. This suggests *P. cinereus* has a larger range of temperature tolerance than *P. shenandoah* (Dallalio et al. 2017). Finally, Chambert et al. (2018) found that although *P. cinereus* populations were relatively stable over 4 y, *P. shenandoah* experienced high turnover in occupancy.

Community ecology: Other salamanders and *P. cinereus* interactions.— Regarding competition with salamanders other than *P. shenandoah*, Petranka's (1998) comments are limited. At that time, research summarized by Petranka (1998) indicated that interspecific competition for food between *P. cinereus* and *P. hoffmani* is unlikely and that dietary overlap between *P. cinereus* and *P. wehrlei* occurs but competition for food is unknown. Petranka (1998) also briefly summarizes interactions of *P. cinereus* with two more distantly related salamanders. Adult *P. cinereus* display similar levels of aggression towards and defend territories against juvenile *P. glutinosus* as they would towards adult conspecifics. *Desmognathus ochrophaeus* defends cover objects from *P. cinereus* and drives *P. cinereus* out of occupied territories (Petranka 1998).

Studies since Petranka (1998) have further described interactions between *P. cinereus* and other closely related salamander species. Multiple studies have examined one-on-one interactions between *P. cinereus* and other small-bodied *Plethodon*, looking for evidence for character displacement or competitive exclusion. Character displacement in both head morphology and diet is supported for *P. cinereus* and *P. hoffmani* (Adams 2000; Adams and Rohlf 2000), but not for teeth number or jaw muscle mass (Swart and Adams 2004). Although the microhabitats between these two species are not significantly different (Carlson et al. 2016), Jaeger et al. (2002b) found behavioral differences that may drive character displacement: *P. cinereus* is more aggressive and less submissive than both allopatric and sympatric *P. hoffmani*. They suggest that the boundary between the two species is either static, because of the aggressive superiority of *P. cinereus* and the exploitative superiority of *P. hoffmani* from eating larger prey, or that *P. cinereus* is slowly intruding on the range of *P. hoffmani* (Jaeger et al. 2002b).

Character displacement has also been supported for sympatric *P. cinereus* and *P. nettingi* (Adams et al. 2007; Adams 2011). Both species are smaller when in sympatry than when in allopatry, and sympatric populations show greater divergence in head shape between species relative to allopatric populations. These results suggest interspecific competition as a mechanism for phenotypic variation among *Plethodon* species (Adams et al. 2007). Over 32 yr, *P. nettingi* has decreased in abundance, which Kroschel et al. (2014) found may be correlated to *P. cinereus* expanding their range into the higher elevations that *P. nettingi* originally inhabited, but they could not rule out changes in environmental conditions affecting both species.

In Ohio and Kentucky, the ranges of *P. cinereus* and *P. electromorphus* overlap. In Ohio, sympatric localities within the broader counties of sympatry are not common, suggesting competitive interactions between these two species are important in determining species presence (Deitloff et al. 2008). In intraspecific trials, *P. cinereus* was more aggressive than *P. electromorphus*, and in interspecific trials, *P. electromorphus* was more submissive. These results suggest *P. electromorphus* may not be able to expand its range into that of *P. cinereus*, but *P. cinereus* may invade the range of *P. electromorphus* (Deitloff et al. 2008). In sympatric populations, both *P. cinereus* and *P. electromorphus* exhibited more aggressive behaviors and less submissive behaviors than allopatric populations (Deitloff et al. 2009). This study, however, only looked at one sympatric and one allopatric population, and the authors called for future research over the full extent of the overlapping ranges. Site-specific morphological differences also occur in sympatric *P. cinereus* and *P. electromorphus* populations (Deitloff et al. 2013). At some sympatric locations the two species experienced morphological divergence in head shape, while at other sympatric locations, morphological convergence occurred. These results suggest that abiotic and biotic disparities at different locations may be responsible for the morphological variation (Deitloff et al. 2013).

Hedeen (2000), working in both Kentucky and Ohio, found similar results to Deitloff et al. (2008): sympatry between *P. cinereus* and *P. electromorphus* was uncommon, and there seem to be climatic differences that correspond to differences in distribution. *Plethodon electromorphus* was found in drier upslope environments, whereas *P. cinereus* was found in wetter, lower, flatter areas (Hedeen 2000). Note that the populations of *P. electromorphus* sampled by Hedeen (2000) were previously classified as *P. richmondi* and are referred to as such by Hedeen (2000). Highton (1999) reclassified these populations as *P. electromorphus* based on allozyme data.

The ranges of *P. cinereus* and *P. hubrichti* are parapatric, with the range of *P. cinereus* completely surrounding that of *P. hubrichti*. Aasen and Reichenbach (2004) found no significant changes in relative proportions of *P. cinereus* and *P. hubrichti* over 10 yr at three populations in Virginia (one allopatric site for each species, and one sympatric site). Arif et al. (2007) found *P. hubrichti* to be more aggressive and less submissive than *P. cinereus*, but no differences in diet were observed between these two species. Head shape between these two species was different, but there was no evidence of ongoing character displacement in sympatric populations (Arif et al. 2007). The authors hypothesize *P. hubrichti* restricts the range of *P. cinereus*, even though it lives in suitable microclimates for *P. cinereus.* This hypothesis was further supported by Kniowski and Reichenbach (2009) which found that sympatric *P. hubrichti* and *P. cinereus* were similar in microhabitat preferences, movement patterns, growth rates, and adult and juvenile survival rates but differed in size. Sympatric *P. hubrichti* neonates and adults were larger than *P. cinereus* neonates and adults (Kniowski and Reichenbach 2009). A follow-up study observed non-fatal biting by a larger *P. hubrichti* of a smaller *P. cinereus,* suggesting interference competition contributes to the geographic distribution of these species (Kniowski and Pietsch 2015).

Several studies explored the position of *P. cinereus* within the larger woodland salamander community, focusing on its interactions with stream specialists (e.g., *Desmognathus* spp. and *Eurycea* spp.) and large-bodied *Plethodon* like *P. glutinosus.* As described previously in the Predators and Parasites section, it is unclear if *D. fuscus* preys on *P. cinereus* (Jaeger et al. 1998; Ransom and Jaeger 2006). Jaeger et al. (1998) found no evidence that larger *P. glutinosus* eat smaller *P. cinereus*, but a later study found that when sympatric, competition between *P. glutinosus* and *P. cinereus* led to reduced growth in juveniles of both species (Price and Secki Shields 2002). Two other studies support exclusion of *P. cinereus* by *Desmognathus* spp. Grover (2000) found little habitat overlap between *Plethodon* and *Desmognathus*, but some between *Plethodon* and *Eurycea*. Grover and Wilbur (2002) found that *D. fuscus* displaced *P. cinereus* closer to streams, and both abundance and mass of *P. cinereus* increased with distance from streams. When limited to a near-stream habitat, where stream specialist *E. cirrigera* likely outcompetes it, the body condition of *P. cinereus* individuals declined over a 3-wk period (Pasachnik and Ruthig 2004). A removal experiment at a stream/forest ecotone found that removal of *P. cinereus* had no effect on either *P. cinereus* abundance or *Desmognathus* sp. abundance; however, *E. cirrigera* moved closer to streams when *P. cinereus* was removed (Ransom and Jaeger 2008).

Plethodon salamanders are hypothesized to use behavioral mechanisms, such as climbing behaviors, that promote coexistence. A field study conducted by Mezebish et al. (2018) observed the climbing frequencies of three size guilds of *Plethodon* species. The authors found that the smallest species, *P. cinereus,* climbed more frequently than both the intermediate species, *P. montanus,* and the largest species, *P. glutinosus*. *Plethodon cinereus* also increased climbing frequency when exposed to intraspecific competitors but decreased climbing when exposed to interspecific competitors (Mezebish et al. 2018). The differences in climbing behaviors in different-sized *Plethodon* suggest that behavioral niche partitioning may be a mechanism that reduces competitive interactions and allows for the coexistence of species. In the lab, although adult *P. glutinosus* and *P. cinereus* did not directly interact when placed together, *P. cinereus* increased nose tapping behaviors when in the presence of *P. glutinosus* (Mezebish et al. 2018). This suggests that the individuals were chemically aware of the presence of the other. This study also found that more climbing behavior was observed in all species when there was more understory vegetation available to climb on.

Community ecology: Nonsalamander species and *P. cinereus* interactions.— Several studies since Petranka (1998) have described interactions of *P. cinereus* with nonsalamander species, focusing on (1) the potential roles of earthworms beyond simply being a prey item for *P. cinereus*, (2) the relationships between *P. cinereus* and intraguild predators common to the forest floor and soil (e.g., spiders, centipedes, beetles), (3) the role of *P. cinereus* in regulating soil and leaf-litter invertebrate communities, and (4) indirect interactions between *P. cinereus* and other woodland species.

Earthworms are likely to be important to *P. cinereus* community ecology in addition to being a prey item (e.g., Maerz et al. 2005, 2006; see the previous section on Terrestrial Ecology: Diet and Feeding Behavior). The work by Ransom and colleagues, conducted at MLBS in Virginia, focuses on the relationships between native and nonnative earthworms (Annelida) and *P. cinereus*. Cáceres-Charneco and Ransom (2010) found that *P. cinereus* uses earthworm burrows as refuge. In both lab and field, they found that *P. cinereus* was more likely to be under cover objects when earthworms were absent, and more likely to be in burrows when earthworms were present (Cáceres-Charneco and Ransom 2010). Ransom (2017) also observed that salamanders do not seem to distinguish between native vs nonnative earthworms, consuming and using the burrows of all species similarly. Ransom (2012) defines three distinct relationships between earthworms and *P. cinereus*: (1) earthworms are ecosystem engineers, building burrows that salamanders use regularly; (2) earthworms are potential prey for salamanders; and (3) earthworms compete with the other microinvertebrate prey species of *P. cinereus* leading to indirect effects on salamanders. Ransom (2012) found that the strength of these relationships varies by season for the non-native earthworm *Lumbricus terrestris*. Positive effects of ecosystem engineering were important to overwinter survival of adult *P. cinereus*. The positive effect of earthworms as prey was only greater than the negative effect of earthworms as competitors in the summer (Ransom 2012).

In Michigan, a survey by Brunges et al. (2020) investigated the effect of 11 different invasive earthworm species on terrestrial salamander abundance. They found a negative association between salamander counts and the presence of invasive, epigeic (i.e., found in the leaf litter) earthworms but no effect of invasive endogeic (i.e., found underground) earthworms. The authors suggest that this is because epigeic earthworms consume the O-horizon leaf litter layer, which *P. cinereus* depends on for moisture and protection (Brunges et al. 2020). Similarly, in Virginia, Ransom (2017) found that the presence of the invasive endogeic earthworm, *Octolasion tyrtaeum*, had an indirect, negative effect on nighttime *P. cinereus* counts. This earthworm species was also associated with a narrower O-horizon layer suggesting a similar mechanism to that proposed by Brunges et al. (2020). Finally, two studies in Ohio found that nonnative, epigeic *Amynthas* earthworms alter microhabitats and behavior of *P. cinereus*. The first found that earthworm presence decreased leaf litter mass over time, leading salamanders to increase movement, cover object use, and co-occurrence under cover objects with earthworms (Ziemba et al. 2015). A follow-up study found further evidence the salamanders were negatively impacted by *Amynthas* and *Metaphire* spp. (Ziemba et al. 2016). In the lab, salamanders opted for poorer-quality microhabitats and consumed fewer flies when earthworms were present. In the field, salamanders and earthworms shared cover objects much less than expected, and earthworm abundance was negatively associated with juvenile and male salamander abundance (Ziemba et al. 2016).

In Ohio, several studies have explored relationships between *P. cinereus* and spiders, centipedes, and carabid beetles. Anthony et al. (2007) found that *P. cinereus* exhibited more submissive behaviors when exposed to native centipedes as opposed to introduced centipedes, suggesting the presence of learned predator avoidance behaviors in *P. cinereus*. Burgett and Smith (2012) exposed *P. cinereus* to centipedes or conspecifics, and found salamanders showed increased aggression towards centipedes regardless of their residency status but showed no increase of aggression towards conspecifics in either setting. Hickerson et al. (2012) did a predator-removal experiment with the following treatments: *P. cinereus* removal, centipede removal, and a control with no removals. Interactions were complex: Removing either predator changed the abundance of other invertebrate predators (spiders and beetles) and had a mix of effects on invertebrate prey species. There was a negative relationship between spider or centipede abundance and *P. cinereus* abundance, suggesting interference competition between salamanders and the two invertebrate predators (Hickerson et al. 2012). However, there was a positive relationship between *P. cinereus* and carabid beetles. Hickerson et al. (2012) note that these relationships are strongest during the dry summer months, when these species all have fixed territories tied to suitable microhabitats. Interestingly, in the lab, Gall et al. (2003) found evidence to support intraguild predation by carabid beetles on *P. cinereus*. Residents of both species behaved more aggressively than intruders and attacked intruders of both species at similar levels. *Plethodon cinereus* bitten by carabid beetles often produced defensive, adhesive secretions which immobilized the beetles (Gall et al. 2003). Hickerson et al. (2004) found similar levels of interspecific aggression in laboratory mesocosms containing centipedes and *P. cinereus*. In this study, salamanders often escalated interactions to bite intruder centipedes, and did not exhibit biting behavior towards intruding conspecifics (Hickerson et al. 2004). Similarly, Hickerson et al. (2018) found that spiders in the genus *Wadotes* are also perceived by *P. cinereus* to be competitors, not as potential predators or prey. In laboratory trials, *P. cinereus* reacted to intruder *Wadotes* individuals in much the same way as they reacted to conspecific intruders, and there was no evidence of intraguild predation between spiders and adult or juvenile salamanders (Hickerson et al. 2018).

Plethodon cinereus is an important regulator of the composition of soil-litter invertebrate communities and thus, indirectly, the ecosystem processes these invertebrates perform. These interactions are thought to be crucially important for forest health, and often are used to justify the importance of woodland salamanders more generally (e.g., Welsh and Droege 2001; Davic and Welsh 2004). However, the community-level impacts of *P. cinereus* can depend on the habitat and climate context (and see Additional Topics: Ecosystem Ecology for broader impacts). In Ohio, Walton (2005, 2013) and Walton and Steckler (2005) all found that *P. cinereus* does have a top-down regulatory effect on the composition of soil-litter invertebrate communities, but the magnitude and direction of these effects varied both seasonally and annually (Walton 2013). An earlier, 2-yr study found that when leaf-litter mass and moisture were both high (typically in the spring), salamanders exerted stronger, negative top-down effects on mesofaunal invertebrates (Walton 2005). In complementary microcosm experiments, when *P. cinereus* was present, Walton and Steckler (2005) found more podomorphic Collembola, fewer enchytraeid worms, and fewer macroinvertebrate detritivores. Total invertebrate density, and densities of Collembola and Acari (mites) increased more quickly when salamanders were present. The authors argue that salamanders are either preying on larger detritivores that compete with these mesofaunal groups, releasing them from competition, or that salamander fecal matter promotes microflora growth, leading to bottom-up effects that promote mesofaunal population growth (Walton and Steckler 2005). A follow-up microcosm study found that salamander treatments again increased the density of Collembola, but this time only in urban leaf litter, not rural leaf litter (Walton et al. 2006). Other taxa, such as oribatid mites, pseudoscorpions, isopods, and millipedes (Walton et al. 2006), experienced decreased densities in both urban and rural leaf litters when salamanders were present.

Walton (2013) examined these patterns over a longer, 6-yr period and synthesized the complex relationships between *P. cinereus* and the mesofaunal invertebrates with which they share the leaf litter. During this longer study, Walton (2013) found positive, negative, and no effects of *P. cinereus* on invertebrate densities, with strong seasonal variation in strength and direction of the effects of salamanders on several invertebrate taxa. For example, the same negative relationships between *P. cinereus* and mesofaunal invertebrates observed in Walton (2005) were only observed in the spring and became positive relationships in autumn in the longer study (Walton 2013). Walton (2013) convincingly argues two complementary hypotheses to explain the change in dynamics: seasonal changes in prey-selection behavior by *P. cinereus* and seasonal changes in intraguild territoriality between *P. cinereus* and arthropod predators. Both hypotheses are mediated specifically by seasonal change in leaf-litter thickness, and the resulting interaction webs for spring and autumn are well summarized in Walton (2013: fig. 7). We refer the reader to Walton's (2013) detailed discussion of the current support for these two hypotheses as well as starting points for additional experimental tests needed for further understanding.

In contrast, in a 2-yr study in Virginia, Homyack et al. (2010b) found no evidence that *P. cinereus* affected the number of invertebrate taxonomic groups or functional guilds. In New Hampshire, Hocking and Babbitt (2014) found over 4 yr that *P. cinereus* had no effect on intraguild predator abundance (carabid beetles, centipedes, and spiders). Walton (2013) offers testable hypotheses that may explain the lack of patterns found by Homyack et al. (2010b) and Hocking and Babbitt (2014). Additionally, Hickerson et al. (2017) provide a detailed argument that because of the differences both in methodology and duration of Homyack et al. (2010b) and Hocking and Babbitt (2014) compared to those studies discussed previously that do find strong patterns, the former are not directly comparable to the latter. We are sensitive to the Hocking and Babbitt (2014) argument that caution is warranted when using *P. cinereus* as an ecological indicator within a given forest until the local patterns at that site are sufficiently understood. Future studies that use standardized invertebrate sampling methods across sites and detailed, longitudinal data sets that explicitly incorporate seasonal and annual variability (e.g., like Walton 2013) will be important for generalizing the role of plethodontid salamanders in communities and ecosystems.

Finally, a small number of studies have looked at the indirect relationships between *P. cinereus* and other woodland species, including White-tailed Deer (*Odocoileus virginianus*), Garlic Mustard (*Alliaria petiolata*), Spongy Moths (*Lymantria dispar dispar*), and fungal communities. In Ohio, Greenwald et al. (2008) found a positive, indirect effect of deer presence on *P. cinereus* abundance. Salamanders were three times more abundant in deer-permitted control plots compared to deer-exclusion plots. Greenwald et al. (2008) suggest that deer herbivory increases invertebrate species richness through increased nutrient deposition and plant growth, which in turn attracts salamanders. In Massachusetts, Brooks (1999) found that the abundance of *P. cinereus* did not change across forests with higher or lower densities of White-tailed Deer. In Ohio, removal of invasive Garlic Mustard had no effect on *P. cinereus* abundance (Smith 2018). Mitchell (2015) explored how *P. cinereus* counts changed after invasion by Spongy Moths. Despite recovery of the canopy and increased amounts of coarse woody debris, Mitchell (2015) observed a >60% decline in *P. cinereus* counts in 1993 compared to 1988 (prior to the 1989 arrival of Spongy Moths). It is not clear if the decline in *P. cinereus* was related to the arrival of Spongy Moths, other factors, or some combination of these. For interactions between *P. cinereus* and the soil microbial community, please see the forthcoming section Additional Topics: Microbiota.

In the decades since Petranka (1998), the community ecology of *P. cinereus* is one of the fields which has grown the most, but for which there are still many unanswered questions. We encourage the reader interested in these topics to also read Bruce (2008) which thoroughly reviews interspecific competition and intraguild predation in Plethodontidae more generally. Bruce (2008) reviews several studies cited both here and by the three prior reviews (Petranka 1998; Anthony and Pfingsten 2013; Jaeger et al. 2016), offering conclusions which feature potential avenues for future work. Broadly, Bruce (2008) highlights the need for long-term, time-series studies that target the relationship between population growth rates and densities of *Plethodon* spp., as well as the continued development and use of manipulative experiments, emphasizing a need for those in unenclosed field plots. Specifically, regarding *P. cinereus*, Bruce (2008) points out that although we have a good basic understanding of the top-down impacts of *P. cinereus* on their prey, little is known about how those prey exert bottom-up control on *P. cinereus* populations.

In addition to better understanding interspecific competition and intraguild predation within *Plethodon*, continued study of the interactions between *P. cinereus* and its close relatives in *Plethodon* will hopefully help us understand not only how *P. cinereus* was able to spread so far and wide across northeastern North America, but also how reliable of a stand-in *P. cinereus* biology could be for its less abundant, less wide-ranging relatives. The crucial role of *P. cinereus* as an invertebrate mesopredator in northeastern woodlands suggests they interact with many other species, both directly and indirectly, both positively and negatively, and the research reviewed here only begins to reveal the complexity of these dynamics. Importantly, the variation in *P. cinereus* dynamics across both time and space makes generalizing their community-level impacts difficult. The lack of standardized methods for tracking such impacts as well as the short-term nature of most investigations further compounds these difficulties. These difficulties make the "ecological indicator" designation (e.g., Welsh and Droege 2001; Siddig et al. 2019) of *P. cinereus* harder to sell, but we argue that the variation and complexity in *P. cinereus* community dynamics offer countless opportunities for broader ecological research on these topics, lending support to our argument that *P. cinereus* has model organism potential, regardless of its use as or the specific requirements for an indicator species. A coordinated effort that (1) spans several years and surface-active seasons, (2) is replicated across the range of *P. cinereus*, and (3) monitors and measures salamander and invertebrate densities and relevant abiotic covariates (e.g., leaf litter biomass, soil moisture) will be critical in establishing baseline, range-wide understanding for future experimentation. Walton (2013) and Hickerson et al. (2017) both provide robust methodology and foundational knowledge on which to build this research program.

Conservation biology.— Petranka's (1998) summary of the conservation biology of *P. cinereus* was very brief, focusing on sensitivity of *P. cinereus* to soil acidification (e.g., Wyman 1988) and intensive forest harvesting practices (e.g., deMaynadier and Hunter 1995). Historically, there has been very little concern for the impacts of human-mediated effects on *P. cinereus* populations, in part because of the then-growing understanding that *P. cinereus* are remarkably abundant in some forests, with biomass greater than other prominent vertebrate groups (e.g., New Hampshire, Burton and Likens 1975a). However, shortly after the publication of Petranka (1998), Lannoo (2005) was published, comprehensively reviewing contemporary amphibian declines, their hypothesized causes, potential conservation, survey and monitoring strategies, and the statuses of United States species. Highton's (2005) chapter within this volume documents the declines of 44 *Plethodon* species across 205 populations, including *P. cinereus*. Highton (2005) reports that 19 out of 24 populations of *P. cinereus* across eight states (Indiana, Maryland, New York, North Carolina, Tennessee, Pennsylvania, Virginia, and West Virginia) show declines in mean number of individuals collected per person from visits pre-1990 (range = 1956–1986) to visits post-1990 (range = 1990–1999), some of which are quite dramatic (see Highton 2005: table 8-1). These patterns, and those of global amphibian declines more generally (e.g., Alford and Richards 1999; Lannoo 2005; Caruso and Lips 2013), are alarming and suggest that the historically high abundances of *P. cinereus* in northeastern North American forests should not be taken for granted.

Like many of the topics we have reviewed thus far, the conclusions of conservation-focused studies of *P. cinereus* are geographically variable, with many studies finding contradictory patterns, suggesting the importance of understanding both land use history and current anthropogenic threats to best determine the likelihood of persistence for any given population. We found many recent papers that have looked at how *P. cinereus* responds to specific kinds of anthropogenic change, as well as many studies that focus on how to manage *P. cinereus* populations or use *P. cinereus* to manage forest ecosystems. We have separated the more management-focused sources to be summarized under the Additional Topics: Management section, and here focus largely on concerns related to how *P. cinereus* responds to anthropogenic land use changes and climate change. We also limited our discussion of papers that have conservation as a secondary category (Supplemental Material S12; Supplemental Data S11), as these studies are nearly all discussed elsewhere in this review.

Since Petranka (1998), many studies have further explored the sensitivity of *P. cinereus* to anthropogenic influences, despite low prioritization of this species as a conservation concern. deMaynadier and Hunter (1998) found that *P. cinereus* in Maine are sensitive to clear cutting and edge effects, and have an affinity for mature forest. Further, it was suggested that modified, open canopy sites may represent sink habitat, meaning there are significantly more juveniles than adults and these juveniles may not have established territories. Despite this finding, at populations in Connecticut and Massachusetts, Brooks (2001) found that *P. cinereus* abundance only decreases temporarily, both when Eastern Hemlock (*Tsuga canadensis*) is partially harvested as well as when invasion of Hemlock Wooly Adelgid (*Adelges tsugae*) causes Eastern Hemlock defoliation and tree loss. Within 3 yr of initial tree loss, the abundance of *P. cinereus* had already begun to increase (Brooks 2001). Also working in Connecticut, Mossman et al. (2019) found that abundance of *P. cinereus* was the highest in 20–25-yr-old shelterwoods and significantly higher than in mature or unharvested forest sites, suggesting *P. cinereus* may benefit from some infrequent level of disturbance, particularly disturbance that results in increased availability of coarse woody debris, like timber harvesting. This contrasts with the findings of Rodewald and Yahner (1999) in Pennsylvania, who found that harvested areas had no salamanders, and the abundance of *P. cinereus* in mature forest was positively correlated with the number of trees. At Appalachian populations in southwestern Virginia and neighboring West Virginia, Knapp et al. (2003) compared declines in salamander abundance after clear-cutting to six other silvicultural methods, and found that if the canopy was disturbed, the other silvicultural methods were as bad as clear-cutting for salamander abundance. After a forest fire in Nova Scotia, only one *P. cinereus* individual was found alive about 300 m from the edge of the wildfire in an unburned refuge (Russell 2011). No salamanders were found in the burned area when searched over the next 4 mo. This suggests that *P. cinereus* may be negatively affected by wildfires in terms of habitat loss; however, given their ability to persist in subterranean retreats during a wildfire, they likely could move to areas nearby that were not affected by the wildfire once it is safe to do so (Russell 2011).

Various modeling approaches by Leroux et al. (2017) suggest that patch size is more important for persistence of *P. cinereus* populations than either patch isolation or environmental conditions (but see the following discussion of conservation genetics). A model by Venier et al. (2007) based on *P. cinereus* in Ontario concluded that *P. cinereus* are sensitive to changes in habitat availability, regardless of whether the disturbance is caused naturally or from intensive harvesting. As canopy cover and downed coarse woody debris increases, *P. cinereus* abundance increases (Venier et al. 2007). In Indiana, however, while Peele et al. (2017) also found these factors to be positively related to the abundance of *P. cinereus,* neither one had a significant effect on the survival rates of the *P. cinereus*. Otto et al. (2014) found similar importance of canopy cover and coarse woody debris availability in Michigan at the landscape scale, but not at the local scale. A model by Gordon et al. (2012) found that *P. cinereus* abundance decreases following forest harvesting in Ontario. Vanderwel et al. (2011) modeled the value of different habitats following deforestation, using *P. cinereus* data from Québec and Vermont. The habitat value for *P. cinereus* increased after most stages of deforestation, likely due to increases in coarse woody debris, suggesting that *P. cinereus* can recover after disturbances to their environment. A field study in West Virginia by Wood and Williams (2013) found that reclaimed mountaintop removal mines are not suitable habitat for *P. cinereus*, as these habitats favor succession towards a grassland or shrubland habitat than forest. They argue that the recovery of the forest habitat after mountaintop mining may take longer than areas that are clear-cut because of factors like soil compaction.

In Virginia, Marsh and colleagues have published several studies on the effects of roads on *P. cinereus*, many of which we have previously discussed in this monograph (Marsh and Beckman 2004; Marsh et al. 2005, 2007, 2008). From a conservation perspective, both Marsh and Beckman (2004) and Marsh (2007) examine the edge effects of roads. The first study found strong edge effects—fewer *P. cinereus* were found close to roads in all three populations studied. The authors suggest that the decline of *P. cinereus* as you approach a road edge is due to the parallel decline in both soil moisture and cover object area near roads (Marsh and Beckman 2004). Marsh (2007) focused on gated (closed to vehicles) vs. ungated roads and found no edge effects on *P. cinereus* from roads that are narrow and gated, while ungated roads show the same pattern as observed in Marsh and Beckman (2004). Marsh et al. (2005, 2008) both find that roads are dispersal barriers: Marsh et al. (2005) used a displacement and homing experiment and Marsh et al. (2008) measured population genetic structure on different sides of roads of different widths. In Connecticut, Gibbs (1998b) also found roads to be a dispersal barrier for *P. cinereus.*

As reviewed earlier, several studies have explored the relationship between habitat fragmentation and population genetics. Gibbs (1998c) compared continuous to fragmented populations in Connecticut using random amplified polymorphic DNA (RAPD) markers and found that the fragmented populations were more divergent, that is, showed greater genetic structure, compared to the continuous populations. Gibbs (1998c) also noted a difference in morph frequency: fragmented populations were close to 50:50 striped:unstriped, whereas continuous populations were nearly 100% striped. In Québec, Noël et al. (2007) found that urban *P. cinereus* have both lower allelic richness and lower heterozygosity. A follow-up study found that *P. cinereus* showed more genetic differentiation in areas where anthropogenic disturbances have persisted for a longer time (Noël and Lapointe 2010). The authors suggest that this pattern is because *P. cinereus* in these environments tend to have a low effective population size. Further implications from Noël and Lapointe (2010) are that it is important to preserve large, forested areas within cities to increase genetic variation and conserve or increase effective population size. Cosentino and Brubaker (2018) demonstrate the importance of connectivity for post-agricultural recovery. Salamanders were affected by historical land use and were more abundant in areas of historical forest cover. This suggests connectivity between relic source populations and regenerating forests on postagricultural lands is important for colonization of the new forest habitat (Cosentino and Brubaker 2018).

In Ohio and Pennsylvania, Cameron et al. (2019) compare the genetic differentiation and population structure between fragmented populations (Cleveland, Ohio) and continuous populations (Allegheny National Forest, Pennsylvania) to understand the relative roles of genetic drift and effective population size better. In the fragmented landscape, populations did show genetic differentiation and structuring; these patterns were best explained by spatial variation in effective population size and driven by one of the four sampled populations. The three non-differentiated fragmented populations showed levels of gene flow comparable to the four continuous populations. Interestingly, the genetically distinct population in the fragmented landscape had the lowest effective population size, but the largest allelic richness and highest observed heterozygosity within that landscape. The authors argue that this may be due to multiple paternity in *P. cinereus* (see Liebgold et al. 2006) and/or the presence of unsampled populations within the fragmented landscape. In the continuous landscape, populations were not genetically differentiated, lacked structure, and differences in allele frequency between continuous sites were best explained equally by matrix resistance and geographic distance, similar to Noël et al. (2007). Cameron et al. (2019) conclude that the ability of *P. cinereus* to persist in marginal habitats likely allows them to maintain levels of gene flow in highly modified habitats that are similar to those observed in larger forests.

Using a combination of contemporary field measurements of SVL and historical measurements from museum specimens, Caruso et al. (2014) found that the body size of *P. cinereus* has decreased by 7% in several Appalachian Mountain locations over 55 yr. The greatest decreases in body size were in the southern Appalachians, which have had the greatest increase in both drying and warming. The authors hypothesize that this correlation between location and body size likely comes from an increase in metabolic expenditure (Caruso et al. 2014). In contrast, using only museum specimens but including specimens from both high and low elevations, McCarthy et al. (2017) reported a similar precipitation pattern, with body size being negatively correlated precipitation in the driest month, but the opposite temperature pattern: larger *P. cinereus* were correlated with higher mean maximum July temperatures, and specimens on the coastal plain showed a temporal increase in body size correlated with a temporal increase in mean maximum July temperatures.

A third study using only museum specimens looked at morph-specific change in SVL at 37 locations over 43 yr, at high and low elevations (Hantak et al. 2021). This study was summarized in detail in the Systematics and Geographic Variation section; however the patterns documented by Hantak et al. (2021) are more similar to Caruso et al. (2014) than to McCarthy et al. (2017), with both morphs showing decreases in SVL with increases in temperature and increases in SVL with increasing elevation. The strength of these changes was different between the two morphs, with striped morphs responding more strongly to temperature, and unstriped morphs responding more strongly to elevation. Striped morphs also showed a decrease in SVL over time, while SVL in unstriped morphs is increasing over time (Hantak et al. 2021).

Specifically in response to Caruso et al. (2014), and prior to the publication of McCarthy et al. (2017) or Hantak et al. (2021), both Grant (2015) and Connette et al. (2015) offer alternative explanations for shrinking salamanders. They argue that the results of Caruso et al. (2014) could be explained by the sampling approaches used in the study and that both museum specimens and contemporary surface-active individuals likely only represent the surface-active portion of the inferred population. Indeed, in their discussion, McCarthy et al. (2017) argue that they designed their study specifically to address Grant's (2015) criticisms of Caruso et al. (2014). The most recent study by Hantak et al. (2021) suggests complex patterns driving body size responses to abiotic factors, and an impact of color morph, which was not considered in Caruso et al. (2014) or McCarthy et al. (2017). Methodologically, the two more recent studies are difficult to compare. McCarthy et al. (2017) grouped specimens by county and into two time brackets (1950–1970 and 1980–2000), and used mean maximum July temperature for each county in the two time brackets to explore how body size changed in counties which experienced warming vs. counties which did not experience warming. Hantak et al. (2021) focused on 37 geolocations which had sampling over a minimum time series of 20 y, grouped geolocations separated less than 15 km into eight composite sites, and used mean annual temperature for each geolocation and each year of specimen collection. Further work on this topic, which tracks contemporary populations and includes metrics like body size, individual growth rates, and changes in mass across the range over time using spatial capture–recapture methods (e.g., Sutherland et al. 2016) may be able to detect these patterns more confidently.

Although *P. cinereus* is not itself considered a species of conservation concern, it is clearly affected by a variety of land use modifications and climate change, both of which are often anthropogenically caused. Declines in *P. cinereus* populations have been documented (Highton 2005), and population and conservation genetic approaches discussed in detail above suggest that the evolutionary resiliency (sensu Sgrò et al. 2011) of *P. cinereus* may be at risk from continued changing land use and climates. *Plethodon cinereus* also clearly has strong impacts on the ecological community (see the Community Ecology section) such that even slight changes in salamander abundance could have much larger ripple effects throughout the community and ecosystem (Gaston and Fuller 2008). Regular monitoring of common, abundant, not-at-risk species like *P. cinereus* will help conservation biologists detect declines earlier and have a better chance to mitigate their effects (e.g., Gaston and Fuller 2008; Gaston 2010, 2011; Lindenmayer et al. 2011, 2013; Sterrett et al. 2019).

Additional topics: Introduction.— In addition to the miscellaneous physiology and behavior sources we report on previously, we found four additional topics not covered by Petranka (1998) for which there has been enough literature to warrant their own sections in the present review. First, we summarize studies on the ecosystem ecology of *P. cinereus*. Next, we summarize studies that focus on the natural resources management of *P. cinereus* and the forests in which they live. Third, we describe the many studies exploring the skin and gut microbiota of *P. cinereus* and their relationship to disease resistance. Finally, we found several ecotoxicology studies that explore the tolerance of *P. cinereus* to various anthropogenic pollutants, particularly on current and former United States military installations.

Additional topics: Ecosystem ecology.— Petranka (1998) mentions the Burton and Likens (1975a) study at Hubbard Brook Experimental Forest in New Hampshire for their estimates of *P. cinereus* density, but similarly important is Burton and Likens (1975b), a simultaneous study on the energy flow and nutrient cycling that must pass through *P. cinereus*, given its position in the trophic web and the high densities observed at Hubbard Brook. These studies (Burton and Likens 1975a,b) have since been cited by hundreds of subsequent studies, some of which argue for the use of *P. cinereus* as an ecological indicator species (e.g., Welsh and Droege 2001; Siddig et al. 2019), or for the overall importance of plethodontids to terrestrial forest ecosystems (e.g., Davic and Welsh 2004), and indeed have shaped the thinking of many researchers working on North American plethodontid salamanders. As we discuss in Additional Topics: Management, there are challenges to the acceptance and use of *P. cinereus* as an indicator species (e.g., Riedel et al. 2008; Moore and Ouellet 2015). In particular, the wide geographic range and the high tolerance of *P. cinereus* to disturbed habitats (e.g., Mossman et al. 2019) make *P. cinereus* an outlier within Plethodontidae, and a potentially poor proxy for more threatened *Plethodon* salamanders.

Since Petranka (1998), several studies have investigated how *P. cinereus* contribute to ecosystem processes like nutrient cycling or energy movement. Some of these have manipulated densities of *P. cinereus* or examined how natural density variation influences ecosystem processes, albeit with contradictory findings (Wyman 1998; Walton 2005; Sucre et al. 2010; Homyack et al. 2010b; Walker et al. 2014; Hocking and Babbitt 2014; Pelini et al. 2015; Hickerson et al. 2017). In New York, Wyman (1998) found that experimental cages with two or six salamanders (compared to controls with zero salamanders) significantly decreased forest floor prey communities, which had an indirect negative effect on the rate and magnitude of leaf litter decomposition, likely because of *P. cinereus* feeding on leaf shredders. In Ohio, Hickerson et al. (2017) also manipulated *P. cinereus* densities by removal using an open field design and found similar results to Wyman (1998). Repeated removal of salamanders over a 4-yr period increased the rate and magnitude of leaf litter decomposition compared to treatments with fewer or no salamanders removed (Hickerson et al. 2017). In contrast, other experimental studies found no effects of *P. cinereus* on ecosystem measures, such as leaf litter and wood decomposition or nitrogen mineralization rates, among others, even when manipulated densities were as high as 4 salamanders/m^2 (Homyack et al. 2010b in Virginia; Hocking and Babbitt 2014 in New Hampshire; but see discussion of these studies above in Community Ecology). Additionally, Sucre et al. (2010) found that salamander abundance was not a reliable indicator of nitrogen availability in Virginia.

Milanovich and Maerz (2012, 2013) describe the use of stable isotopes from *P. cinereus* tail clips collected from New York for tracking ecosystem nutrient and energy movement. They note that these isotopes are accurate even when the salamander has been fasted for up to 35 d, making their interpretation much easier compared to organisms for which fasting does change these values. Also working in New York, Gilbert et al. (2014) used carbon-13 to understand how carbon from sugar maple (*Acer saccharum*) tree roots moves through the ecosystem and found that *P. cinereus* individuals contained large quantities of root-derived carbon. This was true whether earthworms were part of the treatment conditions or not (Gilbert et al. 2014).

Another line of investigation has made connections between ecosystem changes or elemental gradients and *P. cinereus* (Homyack et al. 2011; Beier et al. 2012; Ochs and Siddig 2017). In recently harvested forests in West Virginia, *P. cinereus* expends more energy on body maintenance, although there were no consistent patterns related to body condition or invertebrate abundance (Homyack et al. 2011). In New York, Beier et al. (2012) found a positive relationship between *P. cinereus* abundance and a well-defined calcium gradient, and in Massachusetts, Ochs and Siddig (2017) found *P. cinereus* was more prevalent in forests with lower soil pH, lower carbon to nitrogen (C:N) ratios, and lower temperatures. The authors note that the first two characteristics, low soil pH and low C:N ratios, are characteristic of Eastern Hemlock stands, which used to be much more common within the range of *P. cinereus* prior to the arrival of Hemlock Wooly Adelgid (Siddig et al. 2019). The loss of Eastern Hemlocks and other ecosystem changes as a result of invasive species who affect fundamental environmental properties relied on by forest floor inhabitants (e.g., soil chemistry, temperature, humidity), may also influence *P. cinereus* (e.g., Cáceres-Charneco and Ransom 2010; Ochs and Siddig 2017). Continental invasions of earthworms from Europe and Asia undoubtedly influence *P. cinereus* in many ways, but especially by changing soil properties and *P. cinereus* behavior, which likely influence the role of salamanders in shaping North American forest ecosystems (Cáceres-Charneco and Ransom 2010; see also the Community Ecology section).

Lastly, as discussed in Community Ecology above, the role of *P. cinereus* on the forest floor as a predator (e.g., Walton 2005; Walker et al. 2014) may influence heterotrophic respiration rates, having measurable implications for climate change in forest soils, but these effects may vary latitudinally (Pelini et al. 2015). The inconsistent results of these studies (see our discussion above, in Community Ecology, as well as Hickerson et al. 2017) are yet another reason it is critical to design robust experiments to ensure comparability across populations and better understand variation in demography and community interactions across the range of *P. cinereus*.

Additional topics: Management.— In Petranka (1998) there was relatively little consideration of management for *P. cinereus* populations or their habitat, presumably because *P. cinereus* is considered a common species throughout its range, despite its proposed sensitivity to changing landscapes driven by human activity and our knowledge of these practices on other woodland salamanders. However, since Petranka (1998), there has been a great deal of research on the impacts of forest management on amphibian communities, including the ubiquitous *P. cinereus*. Here, we summarize those studies which focus on managing forests with explicit mention of impacts to *P. cinereus*.

In an experimental management context (i.e., either manipulated or observational), *P. cinereus* abundance or distribution may be influenced by factors as diverse as prescribed fire (Mitchell 2000), tree harvest management strategy or intensity (Messere and Ducey 1998; Rodewald and Yahner 1999; Harpole and Haas 1999; Yahner et al. 2001a; Duguay and Wood 2002; Perkins and Hunter 2006; Patrick et al. 2006; Homyack and Haas 2009; Strojny and Hunter 2010b; Hocking et al. 2013; MacNeil and Williams 2013b, 2014; Mossman et al. 2019), deer management (Greenwald et al. 2008; see discussion in Community Ecology), managed grazing (Riedel et al. 2008), or subsequently in forests with varying densities and qualities of coarse woody debris (McKenny et al. 2006; Strojny and Hunter 2010a). There is some evidence that plantation-style forests, common on lumber farms, are not suitable for *P. cinereus* (Waldick et al. 1999; Reams et al. 2008) despite the closed canopy, perhaps because of the lack of cover objects.

Studying how timber harvest practices influence *P. cinereus* energetic response, Homyack et al. (2011) reported on short-term effects of forest floor temperatures from overstory removal harvest, which may lead to an energetic cost for *P. cinereus*. The authors also suggest that retaining downed logs and other large woody debris in addition to promoting regrowth of understory may contribute to rapid recovery of forest floor conditions conducive to stable *P. cinereus* populations. Electric transmission right-of-way (ROW) areas are often heavily managed to remove vegetation and to provide continual access for maintenance. Yahner et al. (2001a) report that *P. cinereus* were among the most common amphibians found in these areas and that ROW areas housed a greater diversity of amphibians than adjacent forests; however, the authors do not discuss how detection influenced their results. In a follow-up study, *P. cinereus* were more commonly found in areas in Pennsylvania that are managed through timber harvesting than in areas that are undisturbed (Yahner et al. 2001b), which contradicts the deMaynadier and Hunter (1998) finding that *P. cinereus* prefer interior, mature forests. The work of Yahner et al. (2001b) does fit with the suggestion of Riedel et al. (2008) that *P. cinereus* may be less sensitive to anthropogenic change than previously thought, provided they have appropriate microhabitats (i.e., cool and moist cover objects; but see Wood and Williams 2013 for a counterexample).

Some studies demonstrated no effect of experimental management on *P. cinereus* individuals or populations. Mahoney et al. (2016) showed no effect of shelterwood-burn or fenced shelterwood-burn treatments on *P. cinereus* abundance, but stressed that leaf litter and fine woody debris cover objects were influential on *P. cinereus* abundance when considering best approximating single variable models. Similarly, Moore (2014) used a mesocosm experiment to demonstrate that the addition of lime to acidic, maple forests (liming), has no impact on survival of *P. cinereus*. Cameron et al. (2016) found similar results in the field comparing a long-term liming site to an unlimed control area in Ohio.

In the last two decades, it has been suggested that *P. cinereus* be considered as an indicator species for a variety of ecosystem properties (e.g., Welsh and Ollivier 1998; Welsh and Droege 2001). Siddig et al. (2019) agreed that *P. cinereus* may be an indicator species used to monitor changes in eastern hemlock forest ecosystems because of their sensitivity to key stressors and changing environmental conditions. Along with several studies hypothesizing and testing the connection between a changing climate and color phenotype ratios in a population (see the Systematics and Geographic Variation section), Moore and Ouellet (2015) concluded that climate variables do not influence color phenotype ratios broadly across the range of *P. cinereus*. The indicator species concept (also known as "surrogate species concept") arose as a shortcut approach to evaluating the complex state of ecosystems by measuring a few, relatively inexpensive observable characteristics (Landres et al. 1988; Caro 2010; Lindenmayer et al. 2015). The degree to which *P. cinereus* can successfully be considered an indicator species in the future will depend upon making direct connections between *P. cinereus* and specific drivers of interest as well as understanding the mechanistic relationship between the indicator and ecosystem property of interest, which is often an unobservable ecological process (Fleming et al. 2020).

Additional topics: Microbiota.— Studies that explore the community-level interactions between *P. cinereus* and microbial species generally focus on three distinct groups of microbiota: salamander skin microbiota, salamander gut microbiota, and environmental (typically soil) microbiota. In this section, we discuss all sources which address how *P. cinereus* interacts, directly or indirectly, with microbial taxa. Prior to 1998, information regarding the microbiota that *P. cinereus* interact with was scarce, in part because the technological developments which enabled economical microbial community profiling were only just becoming available. Petranka (1998) mentions that there has been no evidence for antibiotic properties in the skin secretions of brooding females, a claim that has since been refuted by several recent studies that document microbial taxa that produce both antibiotic and antifungal compounds in clinically relevant levels (e.g., Fredericks and Dankert 2000; Harris et al. 2006; Culp et al. 2007; Lauer et al. 2007; Brucker et al. 2008a,b; Becker et al. 2009). Most research to date regarding the skin microbiota of *P. cinereus* has focused on two overarching goals: (1) to identify microbial taxa found on salamander skin and in their guts, and (2) to understand the potential these microbial taxa have to produce antibacterial and antifungal compounds. The latter goal has been specifically focused on those microbiota which may be useful in targeting the deadly amphibian fungal pathogen *Bd*, to which *P. cinereus* is thought to be largely resistant. Compared to these two topics, relatively few studies have looked at the impact of *P. cinereus* on the soil microbial communities.

Fredericks and Dankert (2000) is one of the earliest studies to identify antimicrobial proteins on the skin of *P. cinereus*, shortly after Petranka (1998) was published. However, as this study focused on protein fractions instead of whole-community DNA, they are unable to determine if these compounds are salamander-made or microbe-made. Harris et al. (2006) document three genera of bacteria on the skin of *P. cinereus* that inhibit the growth of *Bd* in challenge assays (*Bacillus*, *Lysobacter*, *Pseudomonas*). Another early study of skin microbes by Culp et al. (2007) isolated five bacterial taxa (*Pseudomonas fluorescens*, *Microbacterium testaceum*, *Flavobacterium johnsoniae*, *Bacillus cereus*, and *Corynebacterium* spp.) and one yeast (*Candida molishiana*), as well as several unidentifiable isolates. Of these, *Pseudomonas fluorescens* was especially notable, because it is known for having antimicrobial and toxic (hydrogen cyanide) properties. Culp et al. (2007) also noted that many of the bacterial colonies were mucoid, and thus are likely involved in preventing salamander skin dehydration.

Shortly after these early studies were published, metagenomic methods became less expensive and more accessible, and most subsequent work using these methods suggests that microbes produce many of the beneficial proteins previously identified by Fredericks and Dankert (2000). Lauer et al. (2007) found that 89% of the salamanders in their sample had strong and/or weak antifungal bacteria on their skin. They used a fungal pathogen, *Mariannaea* sp., isolated from dead *Hemidactylium scutatum* eggs in their challenge assays. Lauer et al. (2007) highlight their discovery of a specific bacterial strain closely related to *Janthinobacterium lividum,* a bacterium which was previously known to produce antifungal compounds. In their study, *J. lividum* was found on every salamander (Lauer et al. 2007). This result has since been confirmed by several additional studies that focus on *J. lividum* and the ability of *P. cinereus* to either resist or quickly recover from *Bd* infection (e.g., Brucker et al. 2008a; Becker et al. 2009; Wiggins et al. 2011; Muletz et al. 2012; Hess et al. 2015). A follow-up study found similar microbial composition at the genus and family levels, but little overlap at the species level, on the skin of confamilial *H. scutatum* (Lauer et al. 2008).

Janthinobacterium lividum makes at least two known antifungal metabolites, indole-3-carboxaldehyde and violacein, that are lethal to *Bd* in naturally occurring concentrations found on the skin of *P. cinereus* (Brucker et al. 2008a). When *Bd* is experimentally introduced salamanders, 8 out of 10 salamanders who died due to *Bd* infection had no violacein-producing microbes and the remaining 2 had lower than average violacein levels (Becker et al. 2009). Other *Bd* inhibiting or mitigating microbial taxa found in the skin or in the guts of *P. cinereus* include *Lysobacter gummosus* (Brucker et al. 2008b), *Pseudomonas reactans* (Harris et al. 2006, 2009), and several additional taxa identified by Muletz-Wolz et al. (2017) and Fontaine et al. (2018). In a lab experiment, Loudon et al. (2014a) cultured bacterial isolates including *Bacillus* spp., *J. lividum*, *Pseudomonas* spp., and *Chitinophaga arvensicola*, from *P. cinereus* as cocultures and monocultures to determine what bacterial species or combinations most successfully inhibit the growth of *Bd*. Metabolites in the co-cultures were most inhibitory to *Bd* as they interact synergistically and additively (Loudon et al. 2014a).

There is some evidence that these protective bacterial taxa can be inoculated on salamanders who lack them, and that inoculation relieves symptoms of infection (Harris et al. 2009; Muletz et al. 2012; Loudon et al. 2014b). Harris et al. (2009) used Provosoli medium to expose individuals of *P. cinereus* to protective *Pseudomonas reactans*, with and without *Bd* present in the same treatment. Salamanders exposed to *Bd* alone lost more body mass compared to both those in the control groups, which were exposed to either sterile medium or *Pseudomonas reactans* alone, and those in the treatment group exposed to *Bd* and *Pseudomonas reactans*. Muletz et al. (2012) sought to use *J. lividum* to protect the globally declining amphibian populations as a result of *Bd*, and learned that through soil bioaugmentation, it is possible to experimentally introduce *J. lividum* into soil which is then environmentally transferred to amphibian skin. Within 5 d post-*Bd* exposure, the environmental transmission of *J. lividum* was able to inhibit the colonization of *Bd* on the skin of *P. cinereus* (Muletz et al. 2012).

Loudon et al. (2014b) identified a "core community" of eight operational taxonomic units (OTUs) which was found on at least 90% of the salamanders throughout the experiment. Their experiment revealed that the most abundant and prevalent OTU was a member of the phylum Verrucomicrobia, and that five out of the eight core OTUs were in the family *Pseudomonadaceae* which all have antifungal properties. Their results also indicate that the availability of different bacteria in the environment influences what bacteria are found on the salamander's skin (Loudon et al. 2014b). Specifically, they suggest that the environment works as a reservoir for bacteria. Without access to this reservoir, the core community of skin microbiota dominates, and the diversity of the microbiome is lower (Loudon et al. 2014b). Loudon et al. (2016) supports these results: 9 out of 12 (75%) OTUs that were overrepresented on *P. cinereus* skin had at least a 97% match to antifungal isolates. They also noted that four of these overrepresented OTUs were part of the core community identified by Loudon et al. (2014b). Loudon et al. (2016) suggest that salamander skin, as an environment, may actively select for bacteria with antifungal activity. Future efforts to protect amphibians from mortality due to diseases such as *Bd* may include exposing captive animals to environmental reservoirs with defensive bacteria. This may improve captive-rearing programs for amphibians to prevent colonization of *Bd* (e.g., Passos et al. 2018).

Protective bacteria for *P. cinereus* against fungal diseases may also originate from the gut of the salamander, although we only found two studies that looked at gut microbes (Wiggins et al. 2011; Fontaine et al. 2018). Wiggins et al. (2011) suggest that the gastrointestinal tract of *P. cinereus* could serve as a reservoir for *J. lividum*. Fontaine et al. (2018) also find evidence of *Janthinobacterium* and other disease resistance related taxa in the guts of *P. cinereus*. This study found an interesting pattern with temperature. Microbial diversity, including those taxa involved in disease resistance, declined at 20°C compared to 10°C and 15°C, and digestive performance was greatest at 15°C. Additionally, the relative abundance of pathogenic taxa increased at 20°C (Fontaine et al. 2018).

In terms of how *P. cinereus* responds to *Bd* infection, a small number of studies have documented behavioral effects of *Bd* infection, loss of body mass, differential infection by color phenotype, and gene expression. As noted earlier in the Predators and Parasites section, natural incidence of *Bd* infection in *P. cinereus* is generally quite low ($\leq$2%, with the exception of a New Brunswick population with infection rates around 13%; Jongsma et al. 2019). In a behavioral study, *Bd*-infected salamanders attacked prey significantly more often than noninfected individuals, and the prevalence of *Bd* among *P. cinereus* decreased over time (Hess et al. 2015). The latter result led Hess et al. (2015) to suggest that *P. cinereus* may have natural resistance to *Bd*. The former result makes biological sense in the context of Harris et al. (2009) and Becker and Harris (2010), which both show that *Bd*-infected *P. cinereus* without protective bacteria lose significantly more body mass than controls (in both studies) and individuals inoculated with protective bacteria (Harris et al. 2009). Additionally, Becker and Harris (2010) showed that a reduction of cutaneous bacteria prior to *Bd* infection led to increased limb-lifting behavior, which had not been observed in this species before, and was only observed in infected individuals.

Venesky et al. (2015) looked at differential effects of *Bd* infection by color phenotype in the laboratory. Unstriped *P. cinereus* had both a higher prevalence of infection and higher mortality due to *Bd* than the striped individuals (Venesky et al. 2015). The authors note that these results conflict with a previously noted connection between high levels of melanin and disease resistance, but that the behavioral differences between morphs (e.g., Venesky and Anthony 2007; Davis and Milanovich 2010; Reiter et al. 2014) may increase the stress experienced by unstriped morphs thus reducing their resistance to infection. Finally, Ellison et al. (2020) found changes in gene expression, mediated by temperature, in *P. cinereus* who were uninfected, recently infected, or naturally recovered from infection with *Bd*. At lower temperatures, inflammation transcripts were more commonly expressed, while at higher temperatures, salamanders shift to increased expression of adaptive immune genes, including MHC (major histocompatibility complex) genes (Ellison et al. 2020).

We found three studies that explore how presence or absence of *P. cinereus* may impact soil microbial communities, and the results are somewhat equivocal (Walker et al. 2014; Hickerson et al. 2017; Walker et al. 2018). Two studies, one based in Ohio (Walker et al. 2014) and the other in West Virginia (Walker et al. 2018), used a metagenomics approach to explore the impact of the removal of *P. cinereus* on the fungal detritivore food web. Fungal community diversity and composition were not affected by removal of *P. cinereus*, but there were significant shifts in relative abundance of the fungal groups (Walker et al. 2014, 2018). Hickerson et al. (2017) used phospholipid fatty acid (PLFA) analysis to explore the effect of *P. cinereus* on the microbial community in Ohio. Although removal of intraguild predators had little effect on soil and leaf litter microbial communities, the treatment in which salamanders were most abundant (centipedes removed) suppressed bacteria, which in turn decreased the rate of leaf litter decomposition (Hickerson et al. 2017).

Additionally, only a small number of studies explored change in microbial communities over space and time (Muletz-Wolz et al. 2017, 2018, 2019; Barnes et al. 2020). The work of Muletz-Wolz and colleagues has explored skin microbial communities across an elevational gradient in Maryland and Virginia. They found that location, rather than host characteristics, was the best predictor of prevalence of antifungal bacteria (Muletz-Wolz et al. 2017); higher elevations had greater alpha diversity of bacterial taxa than lower elevations (Muletz-Wolz et al. 2018); and increasing the pathogen load and increasing temperatures changed the microbial community structure, which suggests that *P. cinereus* may not be resistant to *Bd* in all ecological contexts (Muletz-Wolz et al. 2019). Finally, in New York, Barnes et al. (2020) found that the composition of bacterial communities, but not overall diversity, varied with a land use gradient (urban, suburban, exurban), but there were similar levels of *Bd* inhibition among each of these different land use bacterial communities.

Studying the interactions of *P. cinereus* with skin, gut, and environmental microbes is still a relatively new research focus. We also note that this topic is one of the most geographically restricted, with 65% (17/26) of studies discussed earlier using salamanders from Virginia, and the remaining nine studies using salamanders from adjacent central, mid-Atlantic states (Ohio, West Virginia, Pennsylvania, Maryland, and New York). There is evidence that microbial taxa change over time, space, and with access to soil reservoirs (e.g., Loudon et al. 2014b; Muletz-Wolz et al. 2018; Barnes et al. 2020), thus standardized microbial sampling, such as that described by Walker et al. (2015), is needed throughout the range of *P. cinereus* for comparable data that can then be used to understand the relationships of *P. cinereus* with microbial taxa fully. Other gaps in salamander microbiota research include exploring the distribution of different bacteria across the body regions of the salamander. Culp et al. (2007) suggests there may be a nonrandom distribution of different species in different body regions and that future work should look to swab the whole animal at multiple locations on the body to determine if/where different species may congregate. We also do not fully understand the relative roles and interactions of microbial metabolites versus salamander skin secretions. Lauer et al. (2007) suggest separating and analyzing the antibiotic chemicals produced by the animal from those produced by bacteria on the skin. They also suggest conducting experiments using antibiotics to determine the roles of different cutaneous bacteria.

Additional topics: Ecotoxicology.—The final additional topic that has grown considerably since Petranka (1998) explores the responses of *P. cinereus* to a variety of anthropogenic environmental contaminants. These ecotoxicology papers generally subject individual salamanders to multiple concentrations of compounds with known toxicity in other vertebrates. In most cases, the concentrations tested are well below field values at contaminated sites, and salamanders show some ability to detect and avoid some of these contaminants.

Several studies using salamanders from Massachusetts and Maryland have focused on contaminants commonly found on current and former United States military installations, including RDX (1,3,5-trinitrohexahydro-1,3,5-triazine; Johnson et al. 2004), 2,4-DNT (dinitrotoluene; Johnson et al. 2007), TNT (trinitrotoluene; Bazar et al. 2008), copper (Bazar et al. 2009), lead (Bazar et al. 2010), and HMX (high melting explosive or octahydro-1,3,5,7-tetranitro-1,3,5,7-tetrazocine; Johnson et al. 2010). All of these except HMX had negative effects on *P. cinereus* at the highest concentrations tested (Johnson et al. 2004, 2007, 2010; Bazar et al. 2008, 2009, 2010). The most common symptoms were weight loss, depressed white blood cell counts, and death. Additionally, in the copper treatments, the authors observed lethargy, unresponsiveness, and inhibition of the righting reflex (Bazar et al. 2009). HMX did not seem to affect *P. cinereus*, and the authors suggest that this could be because of differences in how HMX is absorbed through salamander skin versus through the gastrointestinal tract of the other vertebrates tested (Johnson et al. 2010).

Mercury (Hg) concentrations found in *P. cinereus* increase when individuals are exposed to contaminated soil compared to individuals from noncontaminated sites (Bergeron et al. 2010a). Bergeron et al. (2010a) reported higher Hg in *P. cinereus* than any previous literature, but also noted a low sample size of 24 individuals. It is not clear from this study if Hg accumulation has negative effects on the salamanders or if it should be more of a concern for the predators that eat salamanders. A follow-up study found that total Hg and (mono)methylmercury (MMHg) concentrations are positively correlated in *P. cinereus* from contaminated sites (Bergeron et al. 2010b). The same study did not find accumulation of selenium (Se) above what is expected for normal background. Selenium is thought to be antagonistic with Hg, offering some protection from Hg toxicity (Bergeron et al. 2010b). Because of the capacity of *P. cinereus* to take in Hg from the surrounding environment, it is suggested that *P. cinereus* be used as a bioindicator to monitor Hg accumulation in the landscape (Townsend and Driscoll 2013).

Two laboratory studies have demonstrated that *P. cinereus* is able to detect and avoid contaminated soils, suggesting that contaminated sites in nature would simply not be colonized by salamanders. First, Gertzog et al. (2011) found that *P. cinereus* can detect and avoid substrates which have been contaminated with herbicides such as Roundup, Bayer Brushkiller, and Spectracide Brush Killer. Second, Gaglione et al. (2011) found that *P. cinereus* can detect and avoid substrates contaminated with urea. Finally, a third study tested the effects of the microbial pesticide *Bacillus thuringiensis* var. *kurstaki* (*Btk*) on *P. cinereus* abundance or diet in West Virginia and found no adverse effects (Raimondo et al. 2003).

Discussion

Is *Plethodon cinereus* an EEB Model Organism?

In completing the comprehensive review, it is clear that the Duffy et al. (2021: p. 55) requirement that a model system have been studied long enough to generate a “substantive body of knowledge” has been met by the research to date on *P. cinereus*. In defining EEB model systems, Duffy et al. (2021) highlight Travis's (2006: p. 307) related stipulations that “robust inference requires horizontal comparisons and vertical integration.” These, too, have been clearly met by the research to date on *P. cinereus*, which has been used to better understand closely related, but more geographically restricted, taxa (horizontal comparisons) and has been studied at nearly every scale of biological organization (vertical integration; Fig. 3). Outside of those who work on plethodontid salamanders, however, we do not think the EEB community would necessarily designate *P. cinereus* as a model organism—not in the comprehensive way that others readily provide examples such as *Anolis* lizards, *Mimulus* plants, or *Drosophila* flies (e.g., see Duffy et al. 2021: Supplemental Material S1; table S1).

Thus, to date, *P. cinereus* falls short of model organism status. This is likely due in part to many of the broader challenges within EEB fields around developing new model systems. In particular, the broader appeal of *P. cinereus* research and plethodontids as model organisms more generally may have been hampered by a lack of methods standardization, barriers to participation in the field of herpetology (e.g., Perry et al. 2020), funding constraints (e.g., Clutton-Brock and Sheldon 2010), and other limitations imposed on both academic and nonacademic scientists in the United States and Canada (e.g., lack of data sharing ethos). However, with the vast body of knowledge on *P. cinereus*, we have the opportunity to build future work with a deliberate eye towards inclusive, coordinated collaboration with an emphasis on knowledge and data sharing. Specifically, the benefits of collaborative ecological research networks can be leveraged for collecting organismal data at larger temporal and spatial scales than individual researchers (Hughes et al. 2017; Clutton-Brock and Sheldon 2010).

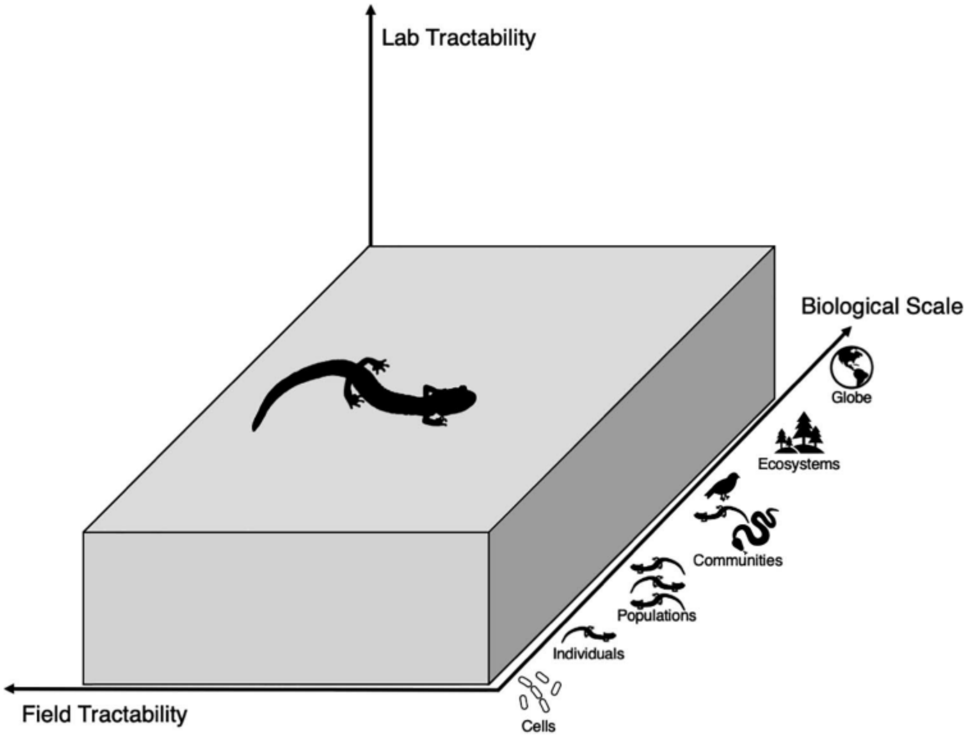

FIG. 3.—The versatility of *P. cinereus* as a model organism in EEB. Salamanders are highly tractable in both lab and field, and at all biological scales through ecosystems. Lab tractability is lower than field tractability because they are a long-lived species and a protocol for controlled breeding in captivity has not been successfully developed yet. Figure adapted from from Duffy et al. (2021: fig. 1).

Applying the Collaborative Research Network Model to *P. cinereus*

Illuminating fundamental phenomena in EEB (Sutherland et al. 2013) not only benefits from the use of diverse model systems (Duffy et al. 2021; Wale and Duffy 2021), but also from long-term data sets (Clutton-Brock and Sheldon 2010). Access to high-speed internet connections and smart devices has rapidly increased, making it easier to manage large collaborative research networks that coordinate large scale experiments and surveys across time and space. One such network, the Salamander Population and Adaptation Research Collaboration Network (SPARCnet) was founded in 2013 by researchers at the United States Geological Survey Amphibian and Reptile Monitoring Initiative (USGS ARMI) and Pennsylvania State University (SPARCnet 2024). Since then, it has grown to include over 30 research collaborators and 13 education collaborators (e.g., nature centers) across 13 states and provinces within the geographic range of *P. cinereus* (Supplemental Material S16; Supplemental Fig. S4, available online).

SPARCnet methodology employs a simple and inexpensive, yet robust and spatially explicit mark-recapture design (Sutherland et al. 2016; Muñoz et al. 2016b; Fleming et al. 2020, 2021; Grant et al. 2024) using standardized ACO plots, arranged in pairs for potential experimental and control studies (e.g., snow removal, forest management). SPARCnet holds annual meetings and has developed research protocols and minimum core data collection agreements among researchers that allow this network to meet the growing needs of long-term studies focusing on changing demography of the focal species, *P. cinereus* (Clutton-Brock and Sheldon 2010). SPARCnet's framework is flexible, allowing individual researchers to design side projects that are site-specific or network-wide. Additionally, the flexibility of SPARCnet structure allows researchers to exploit observations and research questions that emerge in real time (i.e., emergence of disease or toxicology) and work together to study these phenomena across the geographic range in tandem rapidly.

Collaborative research networks provide a solution for consistent data collection methods and help network participants address the many inconsistencies that come with studying a wide-ranging species like *P. cinereus*. It is well known that it is difficult to study patterns from past data based on differences in methodology and confounding factors from data collection (Fraser et al. 2013; Grant 2015), and that EEB studies typically suffer from geographic and taxonomic biases, as we have demonstrated throughout this review (Supplemental Material S15; Supplemental Data S14). A geographically and intellectually distributed network, such as SPARCnet, addresses these concerns to provide a robust spatial and temporal assessment of the current state and change over time of *P. cinereus* populations across its range. The large geographic range and high local abundances make *P. cinereus* a highly accessible model system for a great number of diverse institutions, researchers, and their students. We hope that our experience provides a blueprint for other researchers to more confidently develop a diversity of ecological model systems called for by Duffy et al. (2021).

As we have seen in nearly every section of our review, the great amount of geographic variation in *P. cinereus* biology often leads to puzzling contradictions of *P. cinereus* physiology, behavior, roles in ecosystems when studies are repeated in new locations. These contradictions and their impact on the potential role of *P. cinereus* as an indicator species (especially among color phenotypes; see Systematics and Geographic Variation) have resulted in confusion, valid criticisms, and necessary caution (e.g., Moore and Ouellet 2015). However, considering Duffy et al. (2021) and in the hindsight of this review, we think the inconsistencies—the natural variation of a single species over a wide geographic area—are exactly what makes *P. cinereus* an ideal EEB model organism.

Unlike the other seven of the top eight most well-studied salamander species, *P. cinereus* is the only member of the Plethodontidae (Supplemental Material S1; Table S4, Supplemental Material S3; Supplemental Data S2). As a direct-developing member of the largest family of salamanders, *P. cinereus* is *more* representative of the majority of ecologically and evolutionarily successful salamander taxa than any of the other top seven species. What we learn by studying *P. cinereus* is more likely to apply to vulnerable and endangered plethodontids than what we learn by studying *A. maculatum* or *N. viridescens* (Supplemental Material S1; Table S4). Combined with their large population sizes and position in the forest food web, we see endless potential for illuminating fundamental phenomena in EEB with *P. cinereus*. On top of the overwhelming volume of ecological and behavioral knowledge we have summarized above, the well-supported systematics and evolutionary knowledge of both Plethodontidae and *Plethodon* (e.g., Wake and Larson 1987; Wake 2009; and see Staub and Muller 2017 and Kuchta 2019 for overviews of the work of D. B. Wake and R. Highton, respectively) there is also a very healthy level of recent systematic interest in both the family and the genus (e.g., Wiens et al. 2006; Fisher-Reid and Wiens 2011; Fisher-Reid et al. 2012), making plethodontids truly a model clade, not just *P. cinereus* a model organism.

In terms of the three axes Duffy et al. (2021) include in their Fig. 1, we know, and demonstrate with our review, that *P. cinereus* is both highly lab and field tractable, and research can be and has been done at all biological scales except for global (Fig. 3). That said, there are some weaknesses, particularly when it comes to lab tractability (Fig. 3), which have yet to be satisfactorily addressed, and indeed may never be so. In the field, individuals spend much of the year underground, no matter the broader phenological pattern (Fig. 2), and when they are surface active, they are most active at night, which can be logistically difficult to observe. In the lab, rearing *P. cinereus* has proven difficult for two primary reasons: First, they are a relatively long-lived species. Direct measures of lifespan, based on a single population at the northern range limit, are between 8 and 9 y (Leclair et al. 2006, 2008). Second, controlled laboratory breeding has not yet been possible. Females can be induced to lay fertilized eggs (e.g., Evans et al. 2020), and courtship behaviors can be observed successfully (Dyal 2006; Jaeger et al. 2016), so perhaps one day we will crack the code for controlled breeding of *P. cinereus*, but, as we have argued here, this requires infrastructure, community ethos, and investment from funding agencies.

CONCLUSIONS

(1) Model systems in evolution, ecology, and behavior (EEB) are similar, but also different from those in biomolecular and biomedical sciences. Variation is a feature, not a bug.
(2) As lungless ectotherms, salamanders in the family Plethodontidae have great potential to serve as a model clade within EEB.
(3) One plethodontid in particular, *P. cinereus*, stands out for the overwhelming depth of knowledge accumulated in the last several decades, its critical niche position in forest ecosystems, its accessibility and tractability in both lab and field, and its close, well-studied relationships with other members of its taxonomic family.
(4) In just 22 yr, over 400 papers on all aspects of the evolution, ecology, and behavior of *P. cinereus* have been published in peer-reviewed journals. Although studies are often highly localized and demonstrate high levels of local variation across the large geographic range of *P. cinereus*, they also demonstrate the breadth of EEB fundamental phenomena that can be studied using *P. cinereus*.
(5) *Plethodon cinereus* falls short of model system status because of lack of infrastructure, lack of community ethos, and lack of investment by funding agencies.
(6) The collaborative research network SPARCnet follows in the footsteps of other collaborative research networks to study *P. cinereus* populations cohesively and repeatedly across the geographic range. Local variation is expected and embraced as we leverage our intellectually and geographically distributed network to illuminate fundamental phenomena in EEB through the eyes of a woodland salamander.

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SUPPLEMENTAL MATERIAL

Supplemental material associated with this monograph can be found online at https://doi.org/10.1655/HERPMONOGRAPHS-D-21-00003.S1; https://doi.org/10.1655/HERPMONOGRAPHS-D-21-00003.S2; https://doi.org/10.1655/HERPMONOGRAPHS-D-21-00003.S3; https://doi.org/10.1655/HERPMONOGRAPHS-D-21-00003.S4; https://doi.org/10.1655/HERPMONOGRAPHS-D-21-00003.S5; https://doi.org/10.1655/HERPMONOGRAPHS-D-21-00003.S6; https://doi.org/10.1655/HERPMONOGRAPHS-D-21-00003.S7; https://doi.org/10.1655/HERPMONOGRAPHS-D-21-00003.S8; https://doi.org/10.1655/HERPMONOGRAPHS-D-21-00003.S9; https://doi.org/10.1655/HERPMONOGRAPHS-

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LITERATURE CITED

Aasen, G., and N. Reichenbach. 2004. Is the Red-backed Salamander (*Plethodon cinereus*) encroaching upon populations of the Peaks of Otter Salamander (*P. hubrichti*)? Catesbeiana 24:17–20.

Acord, M.A., C.D. Anthony, and C.-A.M. Hickerson. 2013. Assortative mating in a polymorphic salamander. Copeia 2013:676–683.

Adams, D.C. 2000. Divergence of trophic morphology and resource use among populations of *Plethodon cinereus* and *P. hoffmani* in Pennsylvania: A possible case of character displacement. Pp. 383–395 in Biology of Plethodontid Salamanders (R.C. Bruce, R.G. Jaeger and L.D. Houck, eds.). Springer Science+, USA.

Adams, D.C. 2011. Quantitative genetics and evolution of head shape in *Plethodon* salamanders. Evolutionary Biology 38:278.

Adams, D.C., and F.J. Rohlf. 2000. Ecological character displacement in *Plethodon*: Biomechanical differences found from a geometric morphometric study. Proceedings of the National Academy of Sciences 97:4106–4111.

Adams, D.C., M.E. West, and M.L. Collyer. 2007. Location-specific sympatric morphological divergence as a possible response to species interactions in West Virginia *Plethodon* salamander communities. Journal of Animal Ecology 76:289–295.

Adams, D. C., C.M. Berns, K.H. Kozak, and J.J. Wiens. 2009. Are rates of species diversification correlated with rates of morphological evolution? Proceedings of the Royal Society of London B 276:2729–2738.

Alford, R.A., and S.J. Richards. 1999. Global amphibian declines: A problem in applied ecology. Annual Review of Ecology and Systematics 30:133–165.

AmphibiaWeb. 2024. AmphibiaWeb: Information on Amphibian Biology and Conservation. Available at https://amphibiaweb.org. Accessed on 10 September 2024. University of California, USA.

Anderson, J.T., A.B. Solis, and J.D. Osbourne. 2013. Herpetofaunal abundance in forested edge and interior locations of West Virginia. Pp. 474–486 in Proceedings of the 18th Central Hardwood Forest Conference GTR-NRS-P-117 (G.W. Miller, T.M. Schuler, K.W. Gottschalk, J.R. Brooks, S.T. Grushecky, B.D. Spong, and J.S. Rentch, eds.). U.S. Department of Agriculture, USA.

Angleberger, M.A.P., and J.P. Chinnici. 1975. Dimorphism in the Red-backed Salamander *Plethodon cinereus* at Mountain Lake, Virginia USA. Virginia Journal of Science 26:153–158.

Ankeny, R.A., and S. Leonelli. 2011. What's so special about model organisms? Studies in History and Philosophy of Science Part A 42:313–323.

Anthony, C.D., and R.A. Pfingsten. 2013. Eastern Red-backed Salamander, *Plethodon cinereus*. Pp. 335–360 in Amphibians of Ohio (R.A. Pfingsten, J.G. Davis, T.O. Matson, G.J. Lipps, D. Wynn, and B.J. Armitage, eds.). Ohio Biological Survey, USA.

Anthony, C.D., J.R. Mendelson, and R.R. Simons. 1994. Differential parasitism by sex on plethodontid salamanders and histological evidence for structural damage to the nasolabial groove. The American Midland Naturalist 132:302–307.

Anthony, C.D., C.-A.M. Hickerson, and M.D. Venesky. 2007. Responses of juvenile terrestrial salamanders to introduced (*Lithobius forficatus*) and native centipedes (*Scolopocryptops sexspinosus*). Journal of Zoology 271:54–62.

Anthony, C.D., M.D. Venesky, and C.-A.M. Hickerson. 2008. Ecological separation in a polymorphic terrestrial salamander. Journal of Animal Ecology 77:646–653.

Anthony, C.D., K.E. Jaworski, M. Messner, and C.-A. Hickerson. 2017. Differences in prey availability within the territories of striped and unstriped Eastern Red-backed Salamanders (*Plethodon cinereus*). Herpetological Review 48:509–514.

Anthony, C.D., C.-A.M. Hickerson, T.M. Evers, K.L. Garner, and R.D. Mayer. 2023. Sexually dimorphic biofluorescence of the postcloacal gland in the terrestrial salamander, *Plethodon cinereus*. Journal of Herpetology 57:262–269.

Arif, S., D. Adams, and J. Wicknick. 2007. Bioclimatic modelling, morphology, and behaviour reveal alternative mechanisms regulating the distributions of two parapatric salamander species. Evolutionary Ecology Research 9:843–854.

Arnold, S.J. 1977. The evolution of courtship behavior in New World salamanders with some comments on Old World salamandrids. Pp. 141–183 in The Reproductive Biology of Amphibians (D.H. Taylor and S.I. Guttman, eds.). Springer, USA.

Augustine, L., and M. Neff. 2016. Determining the prevalence of Amphibian Chytrid Fungus (*Batrachochytrium dendrobatidis*) and *Ranavirus* at Long Branch Nature Center in Arlington, Virginia. Catesbeiana 36:35–42.

Avila, L.A., R. Wiggins, E.D. Brodie, Jr., and E.D. Brodie, III. 2012. Garter Snakes do not respond to TTX via chemoreception. Chemoecology 22:263–268.

Barnes, E.M., E.L. Carter, and J.D. Lewis. 2020. Predicting microbiome function across space is confounded by strain-level differences and functional redundancy across taxa. Frontiers in Microbiology 11:101. DOI: https://dx.doi.org/10.3389/fmicb.2020.00101.

Baxter-Gilbert, J., L. King, and J.L. Riley. 2022. First report of eastern Red-backed Salamander (*Plethodon cinereus*) on Newfoundland. The Canadian Field Naturalist 136:5–9.

Bayer, C.S.O., A.M. Sackman, K. Bezold, P.R. Cabe, and D.M. Marsh. 2012. Conservation genetics of an endemic mountaintop salamander with an extremely limited range. Conservation Genetics 13:443–454.

Bazar, M.A., M.J. Quinn, K. Mozzachio, and M.S. Johnson. 2008. Toxicological responses of Red-backed Salamanders (*Plethodon cinereus*) to subchronic soil exposures of 2,4,6-trinitrotoluene. Environmental Toxicology and Chemistry 27:1393–1398.

Bazar, M.A., M.J. Quinn, K. Mozzachio, J.A. Bleiler, C.R. Archer, C.T. Phillips, and M.S. Johnson. 2009. Toxicological responses of Red-backed Salamanders (*Plethodon cinereus*) to soil exposures of copper. Archives of Environmental Contamination and Toxicology 57:116–122.

Bazar, M.A., M.J. Quinn, K. Mozzachio, J.A. Bleiler, C.R. Archer, C.T. Phillips, and M.S. Johnson. 2010. Toxicological responses of Red-Backed Salamander (*Plethodon cinereus*) exposed to aged and amended soils containing lead. Archives of Environmental Contamination and Toxicology 58:1040–1047.

Becker, M.H., and R.N. Harris. 2010. Cutaneous bacteria of the Redback Salamander prevent morbidity associated with a lethal disease. PLoS One 5:e10957.

Becker, M.H., R.M. Brucker, C.R. Schwantes, R.N. Harris, and K.P.C. Minbiole. 2009. The bacterially produced metabolite violacein is associated with survival of amphibians infected with a lethal fungus. Applied and Environmental Microbiology 75:6635–6638.

Becker, S., C. Moorman, C. DePerno, and T. Simons. 2013. Quantifiable long-term monitoring on parks and nature preserves. Southeastern Naturalist 12:339–352.

Beier, C.M., A.M. Woods, K.P. Hotopp, J.P. Gibbs, M.J. Mitchell, M. Dovčiak, D.J. Leopold, G.B. Lawrence, and B.D. Page. 2012. Changes in faunal and vegetation communities along a soil calcium gradient in northern hardwood forests. Canadian Journal of Forest Research 42:1141–1152.

Bellocq, M.I., K. Kloosterman, and S.M. Smith. 2000. The diet of coexisting species of amphibians in Canadian Jack Pine forests. Herpetological Journal 10:63–68.

Bennett, R.M., R.M. Ross, W.A. Lellis, and L.A. Redell. 2003. Terrestrial salamander preference for artificial cover objects made from four species of wood. Journal of the Pennsylvania Academy of Science 76:77–79.

Bergeron, C.M., C.M. Bodinof, J.M. Unrine, and W.A. Hopkins. 2010a. Bioaccumulation and maternal transfer of mercury and selenium in amphibians. Environmental Toxicology and Chemistry 29:989–997.

Bergeron, C.M., C.M. Bodinof, J.M. Unrine, and W.A. Hopkins. 2010b. Mercury accumulation along a contamination gradient and nondestructive indices of bioaccumulation in amphibians. Environmental Toxicology and Chemistry 29:980–988.

Best, M.L., and H.H. Welsh. 2014. The trophic role of a forest salamander: Impacts on invertebrates, leaf litter retention, and the humification process. Ecosphere 5:16. DOI: https://dx.doi.org/10.1890/ES13-00302.1.

Biddle, J.R., A.H. Grant, and E.B. Liebgold. 2017. Factors affecting the growth of Eastern Red-backed Salamanders, *Plethodon cinereus*. Herpetologica 73:89–93.

Blankers, T., D.C. Adams, and J.J. Wiens. 2012. Ecological radiation with limited morphological diversification in salamanders. Journal of Evolutionary Biology 25:634–646.

Bolek, M.G., and J.R. Coggins. 1998. Helminth parasites of the Spotted Salamander *Ambystoma maculatum* and Red-backed Salamander *Plethodon c. cinereus* from northwestern Wisconsin. Journal of the Helminthological Society of Washington 65:98–102.

Bondi, C.A., S. Green, and C.M. Beier. 2015. Evaluation of gastric lavage method for diet analysis of the Eastern Red-backed Salamander (*Plethodon cinereus*). Herpetological Review 46:196–199.

Bondi, C.A., C.M. Beier, P.K. Ducey, G.B. Lawrence, and S. Bailey. 2016. Can the Eastern Red-backed Salamander (*Plethodon cinereus*) persist in an acidified landscape? Ecosphere 7:e01318. DOI: https://dx.doi.org/10.1002/ecs2.1318.

Bondi, C.A., C.M. Beier, M.K. Fierke, and P.K. Ducey. 2019. The role of feeding strategy in the tolerance of a terrestrial salamander (*Plethodon cinereus*) to biogeochemical changes in northern hardwood forests. Canadian Journal of Zoology 97:281–293.

Bonett, R.M., N.M. Ledbetter, A.J. Hess, M.A. Herrboldt, and M. Denoël. 2022. Repeated ecological and life cycle transitions make salamanders an ideal model for evolution and development. Developmental Dynamics 251:957–972.

Bonin, J., and Y. Bachand. 1997. The use of artificial covers to survey terrestrial salamanders in Quebec. Herpetological Conservation 1:175–179.

Brenner, F.J., E.D. Smith, and M.J. Marr. 2005. Factors affecting the distribution of Redback Salamanders (*Plethodon cinereus*) in a second growth forest community. Journal of the Pennsylvania Academy of Science 78:53–56.

Brodie E.D., Jr., R.T. Nowak, and W.R. Harvey. 1979. The effectiveness of antipredator secretions and behavior of selected salamanders against shrews. Copeia 1979:270–274.

Brooks, R.T. 1999. Residual effects of thinning and high White-tailed Deer densities on Northern Redback Salamanders in Southern New England Oak forests. The Journal of Wildlife Management 63:1172–1180.

Brooks, R.T. 2001. Effects of the removal of overstory hemlock from hemlock-dominated forests on Eastern Redback Salamanders. Forest Ecology and Management 149:197–204.

Brown, G.S., L. Pollock, P.D. DeWitt, and N. Dawson. 2020. Responses of terrestrial animals to forest characteristics and climate reveals ecological indicators for sustaining wildlife in managed forests. Forest Ecology and Management 459:117854. DOI: https://dx.doi.org/10.1016/j.foreco.2019.117854.

Bruce, R.C. 2008. Intraguild interactions and population regulation in plethodontid salamanders. Herpetological Monographs 22:31–53.

Brucker, R.M., R.N. Harris, C.R. Schwantes, T.N. Gallaher, D.C. Flaherty, B.A. Lam, and K.P.C. Minbiole. 2008a. Amphibian chemical defense: Antifungal metabolites of the microsymbiont *Janthinobacterium lividum* on the salamander *Plethodon cinereus*. Journal of Chemical Ecology 34:1422–1429.

Brucker, R.M., C.M. Baylor, R.L. Walters, A. Lauer, R.N. Harris, and K.P.C. Minbiole. 2008b. The identification of 2,4-diacetylphloroglucinol as an antifungal metabolite produced by cutaneous bacteria of the salamander *Plethodon cinereus*. Journal of Chemical Ecology 34:39–43.

Brunges, H.J., J.P. Dunn, D.R. Helder, and S. Otieno. 2020. Effects of invasive earthworm feeding guilds and their interactions with physiographic conditions on the relative abundance and distribution of woodland salamanders. Herpetological Conservation and Biology 15:16–24.

Burgett, A.A., and G.R. Smith. 2012. Differential responses of Eastern Red-backed Salamanders (*Plethodon cinereus*) to conspecifics and centipedes. Current Herpetology 31:78–86.

Burton, T.M., and G.E. Likens. 1975a. Salamander populations and biomass in the Hubbard Brook Experimental Forest, New Hampshire. Copeia 1975:541–546.

Burton, T.M., and G.E. Likens. 1975b. Energy flow and nutrient cycling in salamander populations in the Hubbard Brook Experimental Forest, New Hampshire. Ecology 56:1068–1080.

Cabe, P.R., R.B. Page, T.J. Hanlon, M.E. Aldrich, L. Connors, and D.M. Marsh. 2007. Fine-scale population differentiation and gene flow in a terrestrial salamander (*Plethodon cinereus*) living in continuous habitat. Heredity 98:53–60.

Cáceres-Charneco, R.I., and T.S. Ransom. 2010. The influence of habitat provisioning: Use of earthworm burrows by the terrestrial salamander, *Plethodon cinereus*. Population Ecology 52:517–526.

Cameron, A.C., C.-A.M. Hickerson, and C.D. Anthony. 2016. *Plethodon cinereus* (Eastern Red-backed Salamander) not affected by long-term exposure to soil liming. Northeastern Naturalist 23:88–99.

Cameron, A.C., J.J. Anderson, and R.B. Page. 2017. Assessment of intra and interregional genetic variation in the Eastern Red-backed Salamander, *Plethodon cinereus*, via analysis of novel microsatellite markers. PLoS One 12:e0186866. DOI: https://dx.doi.org/10.1371/journal.pone.0186866.

Cameron, A.C., R.B. Page, J.I. Watling, C.-A.M. Hickerson, and C.D. Anthony. 2019. Using a comparative approach to investigate the relationship between landscape genetic connectivity among woodland salamander populations. Conservation Genetics 20:1265–1280.

Carfioli, M.A., H.M. Tiebout, S.A. Pagano, K.M. Heister, and F.C. Lutcher. 2000. Monitoring *Plethodon cinereus* populations: Field tests of experimental coverboard designs. Pp. 463–475 in Biology of Plethodontid Salamanders (R.C. Bruce, R.G. Jaeger, and L.D. Houck, eds.). Springer Science+, USA.

Carlson, B.E., C.J. Thawley, and S.P. Graham. 2016. Natural history of the Valley and Ridge Salamander (*Plethodon hoffmani*): Demography, movement, microhabitats, and abundance. Herpetological Conservation and Biology 11:315–327.

Carlson, T.A.Y., and E.J. Szuch. 2007. Un-weathered (new) artificial cover objects effectively sample plethodontid salamanders in Michigan. Herpetological Review 38:412–415.

Caro, T. 2010. Conservation by Proxy: Indicator, Umbrella, Keystone, Flagship, and Other Surrogate Species. Island Press, USA.

Carpenter, D.W., R.E. Jung, and J.W. Sites. 2001. Conservation genetics of the endangered Shenandoah Salamander (*Plethodon shenandoah*, Plethodontidae). Animal Conservation 4:111–119.

Caruso, N.M., and K.R. Lips. 2013. Truly enigmatic declines in terrestrial salamander populations in Great Smoky Mountains National Park. Diversity and Distributions 19:38–48.

Caruso, N.M., M.W. Sears, D.C. Adams, and K.R. Lips. 2014. Widespread rapid reductions in body size of adult salamanders in response to climate change. Global Change Biology 20:1751–1759.

Casper, G.S. 2005. *Plethodon cinereus* (Green 1918) Eastern Red-backed Salamander. Pp. 796–800 in Amphibian Declines: The Conservation Status of United States Species (M. Lannoo, ed.). University of California Press, USA.

Cassell, R.W., and M.P. Jones. 2005. Syntopic occurrence of the erythristic morph of *Plethodon cinereus* and *Notophthalmus viridescens* in Pennsylvania. Northeastern Naturalist 12:169–172.

Chalmers, R.J., and C.S. Loftin. 2010. *Plethodon cinereus* (Eastern Red-backed Salamander). Wetland habitat. Herpetological Review 41:468–469.

Chambert, T., E.H.C. Grant, D.A.W. Miller, J.D. Nichols, K.P. Mulder, and A.B. Brand. 2018. Two-species occupancy modelling accounting for species misidentification and non-detection. Methods in Ecology and Evolution 9:1468–1477.

Chouinard, A.J. 2012. Rapid onset of mate quality assessment via chemical signals in a woodland salamander (*Plethodon cinereus*). Behavioral Ecology and Sociobiology 66:765–775.

Church, D.R., and R.K. Okazaki. 2002. Seasonal variation of plasma testosterone titers in male redback salamanders, *Plethodon cinereus*. Amphibia-Reptilia 23:93–97.

Ciul, K., L. Simpson, G.R. Smith, and J.E. Rettig. 2010. Evaluation of the rate of artificial coverboard use by the salamander, *Plethodon cinereus*, in the vicinity of natural cover objects. Bulletin of the Maryland Herpetological Society 46:17–19.

Clutton-Brock, T., and B.C. Sheldon. 2010. Individuals and populations: The role of long-term, individual-based studies of animals in ecology and evolutionary biology. Trends in Ecology & Evolution 25:562–573.

Connette, G.M., J.A. Crawford, and W.E. Peterman. 2015. Climate change and shrinking salamanders: Alternative mechanisms for changes in plethodontid salamander body size. Global Change Biology 21:2834–2843.

Connors, L.M., and P.R. Cabe. 2003. Isolation of dinucleotide microsatellite loci from Red-backed Salamander (*Plethodon cinereus*). Molecular Ecology Notes 3:131–133.

Cooper, W.E., Jr., and G.M. Burghardt. 1990. A comparative analysis of scoring methods for chemical discrimination of prey by squamate reptiles. Journal of Chemical Ecology 16:45–65.

Cosentino, B.J., and K.M. Brubaker. 2018. Effects of land use legacies and habitat fragmentation on salamander abundance. Landscape Ecology 33:1573–1584.

Cosentino, B.J., and D.C. Droney. 2016. Movement behaviour of woodland salamanders is repeatable and varies with forest age in a fragmented landscape. Animal Behaviour 121:137–146.

Cosentino, B.J., J.-D. Moore, N.E. Karraker, M. Ouellet, and J.P. Gibbs. 2017. Evolutionary response to global change: Climate and land use interact to shape color polymorphism in a woodland salamander. Ecology and Evolution 7:5426–5434.

Cote, G., S. Getty, A. Vokoun, S. Carmichael, H. Hunt, N. Letton, K.D. McEntire, J.A. Wooten, and C.D. Camp. 2016. A test of scent-trailing as a contributing factor in the climbing behaviour of the Redback Salamander (*Plethodon cinereus*). Amphibia-Reptilia 37:111–116.

CRC (Collaborative Research Centre). 2014. Collaborative Research Centre 806 Database: Maps. Available at https://crc806db.uni-koeln.de/layer/show/6. Accessed on 2 August 2021. University of Cologne, Germany.

Crespi, E.J., and H. Lessig. 2004. Mothers influence offspring body size through post-oviposition maternal effects in the Redbacked Salamander, *Plethodon cinereus*. Oecologia 138:306–311.

Culp, C.E., J.O. Falkinham, III, and L.K. Belden. 2007. Identification of the natural bacterial microflora on the skin of Eastern Newts, Bullfrog tadpoles and Redback Salamanders. Herpetologica 63:66–71.

Cusi, J.C., G. Gagliardi-Urrutia, I.C. Brcko, D.B. Wake, and R. Von May. 2020. Taxonomic status of the Neotropical salamanders *Bolitoglossa altamazonica* and *Bolitoglossa peruviana* (Amphibia: Caudata: Plethodontidae), with the description of a new species from Northern Peru. Zootaxa 4834:365–406.

Dallalio, E.A., A.B. Brand, and E.H.C. Grant. 2017. Climate-mediated competition in a high-elevation salamander community. Journal of Herpetology 51:190–196.

Davic, R.D., and H.H. Welsh. 2004. On the ecological roles of salamanders. Annual Review of Ecology, Evolution, and Systematics 35:405–434.

Davis, A.K., and K. Cecala. 2010. Intraerythrocytic rickettsial inclusions in Ocoee Salamanders (*Desmognathus ocoee*): Prevalence, morphology, and comparisons with inclusions of *Plethodon cinereus*. Parasitology Research 107:363–367.

Davis, A.K., and J.R. Milanovich. 2010. Lead-phase and red-stripe color morphs of Red-backed Salamanders *Plethodon cinereus* differ in hematological stress indices: A consequence of differential predation pressure? Current Zoology 56:238–243.

Davis, A., J. Milanovich, J. DeVore, and J. Maerz. 2009a. An investigation of factors influencing erythrocyte morphology of Red-backed Salamanders (*Plethodon cinereus*). Animal Biology 59:201–209.

Davis, A.K., J.L. DeVore, J.R. Milanovich, K. Cecala, J.C. Maerz, and M.J. Yabsley. 2009b. New findings from an old pathogen: Intraerythrocytic bacteria (Family Anaplasmatacea) in Red-backed Salamanders *Plethodon cinereus*. EcoHealth 6:219–228.

Dawley, E.M., A. Fingerlin, D. Hwang, S.S. John, and C.A. Stankiewicz. 2000. Seasonal cell proliferation in the chemosensory epithelium and brain of Red-backed Salamanders, *Plethodon cinereus*. Brain, Behavior and Evolution 56:1–13.

Dawley, E.M., M. Nelsen, A. Lopata, J. Schwartz, and A. Bierly. 2006. Cell birth and survival following seasonal periods of cell proliferation in the chemosensory epithelia of Red-backed Salamanders, *Plethodon cinereus*. Brain, Behavior and Evolution 68:26–36.

Deitloff, J., D.C. Adams, B.F.M. Olechnowski, and R.G. Jaeger. 2008. Interspecific aggression in Ohio *Plethodon*: Implications for competition. Herpetologica 64:180–188.

Deitloff, J., J.O. Church, D.C. Adams, and R.G. Jaeger. 2009. Interspecific agonistic behaviors in a salamander community: Implications for alpha selection. Herpetologica 65:174–182.

Deitloff, J., J.D. Petersen, and D.C. Adams. 2013. Complex species interactions lead to unpredictable outcomes in *Plethodon*. Herpetologica 69:1–10.

deMaynadier, P.G., and M.L. Hunter. 1995. The relationship between forest management and amphibian ecology: A review of the North American literature. Environmental Reviews 3:230–261.

deMaynadier, P.G., and M.L. Hunter. 1998. Effects of silvicultural edges on the distribution and abundance of amphibians in Maine. Conservation Biology 12:340–352.

Ducey, P.K., M. Messere, K. Lapoint, and S. Noce. 1999. Lumbricid prey and potential herpetofaunal predators of the invading terrestrial flatworm *Bipalium adventitium* (Turbellaria: Tricladida: Terricola). The American Midland Naturalist 141:305–314.

Duellman, W.E., and L. Trueb. 1986. Biology of Amphibians, 1st edition. McGraw Hill, USA.

Duffy, M.A., C. García-Robledo, S.P. Gordon, … L. Zaman. 2021. Model systems in ecology, evolution, and behavior: A call for diversity in our model systems and discipline. The American Naturalist 198:53–68.

Duguay, J.P., and P.B. Wood. 2002. Salamander abundance in regenerating forest stands on the Monongahela National Forest, West Virginia. Forest Science 48:331–335.

Duhaime-Ross, A., G. Martel, and F. Laberge. 2013. Sensory determinants of agonistic interactions in the Red-backed Salamander, *Plethodon cinereus*. Behaviour 150:1467–1489.

Dyal, L.A. 2006. Novel courtship behaviors in three small eastern *Plethodon* species. Journal of Herpetology 40:55–65.

Edwards, E. 2021. Society of Systematic Biologists Presidential Plenary: Rediscovering the Organism in Phylogenetic Biology. Available at https://www.youtube.com/watch?v=335_az6ybXw. Accessed on 14 August 2024. Evolution Meetings, USA.

Ellison, A., K. Zamudio, K. Lips, and C. Muletz-Wolz. 2020. Temperature-mediated shifts in salamander transcriptomic responses to the amphibian-killing fungus. Molecular Ecology 29:325–343.

Evans, A.E., B.R. Forester, E.L. Jockusch, and M.C. Urban. 2018. Salamander morph frequencies do not evolve as predicted in response to 40 years of climate change. Ecography 41:1687–1697.

Evans, A.E., M.C. Urban, and E.L. Jockusch. 2020. Developmental temperature influences color polymorphism but not hatchling size in a woodland salamander. Oecologia 192:909–918.

Faragher, S.G., and R.G. Jaeger. 1997. Distributions of adult and juvenile Red-backed Salamanders: Testing new hypotheses regarding territoriality. Copeia 1997:410–414.

Farallo, V.R., and D.B. Miles. 2016. The importance of microhabitat: A comparison of two microendemic species of *Plethodon* to the widespread *P. cinereus*. Copeia 104:67–77.

Fisher-Reid, M.C., and J.J. Wiens. 2011. What are the consequences of combining nuclear and mitochondrial data for phylogenetic analysis? Lessons from *Plethodon* salamanders and 13 other vertebrate clades. BMC Evolutionary Biology 11:300. DOI: https://dx.doi.org/10.1186/1471-2148-11-300.

Fisher-Reid, M.C., and J.J. Wiens. 2015. Is geographic variation within species related to macroevolutionary patterns between species? Journal of Evolutionary Biology 28:1502–1515.

Fisher-Reid, M.C., K.H. Kozak, and J.J. Wiens. 2012. How is the rate of climatic-niche evolution related to climatic-niche breadth? Evolution 66:3836–3851.

Fisher-Reid, M.C., T.N. Engstrom, C.A. Kuczynski, P.R. Stephens, and J.J. Wiens. 2013. Parapatric divergence of sympatric morphs in a salamander: Incipient speciation on Long Island? Molecular Ecology 22:4681–4694.

Fitzpatrick, B.M., K. Shook, and R. Izally. 2009. Frequency-dependent selection by wild birds promotes polymorphism in model salamanders. BMC Ecology 9:12. DOI: https://dx.doi.org/10.1186/1472-6785-9-12.

Fleming, J., C. Sutherland, S.C. Sterrett, and E.H.C. Grant. 2020. A latent process model approach to improve the utility of indicator species. Oikos 129:1753–1762.

Fleming, J., E.H.C. Grant, S.C. Sterrett, and C. Sutherland. 2021. Experimental evaluation of spatial capture–recapture study design. Ecological Applications 31:e02419. DOI: https://dx.doi.org/10.1002/eap.2419.

Fleming, M.M., L.B. Mills, J.K. Russell, G.R. Smith, and J.E. Rettig. 2011. Effects of trails on Eastern Redback Salamander (*Plethodon cinereus* Green). Herpetology Notes 4:229–232.

Fontaine, S.S., A.J. Novarro, and K.D. Kohl. 2018. Environmental temperature alters the digestive performance and gut microbiota of a terrestrial amphibian. Journal of Experimental Biology 221:jeb187559. DOI: https://dx.doi.org/10.1242/jeb.187559.

Forester, D.C., and C. Anders. 2000. Contributions to the life history of the Redback Salamander, *Plethodon cinereus*: Preliminary evidence for kin recognition. Pp. 407–416 in Biology of Plethodontid Salamanders (R.C. Bruce, R.G. Jaeger, and L.D. Houck, eds.). Springer Science+, USA.

Fraser, D.F. 1980. On the environmental control of oocyte maturation in a plethodontid salamander. Oecologia 46:302–307.

Fraser, L.H., H.A. Henry, C.N. Carlyle, … R. Turkington. 2013. Coordinated distributed experiments: An emerging tool for testing global hypotheses in ecology and environmental science. Frontiers in Ecology and the Environment 11:147–155.

Fredericks, L.P., and J.R. Dankert. 2000. Antibacterial and hemolytic activity of the skin of the terrestrial salamander, *Plethodon cinereus*. Journal of Experimental Zoology 287:340–345.

Frisbie, M.P., and R.L. Wyman. 1991. The effects of soil pH on sodium balance in the Red-backed Salamander, *Plethodon cinereus*, and three other terrestrial salamanders. Physiological Zoology 64:1050–1068.

Gade, M.R., K.C. Donlon, P.R. Gould, and R.R. Wittum. 2017. Female *Plethodon cinereus* cannibalism of an adult conspecific. Herpetology Notes 10:615.

Gaglione, C.M., E.M. O'Meara, K.L. Pence, A.C. Petterson, G.R. Smith, and J.E. Rettig. 2011. Red-backed Salamander, *Plethodon cinereus* (Green, 1818): Avoidance of urea. Herpetology Notes 4:275–277.

Gall, S.B., C.D. Anthony, and J.A. Wicknick. 2003. Do behavioral interactions between salamanders and beetles indicate a guild relationship? The American Midland Naturalist 149:363–374.

Gaston, K.J. 2010. Valuing common species. Science 327:154–155.

Gaston, K.J. 2011. Common ecology. Bioscience 61:354–362.

Gaston, K.J., and R.A. Fuller. 2008. Commonness, population depletion, and conservation biology. Trends in Ecology and Evolution 23:14–19.

Gergits, W.S., and R.G. Jaeger. 1990. Field observations of the behaviors of the Red-backed Salamander, *Plethodon cinereus*: Courtship and agonistic interactions. Journal of Herpetology 24:93–95.

Gertzog, B.J., L.J. Kaplan, D. Nichols, G.R. Smith, and J.E. Rettig. 2011. Avoidance of three herbicide formulations by Eastern Red-backed Salamanders (*Plethodon cinereus*). Herpetological Conservation and Biology 6:237–241.

Gibbons, M.E., A.M. Ferguson, D.R. Lee, and R.G. Jaeger. 2003. Mother–offspring discrimination in the Red-backed Salamander may be context dependent. Herpetologica 59:322–333.

Gibbons, M.E., A.M. Ferguson, and D.R. Lee. 2005. Both learning and heritability affect foraging behaviour of Red-backed Salamanders, *Plethodon cinereus*. Animal Behaviour 69:721–732.

Gibbs, J.P. 1998a. Distribution of woodland amphibians along a forest fragmentation gradient. Landscape Ecology 13:263–268.

Gibbs, J.P. 1998b. Amphibian movements in response to forest edges, roads, and streambeds in Southern New England. The Journal of Wildlife Management 62:584–589.

Gibbs, J.P. 1998c. Genetic structure of Redback Salamander *Plethodon cinereus* populations in continuous and fragmented forests. Biological Conservation 86:77–81.

Gibbs, J.P., and N.E. Karraker. 2006. Effects of warming conditions in Eastern North American forests on Red-backed Salamander morphology. Conservation Biology 20:913–917.

Gilbert, K.J., T.J. Fahey, J.C. Maerz, R.E. Sherman, P. Bohlen, J.J. Dombroskie, P.M. Groffman, and J.B. Yavitt. 2014. Exploring carbon flow through the root channel in a temperate forest soil food web. Soil Biology and Biochemistry 76:45–52.

Gillette, J.R. 2003. Population Ecology, Social Behavior, and Intersexual Differences in a Natural Population of Red-backed Salamanders: A Long-term Field Study. Ph.D. dissertation, University of Louisiana at Lafayette, USA.

Gillette, J.R., and M.G. Peterson. 2001. The benefits of transparency: Candling as a simple method for determining sex in Red-backed Salamanders (*Plethodon cinereus*). Herpetological Review 32:233.

Gillette, J.R., S.E. Kolb, J.A. Smith, and R.G. Jaeger. 2000. Pheromonal attractions to particular males by female Redback Salamanders (*Plethodon cinereus*). Pp. 431–441 in Biology of Plethodontid Salamanders (R.C. Bruce, R.G. Jaeger, and L.D. Houck, eds.). Springer Science+, USA.

Gillilland, M.G., III, and P.M. Muzzall. 2002. Amphibians, trematodes, and deformities: An overview from Southern Michigan. Comparative Parasitology 69:81–85.

Gordon, A., B.A. Wintle, S.A. Bekessy, J.L. Pearce, L.A. Venier, and J.N. Wilson. 2012. The use of dynamic landscape metapopulation models for forest management: A case study of the Red-backed Salamander. Canadian Journal of Forest Research 42:1091–1106.

Gorgolewski, A., J. Caspersen, P. Hazlett, T. Jones, H. Tran, and N. Basiliko. 2016. Responses of Eastern Red-backed Salamander (*Plethodon cinereus*) abundance 1 year after application of wood ash in a northern hardwood forest. Canadian Journal of Forest Research 46:402–409.

Graeter, G.J., B.B. Rothermel, and J.W. Gibbons. 2008. Habitat selection and movement of pond-breeding amphibians in experimentally fragmented pine forests. The Journal of Wildlife Management 72:473–482.

Grant, A.H., and E.B. Liebgold. 2017. Color-biased dispersal inferred by fine-scale genetic spatial autocorrelation in a color polymorphic salamander. Journal of Heredity 108:588–593.

Grant, A.H., T.S. Ransom, and E.B. Liebgold. 2018. Differential survival and the effects of predation on a color polymorphic species, the Red-backed Salamander (*Plethodon cinereus*). Journal of Herpetology 52:127–135.

Grant, E.H.C. 2015. Please don't misuse the museum: "Declines" may be statistical. Global Change Biology 21:1018–1024.

Grant, E.H.C., J. Fleming, E. Bastiaans, … D.A.W. Miller. 2024. Range-wide salamander densities reveal a key component of terrestrial vertebrate biomass in eastern North American forests. Biology Letters 20:20240033. DOI: https://dx.doi.org/10.1098/rsbl.2024.0033.

Gratwicke, B., M. Evans, E.H.C. Grant, J. Greathouse, W.J. McShea, N. Rotzel, and R.C. Fleischer. 2011. Low prevalence of *Batrachochytrium dendrobatidis* detected in Appalachian salamanders from Warren County, Virginia, USA. Herpetological Review 42:217–219.

Graves, B.M., and V.S. Quinn. 2000. Temporal persistence of alarm pheromones in skin secretions of the salamander, *Plethodon cinereus*. Journal of Herpetology 34:287–291.

Greenwald, K.R., L.J. Petit. and T.A. Waite. 2008. Indirect effects of a keystone herbivore elevate local animal diversity. The Journal of Wildlife Management 72:1318–1321.

Griffis, M.A., and R.G. Jaeger. 1998. Competition leads to an extinction-prone species of salamander: Interspecific territoriality in a metapopulation. Ecology 79:2494–2502.

Grover, M.C. 1998. Influence of cover and moisture on abundances of the terrestrial salamanders *Plethodon cinereus* and *Plethodon glutinosus*. Journal of Herpetology 32:489–497.

Grover, M.C. 2000. Determinants of salamander distributions along moisture gradients. Copeia 2000:156–168.

Grover, M.C. 2006. Comparative effectiveness of nighttime visual encounter surveys and cover object searches in detecting salamanders. Herpetological Conservation and Biology 1:93–99.

Grover, M.C., and H.M. Wilbur. 2002. Ecology of ecotones: Interactions between salamanders on a complex environmental gradient. Ecology 83:2112–2123.

Guffey, C., J.G. MaKinster, and R.G. Jaeger. 1998. Familiarity affects interactions between potentially courting territorial salamanders. Copeia 1998:205–208.

Hantak, M.M., and S.R. Kuchta. 2018. Predator perception across space and time: Relative camouflage in a colour polymorphic salamander. Biological Journal of the Linnean Society 123:21–33.

Hantak, M.M., S.R. Kuchta, C.-A.M. Hickerson, and C.D. Anthony. 2015. *Plethodon cinereus* (Eastern Red-backed Salamander). Morphology. Herpetological Review 46:409–410.

Hantak, M.M., D.J. Paluh, and C.-A.M. Hickerson. 2016. Comparison of the diets of sympatric erythristic and striped Morphs of *Plethodon cinereus* (Eastern Red-backed Salamander). Northeastern Naturalist 23:219–228.

Hantak, M.M., R.B. Page, P.E. Converse, C.D. Anthony, C.-A.M. Hickerson, and S.R. Kuchta. 2019. Do genetic structure and landscape heterogeneity impact color morph frequency in a polymorphic salamander? Ecography 42:1383–1394.

Hantak, M.M., K.M. Brooks, C.-A. Hickerson, C.D. Anthony, and S.R. Kuchta. 2020. A spatiotemporal assessment of dietary partitioning between color morphs of a terrestrial salamander. Copeia 2020:727–736.

Hantak, M.M., N.A. Federico, D.C. Blackburn and R.P. Guralnick. 2021. Rapid phenotypic change in a polymorphic salamander over 43 years. Scientific Reports 11:22681.

Harms-Tuohy, C.A., N.V. Schizas, and R.S. Appeldoorn. 2016. Use of DNA metabarcoding for stomach content analysis in the invasive Lionfish *Pterois volitans* in Puerto Rico. Marine Ecology Progress Series 558:181–191.

Harpole, D.N., and C.A. Haas. 1999. Effects of seven silvicultural treatments on terrestrial salamanders. Forest Ecology and Management 114:349–356.

Harris, R.N., T.Y. James, A. Lauer, M.A. Simon, and A. Patel. 2006. Amphibian pathogen *Batrachochytrium dendrobatidis* is inhibited by the cutaneous bacteria of amphibian species. EcoHealth 3:53. DOI: https://dx.doi.org/10.1007/s10393-005-0009-1.

Harris, R.N., A. Lauer, M.A. Simon, J.L. Banning, and R.A. Alford. 2009. Addition of antifungal skin bacteria to salamanders ameliorates the effects of chytridiomycosis. Diseases of Aquatic Organisms 83:11–16.

Hartzell, S.M. 2019. A herpetological survey of the Chincoteague Bay Field Station campus in Accomack County, Virginia. Catesbeiana 39:10–14.

Hass, C.A. 1985. Geographic protein variation in the Red-backed Salamander (*Plethodon cinereus* Green) from the southern part of its range. M.Sc. thesis, University of Maryland, College Park, USA.

Hecker, L., D.M. Madison, R.W. Dapson, and V. Holzherr. 2003. Presence of modified serous glands in the caudal integument of the Red-backed Salamander (*Plethodon cinereus*). Journal of Herpetology 37:732–736.

Hedeen, S.E. 2000. Influence of topography on local distributions of *Plethodon cinereus* and *P. richmondi* (Plethodontidae) in northern Kentucky and southwestern Ohio. Journal of the Kentucky Academy of Science 61:6–9.

Hedrick, B.P., G. Bancroft, F. Riand, and C. Sutherland. 2021. Effects of coverboard age and aging on salamander usage. Herpetological Review 52:6–12.

Heemeyer, J.L., J.A. Homyack, and C.A. Haas. 2007. Retention and readability of visible implant elastomer marks in Eastern Red-backed Salamanders (*Plethodon cinereus*). Herpetological Review 38:425–425.

Hernández-Pacheco, R., C. Sutherland, L.M. Thompson, and K.L. Grayson. 2019. Unexpected spatial population ecology of a widespread terrestrial salamander near its southern range edge. Royal Society Open Science 6:182192. DOI: https://dx.doi.org/10.1098/rsos.182192.

Hesed, K.M. 2012. Uncovering salamander ecology: A review of coverboard design. Journal of Herpetology 46:442–450.

Hess, A., C. McAllister, J. DeMarchi, M. Zidek, J. Murone, and M.D. Venesky. 2015. Salamanders increase their feeding activity when infected with the pathogenic chytrid fungus *Batrachochytrium dendrobatidis*. Diseases of Aquatic Organisms 116:205–212.

Hessel, A.L., W.G. Ryerson, and L.B. Whitenack. 2017. Doing without: Jump performance after tail autotomy in three species of plethodontid salamanders. Herpetologica 73:100–104.

Hickerson, C.-A.M., C.D. Anthony, and J.A. Wicknick. 2004. Behavioral interactions between salamanders and centipedes: Competition in divergent taxa. Behavioral Ecology 15:679–686.

Hickerson, C.-A.M., C.D. Anthony, and B.M. Walton. 2012. Interactions among forest-floor guild members in structurally simple microhabitats. The American Midland Naturalist 168:30–42.

Hickerson, C.-A.M., C.D. Anthony, and B.M. Walton. 2017. Eastern Red-backed Salamanders regulate top-down effects in a temperate forest-floor community. Herpetologica 73:180–189.

Hickerson, C.-A.M., C.D. Anthony, and A.M. Figura. 2018. Behavioral interactions between terrestrial salamanders and spiders: Competition or intraguild predation? Ethology Ecology & Evolution 30:285–296.

Highton, R. 1975. Geographic variation in genetic dominance of the color morphs of the Red-backed Salamander, *Plethodon cinereus*. Genetics 80:363–374.

Highton, R. 1977. Comparison of microgeographic variation in morphological and electrophoretic traits. Evolutionary Biology 10:397–436.

Highton, R. 1999. Geographic protein variation and speciation in the salamanders of the *Plethodon cinereus* group with the description of two new species. Herpetologica 55:43–90.

Highton, R. 2005. Declines of Eastern North American woodland salamanders (*Plethodon*). Pp. 34–46 in Amphibian Declines: The Conservation Status of United States Species (M. Lannoo, ed.). University of California Press, USA.

Highton, R., and A. Larson. 1979. The genetic relationships of the salamanders of the genus *Plethodon*. Systematic Biology 28:579–599.

Highton, R., and T.P. Webster. 1976. Geographic protein variation and divergence in populations of the salamander *Plethodon cinereus*. Evolution 30:33–45.

Highton, R., A.P. Hastings, C. Palmer, R. Watts, C.A. Hass, M. Culver, and S.J. Arnold. 2012. Concurrent speciation in the eastern woodland salamanders (Genus *Plethodon*): DNA sequences of the complete albumin nuclear and partial mitochondrial 12s genes. Molecular Phylogenetics and Evolution 63:278–290.

Hocking, D.J., and K.J. Babbitt. 2014. Effects of Red-backed Salamanders on ecosystem functions. PLoS One 9:e86854. DOI: https://dx.doi.org/10.1371/journal.pone.0086854.

Hocking, D.J., K.J. Babbitt, and M. Yamasaki. 2013. Comparison of silvicultural and natural disturbance effects on terrestrial salamanders in northern hardwood forests. Biological Conservation 167:194–202.

Homyack, J.A., and C.A. Haas. 2009. Long-term effects of experimental forest harvesting on abundance and reproductive demography of terrestrial salamanders. Biological Conservation 142:110–121.

Homyack, J.A., C.A. Haas, and W.A. Hopkins. 2010a. Influence of temperature and body mass on standard metabolic rate of Eastern Red-backed Salamanders (*Plethodon cinereus*). Journal of Thermal Biology 35:143–146.

Homyack, J.A., E.B. Sucre, C.A. Haas, and T.R. Fox. 2010b. Does *Plethodon cinereus* affect leaf litter decomposition and invertebrate abundances in mixed oak forest? Journal of Herpetology 44:447–456.

Homyack, J.A., C.A. Haas, and W.A. Hopkins. 2011. Energetics of surface-active terrestrial salamanders in experimentally harvested forest. The Journal of Wildlife Management 75:1267–1278.

Houck, L.D., and S.J. Arnold. 2003. Courtship and mating behavior. Pp. 383–424 in Phylogeny and Reproductive Biology of Urodela (D.M. Sever, ed.). Science Publishers, USA.

Hughes, B.B., R. Beas-Luna, A.K. Barner, … M.H. Carr. 2017. Long-term studies contribute disproportionately to ecology and policy. BioScience 67:271–281.

Hughes, M., R. Petersen and R.M. Duffield. 1999. *Plethodon cinereus* (Red-backed Salamander). Habitat. Herpetological Review 30:160–160.

Hurst, L.M., and G.R. Smith. 2006. Response of *Plethodon cinereus* to chemical cues from different numbers of conspecifics. Bulletin of the Maryland Herpetological Society 42:144–148.

IUCN (International Union for Conservation of Nature). 2020. The IUCN Red List of Threatened Species, Version 2020-2. Available at https://www.iucnredlist.org/en. Accessed 11 October 2020.

Ivanov, K., O.M. Lockhart, J. Keiper, and B.M. Walton. 2011. Status of the exotic ant *Nylanderia flavipes* (Hymenoptera: Formicidae) in northeastern Ohio. Biological Invasions 13:1945–1950.

Iverson, J.P., and G.R. Smith. 2010. Substrate and cover object choice by the Red-backed Salamander (*Plethodon cinereus*). Bulletin of the Maryland Herpetological Society 46:13–16.

Jaeger, R.G. 1970. Potential extinction through competition between two species of terrestrial salamanders. Evolution 24:632–642.

Jaeger, R.G. 1971a. Competitive exclusion as a factor influencing the distributions of two species of terrestrial salamanders. Ecology 52:632–637.

Jaeger, R.G. 1971b. Moisture as a factor influencing the distributions of two species of terrestrial salamanders. Oecologia 6:191–207.

Jaeger, R.G. 1972. Food as a limited resource in competition between two species of terrestrial salamanders. Ecology 53:535–546.

Jaeger, R.G. 1974. Interference or exploitation? A second look at competition between salamanders. Journal of Herpetology 8:191–194.

Jaeger, R., C. Gabor, and H. Wilbur. 1998. An assemblage of salamanders in the southern Appalachian Mountains: Competitive and predatory behavior. Behaviour 135:795–821.

Jaeger, R.G., M.G. Peterson, G. Gollmann, B. Gollmann, and V.R. Townsend. 2001. Salamander social strategies: Living together in female–male pairs. Journal of Herpetology 35:335–338.

Jaeger, R.G., J.R. Gillette, and R.C. Cooper. 2002a. Sexual coercion in a territorial salamander: Males punish socially polyandrous female partners. Animal Behaviour 63:871–877.

Jaeger, R.G., E.D. Prosen, and D.C. Adams. 2002b. Character displacement and aggression in two species of terrestrial salamanders. Copeia 2002:391–401.

Jaeger, R.G., B. Gollmann, C.D. Anthony, C.R. Gabor, and N.R. Kohn. 2016. Behavioral Ecology of the Eastern Red-backed Salamander: 50 Years of Research, 1st edition. Oxford University Press, USA.

Jaramillo, A.F., I. De La Riva, J.M. Guayasamin, J.C. Chaparro, G. Gagliardi-Urrutia, R.C. Gutiérrez, I. Brcko, C. Vilà, and S. Castroviejo-Fisher. 2020. Vastly underestimated species richness of Amazonian salamanders (Plethodontidae: *Bolitoglossa*) and implications about plethodontid diversification. Molecular Phylogenetics and Evolution 149:106841. DOI: https://dx.doi.org/10.1016/j.ympev.2020.106841.

Jaworski, K.E., M.S. Lattanzio, C.-A.M. Hickerson, and C.D. Anthony. 2018. Male mate preference as an agent of fecundity selection in a polymorphic salamander. Ecology and Evolution 8:8750–8760.

Johnson, M.S., H.I. Paulus, C.J. Salice, R.T. Checkai, and M. Simini. 2004. Toxicologic and histopathologic response of the terrestrial salamander *Plethodon cinereus* to soil exposures of 1,3,5-trinitrohexahydro-1,3,5-triazine. Archives of Environmental Contamination and Toxicology 47:496–501.

Johnson, M.S., J. Suski, and M.A. Bazar. 2007. Toxicological responses of Red-backed Salamanders (*Plethodon cinereus*) to subchronic soil exposures of 2,4-dinitrotoluene. Environmental Pollution 147:604–608.

Johnson, M.S., C.A. McFarland, M.A. Bazar, M.J. Quinn, E.M. LaFiandra, and L.G. Talent. 2010. Toxicity of octahydro-1,3,5,7-tetranitro-1,3,5,7-tetrazocine (HMX) in three vertebrate species. Archives of Environmental Contamination and Toxicology 58:836–843.

Jongsma, G.F.M. 2012a. *Plethodon cinereus* (Eastern Red-backed Salamander). Morphology. Herpetological Review 43:318–318.

Jongsma, G.F.M. 2012b. *Plethodon cinereus* (Eastern Red-backed Salamander). Morphology. Herpetological Review 43:460–460.

Jongsma, G.F.M., M.A. Empey, C.M. Smith, A.M. Bennett, and D.E. McAlpine. 2019. High prevalence of the amphibian pathogen *Batrachochytrium dendrobatidis* in plethodontid salamanders in protected areas in New Brunswick, Canada. Herpetological Conservation and Biology 14:91–96.

Jordan, M.A., D.A. Morris, and S.E. Gibson. 2008. The influence of historical landscape change on genetic variation and population structure of a terrestrial salamander (*Plethodon cinereus*). Conservation Genetics 10:1647. DOI: https://dx.doi.org/10.1007/s10592-008-9741-8.

Jung, R.E., S. Droege, J.R. Sauer, and R.B. Landy. 2000a. Evaluation of terrestrial and streamside salamander monitoring techniques at Shenandoah National Park. Environmental Monitoring and Assessment 63:65–79.

Jung, R.E., W.L. Ward, C.O. King, and L.A. Weir. 2000b. *Plethodon cinereus* (Redback Salamander). Predation. Herpetological Review 31:98–99.

Karuzas, J.M., J.C. Maerz, and D.M. Madison. 2004. An alternative hypothesis for the primary function of a proposed mate assessment behaviour in Red-backed Salamanders. Animal Behaviour 68:489–494.

Kerby, J.L., K.L. Richards-Hrdlicka, A. Storfer, and D.K. Skelly. 2010. An examination of amphibian sensitivity to environmental contaminants: Are amphibians poor canaries? Ecology Letters 13:60–67.

Kerney, R. 2011. Embryonic staging table for a direct-developing salamander, *Plethodon cinereus* (Plethodontidae). The Anatomical Record 294:1796–1808.

Kerney, R.R., D.C. Blackburn, H. Müller, and J. Hanken. 2012. Do larval traits re-evolve? Evidence from the embryogenesis of a direct-developing salamander, *Plethodon cinereus*. Evolution 66:252–262.

Keyser, P.D., D.J. Sausville, W.M. Ford, D.J. Schwab, and P.H. Brose. 2004. Prescribed fire impacts to amphibians and reptiles in shelterwood-harvested oak-dominated forests. Virginia Journal of Science 55:159–168.

Kight, S.L., C. Eadie, D. Lynch, J. Coelho, and A. Dewera. 2005. Classical conditioning of Red-backed Salamanders, *Plethodon cinereus*. Bulletin of the Maryland Herpetological Society 41:68–84.

King, R.B., M.J. Oldham, W.F. Weller, and D. Wynn. 1997. Historic and current amphibian and reptile distributions in the island region of Western Lake Erie. The American Midland Naturalist 138:153–173.

Kleeberger, S.R., and J.K. Werner. 1982. Home range and homing behavior of *Plethodon cinereus* in Northern Michigan. Copeia 1982:409–415.

Knapp, S.M., C.A. Haas, D.N. Harpole, and R.L. Kirkpatrick. 2003. Initial effects of clearcutting and alternative silvicultural practices on terrestrial salamander abundance. Conservation Biology 17:752–762.

Kniowski, A., and R. Pietsch. 2015. *Plethodon hubrichti* (Peaks of Otter Salamander) behavior. Herpetological Review 46:71–71.

Kniowski, A., and N. Reichenbach. 2009. The ecology of the Peaks of Otter Salamander (*Plethodon hubrichti*) in sympatry with the Eastern Red-backed Salamander (*Plethodon cinereus*). Herpetological Conservation and Biology 4:285–294.

Kolozsvary, M.B., and R.K. Swihart. 1999. Habitat fragmentation and the distribution of amphibians: Patch and landscape correlates in farmland. Canadian Journal of Zoology 77:1288–1299.

Kozak, K.H., and J.J. Wiens. 2010. Niche conservatism drives elevational diversity patterns in Appalachian salamanders. The American Naturalist 176:40–54.

Kozak, K.H., R.W. Mendyk, and J.J. Wiens. 2009. Can parallel diversification occur in sympatry? Repeated patterns of body-size evolution in coexisting clades of North American salamanders. Evolution 63:1769–1784.

Kraemer, A.C., and D.C. Adams. 2014. Predator perception of Batesian mimicry and conspicuousness in a salamander. Evolution 68:1197–1206.

Kraemer, A.C., J. Kissner, and D.C. Adams. 2012. Morphological colorchange in the Red-backed Salamander (*Plethodon cinereus*) while kept in captivity. Copeia 2012:748–755.

Kraemer, A.C., J.M. Serb, and D.C. Adams. 2015a. Batesian mimics influence the evolution of conspicuousness in an aposematic salamander. Journal of Evolutionary Biology 28:1016–1023.

Kraemer, A.C., J.M. Serb, and D.C. Adams. 2015b. Model toxin level does not directly influence the evolution of mimicry in the salamander *Plethodon cinereus*. Evolutionary Ecology 29:511–523.

Kraemer, A.C., J.M. Serb, and D.C. Adams. 2016. Both novelty and conspicuousness influence selection by mammalian predators on the colour pattern of *Plethodon cinereus* (Urodela: Plethodontidae). Biological Journal of the Linnean Society 118:889–900.

Kroschel, W.A., W.B. Sutton, C.J.W. McClure, and T.K. Pauley. 2014. Decline of the Cheat Mountain Salamander over a 32-year period and the potential influence of competition from a sympatric species. Journal of Herpetology 48:415–422.

Kuchta, S.R. 2019. Historical Perspective: Richard Highton. Copeia 107:365–372.

Kuchta, S.R., M.M. Hantak, B.P. Waldron, C.-A.M. Hickerson, R.M. Lehtinen, and C.D. Anthony. 2022. Hybridization between the woodland salamanders *Plethodon cinereus* and *P. electromorphus* is not widespread. Ichthyology and Herpetology 110:430–438.

Kunkel, C.L., C.D. Anthony, C.-A.M. Hickerson, and R.C. Feldhoff. 2019. Species variation in a pheromone complex is maintained at the population level in the Eastern Red-backed Salamander. Journal of Herpetology 53:173–178.

Lancaster, D.L., and S.E. Wise. 1996. Differential response by the Ringneck Snake, *Diadophis punctatus*, to odors of tail-autotomizing prey. Herpetologica 52:98–108.

Landres, P.B., J. Verner, and J.W. Thomas. 1988. Ecological uses of vertebrate indicator species: A critique. Conservation Biology 2:316–328.

Lannoo, M. (ed.). 2005. Amphibian Declines: The Conservation Status of United States Species, 1st edition. University of California Press, USA.

Lauer, A., M.A. Simon, J.L. Banning, E. André, K. Duncan, and R.N. Harris. 2007. Common cutaneous bacteria from the Eastern Red-backed Salamander can inhibit pathogenic fungi. Copeia 2007:630–640.

Lauer, A., M.A. Simon, J.L. Banning, B.A. Lam, and R.N. Harris. 2008. Diversity of cutaneous bacteria with antifungal activity isolated from female four-toed salamanders. The ISME Journal 2:145–157.

Leclair, M.H., M. Levasseur, and R. Leclair, Jr. 2006. Life-history traits of *Plethodon cinereus* in the northern parts of its range: Variations in population structure, age and growth. Herpetologica 62:265–282.

Leclair, M.H., M. Levasseur, and R. Leclair. 2008. Activity and reproductive cycles in northern populations of the Red-backed Salamander, *Plethodon cinereus*. Journal of Herpetology 42:31–38.

LeGros, D.L. 2018. The use of an anthropogenic structure by Eastern Red-backed Salamander (*Plethodon cinereus*). The Canadian Field-Naturalist 132:58–60.

Lehtinen, R.M., A.F. Steratore, M.M. Eyre, E.S. Cassagnol, M.L. Stern, and H.A. Edgington. 2016. Identification of widespread hybridization between two terrestrial salamanders using morphology, coloration, and molecular markers. Copeia 104:132–139.

Lemen, C.A., and P.W. Freeman. 1985. Tracking mammals with fluorescent pigments: A new technique. Journal of Mammalogy 66:134–136.

Leonelli, S., and R.A. Ankeny. 2013. What makes a model organism? Endeavour 37:209–212.

Leroux, S.J., C.H. Albert, A.-S. Lafuite, B. Rayfield, S. Wang, and D. Gravel. 2017. Structural uncertainty in models projecting the consequences of habitat loss and fragmentation on biodiversity. Ecography 40:36–47.

Lewis, Z.R., R. Kerney, and J. Hanken. 2022. Developmental basis of evolutionary lung loss in plethodontid salamanders. Science Advances 8:eabo6108.

Liebgold, E.B. 2014. The influence of social environment: Behavior of unrelated adults affects future juvenile behaviors. Ethology 120:388–399.

Liebgold, E.B. 2019. A tale of two tails: A rare occurrence of tail bifurcation in the Red-backed Salamander (*Plethodon cinereus*). Herpetological Bulletin 148:35–36.

Liebgold, E.B., and P.R. Cabe. 2008. Familiarity with adults, but not relatedness, affects the growth of juvenile Red-backed Salamanders (*Plethodon cinereus*). Behavioral Ecology and Sociobiology 63:277.

Liebgold, E.B., and C.J. Dibble. 2011. Better the devil you know: Familiarity affects foraging activity of Red-backed Salamanders, *Plethodon cinereus*. Animal Behaviour 82:1059–1066.

Liebgold, E.B., P.R. Cabe, R.G. Jaeger, and P.L. Leberg. 2006. Multiple paternity in a salamander with socially monogamous behaviour. Molecular Ecology 15:4153–4160.

Liebgold, E.B., E.D. Brodie, and P.R. Cabe. 2011. Female philopatry and male-biased dispersal in a direct-developing salamander, *Plethodon cinereus*. Molecular Ecology 20:249–257.

Lindenmayer, D.B., J.T. Wood, L. McBurney, C. MacGregor, K. Youngentob, and S.C. Banks. 2011. How to make a common species rare: A case against conservation complacency. Biological Conservation 144:1663–1672.

Lindenmayer, D.B., M.P. Piggott, and B.A. Wintle. 2013. Counting the books while the library burns: Why conservation monitoring programs need a plan for action. Frontiers in Ecology and the Environment 11:549–555.

Lindenmayer, D., P. Barton, and J. Pierson (eds.). 2015. Indicators and Surrogates of Biodiversity and Environmental Change. CRC Press, USA.

Lotter, F. 1978. Reproductive ecology of the salamander *Plethodon cinereus* (Amphibia, Urodela, Plethodontidae) in Connecticut. Journal of Herpetology 12:231–236.

Lotter, F., and N.J. Scott. 1977. Correlation between climate and distribution of the color morphs of the salamander *Plethodon cinereus*. Copeia 1977:681–690.

Loudon, A.H., J.A. Holland, T.P. Umile, E.A. Burzynski, K.P.C. Minbiole, and R.N. Harris. 2014a. Interactions between amphibians' symbiotic bacteria cause the production of emergent anti-fungal metabolites. Frontiers in Microbiology 5:441. DOI: https://dx.doi.org/10.3389/fmicb.2014.00441.

Loudon, A.H., D.C. Woodhams, L.W. Parfrey, H. Archer, R. Knight, V. McKenzie, and R.N. Harris. 2014b. Microbial community dynamics and effect of environmental microbial reservoirs on Red-backed Salamanders (*Plethodon cinereus*). The ISME Journal 8:830–840.

Loudon, A.H., A. Venkataraman, W. Van Treuren, D.C. Woodhams, L.W. Parfrey, V.J. McKenzie, R. Knight, T.M. Schmidt, and R.N. Harris. 2016. Vertebrate hosts as islands: Dynamics of selection, immigration, loss, persistence, and potential function of bacteria on salamander skin. Frontiers in Microbiology 7:333. DOI: https://dx.doi.org/10.3389/fmicb.2016.00333.

Lowe, J. 2004. Rates of Tricaine methanesulfonate (MS-222) anesthetization in relation to pH and concentration in five terrestrial salamanders. Herpetological Review 35:352–254.

Luymes, N., and P. Chow-Fraser. 2019. Optimizations for time and effort in long-term monitoring: A case study using a multidecadal terrestrial salamander monitoring program. Environmental Monitoring and Assessment 191:597. DOI: https://dx.doi.org/10.1007/s10661-019-7759-7.

MacNeil, J.E., and R.N. Williams. 2013a. Effectiveness of two artificial cover objects in sampling terrestrial salamanders. Herpetological Conservation and Biology 8:552–560.

MacNeil, J.E., and R.N. Williams. 2013b. Relative abundance and species richness of terrestrial salamanders on hardwood ecosystem experiment sites before harvesting. Pp. 142–150 in The Hardwood Ecosystem Experiment: A Framework for Studying Responses to Forest Management (R.K. Swihart, M.R. Saunders, R.A. Kalb, G.S. Haulton, and C.H. Michler, eds.). U.S. Department of Agriculture, USA.

MacNeil, J.E., and R.N. Williams. 2014. Effects of timber harvests and silvicultural edges on terrestrial salamanders. PLoS One 9:e114683. DOI: https://dx.doi.org/10.1371/journal.pone.0114683.

Madison, D.M., K. Wareing, and J.C. Maerz. 1999a. Oviposition behavior in the Red-backed Salamander (*Plethodon cinereus*): Implications of suspending a clutch. Herpetological Review 30:209–210.

Madison, D.M., J.C. Maerz, and J.H. McDarby. 1999b. Optimization of predator avoidance by salamanders using chemical cues: Diet and diel effects. Ethology 105:1073–1086.

Madison, D.M., A.M. Sullivan, J.C. Maerz, J.H. McDarby, and J.R. Rohr. 2002. A complex, cross-taxon, chemical releaser of antipredator behavior in amphibians. Journal of Chemical Ecology 28:2271–2282.

Maerz, J., E. Myers, and D. Adams. 2006. Trophic polymorphism in a terrestrial salamander. Evolutionary Ecology Research 8:23–35.

Maerz, J.C., and J.M. Karuzas. 2003. *Plethodon cinereus* (Eastern Red-backed Salamander). Cannibalism. Herpetological Review 34:354–354.

Maerz, J.C., and D.M. Madison. 2000. Environmental variation and territorial behavior in a terrestrial salamander. Pp. 395–406 in Biology of Plethodontid Salamanders (R.C. Bruce, R.G. Jaeger, and L.D. Houck, eds.). Springer Science+, USA.

Maerz, J.C., N.L. Panebianco, and D.M. Madison. 2001. Effects of predator chemical cues and behavioral biorhythms on foraging activity of terrestrial Salamanders. Journal of Chemical Ecology 27:1333–1344.

Maerz, J.C., J.M. Karuzas, D.M. Madison, and B. Blossey. 2005. Introduced invertebrates are important prey for a generalist predator. Diversity and Distributions 11:83–90.

Mahoney, K.R., K.R. Russell, W.M. Ford, J.L. Rodrigue, J.D. Riddle, T.M. Schuler, and M.B. Adams. 2016. Woodland salamander responses to a shelterwood harvest-prescribed burn silvicultural treatment within Appalachian mixed-oak forests. Forest Ecology and Management 359:277–285.

Marsh, D.M. 2007. Edge effects of gated and ungated roads on terrestrial salamanders. The Journal of Wildlife Management 71:389–394.

Marsh, D.M., and N.G. Beckman. 2004. Effects of forest roads on the abundance and activity of terrestrial salamanders. Ecological Applications 14:1882–1891.

Marsh, D.M., and M.A. Goicochea. 2003. Monitoring terrestrial salamanders: Biases caused by intense sampling and choice of cover objects. Journal of Herpetology 37:460–466.

Marsh, D.M., K.A. Thakur, K.C. Bulka, and L.B. Clarke. 2004. Dispersal and colonization through open fields by a terrestrial, woodland salamander. Ecology 85:3396–3405.

Marsh, D.M., G.S. Milam, N.P. Gorham, and N.G. Beckman. 2005. Forest roads as partial barriers to terrestrial salamander movement. Conservation Biology 19:2004–2008.

Marsh, D.M., R.B. Page, T.J. Hanlon, … P.R. Cabe. 2007. Ecological and genetic evidence that low-order streams inhibit dispersal by Red-backed Salamanders (*Plethodon cinereus*). Canadian Journal of Zoology 85:319–327.

Marsh, D.M., R.B. Page, T.J. Hanlon, R. Corritone, E.C. Little, D.E. Seifert, and P.R. Cabe. 2008. Effects of roads on patterns of genetic differentiation in Red-backed Salamanders, *Plethodon cinereus*. Conservation Genetics 9:603–613.

Marsh, D.M., F.W. Townes, K.M. Cotter, K. Farroni, K.L. McCreary, R.L. Petry, and J.M. Tilghman. 2019. Thermal preference and species range in mountaintop salamanders and their widespread competitors. Journal of Herpetology 53:96–103.

Martin, A.M., and M.M. Hantak. 2011. *Plethodon cinereus* (Eastern Red-backed Salamander). Tenacity and homing. Herpetological Review 42:581–582.

Mathis, A. 1989. Do seasonal spatial distributions in a terrestrial salamander reflect reproductive behavior or territoriality? Copeia 1989:788–791.

Mathis, A. 1991. Territories of male and female terrestrial salamanders: Costs, benefits, and intersexual spatial associations. Oecologia 86:433–440.

Mathis, A., and D. Lancaster. 1998. Response of terrestrial salamanders to chemical stimuli from distressed conspecifics. Amphibia-Reptilia 19:330–335.

McCarthy, T., P. Masson, A. Thieme, P. Leimgruber, and B. Gratwicke. 2017. The relationship between climate and adult body size in Redback Salamanders (*Plethodon cinereus*). Geo: Geography and Environment 4: e00031. DOI: https://dx.doi.org/10.1002/geo2.31.

McGhee, J.D. 2013. Preliminary estimation of capture rates for Red-backed Salamanders at the Randolph-Macon College Environmental Field Station, Doswell, Virginia. Catesbeiana 33:62–66.

McGhee, J.D., and M.D. Killian. 2012. Exploratory modeling indicates Red-backed Salamander detections are sensitive to soil pH at C.F. Phelps Wildlife Management Area, Virginia. Virginia Journal of Science 63:137–144.

McKenny, H.C., W.S. Keeton, and T.M. Donovan. 2006. Effects of structural complexity enhancement on Eastern Red-backed Salamander (*Plethodon cinereus*) populations in northern hardwood forests. Forest Ecology and Management 230:186–196.

Meche, G., and R.G. Jaeger. 2002. Associations of male Red-backed Salamanders with tail-intact versus tail-autotomized females during the courtship season. Journal of Herpetology 36:532–535.

Mendyk, R.W., L. Augustine, and G. Montague. 2010. *Plethodon cinereus* (Red-backed Salamander). Leucism. Herpetological Review 41:189–190.

Meshaka, W.E., and D. Wright. 2017. Selected life history traits of the Eastern Red-backed Salamander, *Plethodon cinereus* (Green), at a suburban residence in south central Pennsylvania. Journal of the Pennsylvania Academy of Science 91:95–104.

Meshaka, W.E., C.G. Lindsay, A.L. Mack, and M.L. McCallum. 2019. A survey of terrestrially active salamanders from two different woodlands at the Powdermill Nature Reserve, Pennsylvania. Northeastern Naturalist 26:629–640.

Messere, M., and P.K. Ducey. 1998. Forest floor distribution of northern Redback Salamanders, *Plethodon cinereus*, in relation to canopy gaps: First year following selective logging. Forest Ecology and Management 107:319–324.

Mezebish, T.D., A. Blackman, and A.J. Novarro. 2018. Salamander climbing behavior varies among species and is correlated with community composition. Behavioral Ecology 29:686–692.

Milanovich, J.R., and J.C. Maerz. 2012. Assessing the use of non-lethal tail clips for measuring stable isotopes of plethodontid salamanders. Herpetological Conservation and Biology 7:67–74.

Milanovich, J.R., and J.C. Maerz. 2013. Realistic fasting does not affect stable isotope levels of a metabolically efficient salamander. Journal of Herpetology 47:544–548.

Mitchell, J.C. 2000. Observations on amphibians and reptiles in burned and unburned forests on the upper Coastal Plain of Virginia. Virginia Journal of Science 51:199–203.

Mitchell, J.C. 2015. Amphibian and small mammal assemblages in a Northern Virginia forest before and after defoliation by Gypsy Moths (*Lymantria dispar*). Virginia Journal of Science 66:403–411.

Mitchell, J.C., S.C. Rinehart, J.F. Pagels, K.A. Buhlmann, and C.A. Pague. 1997. Factors influencing amphibian and small mammal assemblages in central Appalachian forests. Forest Ecology and Management 96:65–76.

Monti, L., M. Hunter, and J. Witham. 2000. An evaluation of the artificial cover object (ACO) method for monitoring populations of the Redback Salamander *Plethodon cinereus*. Journal of Herpetology 34:624–629.

Moore, A.L., C.E. Williams, and W.J. Moriarity. 2000. Species composition of salamander assemblages in Allegheny Plateau riparian forests. Journal of the Pennsylvania Academy of Science 74:24–28.

Moore, A.L., C.E. Williams, T.H. Martin, and W.J. Moriarity. 2001. Influence of season, geomorphic surface and cover item on capture, size and weight of *Desmognathus ochrophaeus* and *Plethodon cinereus* in Allegheny Plateau riparian forests. The American Midland Naturalist 145:39–45.

Moore, J.-D. 2005. Use of native dominant wood as a new coverboard type for monitoring Eastern Red-backed Salamanders. Herpetological Review 36:268–271.

Moore, J.-D. 2009. Comparison of a population of Eastern Red-backed Salamanders, *Plethodon cinereus*, under native dominant wood coverboards and natural cover objects. The Canadian Field-Naturalist 123:210–214.

Moore, J.-D. 2014. Short-term effect of forest liming on Eastern Red-backed Salamander (*Plethodon cinereus*). Forest Ecology and Management 318:270–273.

Moore, J.-D., and M. Ouellet. 2014. A review of colour phenotypes of the Eastern Red-backed Salamander, *Plethodon cinereus*, in North America. The Canadian Field-Naturalist 128:250–259.

Moore, J.-D., and M. Ouellet. 2015. Questioning the use of an amphibian colour morph as an indicator of climate change. Global Change Biology 21:566–571.

Moore, J.-D., and R.L. Wyman. 2010. Eastern Red-backed Salamanders (*Plethodon cinereus*) in a highly acid forest soil. The American Midland Naturalist 163:95–105.

Moreno, G. 1989. Behavioral and physiological differentiation between the color morphs of the salamander, *Plethodon cinereus*. Journal of Herpetology 23:335–341.

Mossman, A., M.R. Lambert, M.S. Ashton, J. Wikle, and M.C. Duguid. 2019. Two salamander species respond differently to timber harvests in a managed New England forest. PeerJ 7:e7604. DOI: https://dx.doi.org/10.7717/peerj.7604.

Muletz, C., N.M. Caruso, R.C. Fleischer, R.W. McDiarmid, and K.R. Lips. 2014. Unexpected rarity of the pathogen *Batrachochytrium dendrobatidis* in Appalachian *Plethodon* Salamanders: 1957–2011. PLoS One 9: e103728. DOI: https://dx.doi.org/10.1371/journal.pone.0103728.

Muletz, C.R., J.M. Myers, R.J. Domangue, J.B. Herrick, and R.N. Harris. 2012. Soil bioaugmentation with amphibian cutaneous bacteria protects amphibian hosts from infection by *Batrachochytrium dendrobatidis*. Biological Conservation 152:119–126.

Muletz-Wolz, C.R., G.V. DiRenzo, S.A. Yarwood, E.H.C. Grant, R.C. Fleischer, and K.R. Lips. 2017. Antifungal bacteria on woodland salamander skin exhibit high taxonomic diversity and geographic variability. Applied and Environmental Microbiology 83:e00186–17. DOI: https://dx.doi.org/10.1128/AEM.00186-17.

Muletz-Wolz, C.R., S.A. Yarwood, E.H.C. Grant, R.C. Fleischer, and K.R. Lips. 2018. Effects of host species and environment on the skin microbiome of Plethodontid salamanders. Journal of Animal Ecology 87:341–353.

Muletz-Wolz, C.R., R.C. Fleischer, and K.R. Lips. 2019. Fungal disease and temperature alter skin microbiome structure in an experimental salamander system. Molecular Ecology 28:2917–2931.

Müller, B., and U. Grossniklaus. 2010. Model organisms—A historical perspective. Journal of Proteomics 73:2054–2063.

Muñoz, D.J. 2018. Caudata: *Plethodon cinereus* (Eastern Red-backed Salamander) Fluorescence. Herpetological Review 49:512–513.

Muñoz, D.J., K.M. Hesed, E.H.C. Grant, and D.A.W. Miller. 2016a. Evaluating within-population variability in behavior and demography for the adaptive potential of a dispersal-limited species to climate change. Ecology and Evolution 6:8740–8755.

Muñoz, D.J., D.A.W. Miller, C. Sutherland, and E.H.C. Grant. 2016b. Using spatial capture–recapture to elucidate population processes and space-use in herpetological studies. Journal of Herpetology 50:570–581.

Murray, D.L., and C.L. Jenkins. 1999. Perceived predation risk as a function of predator dietary cues in terrestrial salamanders. Animal Behaviour 57:33–39.

Muzzall, P.M., C.R. Peebles, and T.M. Burton. 1997. Endoparasites of plethodontid salamanders from Paradise Brook, New Hampshire. The Journal of Parasitology 83:1193–1195.

Myers, E.M., and D.C. Adams. 2008. Morphology is decoupled from interspecific competition in *Plethodon* salamanders in the Shenandoah Mountains, USA. Herpetologica 64:281–289.

Nagel, J.W. 1977. Life History of the Red-backed Salamander, *Plethodon cinereus*, in Northeastern Tennessee. Herpetologica 33:13–18.

Ng, M.Y., and H.M. Wilbur. 1995. The cost of brooding in *Plethodon cinereus*. Herpetologica 51:1–8.

Noël, S., and F.-J. Lapointe. 2010. Urban conservation genetics: Study of a terrestrial salamander in the city. Biological Conservation 143:2823–2831.

Noël, S., M. Ouellet, P. Galois, and F.-J. Lapointe. 2007. Impact of urban fragmentation on the genetic structure of the Eastern Red-backed Salamander. Conservation Genetics 8:599–606.

Novarro, A.J., A. Blackman, and S.D. Bailey. 2017. Tricaine methanesulfonate (MS-222) as a short-term anesthetic for the Eastern Red-backed Salamander *Plethodon cinereus*. Herpetological Review 48:320–322.

Novarro, A.J., C.R. Gabor, C.B. Goff, T.D. Mezebish, L.M. Thompson, and K.L. Grayson. 2018. Physiological responses to elevated temperature across the geographic range of a terrestrial salamander. Journal of Experimental Biology 221:jeb178236. DOI: https://dx.doi.org/10.1242/jeb.178236.

Ochs, A., and A.A.H. Siddig. 2017. Response of Red-backed Salamanders (*Plethodon cinereus*) to changes in Hemlock forest soil driven by invasive Hemlock Woolly Adelgid (*Adelges tsugae*). Environments 4:8. DOI: https://dx.doi.org/10.3390/environments4010008.

Orlofske, S.A., K.L. Grayson, and W.A. Hopkins. 2009. The effects of fluorescent tracking powder on oxygen consumption in salamanders using either cutaneous or bimodal respiration. Copeia 2009:623–627.

Orr, J.M., and C.H. Ernst. 2005. *Plethodon cinereus* (Eastern Red-backed Salamander). Early nesting. Herpetological Review 36:296–296.

Otaibi, B.W., Q.K. Johnson, and B.J. Cosentino. 2017. Postautotomy tail movement differs between colour morphs of the Red-backed Salamander (*Plethodon cinereus*). Amphibia-Reptilia 38:395–399.

Otto, C.R.V., and G.J. Roloff. 2011. Comparing cover object and leaf litter surveys for detecting Red-backed Salamanders, *Plethodon cinereus*. Journal of Herpetology 45:256–260. DOI: https://dx.doi.org/10.1670/10-039.1.

Otto, C.R.V., L.L. Bailey, and G.J. Roloff. 2013. Improving species occupancy estimation when sampling violates the closure assumption. Ecography 36:1299–1309.

Otto, C.R.V., G.J. Roloff, and R.E. Thames. 2014. Comparing population patterns to processes: Abundance and survival of a forest salamander following habitat degradation. PLoS One 9:e93859. DOI: https://dx.doi.org/10.1371/journal.pone.0093859.

Ousterhout, B.H., and E.B. Liebgold. 2010. Dispersal versus site tenacity of adult and juvenile Red-backed Salamanders (*Plethodon cinereus*). Herpetologica 66:269–275.

Palmer, C.A., R.A. Watts, R.G. Gregg, M.A. McCall, L.D. Houck, R. Highton, and S.J. Arnold. 2005. Lineage-specific differences in evolutionary mode in a salamander courtship pheromone. Molecular Biology and Evolution 22:2243–2256.

Palmer, C.A., R.A. Watts, L.D. Houck, A.L. Picard, and S.J. Arnold. 2007. Evolutionary replacement of components in a salamander pheromone signaling complex: More evidence for phenotypic-molecular decoupling. Evolution 61:202–215.

Palmer, C.A., R.A. Watts, A.P. Hastings, L.D. Houck, and S.J. Arnold. 2010. Rapid evolution of plethodontid modulating factor, a hypervariable salamander courtship pheromone, is driven by positive selection. Journal of Molecular Evolution 70:427–440.

Paluh, D.J., C. Eddy, K. Ivanov, C.-A.M. Hickerson, and C.D. Anthony. 2015. Selective foraging on ants by a terrestrial polymorphic salamander. The American Midland Naturalist 174:265–277.

Pasachnik, S., and G.R. Ruthig. 2004. Versatility of habitat use in three sympatric species of plethodontid salamanders. Journal of Herpetology 38:434–437.

Passos, L.F., G. Garcia, and R.J. Young. 2018. Comparing the bacterial communities of wild and captive Golden Mantella Frogs: Implications for amphibian conservation. PLoS One 13:e0205652. DOI: https://dx.doi.org/10.1371/journal.pone.0205652.

Patrick, D.A., M.L. Hunter, and A.J.K. Calhoun. 2006. Effects of experimental forestry treatments on a Maine amphibian community. Forest Ecology and Management 234:323–332.

Peele, J., C. Nix, P. Ruhl, R. Chapman, P. Zollner, and M.R. Saunders. 2017. Effects of woody biomass harvests on a population of plethodontid salamanders in Southeast Indiana. The American Midland Naturalist 178:132–143.

Pelini, S.L., A.M. Maran, A.R. Chen, J. Kaseman, and T.W. Crowther. 2015. Higher trophic levels overwhelm climate change impacts on terrestrial ecosystem functioning. PLoS One 10:e0136344. DOI: https://dx.doi.org/10.1371/journal.pone.0136344.

Perkins, D.W., and M.L. Hunter. 2006. Effects of riparian timber management on amphibians in Maine. The Journal of Wildlife Management 70:657–670.

Perry, G., E. Muths, M.L. Crump, C. Distel, R.W. Hansen, M.B. Harvey, J. Rowe, S.C. Walls, and S. Woodley. 2020. Increasing diversity and inclusivity in herpetology: Small but critical steps from the editors of herpetological journals. Herpetological Review 51:765–766.

Peterson, M.G., J.R. Gillette, R. Franks, and R.G. Jaeger. 2000. Alternative life styles in a terrestrial salamander. Pp. 417–430 in Biology of Plethodontid Salamanders (R.C. Bruce, R.G. Jaeger, and L.D. Houck, eds.). Springer Science+, USA.

Petranka, J. 1998. Salamanders of the United States and Canada. Smithsonian Books, USA.

Petruzzi, E.E., P.H. Niewiarowski, and F.B.-G. Moore. 2006. The role of thermal niche selection in maintenance of a colour polymorphism in redback salamanders (*Plethodon cinereus*). Frontiers in Zoology 3:10. DOI: https://dx.doi.org/10.1186/1742-9994-3-10.

Pfingsten, R.A., J.G. Davis, T.O. Matson, G. Lipps Jr., D. Wynn, and B.J. Armitage (eds.). 2013. Amphibians of Ohio. Ohio Biological Survey, USA.

Placyk, J.S., and B.M. Graves. 2001a. Foraging behavior of the Red-backed Salamander (*Plethodon cinereus*) under various lighting conditions. Journal of Herpetology 35:521–524.

Placyk, J.S., and B.M. Graves. 2001b. *Plethodon cinereus* (Red-backed salamander). Site attachment. Herpetological Review 32:246–246.

Placyk, J.S., and B.M. Graves. 2001c. A new technique for observing redback salamanders, *Plethodon cinereus*, in the absence of visual stimuli. Herpetological Review 32:94–95.

Placyk, J.S., and B.M. Graves. 2002. Prey detection by vomeronasal chemoreception in a plethodontid salamander. Journal of Chemical Ecology 28:1017–1036.

Placyk, J.S., L. Torretti, and B.M. Graves. 2000. *Plethodon cinereus* (Red-backed Salamander). Intraspecific aggregation. Herpetological Review 31:167.

Placyk, J.S., M.J. Seider, and J.C. Gillingham. 2002. New herpetological records for High and Hog Islands of the Beaver Archipelago, Charlevoix County, Michigan. Herpetological Review 33:230–230.

Price, J.E., and J.A. Secki Shields. 2002. Size-dependent interactions between two terrestrial amphibians, *Plethodon cinereus* and *Plethodon glutinosus*. Herpetologica 58:141–155.

Pyron, R.A., and J.J. Wiens. 2011. A large-scale phylogeny of Amphibia including over 2800 species, and a revised classification of extant frogs, salamanders, and caecilians. Molecular Phylogenetics and Evolution 61:543–583.

Quinn, V.S., and B.M. Graves. 1999a. A technique for sexing Red-backed Salamanders (*Plethodon cinereus*). Herpetological Review 30:32.

Quinn, V.S., and B.M. Graves. 1999b. Space use in response to conspecifics by the Red-backed Salamander (*Plethodon cinereus*, Plethodontidae, Caudata). Ethology 105:993–1002.

Radomski, T., M.M. Hantak, A.D. Brown, and S.R. Kuchta. 2020. Multilocus phylogeography of Eastern Red-backed Salamanders (*Plethodon cinereus*): Cryptic Appalachian diversity and postglacial range expansion. Herpetologica 76:61–73.

Raimondo, S., T.K. Pauley, and L. Butler. 2003. Potential impacts of *Bacillus thuringiensis* var. *kurstaki* on five salamander species in West Virginia. Northeastern Naturalist 10:25–38.

Ransom, T.S. 2012. Comparison of direct, indirect, and ecosystem engineering effects of an earthworm on the Red-backed Salamander. Ecology 93:2198–2207.

Ransom, T.S. 2017. Local distribution of native and invasive earthworms and effects on a native salamander. Population Ecology 59:189–204.

Ransom, T.S., and R.G. Jaeger. 2006. An assemblage of salamanders in the Southern Appalachian Mountains revisited: Competitive and predatory behavior? Behaviour 143:1357–1382.

Ransom, T.S., and R.G. Jaeger. 2008. Intergeneric salamander interactions across an ecotone. Herpetologica 64:20–31.

Reams, R.D., R. Searcy, J.E. Wyatt, and W.H. Gehrmann. 2008. Habitat utilization by reptiles and amphibians at an urban state park in Indiana. Bulletin of the Chicago Herpetological Society 43:17–20.

Reiter, M.K., C.D. Anthony, and C.-A.M. Hickerson. 2014. Territorial behavior and ecological divergence in a polymorphic salamander. Copeia 2014:481–488.

Renaldo, K., C. Murch, J.-N. Riley, B. Helleman, G. Smith, and J. Rettig. 2011. Substrate preference of Eastern Red-backed Salamanders, *Plethodon cinereus*: A comparison of deciduous and coniferous substrates. Amphibia-Reptilia 32:266–269.

Richmond, L.S., and S.C. Trombulak. 2009. Distribution of Red-backed Salamander (*Plethodon cinereus*) with respect to cover-object characteristics in the Green Mountains of Vermont. Northeastern Naturalist 16:13–26.

Riedel, B.L., K.R. Russell, W.M. Ford, K.P. O'Neill, and H.W. Godwin. 2008. Habitat relationships of Eastern Red-backed Salamanders (*Plethodon cinereus*) in Appalachian agroforestry and grazing systems. Agriculture, Ecosystems & Environment 124:229–236.

Riedel, B.L., K.R. Russell, and W.M. Ford. 2012. Physical condition, sex, and age-class of Eastern Red-backed Salamanders (*Plethodon cinereus*) in forested and open habitats of West Virginia, USA. International Journal of Zoology 2012:e623730. DOI: https://dx.doi.org/10.1155/2012/623730.

Roberts, A.M., and E.B. Liebgold. 2008. The effects of perceived mortality risk on habitat selection in a terrestrial salamander. Behavioral Ecology 19:621–626.

Roble, S.M. 1999. *Plethodon cinereus* (Red-backed Salamander). Catesbeiana 19:33.

Rodewald, A.D., and R.H. Yahner. 1999. Effects of forest management and landscape composition on woodland salamanders. Northeast Wildlife 54:45–54.

Rollinson, N., and D. Hackett. 2015. Experimental evaluation of agonistic behaviour, chemical communication, spacing, and intersexual associations of the Eastern Red-backed Salamander (*Plethodon cinereus*) near its northern range limit. Canadian Journal of Zoology 93:773–781.

Rooney, T.P., C. Antolik, and M.D. Moran. 2000. The impact of salamander predation on Collembola abundance. Proceedings of the Entomological Society of Washington 102:308–312.

Rovito, S.M., G. Parra-Olea, C.R. Vásquez-Almazán, R. Luna-Reyes, and D.B. Wake. 2012. Deep divergences and extensive phylogeographic structure in a clade of lowland tropical salamanders. BMC Evolutionary Biology 12:255.

Rovito, S.M., G. Parra-Olea, E. Recuero, and D.B. Wake. 2015. Diversification and biogeographical history of Neotropical plethodontid salamanders. Zoological Journal of the Linnean Society 175:167–188.

Russell, J.J., J.A. Theriot, P. Sood, … A. Brunet. 2017. Non-model model organisms. BMC Biology 15:55. DOI: https://dx.doi.org/10.1186/s12915-017-0391-5.

Russell, R.W. 2011. *Plethodon cinereus* (Eastern Red-backed Salamander). Wildfire survival. Herpetological Review 42:359–262.

Sawyers, M.S., and C.M.J. Novick. 2011. *Plethodon cinereus* (Eastern Red-backed Salamander). Color variation. Herpetological Review 42:580–581.

Schieltz, J.M., L.M.B. Haywood, and D.M. Marsh. 2010. Effects of cover object spacing on the socioecology of the Red-backed Salamander, *Plethodon cinereus*. Herpetologica 66:276–282.

Schluter, D. 2000. The Ecology of Adaptive Radiation. Oxford University Press, UK.

Sebum, D.C., and E. Mallon. 2017. Has the Eastern Red-backed Salamander (*Plethodon cinereus*) declined in Ontario? The Canadian Field-Naturalist 131:115–119.

Semlitsch, R.D., K.M. O'Donnell, and F.R. Thompson. 2014. Abundance, biomass production, nutrient content, and the possible role of terrestrial salamanders in Missouri Ozark forest ecosystems. Canadian Journal of Zoology 92:997–1004.

Sever, D.M. 1997. Sperm storage in the spermatheca of the Red-back Salamander, *Plethodon cinereus* (Amphibia: Plethodontidae). Journal of Morphology 234:131–146.

Sever, D.M. 2017. Ultrastructure of the mental gland of the Red-backed Salamander, *Plethodon cinereus* (Amphibia: Plethodontidae). Acta Zoologica 98:154–162.

Sever, D.M., and D.S. Siegel. 2006. Sperm aggregations in the spermatheca of the Red Back Salamander (*Plethodon cinereus*). Acta Zoologica 87:331–340.

Sever, D.M., and D.S. Siegel. 2015. Histology and ultrastructure of the caudal courtship glands of the Red-backed Salamander, *Plethodon cinereus* (Amphibia: Plethodontidae). Journal of Morphology 276:319–330.

Sgrò, C.M., A.J. Lowe, and A.A. Hoffman. 2011. Building evolutionary resilience for conserving biodiversity under climate change. Evolutionary Applications 4:326–337.

Sharp, C.C., S.E. Steckler, O.M. Lockhart, and B.M. Walton. 2005. *Plethodon cinereus* (Eastern Red-backed Salamander). Predation. Herpetological Review 36:296–297.

Siddig, A.A., A.M. Ellison, and S. Jackson. 2015. Calibrating abundance indices with population size estimators of Red Back Salamanders (*Plethodon cinereus*) in a New England forest. PeerJ 3:e952. DOI: https://dx.doi.org/10.7717/peerj.952.

Siddig, A.A.H., A. Ochs, and A.M. Ellison. 2019. Do terrestrial salamanders indicate ecosystem changes in New England forests? Forests 10:154. DOI: https://dx.doi.org/10.3390/f10020154.

Silva, M., L.A. Hartling, S.A. Field, and K. Teather. 2003. The effects of habitat fragmentation on amphibian species richness of Prince Edward Island. Canadian Journal of Zoology 81:563–573.

Simons, R.R., B.E. Felgenhauer, and T. Thompson. 1999. Description of the postcloacal glands of *Plethodon cinereus*, the Red-backed Salamander, during bouts of scent marking. Journal of Morphology 242:257–269.

Sint, D., I. Thurner, R. Kaufmann, and M. Traugott. 2015. Sparing spiders: Faeces as a non-invasive source of DNA. Frontiers in Zoology 12:3. DOI: https://dx.doi.org/10.1186/s12983-015-0096-y.

Sites, J.W., M. Morando, R. Highton, F. Huber, and R.E. Jung. 2004. Phylogenetic relationships of the endangered Shenandoah Salamander (*Plethodon shenandoah*) and other salamanders of the *Plethodon cinereus* group (Caudata: Plethodontidae). Journal of Herpetology 38:96–105.

Smith, G.R. 2018. Does removal of invasive garlic mustard affect eastern Red-backed Salamanders? Ecological Restoration 36:113–115.

Smith, G.R., T. Johnson, and W.O. Smith. 2015. Effects of colour morph and season on the dehydration and rehydration rates of *Plethodon cinereus*. Amphibia-Reptilia 36:170–174.

Snyder, R., E. Mausteller, T.J.H. Matlaga, and D.A.W. Miller. 2022. How does landscape permeability affect the movement of Eastern Red-backed Salamanders? Journal of Wildlife Management 86:e22132. DOI: https://dx.doi.org/10.1002/jwmg.22132.

SPARCnet (Salamander Population and Adaptation Research Collaboration Network). 2024. The Salamander Population & Adaptation Research Collaboration Network. Available at http://sparcnet.org/. Accessed 19 September 2024. Salamander Population and Adaptation Research Collaboration Network, USA.

Staub, N.L., and R.L. Mueller. 2017. David Burton Wake. Copeia 105:415–426.

Staub, N.L., A.B. Stiller, and K.M. Kiemnec-Tyburczy. 2020. A new perspective on female-to-male communication in salamander courtship. Integrative and Comparative Biology 60:722–731.

Sterrett, S.C., A.B. Brand, W.R. Fields, R.A. Katz, and E.H.C. Grant. 2015. *Plethodon cinereus* (Eastern Red-backed Salamander). Movement. Herpetological Review 46:71–71.

Sterrett, S.C., R.A. Katz, A.B. Brand, W.R. Fields, A.E. Deitrich, D.J. Hocking, T.M. Foreman, A.N.M. Wiewel, and E.H.C. Grant. 2019. Proactive management of amphibians: Challenges and opportunities. Biological Conservation 236:404–410.

Sterrett, S.C., T.D. Dubreuil, M.J. O'Donnell, A. Brand, and E.H.C. Grant. 2022. Testing assumptions in the use of PIT tags to study movement of *Plethodon* salamanders. Journal of Herpetology 56:146–152.

Strojny, C.J., and M.L. Hunter, Jr. 2010a. Comparing relative abundance of amphibians in forest canopy gaps of natural origin vs. timber harvest origin. Animal Biodiversity and Conservation 33:1–13.

Strojny, C.J., and M.L. Hunter, Jr. 2010b. Log diameter influences detection of Eastern Red-backed Salamanders (*Plethodon cinereus*) in harvest gaps, but not in closed-canopy forest conditions. Herpetological Conservation and Biology 5:80–85.

Stuczka, A., C.-A. Hickerson, and C. Anthony. 2016. Niche partitioning along the diet axis in a colour polymorphic population of Eastern Red-backed Salamanders, *Plethodon cinereus*. Amphibia-Reptilia 37:283–290.

Sucre, E.B., J.A. Homyack, T.R. Fox, and C.A. Haas. 2010. The influence of Red-backed Salamanders (*Plethodon cinereus*) on nutrient cycling in Appalachian hardwood forests. Pp. 487–493 in Proceedings of the 14th Biennial Southern Silvicultural Research Conference (J.A. Stanturf, ed.). U.S. Department of Agriculture, USA.

Sugalski, M.T., and D.L. Claussen. 1997. Preference for soil moisture, soil pH, and light intensity by the salamander, *Plethodon cinereus*. Journal of Herpetology 31:245–250.

Sullivan, A., J. Rohr, and D. Madison. 2003. Behavioural responses by Red-backed Salamanders to conspecific and heterospecific cues. Behaviour 140:553–564.

Sullivan, A.M., and G. Jensen. 2013. A study of the sensitivity of *Plethodon cinereus* (Caudata: Plethodontidae) to damage-released cues from conspecifics. Journal of Herpetology 47:585–589.

Sullivan, A.M., J.C. Maerz, and D.M. Madison. 2002. Anti-predator response of Red-backed Salamanders (*Plethodon cinereus*) to chemical cues from Garter Snakes (*Thamnophis sirtalis*): Laboratory and field experiments. Behavioral Ecology and Sociobiology 51:227–233.

Sullivan, A.M., D.M. Madison, and J.R. Rohr. 2004. Variation in the antipredator responses of three sympatric plethodontid salamanders to predator-diet cues. Herpetologica 60:401–408.

Sullivan, A.M., A.L. Picard, and D.M. Madison. 2005. To avoid or not to avoid? Factors influencing the discrimination of predator diet cues by a terrestrial salamander. Animal Behaviour 69:1425–1433.

Sutherland, C., D.J. Muñoz, D.A.W. Miller, and E.H.C. Grant. 2016. Spatial capture–recapture: A promising method for analyzing data collected using artificial cover objects. Herpetologica 72:6–12.

Sutherland, W.J., R.P. Freckleton, H.C.J. Godfray, … T. Wiegand. 2013. Identification of 100 fundamental ecological questions. Journal of Ecology 101:58–67.

Swart, C.C., and D.C. Adams. 2004. The role of muscle mass and tooth number in ecological character displacement between *Plethodon cinereus* and *P. hoffmani* (Caudata: Plethodontidae). Herpetologica 60:408–413.

Takahashi, M.K., and T.K. Pauley. 2010. Resource allocation and life history traits of *Plethodon cinereus* at different elevations. The American Midland Naturalist 163:87–94.

Telfer, A.C., and F. Laberge. 2013. Responses of Eastern Red-backed Salamanders (*Plethodon cinereus*) to chemical cues of prey presented in soluble and volatile forms. Physiology & Behavior 114–115:6–13.

Tornick, J.K. 2010. Factors affecting aggression during nest guarding in the Eastern Red-backed Salamander (*Plethodon cinereus*). Herpetologica 66:385–392.

Townsend, J.M., and C.T. Driscoll. 2013. Red-backed Salamander (*Plethodon cinereus*) as a bioindicator of mercury in terrestrial forests of the northeastern United States. Ecological Indicators 34:168–171.

Travis, J. 2006. Is it what we know or who we know? Choice of organism and robustness of inference in ecology and evolutionary biology (American Society of Naturalists Presidential Address). The American Naturalist 167:303–314.

Uller, C., R. Jaeger, G. Guidry, and C. Martin. 2003. Salamanders (*Plethodon cinereus*) go for more: Rudiments of number in an amphibian. Animal Cognition 6:105–112.

Vanderwel, M.C., J.P. Caspersen, J.R. Malcolm, M.J. Papaik, and C. Messier. 2011. Structural changes and potential vertebrate responses following simulated partial harvesting of boreal mixedwood stands. Forest Ecology and Management 261:1362–1371.

Velo-Antón, G., K.R. Zamudio, and A. Cordero-Rivera. 2012. Genetic drift and rapid evolution of viviparity in insular fire salamanders (*Salamandra salamandra*). Heredity 108:410–418.

Venesky, M.D., and C.D. Anthony. 2007. Antipredator adaptations and predator avoidance by two color morphs of the Eastern Red-backed Salamander, *Plethodon cinereus*. Herpetologica 63:450–458.

Venesky, M.D., A. Hess, J.A. DeMarchi, A. Weil, J. Murone, C.-A.M. Hickerson, and C.D. Anthony. 2015. Morph-specific differences in disease prevalence and pathogen-induced mortality in a terrestrial polymorphic salamander. Journal of Zoology 295:279–285.

Venier, L.A., J.L. Pearce, B.A. Wintle, and S.A. Bekessy. 2007. Future forests and indicator-species population models. The Forestry Chronicle 83:36–40.

VertNet. 2021. VertNet-Home. Available at http://www.vertnet.org/index.html. Accessed 28 July 2021. National Science Foundation, USA.

Wake, D.B. 1970. The abundance and diversity of tropical salamanders. The American Naturalist 104:211–213.

Wake, D.B. 2009. What salamanders have taught us about evolution. Annual Review of Ecology, Evolution, and Systematics 40:333–352.

Wake, D.B., and J. Hanken. 2004. Direct development in the lungless salamanders: What are the consequences for developmental biology, evolution and phylogenesis? International Journal of Developmental Biology 40:859–869.

Wake, D.B., and A. Larson. 1987. Multidimensional analysis of an evolving lineage. Science 238:42–48.

Wake, D.B., and J.F. Lynch. 1976. The distribution, ecology, and evolutionary history of plethodontid salamanders in tropical America. Science Bulletin of the Natural History Museum of Los Angeles County 25:1–65.

Waldick, R.C., B. Freedman, and R.J. Wassersug. 1999. The consequences for amphibians of the conversion of natural, mixed-species forests to conifer plantations in southern New Brunswick. Canadian Field-Naturalist 113:408–418.

Waldron, B.P., S.R. Kuchta, M.M. Hantak, C.-A.M. Hickerson, and C.D. Anthony. 2019. Genetic analysis of a cryptic contact zone between mitochondrial clades of the Eastern Red-backed Salamander, *Plethodon cinereus*. Journal of Herpetology 53:144–153.

Wale, N., and M.A. Duffy. 2021. The use and underuse of model systems in infectious disease ecology and evolutionary biology. The American Naturalist 198:69–92.

Walker, D.M., B.R. Lawrence, D. Esterline, S.P. Graham, M.A. Edelbrock, and J.A. Wooten. 2014. A metagenomics-based approach to the top-down effect on the detritivore food web: A salamanders influence on fungal communities within a deciduous forest. Ecology and Evolution 4:4106–4116.

Walker, D.M., B.R. Lawrence, D. Esterline, M. McAndrew, J. Edelbrock, S.P. Graham, and C. Kelehear. 2015. A novel protocol for washing environmental microbes from amphibian skin. Herpetological Review 46:349–353.

Walker, D.M., C.M. Murray, D. Talbert, P. Tinker, S.P. Graham, and T.W. Crowther. 2018. A salamander's top-down effect on fungal communities in a detritivore ecosystem. FEMS Microbiology Ecology 94:fiy168. DOI: https://dx.doi.org/10.1093/femsec/fiy168.

Walton, B.M. 2005. Salamanders in forest-floor food webs: Environmental heterogeneity affects the strength of top-down effects. Pedobiologia 49:381–393.

Walton, B.M. 2013. Top-down regulation of litter invertebrates by a terrestrial salamander. Herpetologica 69:127–146.

Walton, B.M., and S. Steckler. 2005. Contrasting effects of salamanders on forest-floor macro- and mesofauna in laboratory microcosms. Pedobiologia 49:51–60.

Walton, B.M., D. Tsatiris, and M. Rivera-Sostre. 2006. Salamanders in forest-floor food webs: Invertebrate species composition influences top–down effects. Pedobiologia 50:313–321.

Watts, R.A., C.A. Palmer, R.C. Feldhoff, P.W. Feldhoff, L.D. Houck, A.G. Jones, M.E. Pfrender, S.M. Rollman, and S.J. Arnold. 2004. Stabilizing selection on behavior and morphology masks positive selection on the signal in salamander pheromone signaling complex. Molecular Biology and Evolution 21:1032–1041.

Wells, K.D. 2007. The Ecology and Behavior of Amphibians. University of Chicago Press, USA.

Welsh, H.H., and S. Droege. 2001. A case for using plethodontid salamanders for monitoring biodiversity and ecosystem integrity of North American forests. Conservation Biology 15:558–569.

Welsh, H.H., and L.M. Ollivier. 1998. Stream amphibians as indicators of ecosystem stress: A case study from California's redwoods. Ecological Applications 8:1118–1132.

Wiens, J.J. 2007. Global patterns of diversification and species richness in Amphibians. The American Naturalist 170:S86–S106.

Wiens, J.J., T.N. Engstrom, and P.T. Chippindale. 2006. Rapid diversification, incomplete isolation, and the "speciation clock" in North American salamanders (genus *Plethodon*): Testing the hybrid swarm hypothesis of rapid radiation. Evolution 60:2585–2603.

Wiggins, P.J., J.M. Smith, R.N. Harris, and K.P.C. Minbiole. 2011. Gut of Red-backed Salamanders (*Plethodon cinereus*) may serve as a reservoir for an antifungal cutaneous bacterium. Journal of Herpetology 45:329–332.

Wilbur, H.M. 1980. Complex life cycles. Annual Review of Ecology and Systematics 11:67–93.

Wilburn, D.B., K.E. Bowen, P.W. Feldhoff, and R.C. Feldhoff. 2014. Proteomic analyses of courtship pheromones in the Redback Salamander, *Plethodon cinereus*. Journal of Chemical Ecology 40:928–939.

Wilk, A.J., K.C. Donlon, and W.E. Peterman. 2020. Effects of habitat fragment size and isolation on the density and genetics of urban Red-backed Salamanders (*Plethodon cinereus*). Urban Ecosystems 23:761–773.

Willey, L.L., and M.T. Jones. 2010. *Plethodon cinereus* (Red-backed Salamander). Elevation. Herpetological Review 41:190–190.

Williams, E.E., R. Highton, and D.M. Cooper. 1968. Breakdown of polymorphism of the Red-backed Salamander on Long Island. Evolution 22:76–86.

Winzeler, M., S. LaGrange, and J.T. Hoverman. 2014. Ranaviruses: Emerging Threat to Amphibians. Forestry and Natural Resources Publication FNR-485-W. Purdue University Cooperative Extension Service, USA.

Wise, S.E., and B.W. Buchanan. 2006. Influence of artificial illumination on the nocturnal behavior and physiology of salamanders. Pp. 221–251 in Ecological Consequences of Artificial Night Lighting (C. Rich and T. Longcore, eds.). Island Press, USA.

Wise, S.E., and R.G. Jaeger. 1998. The influence of tail autotomy on agonistic behaviour in a territorial salamander. Animal Behaviour 55:1707–1716.

Wise, S.E., and R.G. Jaeger. 2016. Seasonal and geographic variation in territorial conflicts by male Red-backed Salamanders. Behaviour 153:187–207.

Wise, S.E., A. Rohacek, A.E. Scanlon, T. Cabrera, and B.W. Buchanan. 2022. The effects of artificial night lighting on tail regeneration and prey consumption in a nocturnal salamander (*Plethodon cinereus*) and on the behavior of fruit fly prey (*Drosophila virilis*). Animals 12:2105.

Wood, P.B., and J.M. Williams. 2013. Terrestrial salamander abundance on reclaimed mountaintop removal mines. Wildlife Society Bulletin 37:815–823.

Woolbright, L.L., and C.P. Martin. 2014. Seasonal migration by Red-backed Salamanders, *Plethodon cinereus*. Journal of Herpetology 48:546–551.

Wunder, J.L., N.M. Lampazzi, K.D. Acre, … M.K. Takahashi. 2012. Promoting amphibian conservation through the college classroom: Detection of *Batrachochytrium dendrobatidis* among local amphibians. Herpetological Conservation and Biology 7:462–469.

Wyman, R.L. 1988. Soil acidity and moisture and the distribution of amphibians in five forests of southcentral New York. Copeia 1988:394–399.

Wyman, R.L. 1998. Experimental assessment of salamanders as predators of detrital food webs: Effects on invertebrates, decomposition and the carbon cycle. Biodiversity and Conservation 7:641–650.

Yahner, R.H., W.C. Bramble, and W.R. Byrnes. 2001a. Response of amphibian and reptile populations to vegetation maintenance of an electric transmission line right-of-way. Journal of Arboriculture 27:215–221.

Yahner, R.H., N.H. Piergallini, and B.D. Ross. 2001b. Survey of amphibians and reptiles in two types of managed forests in central Pennsylvania. Journal of the Pennsylvania Academy of Science 74:48–51.

Young, G.I., and R.H. Yahner. 2003. Distribution of, and microhabitat use by, woodland salamanders along forest-farmland edges. Canadian Field-Naturalist 117:19–24.

Yu, Z., R. Dickstein, W.E. Magee, and J.R. Spotila. 1998. Heat shock response in the salamanders *Plethodon jordani* and *Plethodon cinereus*. Journal of Thermal Biology 23:259–265.

Yurewicz, K.L., and H.M. Wilbur. 2004. Resource availability and costs of reproduction in the salamander *Plethodon cinereus*. Copeia 2004:28–36.

Ziemba, J.L., A.C. Cameron, K. Peterson, C.-A.M. Hickerson, and C.D. Anthony. 2015. Invasive Asian earthworms of the genus *Amynthas* alter microhabitat use by terrestrial salamanders. Canadian Journal of Zoology 93:805–811.

Ziemba, J.L., C.-A.M. Hickerson, and C.D. Anthony. 2016. Invasive Asian earthworms negatively impact keystone terrestrial salamanders. PLoS One 11:e0151591. DOI: https://dx.doi.org/10.1371/journal.pone.0151591.

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