

Eastern red-backed salamanders: A comprehensive review of an undervalued model in evolution, ecology, & behavior

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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 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 have a wealth of accumulated knowledge on which current research programs build. A recent call within EEB to invest in the inclusive development of diverse model systems and scientists has led us to evaluate the standing of the widespread, abundant, terrestrial salamander we study, the eastern red-backed salamander (*Plethodon cinereus*). We first look at salamanders as EEB models more generally, to determine where *P. cinereus* fits in this broader context. We next present a comprehensive review of the literature on the eastern red-backed salamander (*Plethodon cinereus*) since the last comprehensive review was completed in 1998. The core of our paper reviews 410 recent studies and highlights inconsistencies, gaps in our knowledge, and future directions in the context of the 1998 review. Finally, we present a collaborative research network, SPARCnet, as a nascent infrastructure for continued research on *P. cinereus*. Here, we especially discuss how this type of infrastructure can be broadly applied not just to other salamanders, but to other model systems, so that the future of EEB research may benefit from models which accurately represent, in Darwin's words, "endless forms most beautiful and most wonderful."

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I. Introduction

What defines a model organism for a particular biological field? While this idea has captured much discussion in the biomolecular literature (e.g., Müller & Grossniklaus, 2010; Ankeny & Leonelli, 2011; Leonelli & Ankeny, 2013; Russell *et al.*, 2017), the fields of evolution, ecology, and behavior (hereafter, EEB) have historically focused less on centering their science around specific study systems and more on studying the best system 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). At the Virtual Asilomar American Society of Naturalists Vice Presidential Symposium in January 2021, Duffy *et al.* (2021) laid out a broad and inclusive framework for defining, developing, and nurturing model organisms and model systems in EEB, including describing important contrasts with the biomolecular sciences. Similarly, in a President’s Plenary talk for the Society for Systematic Biologists in June 2021, Erika Edwards discussed the value of a model clade to EEB and systematic biology in particular. In this paper, 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 great depth of knowledge already 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; Jaeger *et al.*, 2016; studies reviewed herein), (2) the critical niche position of woodland salamanders in forest ecosystems (Davic & 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 such a wide range of salamanders given the extensive diversity, abundance (Plethodontidae comprise nearly 2/3 of all salamander species), and well-studied systematics of the family. In making our argument, we review current knowledge of this species to build a resource for scientists looking to work with *P. cinereus* and discuss the next steps in investment and infrastructure needed for model organisms like *P. cinereus* to be successful (Ankeny & Leonelli, 2011; Leonelli & Ankeny, 2013; Duffy *et al.*, 2021; Wale & Duffy, 2021).

To that end, our paper has four overarching goals. First, we briefly discuss the definition and use of model organisms in EEB, highlighting salamanders as good candidates for model organism 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* that has occurred since the last comprehensive review, more than 20 years ago by Petranks (1998). Finally, we discuss the challenges of advancing *P. cinereus* and similarly well-studied species into the next stage of model organism status. Here, we highlight a collaborative research network, SPARCnet (the Salamander Population and Adaptation Research Collaboration Network), which offers a nascent infrastructure necessary for continued development of *P. cinereus* as a model system in EEB.



Figure 1. Top: Geographic range of *Plethodon cinereus* shown as diagonal lines is 1.89 million km² (IUCN, 2020). The blue 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*, from left to right, unstriped, striped, and erythristic (Photos by M.C. Fisher-Reid).

II. Model Systems in Evolution, Ecology, and Behavior

As part of defining what model organisms are for EEB, Duffy *et al.* (2021) summarize the considerations for using model organisms in cellular, molecular, and developmental biology (hereafter collectively referred to as the biomolecular sciences; e.g., Müller & Grossniklaus, 2010; Ankeny & Leonelli, 2011; Leonelli & Ankeny, 2013; Russell *et al.*, 2017), aptly noting that these fields tend to neglect, or even negate, the ecology and evolution of their models. For example, Müller & Grossniklaus (2010) highlight the origins of 19 model organisms and their major contributions to biology. However, the contributions of these 19 taxa to the fields

of EEB are largely overlooked, despite the prominent phylogeny the authors include and implicit nod at EEB when highlighting the discovery of the highly conserved HOX genes in *Drosophila*. Similarly, Russell *et al.* (2017) profile 14 “non-model model organisms” and focus on fundamental phenomena at the scale of molecules, genes, and cells with little regard for EEB fundamental phenomena (as defined by Ankeny & Leonelli, 2011; Leonelli & Ankeny, 2013). 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), however, the fields of EEB are not well-represented in discussions of model organisms as a whole. While both reviews focus on the biomolecular utility of model organisms, the EEB scientific community values many of these same organisms (e.g., *Escherichia coli*, *D. melanogaster*, *Arabidopsis thaliana*; Duffy *et al.*, 2021), often for many of the same reasons (e.g., short generation time, lab tractability). Despite these overlaps in utility for both fields, however, Duffy *et al.* (2021) argue that there are a number of challenges in applying the definition of model organism from the biomolecular sciences to EEB studies. Instead, Duffy *et al.* (2021) propose the following definition for a model system in EEB (p. 55):

“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 Figure 1 in Duffy *et al.*, 2021). 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. Individual organisms are often the smallest unit of interest in EEB, and although the burgeoning fields of molecular ecology, evolutionary genetics, and evolutionary development can focus on molecular mechanisms, the driving questions, even in these more molecular EEB fields, often focus on using molecular tools for understanding the whole organism or higher biological scales. 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, as these factors contribute to both the accessibility and potential for lessons learned studying the model system to have broader applicability.

The exemplary taxa in EEB textbooks and research programs often take the form of model systems: groups of closely related, ecologically diverse species, found in relatively confined 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 our 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) state, EEB scientists “aim to see the forest *and* the trees” (their emphasis; p. 53).

One of the most crucial challenges facing the use of biomolecular model organisms for EEB research is that these lab-evolved populations are often dramatically different from their wild relatives in both ecologically and evolutionarily important ways (Duffy *et al.*, 2021). These model organisms have long been artificially selected by scientists to produce standardized laboratory strains amenable to mass rearing, such that they are often deliberately stripped of both genotypic and phenotypic variation, and the ecological context for this variation. Thus, biomolecular model organisms generally violate one of the primary requirements for a model organism to address EEB-related questions: that an organism or model system be representative of other species and inform our understanding of general principles or fundamental phenomena in the natural world (Wale & Duffy, 2021).

We, therefore, explicitly define the fundamental phenomena of EEB in the context of considering if a species or system can serve as a model organism in EEB (Fig. 2). In evolution, research focuses largely on the survival and reproduction of organisms based on their hereditary phenotypic variation and seeks to explain

how traits change over time in the context of common ancestry. In ecology, research focuses on the spatial and temporal distribution and abundance of organisms, and how their interactions with each other and their abiotic environments drive population and community dynamics (Begon, Townsend, & Harper, 2006). Behavior unites ecology and evolution with the organismal sciences of physiology, genetics, and development to understand the how and why of behavioral traits (i.e., Tinbergen's four questions; (Tinbergen, 1963). Historically thought to be restricted to animals, we now know that evidence of behavior can be found in all life forms, from microbes that cooperate when resources are limited (e.g., *Dictyostelium discoideum*; Devreotes, 1989), to plants that use chemical cues to warn neighbors of impending herbivore attacks (Babikova *et al.*, 2013). We propose that all research questions in EEB can be assigned to one or more of these three broad contexts at their core, thus defining the fundamental phenomena of EEB (Fig. 2).

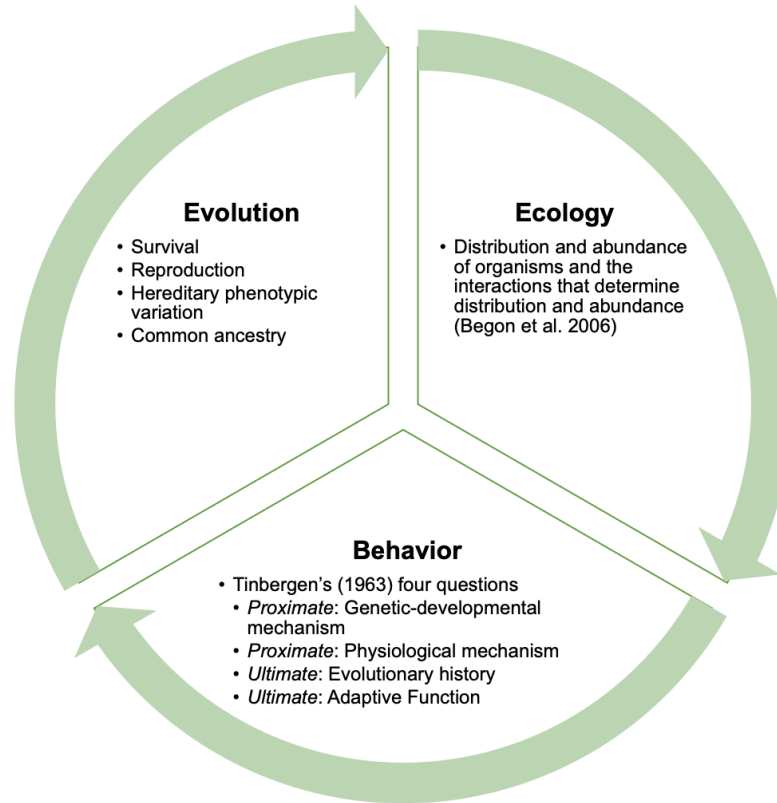


Figure 2. Fundamental phenomena in evolution, ecology, and behavior.

Important to the goals of this manuscript, and rightfully included by Duffy *et al.* (2021), model systems in EEB must contribute to robust inference across these fundamental phenomena (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. 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 communities of woodland salamanders.

III. Salamanders & 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 & Grossniklaus, 2010). In EEB, pond-breeding amphibians have long played a major role in studies of metamorphosis and complex life cycles (Wilbur, 1980). Despite pond-breeding salamanders being more commonly recognized, the salamander family Plethodontidae represents nearly two-thirds of all salamander species (486 of 750; AmphibiaWeb, 2020), and its members occupy a wide range of aquatic and terrestrial microhabitats, often with distinctly different life histories from pond-breeding amphibians (Wake & Lynch, 1976; Petranka, 1998; Blankers, Adams, & Wiens, 2012). Plethodontids are the only salamander family to have radiated extensively in the tropics (tropical bolitoglossines; Wake & Lynch, 1976; Wiens, 2007), and the only family of salamanders with species that have direct development (i.e., no aquatic larval stage; Wake & Hanken, 2004). In fact, because Plethodontidae is the largest salamander family, direct development is actually the most common mode of reproduction in salamanders and was likely a key innovation involved in the diversification of Plethodontidae (Schluter, 2000; Wake & Hanken, 2004). Compared to pond-breeding amphibians, species of plethodontids with direct development generally have high field tractability and site fidelity, while pond-breeders can often only be sampled in large numbers during the brief breeding season. In terms of conservation status, plethodontid species run the gamut from least concern to endangered or data deficient (Table 1; IUCN, 2020).

Table 1. Conservation status for 408 species of Plethodontidae (54% of family) which have been evaluated by the IUCN (IUCN, 2020).

Conservation Status	Number of Plethodontidae Species
Least Concern	94
Near Threatened	35
Vulnerable	65
Endangered	94
Critically Endangered	85
Extinct	2
Data Deficient	33

As amphibians and ectotherms, salamanders are generally sensitive to their environment (Duellman & 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 & 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 due to this environmental sensitivity, several studies have already made the case for the use of plethodontid salamanders in biodiversity and ecosystem monitoring as indicator species (Welsh & Ollivier, 1998; Welsh & Droege, 2001; Best & Welsh, 2014; Farallo & Miles, 2016; Fleming *et al.*, 2020), while others have argued caution when using amphibians as ‘canaries in a coal mine’ for anthropogenic change (Kerby *et al.*, 2010).

The genus *Plethodon* includes 58 terrestrial woodland species found in North America, for which the vast majority of species (49 species) form a clade of eastern *Plethodon*, while the remaining 9 species form a clade of western *Plethodon*, the majority of which are found in the Pacific Northwest (Wiens, Engstrom, & Chippindale, 2006; Fisher-Reid & Wiens, 2015; AmphibiaWeb, 2020). Phylogenetically, *P. cinereus* is a member of the basal clade of the three eastern North American clades of *Plethodon* (Wiens *et al.*, 2006; Fisher-Reid & Wiens, 2015) and it is the sister species to the vulnerable *P. shenandoah* (IUCN, 2020), which, while locally abundant where found, is geographically restricted to three mountaintops in Virginia

(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, and west to Minnesota in the north, and the Appalachians in the south (Fig. 1). Within its range, *P. cinereus* is often locally abundant, with surface density estimates ranging from 0.05 – 3.3 salamanders/m² (Petranka, 1998; Semlitsch, O'Donnell, & Thompson, 2014), and more recent estimates reporting surface densities that can range higher (e.g., Hernández-Pacheco *et al.*, 2019 reported densities of 2.5 – 6.3 salamanders/m² in 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 provide an updated 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 last comprehensive review was conducted over 20 years ago as part of a book detailing the natural history of North American salamanders (Petranka, 1998). In the early 2000s, some authors wrote additional broad overviews of amphibian biology which include species-specific knowledge (Lannoo, 2005; Wells, 2007), but these compendiums largely rely the details found in Petranka (1998), with minimal updates. Fifty years of behavioral research on *P. cinereus* was recently summarized in Jaeger *et al.* (2016) in which the authors highlight Petranka (1998) as the authoritative account for *P. cinereus* life history and ecology (pg. 3). 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.

IV. Methods

(1) Literature Searches

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.

In the family-level search, we searched for each of the ten families of Caudata. Each family was searched to include informal and formal mentions, e.g., we used the topic search keyword **TS=(plethodontid*)** for Plethodontidae (Table 2). There was one family, Proteidae, which returned a large number of non-salamander-related articles. For example, our original search string **TS=(proteid*)** also returned articles on *Proteides* butterflies. We modified the search string for this family only, to restrict results to amphibians (see Table 2). We recorded the number of articles found in these searches, and retained the top three families for the second search (bolded in Table 2). These three families, (Plethodontidae, Salamandridae, and Ambystomatidae) had 3-8x more articles than the next highest family (Hynobiidae; Table 2), and represent the dominant Caudata families and study organisms globally. Together, these three families include 50 genera and represent 85% (640/750 named species; AmphibiaWeb, 2020) of salamander species, with Plethodontidae alone representing 65% (486/750 at the time of the literature search; AmphibiaWeb, 2020) of salamander species.

In the genus-level search, we searched for the name of each genus within three retained families based on lists of genera from AmphibiaWeb (2020). As before, we searched Web of Science All Databases for All Years. These were new searches (i.e., not subsets of the first search) in order to capture articles which do not explicitly list the family name in the title, abstract, or author-provided keywords. Thus, there are numbers in Table 3 for a given genus which are greater than the numbers returned in the family-level search in Table 2. For these searches, genus name was the only keyword used, e.g., **TS=(Plethodon)**. Often, the large numbers

for a given genus are driven by one or two very well-studied species, so our cutoff for a genus to move on to the species-level search was 883, i.e., the number of articles returned for *P. cinereus*'s species-level search (see next paragraph). Thus, we retained the top ten genera for the species-level search (Table 3). Together, these ten genera represent 24% (179/750 named species; AmphibiaWeb, 2020) of salamander species. Search results for all 50 genera are included in Table S1.

In the species-level search, we searched for each of the 179 species within the ten retained genera to determine which species are the most well-studied in EEB as measured by the total number of articles in these fields. As before, we searched the Web of Science All Databases for All Years, however, the species-level search strings included two restrictions to ensure we (1) captured only relevant articles which focused on that species and (2) minimized pseudoreplication. For example, to search for articles on *P. cinereus*, we used the search string: TS=("Plethodon cinereus") NOT KP=("Plethodon cinereus") AND DT=(ARTICLE). This restricted the topic search to title, abstract, and author-provided keywords, and eliminated irrelevant sources which are included in topic searches because the scientific name is found in the Keywords Plus (KP) field. KP is an algorithmically generated field based on the references of sources (Clarivate, 2021), and it can inflate results if an article on a closely related species regularly cites articles with the focal species in the article titles. Limiting the document type (DT) to articles reduces instances of pseudoreplication, as data sets, FigShare figures, and conference abstracts associated with a single published study are all counted as individual records if document type is not restricted. As it is standard practice to state scientific names at least once in published literature in EEB, we did not include common names in our search, nor did we include any subgenera listed on AmphibiaWeb (2020). Any species with > 800 articles (N = 8, 4.5% of species searched) were retained (Table 4) and the full records of all articles were exported from Web Of Science as tab-delimited files to be further processed in Excel. For each of these eight species, we retained articles that were broadly in the fields of natural history, ecology, evolutionary biology, behavior, or conservation biology, and discarded articles that were not in these fields. We did this by sorting the Web of Science results by source (SO; journal title) and then examining the titles and, if necessary, the abstracts of articles in all records, paying special attention to records in both broad-scope journals (e.g., *Nature*, *Science*), and journals that do not typically publish EEB-related studies (e.g., *Developmental Biology*, *Journal of Cell Science*). Macroevolutionary articles using salamanders to explore broad questions in vertebrate evolution were also discarded, as these did not focus on the microevolution of the focal species. All discarded articles deemed outside the intended scope of our review based on these criteria, as well as any duplicate records were moved to a second tab (Tables S3-S10), and not included in the final tallies for the species-level search (Table 4). This filtering step was particularly important for species that are used heavily in cell and developmental biology research. For example, the axolotl (*Ambystoma mexicanum*), is a model laboratory organism for developmental biology, limb regeneration, embryology, and several other applied biomolecular fields, and articles in these fields are not concerned with the axolotl's natural history, ecology, evolution, or behavior. In the supplement, we report the raw number of articles returned for all 179 species (Table S2), and include the lists of retained EEB sources vs. removed non-EEB sources for each of the eight focal species (Tables S3-S10).

(2) Estimation of Geographic Range Size

We expected geographic range size to be related to how well-studied an organism is in EEB due to accessibility: species with larger geographic ranges offer greater opportunities for more individual scientists to study their local population. In order to determine how wide-ranging *P. cinereus* is compared to other salamanders, we downloaded geographic range data from the IUCN Red List for all 607 salamander species for which data was available as a single shapefile (IUCN, 2020). Using QGIS 3.12, we estimated the area (km²) of all polygons using the field calculator formula \$area, and summed polygons for each species using the Dissolve with Stats plugin.

(3) Comprehensive Literature Review of *P. cinereus*

Finally, we conducted a comprehensive literature review of articles on *P. cinereus* that were published after Petranka (1998). We started with the 677 EEB articles that remained from our species-level Web of Science search (Table S8) and cross-referenced this list with sources cited by Petranka (1998) in his chapter on *P. cinereus* (pg. 335–346). Of these 677 articles, 361 articles were published after Petranka (1998) went to press, covering 1997–2020. To these, we added an additional 49 recent studies (spanning 2005–2020) which were not recovered by Web of Science, but which we knew of based on our own prior knowledge of the *P. cinereus* literature (Greenhalgh & Peacock, 2005). This brought the total number of sources to be reviewed to 410, spanning 1997 – June 2020. We next categorized these articles based on what biological scale or fundamental phenomena they focused on, using a combination of Petranka’s (1998) section headers and the section headers for species accounts on AmphibiaWeb (2020) as our categories (Table S11). Articles were categorized into a primary and secondary category based on titles and abstracts. One criticism of the *P. cinereus* literature we were aware of going into this review was that most studies are geographically limited to a single population or geographic region within the geographic range. In order to quantify this, we recorded the source location of the salamanders used in each study (state or province) while we categorized. Studies that included salamanders from multiple states were counted for each state (e.g., Fisher-Reid *et al.*, 2013 included field data from NY, CT, and NJ, and was counted once for each of these three states), bringing our total number of study locations to 458. From this number, we excluded one study from Tennessee (Fitzpatrick, Shook, & Izally, 2009) because it was not actually conducted within the range of *P. cinereus*, but within the range of congener *P. ventralis*. Of the remaining 457 study locations, seven studies were considered range-wide (1.5%), and two studies had unknown sources of salamanders (0.4%), and were excluded from further analyses. Our final number of study locations was 448.

Once categorized, we divided the studies equally among all authors to be read and summarized. We kept our summaries to a few sentences recorded in a “Key Results” field in a shared spreadsheet (Table S11). From these single article summaries, we then drafted category summaries and aligned these with Petranka (1998) chapter headers, which comprise the Comprehensive Literature Review section below. In reviewing the post-Petranka (1998) literature on *P. cinereus*, we hope to first provide a much-needed update on the current state of knowledge on *P. cinereus*, one which thoroughly examines the geographic variation, gaps in our knowledge, and lays out future research directions. Second, we demonstrate how our research network, SPARCnet, is poised to embrace the geographic variation, collect standardized long-term demographic data, and run statistically robust field-based experiments.

V. Results

(1) Literature Searches

Results for the family-level and genus-level searches are shown in Table 2 and Table 3, respectively, and the full results for all 50 genera are in Table S1 and for all 179 species in Table S2. In the species-level search (Table 4), in terms of raw numbers of articles in EEB related fields compared to non-EEB related fields, *P. cinereus* comes out 5th, 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 pond-breeding species with an aquatic larval stage. *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, 2020), and the only salamander family with direct developing species (Wake & 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*; Table S4).

Table 2. Family-level searches in Web of Science (WoS). All searches were conducted on 18 June 2020. Bolded taxa were retained for the genus level search.

Salamander Family	Family Search String	Number of articles found (WoS All Databases, 1864-2020)	Number of Species (AmphibiaWeb 2020)
Ambystomatidae	TS=(ambystomatid*)	4396	32
Amphiumidae	TS=(amphiumid*)	514	3
Cryptobranchidae	TS=(cryptobranchid*)	919	4
Dicamptodontidae	TS=(dicamptodontid*)	306	4
Hynobiidae	TS=(hynobiid*)	1656	82
Plethodontidae	TS=(plethodontid*)	6385	486
Proteidae	TS=(proteid* AND (amphibia* OR caudat* OR salamander* OR urodel*))	1294	8
Rhyacotritonidae	TS=(rhyacotritonid*)	14	4
Salamandridae	TS=(salamandrid*)	13114	122
Sirenidae	TS=(sirenid*)	456	5

Table 3. Genus-level searches in Web of Science (WoS). The top 10 salamander genera with the highest number of articles are shown here. All of these were retained for the next stage of searching as they all contained more articles than the number of articles for *P. cinereus* 's species-level search (833), while the remaining 40 genera fell short of this value. Search results for all 50 genera are reported Table S1. All searches were conducted on 18 June 2020.

Family	Genus Search String	Number of articles found (WoS All Databases, 1864-2020)	Number of Species
Salamandridae	TS=(<i>Taricha</i>)	1337	4
Plethodontidae	TS=(<i>Eurycea</i>)	1463	33
Plethodontidae	TS=(<i>Desmognathus</i>)	1700	22
Salamandridae	TS=(<i>Cynops</i>)	1846	9
Salamandridae	TS=(<i>Pleurodeles</i>)	2438	3
Salamandridae	TS=(<i>Notophthalmus</i>)	2527	3
Plethodontidae	TS=(<i>Plethodon</i>)	3040	58
Salamandridae	TS=(<i>Salamandra</i>)	3054	6
Salamandridae	TS=(<i>Triturus</i>)	9292	9
Ambystomatidae	TS=(<i>Ambystoma</i>)	10937	32

Table 4. Species-level searches in Web of Science. The top eight salamander species with the highest raw number of articles are shown here. The raw number includes all results for a given search string, while the adjacent column on the right includes only those articles directly related to the natural history, ecology, and evolution of the species (with duplicates removed). Raw number search results and search strings for all 179 species are reported in Table S2, and article lists for each of these eight species are reported in Tables S3-S10. All searches were conducted on 18 June 2020.

Geographic Region	Geographic Range Size (km ² ; IUCN 2020)	IUCN Threat Status	Family	S
Mexico	1.03 x 10 ²	Critically Endangered	Ambystomatidae	A
Europe	4.37 x 10 ⁶	Least Concern	Salamandridae	T
North America	5.15 x 10 ⁶	Least Concern	Ambystomatidae	A
North America	6.66 x 10 ⁶	Least Concern	Salamandridae	M
Europe	2.16 x 10 ⁶	Least Concern	Salamandridae	S
North America	3.11 x 10 ⁶	Least Concern	Ambystomatidae	A
Japan	2.87 x 10 ⁵	Near Threatened	Salamandridae	C
North America	1.89 x 10 ⁶	Least Concern	Plethodontidae	F

(2) Estimation of Geographic Range Size

Among all salamanders for which range data was available (N = 607; IUCN, 2020), *P. cinereus* has the 11th largest range (Table S12). Among the top eight most well-studied salamander species (Table 4), 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 km²; Table 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 km² (Table 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 to Bolivia and from Ecuador 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 plethodontids.

(3) Comprehensive Literature Review of *P. cinereus*

The following sections summarize the results of our comprehensive literature review of *P. cinereus* research since Petranks (1998) and published prior to our search date in June 2020. We use the same section headers as Petranks (1998), but we have added subheaders for larger topics. We follow Petranks’s (1998) organization of topics closely. We have taken special care to note when more recent research (1) supports what is written in Petranks (1998), (2) fills in a gap in understanding which Petranks (1998) identified, or (3) contradicts what is written in Petranks (1998). In the supplement, we include our categorization and key results summaries of these sources which we used to organize this review (Table S11). We also include the full list of sources returned by Web of Science on *P. cinereus* (Table S8) and note which of these were cited by Petranks, (1998) for completeness (Table S13).

(a) Identification

Petranks (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 Petranks (1998), documentation of other color phenotype anomalies (e.g., leucistic) from throughout the geographic range have been published regularly, often in *Herpetological Review*’s Natural History Notes section (e.g., Mendyk, Augustine, & Montague, 2010; Sawyers & Novick, 2011; Jongsma, 2012a, 2012b). Recently, Moore & Ouellet (2014) reviewed color phenotypes in *P. cinereus*, summarizing eight diagnosable color phenotypes with photographs. Moore & Ouellet (2014) provide a dichotomous key for identifying the color phenotypes and are maintaining an open-access database of photographs and provide 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 & 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, while the remaining five color phenotypes (iridistic, albino, leucistic, amelanistic, melanistic) are somewhat rare anomalies with patchy observations throughout the range.

Additional work on color phenotypes since Petranka (1998) includes studies on the expression of different color phenotypes over time and over development. Over time, Kraemer, Kissner, & Adams (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 hypothesize that the changes in brightness were due to upregulation of dermal pigments (Kraemer *et al.*, 2012), but note 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 development, Evans, Urban, & Jockusch (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 these apart.

SPARCnet research has revealed an additional interesting trait related to skin phenotypes; one that is possibly sexually dimorphic. Muñoz (2018) describes natural green fluorescence under a blacklight on the ventral side of tails for 45 salamanders in Pennsylvania. Muñoz (2018) observed ventral tail fluorescence during the autumn (September to November) 2014 season and notes that the trait occurred more frequently in males (N=33) than females (N=12). In Massachusetts, one of us documented the same ventral fluorescence in 78 individual salamanders during the autumn 2019 season (M.C.F.-R.; unpublished data), as well as in a handful of individuals in the autumn seasons of 2017 and 2018 (prior to intentionally recording these observations; Fig. S1). In 2019, we also observed a strong male bias in fluorescence (N = 71 males; 3 females; 4 unknowns) and we observed that fluorescence persists for several weeks, as 11 individuals recaptured 2-4 times (mean: 2.4) during the same season exhibited fluorescence each time they were caught (sample dates are generally [?] 7 days apart). Munoz (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.

Petranka (1998) notes minimal sexually dimorphic traits in *P. cinereus*, with sexually active males showing swollen nasolabial grooves, hedonic glands, and a mental gland. Two additional studies have been published since which describe non-invasive methods for sexing adult salamanders. Quinn & Graves (1999b) report on sexual dimorphism in the inter-nares distance (distance between nares and snout tip). They show that males had significantly larger inter-nares distances than females, for salamanders whose sex was confirmed by dissection. While this trait is extremely useful for sexing preserved specimens without dissection, it is more difficult to use in field or laboratory settings with live animals. Measuring inter-nares distance on a live animal requires that the animal be cooled on ice prior to measuring, thus this method may not be practical in all field situations (Quinn & Graves, 1999b). Gillette & 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). 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), one can determine sex. Gravid females can also have their eggs counted by pressing gently on the body wall to make the individual eggs visible through the ventral skin. Like any method for determining sex, candling has trouble distinguishing between sub-adult females with no eggs and sub-adult males with undeveloped testes,

however, in our experience, it works well on adult salamanders (i.e., greater than 35 mm snout-vent-length (SVL); Petranka, 1998).

(b) Systematics and Geographic Variation

Genetic and bioinformatics tools for understanding the systematics and geographic variation of *P. cinereus* were only just becoming inexpensive and commonplace in 1998. The studies which Petranka (1998) cites on this topic are even older and rely exclusively on allozyme data to distinguish species-level and population-level genetic variation (Highton & Webster, 1976; Highton & 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 phylogenetic methods (e.g., Wiens *et al.*, 2006; Fisher-Reid & 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, p. 199; Sites *et al.*, 2004; Wiens *et al.*, 2006; Highton *et al.*, 2012) and the closely related southern red-backed salamander (*P. serratus*; Wiens *et al.*, 2006; Highton *et al.*, 2012). At the time of our literature search, there was no published evidence of hybridization between *P. cinereus* and *P. shenandoah* (Carpenter, Jung, & Sites, 2001), or between *P. cinereus* and either *P. shenandoah* or *P. serratus* (Bayer *et al.*, 2012). However, rare hybrids between *P. cinereus* and *P. shenandoah* have recently been documented (E.H.C. Grant, *pers. comm.*). There is also evidence of extensive hybridization between *P. cinereus* and *P. electromorphus* in Ohio (Lehtinen *et al.*, 2016). Phylogenetically, *P. electromorphus* belongs to the *cinereus* clade and last shared a common ancestor with *P. cinereus* roughly 10 million years ago (Wiens *et al.*, 2006). The results of Lehtinen *et al.* (2016) suggest there may be more cryptic hybridization yet to be found between *P. cinereus* and sympatric congeners within the *cinereus* clade.

The systematics of plethodontid salamanders has been one of the most active areas of research, both prior to Petranka's (1998) chapter, and after it. Because they are the largest family of salamanders, and the only group of salamanders to radiate in the tropics (Wake & Lynch, 1976; Wiens, 2007), there has been much interest using them to study evolutionary questions in a phylogenetic context. From a systematics perspective, *P. cinereus* appears to behave as a single evolutionary species (i.e., individuals from across the range form a single phylogenetic lineage (Wiens *et al.*, 2006; Fisher-Reid & 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*.

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. This observation supports a post-glaciation range expansion from southern refugia, and has been further supported by more recent studies using either microsatellites (e.g., Cameron, Anderson, & Page, 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 & Cabe (2003) published the first set of microsatellite markers for *P. cinereus* from a well-studied Virginia population, which have been widely used by researchers to test hypotheses of detectable 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 (Gibbs, 1998c; Noel *et al.*, 2007; Noel & Lapointe, 2010; Wilk, Donlon, & Peterman, 2020), kin discrimination (Liebgold & Cabe, 2008), influence of historical landscape change on population structure (Jordan, Morris, & Gibson, 2008), and color-biased dispersal (Grant & Liebgold, 2017). The results of these studies are discussed in detail in the appropriate section later in this review. Here, we only note that Cabe *et al.* (2007)

found low-level but detectable population structure over 2 km of continuous habitat in Virginia, consistent with an isolation-by-distance model, and no evidence for sex-biased dispersal. Grant & Liebgold (2017) also found no evidence for sex-biased dispersal, but did find evidence for color-biased dispersal. In this Maryland population, striped salamanders showed population genetic evidence of philopatry, while unstriped salamanders showed population genetic evidence of dispersal (Grant & Liebgold, 2017). It remains to be seen if this pattern exists in other populations.

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 they were developed in (e.g., Cameron *et al.*, 2017). In completing this review, we expected that many of the studies on *P. cinereus* are done on a small subset of populations. This is, in fact, the case, with just over half of the reviewed studies occurring in or using salamanders from Virginia (29.5% of studies reviewed), Ohio (13.2% of studies reviewed) or Pennsylvania (9.6% of studies reviewed), and indeed a large number of the population genetic studies mentioned here have limited geographic coverage (see additional comments below; Fig. 3; Table S14).

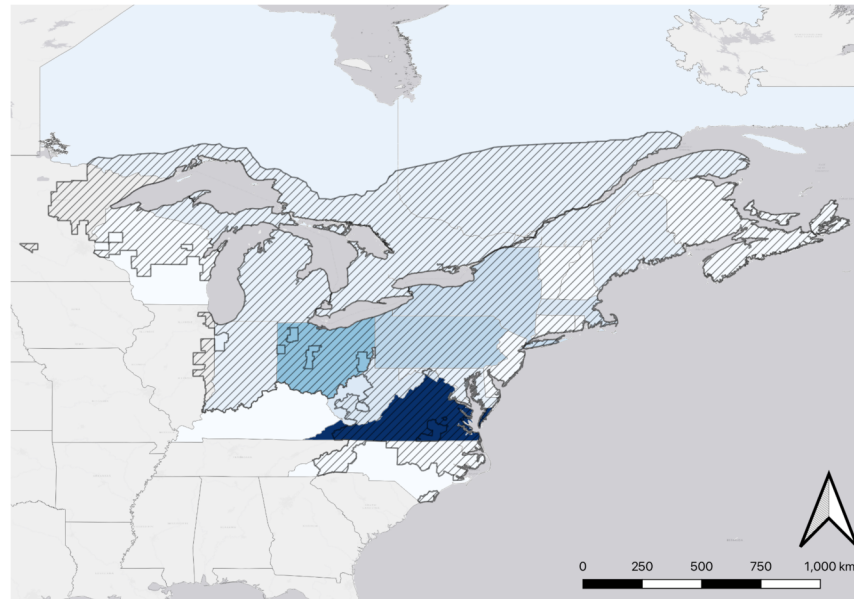


Figure 3. Heatmap of proportion of studies on *P. cinereus* from different states and provinces since Petranks (1998) was published. Darker shades of blue indicate a higher proportion of studies. Studies that included salamanders from multiple states were counted for each state for a total $N = 448$. Slightly more than half of all studies (52.2%) use salamanders from Virginia, Ohio, and Pennsylvania. The geographic range of *P. cinereus* is overlaid as a gray diagonal lines.

Petranks (1998) focuses much of the discussion of geographic variation on ratios of color phenotypes across the range, hypothesizes 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 Petranks (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 three to five decades later (e.g., through confirmation of earlier records in King *et al.*, 1997; Fisher-Reid *et al.*, 2013; Hantak *et al.*, 2015; Evans *et al.*, 2018); although, see discussion of Grant, Ransom, & Liebgold, 2018 below). Less clear is the hypothesized relationships between color phenotypes, their physiology, and climate. At the time Petranka (1998) wrote his chapter on *P. cinereus*, there was evidence that striped morphs were more common in cooler climates (i.e., higher latitudes; Test, 1952; Lotter & Scott, 1977) and evidence that unstriped morphs had a physiology consistent with being more tolerant of warmer conditions than striped morphs (Moreno, 1989). 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, Niewiarowski, & Moore, 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, Johnson, & Smith (2015) found that, while both morphs were equally able to resist water loss, striped morphs recovered from dehydration more successfully than unstriped morphs, particularly in autumn.

Gibbs & Karraker (2006) show that frequencies of the unstriped morph have increased with sampling year alongside increasing global temperatures, supporting work cited in Petranka (1998) and implying that the unstriped morph may become more common as global temperatures increase due to climate change. However, Moore & 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) combine the Gibbs & Karraker (2006) and Moore & Ouellet (2015) data sets and find 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 due to global climate change (Cosentino *et al.*, 2017).

Cosentino *et al.* (2017) note in their discussion, and we agree with their conclusion, that the many studies examining traits between color phenotypes (e.g., Petruzzi *et al.*, 2006; Anthony, Venesky, & Hickerson, 2008; Davis & Milanovich, 2010; Fisher-Reid *et al.*, 2013; Smith *et al.*, 2015; Muñoz *et al.*, 2016a; Cosentino & Droney, 2016) suffer from being limited to a single population or geographic region. To this we add the additional caution that these studies are generally measuring only the surface-active frequency of the color morphs, not the true population-level frequency. Spatial capture-recapture methods, like those used by SPARCnet participants (see below), can better estimate population-level frequencies, but require more consistent and more detailed population monitoring (e.g., Sutherland *et al.*, 2016). Knowing of the existence of geographic limitations in the *P. cinereus* literature from the outset, we recorded the geographic location of each of the 410 studies we reviewed in depth (Table S14; studies with multiple locations counted once for each location; see Methods). Excluding range-wide studies and those with unknown locations, we found that just over half (52.2%; $N = 234/448$) of the studies conducted on *P. cinereus* since Petranka (1998) are from just three states in the center/southern part of the range: Virginia (29.5% of studies reviewed), Ohio (13.2%), and Pennsylvania (9.6%; Fig. 3). Nearly one third of the Virginia studies are from Mountain Lake Biological Station (MLBS; 9.2% of all studies reviewed), a field station in southwestern Virginia, at elevation (~1100-1200 m), and with its own unique pattern of color phenotype frequencies (Angleberger & Chinnici, 1975). As we conclude below, our hope is that the distributed nature of SPARCnet participants throughout the range of *P. cinereus* can begin to more robustly address the geographic variation and contradictory results uncovered when exploring differences between color phenotypes.

Fisher-Reid & 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 eight other species of *Plethodon*, while another 14 species are fixed for either the striped or unstriped morph (seven species each). All of the polymorphic and monomorphic species are in the three basal groups 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 & Wiens, 2015). Interestingly, there is a strong relationship between color phenotype and climate between species that 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 & Wiens, 2015). Only *P. cinereus* and a western species, *P. vehiculum*, show significant climate-morphology relationships, and they are not identical (Fisher-Reid & Wiens, 2015).

Several studies since Petranka (1998), have explored the variation of color phenotypes in *P. cinereus* for reasons other than climate, three focusing on selection imposed by predators using clay models (Fitzpatrick *et al.*, 2009; Kraemer, Serb, & Adams, 2016; Grant *et al.*, 2018), and two focusing on genetic structure and landscape heterogeneity (Fisher-Reid *et al.*, 2013; Hantak *et al.*, 2019). Fitzpatrick *et al.* (2009) found that avian predators will attack the more common morph when presented with striped and unstriped clay models at varying frequencies, suggesting negative frequency-dependent selection is acting to maintain color polymorphism. However, most populations in the literature have morph frequencies that are not 50:50 striped:unstriped (Petranka, 1998; Cosentino *et al.*, 2017), as would be expected if negative frequency-dependent selection were the only or the predominant factor determining color phenotype frequencies.

Kraemer *et al.* (2016) used a clay model approach to test for predation selection on color phenotype (striped, unstriped, and erythristic) imposed by mammals. In this study, the authors found complex results driving mammalian predator attacks on the clay models which include both directional selection favoring inconspicuousness and, more strongly, frequency-dependent selection favoring novel coloration. 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 three years of mark-recapture of a Maryland population on the Delmarva Peninsula (i.e., the peninsula includes portions of Delaware, Maryland, and Virginia) to explore morph-specific differences in survival. Delmarva is another location with its own unique color phenotype frequencies (Petranka, 1998). Similar to Long Island, there is a gradient 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, while mammals showed no differential predation by color phenotype (Grant *et al.* 2018). Interestingly, Grant *et al.* (2018) show color phenotype frequencies that are opposite 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 three years 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 be stable over 40 years. It would be interesting to completely resurvey Highton's (1977) localities and follow Cosentino *et al.*'s (2017) modeling methods 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 color phenotype frequencies in *P. cinereus*. Williams, Highton, & Cooper (1968) were the first to note that the typical 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 the 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 salamanders at these localities also show significant differences in morphology, microclimate, and macroclimate. 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. In northern Ohio, Hantak *et al.* (2019) focus 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 find a complex interaction between gene flow, genetic drift, and natural selection working together to explain morph frequencies, similar to Kraemer *et al.* (2016). Using ecological niche modeling, Hantak *et al.* (2019) found waterways were the most important factor in explaining morph frequency variation, likely, as the authors suggest, because they are strong dispersal barriers.

Taken together, these many studies exploring color polymorphism 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 Hantak *et al.* (2019)'s discussion on the complex maintenance of color polymorphism in *P. cinereus* for additional thoughts on the complexity of color polymorphism in *P. cinereus*. 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 below in our section below on Microbiota and Disease, however in the context of geographic variation, they sampled the skin microbial communities of 37 *P. cinereus* individuals across three localities in the central Appalachians, one locality encompassed an elevation gradient. As other microbial studies have found (see below), they found 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 (OH) clade to striped males from the Pennsylvania (PA) 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. This suggests that the two clades, OH and PA, are not yet reproductively isolated from each other.

(c) 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 notes that *P. cinereus* adults can be found in deciduous, northern conifer, and mixed deciduous-conifer habitats throughout their range, but reach their greatest densities in well-drained, mature forests with deep soils. He also notes that populations are absent or at low densities in highly acidic soils, perennially wet soils, and shallow, rocky soils (Petranka, 1998).

In compiling the more recent literature on the distribution and adult habitats of *P. cinereus* we noted 25 sources which simply document that *P. cinereus* was present at a given study site and categorized these as Regional Herpetofaunal Lists (Table 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 only found two sources explicitly documenting new records of *P. cinereus*. The first, Placyk, Seider, & Gillingham (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 recorded a new, high latitude elevation record for *P. cinereus*, found at 1173 m in Maine, which is considered subalpine (Willey & Jones, 2010). Only 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, thus we doubt they represent true absences or declines in density (Fig. 4). Silva *et al.* (2003) does note that prior work has shown *P. cinereus* is generally rare on Prince Edward Island, Canada, however a survey in October or April would provide a clearer picture of the actual abundance. In general, the autumn season, particularly October, has the highest detection rates (e.g., Leclair, Levasseur, & Leclair, 2008; McGhee, 2013; Sutherland *et al.*, 2016), while 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. 4).

More of the work since (Petranka, 1998) has focused on the microhabitat preferences of both adult and juvenile salamanders, particularly with regards to sampling methods using natural vs. artificial cover objects (NCOs vs. ACOs). We categorized more than 50 studies as focusing on adult and/or juvenile habitat, as well as an additional 19 studies which test a variety of sampling methods based on presumed habitat preferences. Of those latter 19 studies, 18 are focused on ACO 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*, one which SPARCnet employs. 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 & Roloff, 2011) and several found ACO surveys are comparable to NCO surveys (e.g., Monti, Hunter, & Witham, 2000; Grover, 2006; Moore, 2009; Ciul *et al.*, 2010).

In terms of best practices, wood boards (MacNeil & Williams, 2013), resting directly on the ground (Carfioli *et al.*, 2000), and sampled no more frequently than once per week (Marsh & Goicochea, 2003; Otto, Bailey, & Roloff, 2013) have the highest encounter rates. ACOs are colonized by salamanders within 2 months of installation (Bonin & Bachand, 1997), and 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 & Szuch, 2007). That said, recent SPARCnet work has shown ACO age to be important, with older boards capturing more salamanders than younger 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 & Goicochea, 2003), but other studies from Maine and Québec found no age/size differences between ACO and NCOs (Monti *et al.*, 2000; Moore, 2009). Siddig, Ellison, & Jackson (2015) found that ACO surveys overestimate the true density of salamanders, while NCO surveys underestimate the true density, when true density was estimated from removal. However, the sampling in Siddig *et al.* (2015) was done in July in Massachusetts, when surface densities are at or approaching their lowest (see below and Fig. 4), and so should be repeated during the autumn or spring surface-active seasons for accuracy. Work by SPARCnet members has found that, while estimates of space use and detectability are both sensitive to the spacing and extent of an ACO array, estimates of population density are robust to both spacing and extent (Fleming *et al.*, 2021).

Beyond comparisons of ACOs vs. NCOs, several studies find that while you can find *P. cinereus* in the leaf litter, they are more likely to be encountered under cover objects (Moore *et al.*, 2001; Otto & Roloff, 2011; McGhee, 2013). Preference for woody NCOs vs. rocky NCOs varies by study location. In Ohio, woody NCOs were preferred (Iverson & Smith, 2010), while in Vermont, rocky NCOs were preferred (Richmond & Trombulak, 2009). Positive correlations between cover object size (either diameter or area) and salamander size (mass, snout-vent-length) are inconsistent in those studies which have explored the relationship; e.g., Moore *et al.* (2001) and Strojny & Hunter (2010a) find these correlations, while others found no relationship between cover object size and salamander size (Faragher & Jaeger, 1997; Moore, 2005, 2009).

A study in Vermont by McKenny, Keeton, & Donovan (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 & Hunter (2010a) suggest that large coarse woody debris is important based on their study in Maine finding salamanders to be more abundant under logs of larger diameter in canopy gaps after timber harvest. Leaf litter preferences are inconsistent within the same study site, suggesting that individual preferences are highly variable over time (Iverson & Smith, 2010; Renaldo *et al.*, 2011). Iverson & Smith (2010) found no preference for deciduous vs. pine leaf litter, while 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 (1998)'s notes that *P. cinereus* is uncommonly found on perennially wet or highly acidic soils: Chalmers & 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.*, 2001 in Pennsylvania; Anderson, Solis, & Osbourne, 2013 in West Virginia, and 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 & Wyman (2010) found a seemingly healthy population of *P. cinereus* in an extremely acidic forest in Québec, Canada. There, the pH under coverboards ranged from 3.1 to 5.2, and 82% of captures over five years were from coverboards with a soil pH [?] 3.8. The Quebec population also had larger salamanders (both in body size and mass; Moore & Wyman, 2010) compared to other studies, directly contradicting an earlier study which suggests low pH substrates cause a loss of body mass (Frisbie & Wyman, 1991). Similarly, Bondi *et al.* (2016) found *P. cinereus* to occupy a wider range of soil pH than earlier studies, five 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). While 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 ~5 to ~6.5 and found that the abundance of *P. cinereus* increased under coverboards with ash compared to those without ash.

Three additional sources found *P. cinereus* in novel environments. Hughes, Petersen, & Duffield (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 hours. Individual identification was confirmed using photographs of the spotting pattern on the head and tail (LeGros, 2018). To these observations we add two novel environment observations by SPARCnet members, both in Maryland: a gravid female under an old tire in a suburban backyard, and a salamander more than a meter underground found while installing a flagpole in a different suburban yard (E.H.C. Grant; *pers. comm.*)

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. In the laboratory, individuals from an Ohio population preferred high pH, shaded habitat with medium-high moisture (Sugalski & 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, Smith, & Marr (2005) found the presence of *P. cinereus* was correlated with soil moisture and temperature, and indirectly correlated with litter depth. Not surprisingly, given the species is fully terrestrial, they also found that *P. cinereus* presence was not related to either distance or direction from vernal pools (Brenner *et al.*, 2005). In the field, Farallo & Miles (2016) compared the microhabitat characteristics of *P. cinereus* to two microendemic species, *P. sherando* and *P. hubrichti* in Virginia. They found evidence for active seeking-out of preferred habitats, as measured by temperature and moisture levels of the air and soil in all three species, as well as some evidence of microclimatic niche differentiation between all three species, suggesting character displacement when *P. cinereus* is sympatric with the microendemic species (Farallo & 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; levels which 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 & Chow-Fraser (2019) found populations to be stable over an 18-year sample period with an average temperature of 12°C during the spring and autumn active seasons. This study

also argues that monitoring programs which hope to detect population declines should plan on sampling for at least a decade in order to more accurately estimate occupancy (Luymes & Chow-Fraser, 2019).

Kolozsvary & 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. A regression modeling study based on presence/absence data from a location in northern Virginia also found pH variability to be important in detecting *P. cinereus* (McGhee & Killian, 2012), suggesting salamanders actively select “good” microhabitat patches within less desirable patches. However, their sample size for their presence data was very low ($N = 42$ salamanders over 2 years; presence detected on 29% of transects) compared to their absence data. McGhee & Killian (2012) argue that at their location, soil pH may be more important in determining which habitats salamanders avoid (low pH with low pH variability). In Ontario, Brown *et al.* (2020) found that 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 & 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 non-relative conspecific female. Hurst & Smith (2006) found that females will avoid areas with cues from five or more conspecifics, while males do not discriminate. These two studies as well as much of the work detailed in Jaeger *et al.* (2016) imply that *P. cinereus* can not only recognize kin vs. non-kin, and conceptualize the number of individuals in an area, but use this information to inform movement decisions. In West Virginia, Riedel, Russell, & Ford (2012) found that juveniles may actively avoid or be unable to compete for limited cover in non-forested habitats (e.g., meadows, pastures) that adults appear to live in without issue.

(d) 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, while females breed biennially in most populations, particularly in more northern portions of the range where the active season is shorter. That said, Petranka (1998) notes that there is some evidence that larger females can breed annually even in more northern populations (> 44 mm SVL in Connecticut; Lotter, 1978). Courtship follows behaviors stereotypical of other plethodontids (Arnold, 1977), including 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 that females pick up by walking over it. It had also been observed that intruder males could disrupt courtship by biting the courting male. Lastly, (Petranka, 1998) described a 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* has previously been well-reviewed in Jaeger *et al.* (2016).

Extensive work has been done to characterize the sexually dimorphic glands used in courtship by *P. cinereus* from the same population in Indiana. Sever (1997) observed that females usually store sperm for three to four months, and up to nine months if mating occurred right before the winter hibernation period, however, contrary to other locations and 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 & Siegel, 2006), and also confirmed the predominance of spring mating in this population based on absence of sperm in females collected in October compared to those collected in April. Sever & Siegel (2015) found seasonal differences in the size and secretory activity of caudal courtship glands in males, with the greatest size and secretory activity occurring in April and October. Mental glands in males show similar seasonal changes in size and secretory activity (Sever, 2017). Related to these patterns, Church & 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 mid-summer (July) and reaching its lowest point in the winter hibernation season (November - March).

In Virginia, Simons, Felgenhauer, & Thompson (1999) identified and described several mucous and serous glands in the shoulder and postcloacal region of *P. cinereus*. This study 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 while the S2 serous glands are used in nutrient storage and defense. More recently, there has been a focus on the pheromones used during courtship. Wilburn *et al.* (2014) notes the presence of three pheromones: the plethodontid receptivity factor (PRF), the plethodontid modulating factor (PMF), and the sodefrin precursor-like factor (SPF). They hypothesize that PRF is replacing SPF in *P. cinereus* due to only trace amounts of SPF being found. It is also interesting to note that while *P. cinereus* has evolved to produce PRF, it has not evolved to utilize the newer olfactory method to deliver courtship pheromones. As noted above, Kunkel *et al.* (2019) found population-level differences in pheromone chemistry, but not enough to prevent gene flow across two phylogeographic clades.

At the northern range limit, Leclair, Levasseur, & Leclair (2006) and Leclair *et al.* (2008) have documented a much more delayed reproductive phenology in *P. cinereus*, particularly in females. In a Quebec population, males become sexually mature between 3-5 years old and reproduce annually, while females were mostly unable to reproduce until 4-6 years old (Leclair *et al.*, 2008), much later than earlier studies conducted in more southern populations (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 years and it takes three years 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 due to 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, while female-female pairs were uncommon and male-male pairs were very rare (Peterson *et al.*, 2000). Peterson *et al.* (2000) hypothesizes same-sex pairs occur coincidentally due to limited territory space. Meche & Jaeger (2002) found no evidence for males preferring tail-intact over tail-autotomized females. In Ohio, Anthony *et al.* (2008) and Acord, Anthony, & Hickerson (2013) both observed that male-female pairs are usually the of same color phenotype, suggesting positive assortative mating by color. However, a follow-up study by Jaworski *et al.* (2018) found that striped males cannot differentiate between female color phenotypes and thus showed no preference for either striped or unstriped females, but males did show preference for larger females. Preference for larger female size by males was also observed in Anthony *et al.* (2008) and Acord *et al.* (2013). There is some evidence that *P. cinereus* follow social monogamy for a mating strategy. Several articles (e.g., Guffey, MaKinster, & Jaeger, 1998; Gillette *et al.*, 2000; Jaeger *et al.*, 2001; Jaeger, Gillette, & Cooper, 2002) support this, 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.* (2002) hypothesizes that *P. cinereus* uses sexual coercion against polygamous partners. For a thorough review of the behavioral work on *P. cinereus*, particularly as it pertains to courtship and territoriality, we recommend Jaeger *et al.* (2016).

Atypical courtship behaviors have also 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 (fftsw), not observed in two other plethodontids studied in the same paper. However, data suggested that fftsw 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 was recently reviewed by Staub, Stiller, & Kiemnec-Tyburczy

(2020). They specifically describe a more active role for females in courtship than historical studies would suggest, a pattern not unique to salamanders as EEB fields achieve greater gender parity in both scientists and their science (Staub *et al.*, 2020).

Several studies since Petranks have further investigated the fecal pellet squashing behavior. Karuzas, Maerz, & Madison (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 Petranks (1998) that the behavior is used to assess conspecifics' diets, but hypothesize that the behavior is not limited to the context of mate selection. Chouinard (2012) suggests that fecal pellets may also not be necessary 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. We also do not know how the sperm from different males interact. There are additional gaps in our knowledge surrounding how/why males and females may occupy the same cover object, and if there is any geographic variation in social behavior (almost all of the research surrounding mating strategies has been done with individuals from MLBS). Related to this, more field research should be performed in order 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, since previous research assumes they perform similar roles in *P. cinereus* as in other tested plethodontids.

(e) Reproductive Strategy

In this section, Petranks (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 Petranks (1998) reported observations of oviposition 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 there is 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 (Petranks, 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. Petranks (1998) notes that northern or high elevation females tend to oviposit in cavities within decaying logs or beneath rocks and logs, while oviposition in southern populations was typically observed in subsurface retreats created by other animals. Petranks (1998) describes the gross anatomy of eggs and their arrangement in the clutch, generally suspended from the roof of the cavity in a grape-like cluster. Petranks (1998) also reports clutch sizes and ovarian egg counts from several locations, with an average clutch size between 6-9 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 six weeks, and Petranks (1998) reported several populations where hatching occurs in August or September. During the time of Petranks (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.

Since *P. cinereus* does not oviposit naturally in the lab (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 Petranks (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 what was reported in (Petranks, 1998), occurring fre-

quently around June (Piersol, 1910; Burger, 1935; Bishop, 1941; Lynn & Dent, 1941; Sayler, 1966), although a nest in Virginia was found as early as April (Orr & Ernst, 2005). Madison, Wareing, & Maerz (1999) 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 hours. 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.* (1999) hypothesized that this 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 & Wilbur, 2004). Madison *et al.* (1999) also hypothesize 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.

While controlled breeding is not generally possible in the lab (Petranka, 1998), cross-fostering experiments are possible. Crespi & 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 parental care: 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 & Lessig, 2004).

Kerney (2011) created a complete larval staging table for *P. cinereus*, showing the development of embryos over 72 days 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).

Brooding females were more likely to abandon clutches in low-resource conditions (Yurewicz & 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 & Wilbur (2004) also found that females were less likely to abandon or cannibalize larger (about eight eggs) clutches, indicating that the high energetic cost of brooding outweighs the fitness value of smaller (about five eggs) clutches. However, another study showed that brooding females defended large (ten eggs) and small (four eggs) clutches with equal aggressiveness (Tornick, 2010). These results seem contradictory about the ability of females to differentiate between clutch sizes and make energetic investment decisions accordingly, but the discrepancy may be due to the failure of Tornick (2010) study to 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 non-invasive. However, no studies have yet determined the relationship between ovarian egg counts and actual clutch size. Since *P. cinereus* are known to reabsorb eggs (Ng & Wilbur, 1995), is it unclear how reliable this method is for predicting clutch size.

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.*, 1999). More field-based studies and observations of reproduction and brooding are necessary for confidence in the results from laboratory studies. Future studies should also determine the accuracy of using ovarian egg counts to predict clutch size, as gravid females are much easier to capture 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 which have been studied are at elevation (i.e., at MLBS; Crespi & Lessig, 2004; Yurewicz & Wilbur, 2004), and have their own local phenology distinct

from the both southern and northern low elevation populations (Fig. 4), suggesting their results may not be generalizable to those regions.

(f) Terrestrial Ecology

The terrestrial ecology section is the most lengthy 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. Briefly, Petranka (1998) covers the following topics in the following order in his terrestrial ecology section: diet, juvenile habitat and development, density estimates and habitat preferences, feeding behavior, surface activity timing and behavior, and social behaviors and territoriality. There are some overlapping topics with other sections, for example juvenile habitat can just as easily be discussed in the Distribution and Adult Habitat section above, which we opted to do, as well as some spatially disjunct topics within Petranka (1998) which we have opted to combine (i.e., diet and feeding behaviors). Finally, we end this section with a catchall section on studies of general behavior not directly related to any of the preexisting categories in this or other sections.

(i) Diet and Feeding Behavior

Petranka (1998) described the diet of *P. cinereus* as any palatable metazoan prey an individual can capture and that, while variable, there are not 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 Petranka (1998) also notes that individuals have been observed to climb vegetation to forage. There was also limited evidence for winter feeding in underground retreats at a population in Indiana, based on the stomach contents of specimens dug out of abandoned ant mounds (Petranka, 1998). Adult *P. cinereus* were known to use both visual and olfactory cues to find prey and had 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 (Petranka, 1998).

At least 34 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 14 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, Kloosterman, & Smith, 2000; Rooney, Antolik, & Moran, 2000; Adams & Rohlf, 2000; Maerz & Karuzas, 2003; Maerz *et al.*, 2005; Maerz, Myers, & Adams, 2006; Arif, Adams, & Wicknick, 2007; Anthony *et al.*, 2008; Ivanov *et al.*, 2011; Bondi, Green, & Beier, 2015; Bondi *et al.*, 2019; Paluh *et al.*, 2015; Stuczka, Hickerson, & Anthony, 2016; Hantak, Paluh, & Hickerson, 2016). 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 non-native prey, finding evidence that non-native 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). While 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 non-lethal 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 which provide additional confirmation of cannibalism in the field (Maerz & Karuzas, 2003; Gade *et al.*, 2017).

Several studies have explored head morphology in *P. cinereus* and other congeners (e.g., Adams & Rohlf, 2000; Maerz *et al.*, 2006; Arif *et al.*, 2007; Adams, 2011), exploring 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 below. 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 behaviors, including territoriality and general foraging activity, has also been studied in detail. Maerz & Madison (2000) is a complementary field-based study to the primarily lab-based studies of Jaeger *et al.* (2016) which shows that territoriality is correlated to food density. They found that body size was positively correlated with both total number and volume of prey when prey was at low density. When prey was at high density, there was lower shelter fidelity, and greater same-sex cohabitation of cover objects among females (Maerz & Madison, 2000). Anthony *et al.* (2008, 2017) explore the relationship between diet and color phenotype in Ohio. Anthony *et al.* (2008) found that striped morphs eat more diverse and more profitable (easier to digest) prey than unstriped individuals, while the follow-up study found that striped morphs resided on territories with a greater abundance of available prey items (Anthony *et al.*, 2017). Together with a related study from the same population on morph-specific aggression by Reiter, Anthony, & Hickerson (2014), these three studies suggest that striped morphs may competitively exclude unstriped morphs from territories with larger quantities of more energetically profitable prey. In contrast, at a different Ohio locality, Hantak *et al.* (2016) found no significant differences between the diets of sympatric striped and erythristic morphs.

More recent work confirms that *P. cinereus* forage at all times of day, although night foraging is likely the predominant mode (Placyk & Graves, 2001a; Liebgold & Dibble, 2011). Night-active salamanders had higher mass, and there was lower prey abundance in their field enclosures, compared to enclosures with less night-active salamanders (Liebgold & Dibble, 2011). At night, olfactory cues are thought to be most important, as evidenced by increased nose tapping in the dark (Placyk & Graves, 2001a), and decreased predation efficiency when the vomeronasal system is impaired (Placyk & Graves, 2002). Telfer & 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, Panebianco, & Madison (2001), which found that foraging activity was reduced when exposed to water soiled by a garter snake. Social hierarchies also appear to influence foraging activity. Liebgold & 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.

Gibbons, Ferguson, & Lee (2005) found that while there is a genetic component to foraging efficiency, learning and exposure to prey can improve foraging efficiency over time. Petranksa (1998) noted that climbing behavior was likely a foraging tactic, and the results of Cote *et al.* (2016) seem to confirm 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. Finally, a small number of studies explore interference competition between *P. cinereus* and non-salamander predators: centipedes (Hickerson, Anthony, & Walton, 2012) and spiders (Hickerson, Anthony, & Figura, 2018). These studies are discussed in more detail in the Community Ecology section below.

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 20degC, while digestion efficiency was the greatest at 15degC (Fontaine, Navarro, & Kohl, 2018). Two studies have explored the use of stable isotope analysis to study diet

and other factors (e.g., ecosystem level nutrient cycling; Milanovich & Maerz, 2012, 2013). These studies are discussed in more detail in the Ecosystem Ecology section below.

(ii) 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. Therefore, Petranka (1998) concluded, counts of salamanders on the surface and less robust mark-recapture methods (e.g., using toe-clips for marking) likely underestimate the true population size. Estimates of density from a variety of locations ranged from 0.21 salamanders/m² in Pennsylvania (Klein, 1960) to 2.8 salamanders/m² in Virginia (Jaeger, 1980; Mathis, 1991).

Several recent studies that have quantified salamander density in the field. However, one study at the southern range edge in Virginia, indicates that density can be much higher than previous estimates, from 2.49 to 6.26 salamanders/m² per plot surveyed over two years (Hernandez-Pacheco *et al.*, 2019; Fig. S2). Most recent papers focus on how salamander abundance is impacted by human activities. These are discussed in more detail in the Conservation Biology and Additional Topics: Management sections below, but here we briefly describe the impact of roads, forest-farm edges, and after prescribed fire on counts of surface-active salamanders. *Plethodon cinereus* occupies forested locations along an urban to rural gradient (Gibbs, 1998b). However, salamander counts are reduced near gravel roads and is likely due to a reduction in soil moisture near roads (Marsh & Beckman, 2004). Dry conditions at forest-farm edges also lead to reduced counts of salamanders in these ecotones (Young & Yahner, 2003). An experimental study corroborates these observational patterns, 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 to 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) and (Seburn & Mallon, 2017) found no decline in *P. cinereus* counts over a 20 year period in Ontario.

(iii) Seasonal Activity and Dispersal

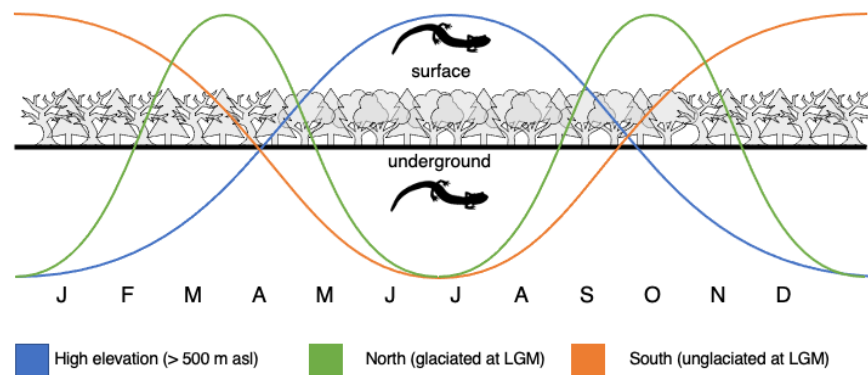


Figure 4. Three regional phenologies of *P. cinereus* surface activity throughout their large range. Biogeographic break points between the three phenologies are approximate based on our experience working with

this species and four studies (Leclair *et al.*, 2008; Becker *et al.*, 2013; Meshaka & 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.

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 (north in Fig. 4). One study found *P. cinereus* as deep as 1 m in winter (Grizzell, 1949). A study by Heatwole (1960) demonstrated that *P. cinereus* relies on the burrows and tunnels made by other fossorial species to retreat underground, and is likely incapable of doing much more than enlarging existing burrows. Petranka (1998) did not mention any studies on natural dispersal or migration, but did highlight how *P. cinereus* can return to its original location after a 90 m displacement (Kleeberger & Werner, 1982).

Based Petranka (1998)'s summary, our own field experience with this species throughout its range, and the four supporting studies described below, we depict the surface activity phenology of *P. cinereus* in Figure 4. There are at least three regional phenologies of surface activity which depend on latitude (north vs. south) and elevation (high vs. low). We hypothesize the latitudinal break between the northern and southern phenologies (Fig. 4) is near the extent of the Wisconsin ice sheet extent at the last glacial maximum (LGM; Fig 1). In support of this hypothesis, Meshaka & Wright (2017) studied a southern Pennsylvania population of *P. cinereus* approximately 150-200 km south of the LGM ice edge, and found it 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). Leclair *et al.* (2008) examines 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 above discussion in Breeding and Courtship; Leclair *et al.*, 2008). Finally, both Becker *et al.* (2013) and Hernández-Pacheco *et al.* (2019) documented the southern phenology of continuous winter activity (Fig. 4) in Cary, North Carolina and Richmond, Virginia, respectively. Both Petranka (1998) and our 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 the cues are which prompt vertical movement, or even how deep individuals can or will go during stressful seasons.

More recent studies 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 spring and down in autumn were reported in New York (Woolbright & Martin, 2014). The authors suggest that this movement is in response to increased availability of crevices in rocks uphill allowing 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, 1998a). 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 forest. Similarly, small streams also reduce return rates of salamanders after displacement (Marsh *et al.*, 2007), and both roads and streams limit gene flow, suggesting these landscape features act as dispersal barriers for *P. cinereus* (Marsh *et al.*, 2007, 2008).

We still know relatively little about natural dispersal distances of *P. cinereus*. Both Petranka (1998) and Williams *et al.* (1968) 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 years after the Wisconsin glacier receded; a distance of at least 1000 km, suggesting dispersal rates are between 67 – 100 m (0.067 – 0.1 km) per year. Previously mentioned mark-recapture studies (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; Hantak *et al.*, 2019) suggest that, while 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) 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 to 143 m (Sterrett *et al.* 2015). Dispersing individuals are likely “floaters” - young adults without territories who readily colonize available habitat. 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 one year of installation by young adult (based on SVL) *P. cinereus* in Virginia.

The low dispersal needs of individuals likely helps *P. cinereus* persist in small forest fragments where other amphibians with greater dispersal needs have been extirpated (Gibbs, 1998a). It is unclear if *P. cinereus* engages in sex-biased dispersal. Two studies, both conducted at MLBS in Virginia, either found no evidence of sex-biased dispersal (Cabe *et al.*, 2007) or found evidence females being more philopatric than males, confirmed through lack of genetic structure at short distances in males and greater overall dispersal distances of males (Liebgold, Brodie, & Cabe, 2011). A more recent study using similar methods for a Maryland population did not find any evidence for sex-biased dispersal (Grant & Liebgold, 2017). Individual movement behavior is highly repeatable (Cosentino & Droney, 2016). 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 & Droney, 2016).

(iv) Territories and Home Range Size

Petranka (1998) devoted several pages to territoriality in both sexes and age classes of *P. cinereus*. Much of the work he cites and 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, or (2) from non-MLBS locations. Reference information for all studies on this topic returned by our literature search are included in Table S11. We encourage those interested in territoriality and aggression in *P. cinereus*, which Petranka (1998) notes is a model organism for studying the ecology and evolution of these behaviors, 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, the average home range area was estimated to be 0.16 to 0.33 m² with no significant differences between males, females or juveniles. Daily movement of surface-active individuals was estimated at 0.43 m, with increases reported during and after precipitation events (Petranka, 1998). The home range of *P. cinereus* was estimated to be 13 m² for males and juveniles and 24 m² for females, and displaced individuals are able to return home at distances of 30–90 m (with declining success at longer distances). Petranka (1998) states that the exact reason *P. cinereus* holds territories is unknown, but it is hypothesized territories are used to defend food, defend or attract mates, and/or defend suitable microhabitats. Petranka (1998) notes that it is believed a large proportion of individuals are floaters that do not hold territories, based on the results of removal experiments (see also Terrestrial Ecology: Seasonal Activity and Dispersal, above). Larger individuals are able to 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).

Much of the Jaeger *et al.* (2016) work on territoriality is lab-based, using MLBS- or Virginia-sourced salamanders. Maerz & Madison (2000) offer one of the earliest field based studies of territorial behavior and its relationship to food availability. At sites in New York and 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 sites 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 for female availability (Maerz & Madison 2000).

Multiple field studies from northern locales have reported aggregations of *P. cinereus* under a single cover object. Quinn & Graves (1999a) and Placyk, Torretti, & Graves (2000) document this for populations in Michigan. In Ontario, Rollinson & Hackett (2015), found modest aggressive behavior in males during the breeding season, but a random distribution of adults during the nonbreeding season. These studies suggest that cooler climates may favor reduced territoriality, since daily foraging activity is generally less restricted than in southern populations. However, this pattern was not found by (Jaeger *et al.*, 2016), who almost exclusively used salamanders sourced from high elevation populations (MLBS and Shenandoah National Park). While the climates of northern latitudes and high elevations are similar, the artificial environment of a laboratory in which most Jaeger *et al.* (2016) studies occurred may influence the expression of territorial behaviors in *P. cinereus*. Thus, we are not sure geography alone explains why Michigan and Ontario salamanders appear to be less territorial than high elevation Virginia salamanders. Additionally, one of us (K.L.G.) has seen multiple large aggregations (N [?] 7) under a single coverboard at a low elevation southern site (Richmond, Virginia; Fig. S2), which also has some of the highest reported densities for this species (Hernandez-Pacheco *et al.*, 2019).

Chemical communication is still thought to be very important in territory establishment, identification of individuals, and even determination of potential predation risk. Sullivan, Rohr, & Madison (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 non-injured 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 non-injured earthworms (Sullivan *et al.*, 2003). Duhaime-Ross, Martel, & Laberge (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. 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 cellular proliferation in May and June, and Dawley *et al.* (2006) found a subsequent increase of apoptotic activity in July, suggesting the importance of these cells during the nonbreeding summer months, when territorial behavior is believed to be strongest (Jaeger *et al.*, 2016).

Site fidelity has been explored in Michigan, Ohio, and Virginia. In Michigan, Placyk & Graves (2001b) found the same individual under the same cover object one year apart. In Ohio, Martin & 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 & Liebgold, 2010). This study also found low levels of between year movements (0.85–1.22 m/year), suggesting high site fidelity (Ousterhout & Liebgold, 2010). To this we note that we have all seen some level of site fidelity across both seasons and years in our SPARCnet plots in Massachusetts, Virginia, Michigan, Pennsylvania, and New Jersey (M.C.F.R., K.L.G., L.S.M., T.H.J.M. and S.C.S.; unpublished data), but we have not yet quantified these patterns.

Recently, with the advent of visual implant elastomer (VIE) marking methods (Heemeyer, Homyack, & Haas, 2007), studies have explored field-based space use in *P. cinereus*. In Virginia, Schieltz, Haywood, & Marsh (2010) found that adults often use more than one cover object, regardless of spacing between cover objects,

with males never occupying adjacent cover objects. Munoz *et al.* (2016b) used spatial capture-recapture (SCR) to understand space use, dispersal patterns, and density in Pennsylvania. This SPARCnet site found densities around 0.423–0.473 salamanders/m². Contrary to what is reported in Petranka (1998), Munoz *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 (Munoz *et al.*, 2016b). As described above, young adult floaters will quickly take over new habitat when it becomes available (Marsh *et al.*, 2004).

In Ohio, two studies explore territoriality differences between color morphs, and a third studies 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 studies we categorized into this topic are from MLBS or other Virginia locations (N = 21/35; Table S11, Fig. 3). Future work which 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 which 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.

(v) Miscellaneous Behavior and Sampling Methods

In the course of our review, we found 24 studies that we initially classified as belonging to the primary category “other,” with further comments that these studies related to physiology, behavior, or sensory ecology. Many of these studies were folded into the discussion of their secondary category, and those (N = 9) which remained difficult to place in other sections of the review are summarized here. Generally, these sources focus on behavior that is not directly related to breeding and courtship, foraging, territoriality (all discussed above), or anti-predator tactics (discussed in next section, below).

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.

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 non-destructive method of tracking population health over time. Fluorescent powder pigment has been used with success to track amphibian, reptile, and small mammal movement over short durations (e.g., Lemen & Freeman, 1985; Graeter, Rothermel, & Gibbons, 2008; Roberts & Liebgold, 2008), and Orlofske, Grayson, & Hopkins (2009) was the first study to explicitly test how the fluorescent powders affect respiration and metabolism in a lungless amphib-

ian 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, Haas, & Hopkins (2010) 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 & 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, Grant, & Liebgold (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).

The last two behavioral studies that were difficult to categorize both explored the social context of juvenile salamander behavior. Liebgold & 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 & Cabe, 2008). Liebgold (2014) followed up on this by testing the presence of territorial adults on juvenile behavior using salamanders from Michigan (presumably non-territorial) and Virginia (presumably territorial; see above). 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 non-territorial adults.

(g) Predators and Defense

Petranka (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 which suggests that ringneck snakes may be able to distinguish the scent of *P. cinereus* from non-edible prey and even distinguish particular parts of the body (i.e., tail vs. body; Lancaster & 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 appears 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 of these. Below, 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 a large number of 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, the Additional Topics: Microbiota and Disease section below.

(i) Predators and Parasites

Since Petranks (1998), a small number of studies have documented unusual predators for *P. cinereus*. Jung *et al.* (2000) 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. Most studies of anti-predator responses use chemical cues from *T. sirtalis* fed a diet of *P. cinereus*, other salamander species, or earthworms. These are summarized in the next subsection.

There has been more work done on the parasites of *P. cinereus*, with several studies documenting helminth infections. Muzzall, Peebles, & Burton (1997) and Bolek & Coggins (1998) document several species of trematode, nematode, and protozoan parasites on *P. cinereus*. Most salamanders in Muzzall *et al.* (1997) hosted at least one parasite, and the trematode (*Brachycoelium* spp.) was most common in *P. cinereus* from New Hampshire. In Wisconsin, (Bolek & 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 (Gilliland & Muzzall, 2002) again found high rates of helminth infection, but no evidence that these parasites caused limb deformities. Most studies which have tested wild populations have found low prevalence of the amphibian pathogens *Ranavirus* or *Bd* on the skin of *P. cinereus* (e.g., Gratwicke *et al.*, 2011; Wunder *et al.*, 2012; Muletz *et al.*, 2012; Augustine & 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.

Rickettsial intracellular pathogens may also influence *P. cinereus* ecology and health. An rickettsial intraerythrocytic pathogen of the family Anaplasmataceae 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, as they 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 infecting plethodontid salamanders differentially by sex (Anthony, Mendelson, & Simons, 1994). A follow-up study by (Davis & Cecala, 2010) focused on *Desmognathus ocoee* found *Rickettsia* spp. bacteria, which are obligate intracellular parasites, at a high rate (35% of *D. ocoee* individuals). This is much higher than infection rates in *P. cinereus* (8%), and appeared to be a different type of *Rickettsia* spp. The authors suggest that the difference in prevalence between the two plethodontids is likely due to the difference in their habitat use: *P. cinereus* are completely terrestrial while *Ocoee* salamanders are semi-aquatic, therefore they contract different species of *Rickettsia* (Davis & Cecala, 2010).

There are conflicting reports as to whether or not northern dusky salamanders (*D. fuscus*) eat *P. cinereus*. Jaeger, Gabor, & Wilbur (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 & 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 the mesocosms. Other large salamanders likely to prey on *P. cinereus* where their ranges overlap include *Gyrinophilus porphyriticus* and *D. quadrimaculatus* (Petranks, 1998).

(ii) 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 morphs respond differently

to predators. In Ohio, Venesky & 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, while 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 & 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 & Anthony, 2007). After simulated predation (i.e., a tail clip), Otaibi, Johnson, & Cosentino (2017) found that the autotomized tails of striped morphs move longer and faster than those of unstriped morphs.

While differential predation by color is well-documented, which morph gets predated on more seems to depend on the population and the predator (see additional discussion above in Systematics and Geographic Variation). 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 by Kraemer *et al.* (2016; see above). In Maryland, Grant *et al.* (2018) found positive frequency dependent selection favoring the more common unstriped morph. Striped morphs were attacked more often by avian predators and had lower survival rates over three years than 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 & 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 & 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. 1; Kraemer & Adams, 2014; Kraemer, Serb, & Adams, 2015a, 2015b). Mimicry by *P. cinereus* may also be more successful through differences in color, not brightness (Kraemer & Adams, 2014). Of the predators tested, only birds can determine the difference between newts and striped *P. cinereus* based upon color, not snakes or mammals (Kraemer & Adams, 2014). Further, newt toxicity does not influence the occurrence of mimicry or the evolution of the mimic phenotype (Kraemer *et al.*, 2015b).

(iii) 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 & Lancaster (1998) demonstrated that exposure to water which previously held stressed conspecifics lead 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 minutes after the alarm pheromone had been collected (Graves & Quinn, 2000). In New York, Sullivan & Jensen (2013) further found that after exposure to different concentrations of damage-released conspecific cues, *P. cinereus* significantly decreased their activity compared to control, but did not discriminate between the differing concentrations of the cue. After simulated predation by tail clips, Roberts & 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 & 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.

Studies which examine salamander responses to garter snake cues have mostly been done using salamanders from upstate New York. A similar pattern of predator avoidance as observed by Murray & Jenkins (1999) was found by Madison *et al.* (2002), although the latter study found 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, Maerz, & Madison (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 added that *P. cinereus* also avoided chemical cues from garter snakes fed *E. bislineata*, suggesting that phylogenetically related species display similar antipredator behaviors and can also discriminate against predator diet cues, which may be linked to an overlap in microhabitat (Sullivan, Madison, & Rohr, 2004). Sullivan, Picard, & Madison (2005) further describes 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 discussed above, *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 & Jaeger (1998) found that in territorial contexts, their own 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. In the lab, Meche & Jaeger (2002) found that males did not distinguish between tailed or tailless females, however, in the field, they found males associated with tailless females more often. Meche & 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 & Wilbur (2004) found that tail loss is energetically costly to females, those with lost or regenerating tails made fewer ova. Meshaka & 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.* (1999) documented the importance of having a tail for proper clutch suspension, it is likely that females are under stronger selection for caution regarding situations that might result in a lost tail than either males or juveniles. (Hessel, Ryerson, & Whitenack, 2017) found no significant difference in jumping or mobility between individuals with and without tails. 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.M. and K.N.S.) have also seen tail bifurcation in the course of our own field work in Pennsylvania (Figure S3).

(h) Community Ecology

Petranka's (1998) section on community ecology is limited to *P. cinereus*' interactions with other salamanders, particularly congeners most closely related to it. The section focuses primarily on interactions (or lack thereof) with its sister species, *Plethodon shenandoah*. According to Petranka, (1998), *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's (1970) work, which suggests that this is only apparently true. Jaeger (1970) could only find "coexistence" in *P. shenandoah* existing in five talus isolates surrounded by continuous non-talus 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*. 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 non-salamander species. We have organized this section to start by reviewing the more recent research on *P. shenandoah* and *P. cinereus*, move on studies on interactions with other salamander species, and then discuss those studies focused on how *P. cinereus* interacts with non-salamander species.

(i) *P. shenandoah* and *P. cinereus* Interactions

Recent research has found evidence to further strengthen Jaeger's (1972) argument that *P. cinereus* adults may exclude *P. shenandoah* juveniles. Myers & 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* due to its susceptibility to desiccation (Petranka, 1998; Myers & Adams, 2008). An early genetics study on *P. cinereus* and *P. shenandoah* found no evidence of introgression or hybridization (Carpenter *et al.*, 2001), however rare hybrids have been more recently documented using both genetics and morphology (E.H.C. Grant, *pers. comm.*), suggesting a more complex dynamic exists between the two species than previously thought.

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, Brand, & Grant, 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 while *P. cinereus* populations were relatively stable over four years, *P. shenandoah* experienced high turnover in occupancy.

(ii) Other salamanders and *P. cinereus* Interactions

Regarding competition with salamanders other than *P. shenandoah*, Petranka's (1998) comments are limited. At that time, research 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). Petranka (1998) also briefly describes 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 & Rohlf, 2000), but not for teeth number or jaw muscle mass (Swart & Adams,

2004). While the microhabitats between these two species are not significantly different (Carlson, Thawley, & Graham, 2016), Jaeger *et al.* (2002) 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, due to 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.*, 2002).

Character displacement has also been supported for sympatric *P. cinereus* and *P. nettingi* (Adams, West, & Collyer, 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 years, *P. nettingi* has decreased in abundance, which Kroschel *et al.* (2014) found may be correlated to *P. cinereus* expanding their territory into the higher elevations that *P. nettingi* originally inhabited, but they could not rule out changes in environmental conditions affecting both species.

The ranges of *P. cinereus* and *P. electromorphus* overlap, however sympatric localities are not common, suggesting competitive interactions are important (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, Petersen, & Adams, 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). Similarly, in Kentucky and Ohio, *P. cinereus* overlaps with *P. richmondi*, however sympatry is uncommon, and there seem to be climatic differences which correspond to differences in distribution (Hedeen, 2000). *Plethodon richmondi* was found in drier, upslopes compared, while *P. cinereus* was found in wetter, lower, flatter areas (Hedeen, 2000).

The ranges of *P. cinereus* and *P. hubrichti* are parapatric, with the range of *P. cinereus* completely surrounding that of *P. hubrichti*. Aasen & Reichenbach (2004) found no significant encroachment of *P. cinereus* on *P. hubrichti*. Arif *et al.* (2007) found *P. hubrichti* to be more aggressive and less submissive than *P. cinereus*, but no differences in diet. 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 suggest *P. hubrichti* restricts the range of *P. cinereus*, even though it lives in suitable microclimates for *P. cinereus*. This was further supported by Kniowski & 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 & 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 & Pietsch, 2015).

A number of 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 above in the Predators and Parasites section, it is unclear if *D. fuscus* preys on *P. cinereus* (Jaeger *et al.*, 1998; Ransom & Jaeger, 2006). Jaeger *et al.* (1998) additionally found no evidence that larger *P. glutinosus* eat smaller *P. cinereus* but a later study finds that when sympatric, *P. glutinosus* and *P. cinereus* reduce each others' growth (Price & 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 & 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, the body condition of *P. cinereus* individuals declines over a three week period, where stream specialist *E. cirrigera* likely outcompetes it (Pasachnik & 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 & Jaeger, 2008).

Plethodon salamanders are hypothesized to use behavioral mechanisms, such as climbing behaviors, that promote coexistence. A field study conducted by Mezebish, Blackman, & Novarro (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. The abundance of intraspecific competitors also resulted in an increase in climbing behavior in *P. cinereus* (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, while 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.

(iii) Non-salamander Species and *P. cinereus* Interactions

Several studies since Petranka (1998) have described interactions of *P. cinereus* with non-salamander species, largely focusing on relationships with intraguild predators common to the forest floor and soil (e.g., spiders, centipedes, beetles, earthworms). The majority of recent work, conducted at MLBS in Virginia, focuses on the relationships between native and non-native earthworms (Annelida) and *P. cinereus*. Caceres-Charneco & 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 (Caceres-Charneco & Ransom, 2010). Ransom (2017) also observed that salamanders do not seem to distinguish between native vs. non-native earthworms, both 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 other microinvertebrate prey species leading to indirect effects on salamanders. Ransom (2012) finds 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 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 non-native *Amyntas* 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 *Amyntas* and *Metaphire* spp. (Ziemba, Hickerson, & Anthony, 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, Hickerson, & Venesky (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 & 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 removal experiment with *P. cinereus*- and centipede-removal treatments. Interactions were complex: removing either predator changed the abundance of other invertebrate predators, 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, Anthony, & Wicknick (2003) find a negative relationship between carabid beetles and *P. cinereus*. Residents of both species behaved more aggressively than intruders, and attacked intruders of both species at similar levels. Hickerson *et al.* (2018) found that spiders in the genus *Wadotes* are perceived as competitors by *P. cinereus* in laboratory trials, and there was no evidence of intraguild predation between spiders and salamanders.

Several studies explore the role of *P. cinereus* in regulating the composition of soil-litter invertebrate communities and ecosystem processes. 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 & Droegge, 2001; Davic & Welsh, 2004). In reviewing the literature on this topic, we find many sources do support the important role of *P. cinereus* in forest ecosystems, however, at least two studies found no direct effects of *P. cinereus* on a variety of community and ecosystem processes (Homyack *et al.*, 2010; Hocking & Babbitt, 2014). Here, we focus on the community level impacts of *P. cinereus*, and summarize ecosystem level impacts in the Additional Topics: Ecosystem Ecology below.

In Ohio, both Walton (2005) and Walton & Steckler (2005) found that *P. cinereus* does affect the composition of soil-litter invertebrate communities, but these effects vary seasonally. When leaf litter mass and moisture were both high, salamanders exerted stronger top-down effects on mesofaunal invertebrates (Walton, 2005). In microcosm experiments, when *P. cinereus* was present, Walton & Steckler (2005) found more podomorph 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 by being present, salamander fecal matter promotes microflora growth. A follow-up study found that salamander treatments again increased the density of Collembola, but this time only in urban leaf litter, not rural leaf litter (Walton, Tsatiris, & Rivera-Sostre, 2006). Other taxa experienced decreased densities in both urban and rural leaf litters when salamanders were present: oribatid mites, pseudoscorpions, isopods, and millipedes (Walton *et al.*, 2006). In contrast, in Virginia, Homyack *et al.* (2010) found no evidence that *P. cinereus* affected the number of invertebrate taxonomic groups or functional guilds. Hocking & Babbitt (2014) found similar results in New Hampshire. In their study, *P. cinereus* had no effect on intraguild predator abundance (carabid beetles, centipedes, and spiders). We feel these conflicting results are to be expected, given the large geographic range and diversity of forest types that *P. cinereus* finds itself in, however, they make generalizations about the role of plethodontid salamanders in these communities and ecosystems difficult, and caution is warranted using *P. cinereus* as an ecological indicator within a given forest until local patterns are sufficiently understood.

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*), and *Lymantria dispar dispar* (LDD) moths, and fungal communities. In Ohio, Greenwald, Petit, & Waite (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). Two studies, one based in Ohio (Walker *et al.*, 2015) 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). Mitchell (2015) explored how *P. cinereus* counts changed before and after invasion by LDD 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 LDD moths). It is not clear if the decline in *P. cinereus* was related to the arrival of LDD moths, other factors, or a combination of these.

(i) Conservation Biology

Petranka's (1998) account 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 & Hunter, 1995). Due to the ubiquitous ecology of *P. cinereus*, there was very little concern for the impacts of human-mediated effects on *P. cinereus* populations due in part to 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 & Likens, 1975a). Like many of the topics we 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 which 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 header below, 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 which have conservation as a secondary category (Table S11), as these studies are nearly all discussed elsewhere in our 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 & Hunter (1998) found that *P. cinereus* in Maine are sensitive to clear cutting and edge effects, and that *P. cinereus* 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, Brooks (2001) found that *P. cinereus* abundance only decreases temporarily, both when eastern hemlock is partially harvested as well as when woolly adelgid invasions causes hemlock defoliation and tree loss. Within three years of initial tree loss, the abundance of *P. cinereus* had already begun to increase (Brooks, 2001). Mossman *et al.* (2019) found that abundance of *P. cinereus* were the highest in 20-25 year-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 & 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.

Knapp *et al.* (2003) compared declines in salamander abundance due to 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 meters 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 four months. 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 have the ability to 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 discussion of conservation genetics below). 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, Roloff, & Thames (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 Quebec 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* are capable of recovering after disturbances to their environment. A field study in West Virginia by Wood & Williams (2013) found that reclaimed mountaintop removal mines are not suitable habitat for *P. cinereus*, as they favor more of 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 due to factors like soil compaction.

In Virginia, D.M. Marsh and colleagues have published a number of studies on the effects of roads on *P. cinereus*, many of which we have previously discussed above (Marsh & Beckman, 2004; Marsh *et al.*, 2005, 2007, 2008). From a conservation perspective, both (Marsh & Beckman, 2004) and (Marsh *et al.*, 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 & 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 & Beckman, 2004). Marsh *et al.* (2005, 2008) both find that roads are dispersal barriers, using a displacement and homing experiment (Marsh *et al.*, 2005) and measures of population genetic structure (Marsh *et al.*, 2008). A similar study by (Gibbs, 1998a) in Connecticut also found roads to be a dispersal barrier for *P. cinereus*.

As mentioned earlier, several studies have explored the relationship between habitat fragmentation and population genetics. Gibbs (1998c) compared continuous to fragmented populations in Connecticut and found that the fragmented populations were more divergent (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, while continuous populations were nearly 100% striped. In Quebec, Noel *et al.* (2007) found that urban *P. cinereus* have both lower allelic richness and lower heterozygosity. A follow up study found that *P. cinereus* show more genetic differentiation in areas where anthropogenic disturbances have persisted for a longer time (Noel & Lapointe, 2010). The authors suggest that this is because *P. cinereus* in these environments tend to have a low effective population size. Further implications from Noel & Lapointe (2010) are that it is important to preserve large, forested areas within cities in order to increase genetic variation and conserve or increase effective population size. Cosentino & 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 connec-

tivity between relic source populations and regenerating forests on post-agricultural lands is important for colonization of the new forest habitat (Cosentino & Brubaker, 2018).

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 years. The greatest decreases in body size was in the southern Appalachians, which have had the greatest 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 the Appalachian mountains and coastal plain, 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. Specifically in response to Caruso *et al.* (2014), and prior to the publication of McCarthy *et al.* (2017), both Grant (2015) and Connette, Crawford, & Peterman (2015) offer alternative explanations for shrinking salamanders. They argue that Caruso *et al.*'s (2014) results could be explained by the sampling approaches used in the study and that both museum specimens and contemporary surface-active individuals likely only represent a portion of the inferred population. Further work on this topic which tracks populations across the range over time using robust spatial capture-recapture methods (e.g., Sutherland *et al.*, 2016) should be able to more confidently detect these patterns.

(j) Additional Topics

In addition to the miscellaneous physiology and behavior sources we report on above, we found at least four additional topics not covered by Petranks (1998), which we feel there has been enough literature to warrant their own sections. First, we present studies on the ecosystem ecology of *P. cinereus*, a topic we found strangely absent from Petranks (1998). Next, we summarize studies which 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 which explore the tolerance of *P. cinereus* to various anthropogenic pollutants common to current and former United States military installations.

(i) Ecosystem Ecology

There are surprisingly no references to the role of *P. cinereus* in ecosystem level processes in Petranks's (1998) otherwise thorough species account. Petranks (1998) mentions Burton & Likens' (1975a) study at Hubbard Brook Experimental Forest in New Hampshire for their estimates of *P. cinereus* density, but Petranks (1998) does not cite or mention Burton & Likens (1975b), a simultaneous study on the energy flow and nutrient cycling that must pass through *P. cinereus*, given their position in the trophic web and the high densities observed at Hubbard Brook. Neither study is restricted to *P. cinereus*, however, *P. cinereus* far outweighs the estimated biomass contributed by the other salamander species (Burton & Likens, 1975a, 1975b). The pair of Burton & Likens' (1975a, 1975b) studies have since been cited by hundreds of subsequent studies, some of which argue for the use of *P. cinereus* as an ecosystem indicator species (e.g. Welsh & Droege, 2001; Siddig, Ochs, & Ellison, 2019), or for the overall importance of plethodontids to terrestrial forest ecosystems (e.g., Davic & Welsh, 2004), and indeed have shaped the thinking of many researchers working on North American plethodontid salamanders since (but see Riedel *et al.*, 2008 and Moore & Ouellet, 2015 for caution about the use of *P. cinereus* as an indicator species). Thus, we found it odd that ecosystem ecology was neglected by Petranks (1998), although this seems to be the case for all species accounts throughout the book.

Since Petranks (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.*, 2010; Walker *et al.*, 2014; Hocking & Babbitt, 2014; Pelini *et al.*, 2015; Hickerson, Anthony, & Walton, 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 leaf litter decomposition, likely due to *P. cinereus* feeding on leaf shredders. In Ohio, Hickerson *et al.* (2017) also manipulated *P. cinereus* densities by removal and found comparable treatment effects in reducing leaf litter decomposition but also on microbial communities. 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/m² (Homyack *et al.*, 2010; Hocking & Babbitt, 2014). Additionally, (Sucre *et al.*, 2010) found that salamander abundance was not a reliable indicator of nitrogen availability.

Milanovich & Maerz (2012, 2013) describe the use of stable isotopes from *P. cinereus* tail clips 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 days, making their interpretation much easier compared to organisms for which fasting does change these values. (Gilbert *et al.*, 2014) use 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 to *P. cinereus* populations or energetics (Homyack, Haas, & Hopkins, 2011; Beier *et al.*, 2012; Ochs & 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, while in Massachusetts, Ochs & 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 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 hemlocks and other massive ecosystem changes as a result of invasive species who affect fundamental environmental properties relied on by forest floor inhabitants (e.g. soil chemistry, temperature), may also influence *P. cinereus* (e.g., Caceres-Charneco & Ransom, 2010; Ochs & Siddig, 2017). Continental invasions of earthworms 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 (Caceres-Charneco & Ransom, 2010; see also Community Ecology section above).

Lastly, as discussed in Community Ecology above, *P. cinereus*' role on the forest floor as a top 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 discussion above and in Community Ecology) are yet another reason it is critical to design robust experiments to better understand variation in demography and community interactions across the range of *P. cinereus* (see section below on SPARCnet).

(ii) Management

In Petranks (1998) there was relatively little consideration of management for *P. cinereus* populations or their habitat, presumably because *P. cinereus* is considered to be 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 Petranks (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 & Ducey, 1998; Rodewald & Yahner, 1999; Harpole & Haas, 1999; Yahner, Bramble, & Byrnes, 2001a; Duguay & Wood, 2002; Perkins & Hunter, 2006; Patrick, Hunter, & Calhoun, 2006; Homyack & Haas, 2009; Strojny & Hunter, 2010b; Hocking, Babbitt, & Yamasaki, 2013; MacNeil & Williams, 2014; Mossman *et al.*, 2019), deer management (Greenwald *et al.*, 2008; see discussion in Community Ecology above), managed grazing (Riedel *et al.*, 2008), or subsequently in forests with varying densities and qualities of coarse woody debris (McKenny *et al.*, 2006; Strojny & Hunter, 2010a). There is some evidence that plantation-style forests, common on lumber farms, are not suitable for *P. cinereus* (Waldick, Freedman, & Wassersug, 1999; Reams *et al.*, 2008) despite the closed canopy, perhaps due to 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, Piergallini, & Ross, 2001b), which contradicts (deMaynadier & Hunter, 1998)'s finding that *P. cinereus* prefer interior, mature forests. (Yahner *et al.*'s (2001b) work does fit with Riedel *et al.*'s (2008) suggestion 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 & Williams, 2013 for a counter example).

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 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 liming, or the addition of lime to acidic, maple forests, has no impact on survival of *P. cinereus*. Cameron, Hickerson, & Anthony (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 & Ollivier, 1998; Welsh & Droege, 2001). Siddig *et al.* (2019) agreed that *P. cinereus* may be an indicator species used to monitor changes in eastern hemlock forest ecosystems due to 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 Systematics and Geographic Variation, above), Moore & 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, Verner, & Thomas, 1988; Caro, 2010; Lindenmayer, Barton, & Pierson, 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 mecha-

nistic relationship between the indicator and ecosystem property; often an unobservable ecological process (Fleming *et al.*, 2020).

(iii) Microbiota

Information regarding the microbiota living on the skin of *P. cinereus* prior to 1998 was scarce, partly due to the early stages of the necessary technology for microbial community profiling available at that time. Petranks (1998) mentions that there has been no evidence for antibiotic properties in the skin secretions of brooding females, a claim which has since been refuted by several recent studies which document microbial taxa which produce both antibiotic and antifungal compounds in clinically relevant levels (e.g., Fredericks & Dankert, 2000; Harris *et al.*, 2006; Culp, Falkinham, & Belden, 2007; Lauer *et al.*, 2007; Brucker *et al.*, 2008a, 2008b; 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 for the production of 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, *Batrachochytrium dendrobatidis* (hereafter, *Bd*), to which *P. cinereus* is thought to be largely resistant to.

Fredericks & Dankert (2000) is one of the earliest studies to identify antimicrobial proteins on the skin of *P. cinereus*, shortly after Petranks (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 four bacteria (*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 since 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, 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 & 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, *Mar- iannaea* 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 bacteria 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 which focus on *J. lividum* and *P. cinereus*'s ability to either resist or quickly recover from *Bd* infection (e.g., (Brucker *et al.*, 2008b; 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 *P. cinereus*'s skin (Brucker *et al.*, 2008b). When *Bd* is experimentally introduced salamanders, eight out of ten salamanders who died due to *Bd* infection had no violacein-producing microbes and the remaining two 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.*, 2008a), *Pseudomonas reactans* (Harris *et al.*, 2006), and several 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*, *Pseu-*

domonas spp., and *Chitinophaga arvensicola*, from *P. cinereus* as co-cultures and mono-cultures 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). *Pseudomonas* sp. was found to prevent weight loss observed in *Bd* treatments by (Harris *et al.*, 2006). There is some evidence that these protective taxa can be inoculated on salamanders who lack them (Muletz *et al.*, 2012; Loudon *et al.*, 2014b). 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 five days 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. 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.* (2016) supports these results: nine out of 12 (75%) OTUs that were over-represented on *P. cinereus* skin had at least a 97% match to antifungal isolates. They also noted that four of these over-represented OTUs were part of the core community identified by Loudon *et al.* (2014b). Loudon *et al.* (2016) suggests 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, Garcia, & Young, 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 20oC compared to 10oC and 15oC, and digestive performance was greatest at 15oC. Additionally, the relative abundance of pathogenetic taxa increased at 20oC (Fontaine *et al.*, 2018).

In terms of how *P. cinereus* responds to *Bd* infection, there have been a small number of studies which document behavioral effects of *Bd* infection, 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 ([?] 2%; with the exception of a New Brunswick population whose infection rates are around 13%; Jongsma *et al.*, 2019). In a behavioral study, *Bd* -infected salamanders attacked prey significantly more often than non-infected individuals and the prevalence of *Bd* among *P. cinereus* decreased over time (Hess *et al.*, 2015). The authors suggest that *P. cinereus* may have natural resistance to *Bd* (Hess *et al.*, 2015). 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 & Anthony, 2007; Davis & 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 only found one study which looks at how presence or absence of *P. cinereus* may impact soil microbial communities, and the results are somewhat equivocal (Hickerson *et al.*, 2017). While 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 explore change in microbial communities over space and time (Muletz-Wolz *et al.*, 2017, 2018; Muletz-Wolz, Fleischer, & Lips, 2019; Barnes, Carter, & Lewis, 2020). The work of C.R. 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 71% (17/24) of studies discussed above using salamanders from Virginia, and the remaining seven 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* to fully understand its relationships with microbial taxa.

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 non-random 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. As we noted above, this field is lacking in geographical diversity, despite multiple studies finding local differences in microbial taxa (e.g., Muletz-Wolz *et al.* 2017; Barnes *et al.*, 2020). We also do not fully understand the relative roles and interactions of microbial metabolites versus salamander skin secretions. Lauer *et al.* (2007) suggests 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.

(iv) Ecotoxicology

The final additional topic that has grown since Petranka (1998) explores the responses of *P. cinereus* to a variety of anthropogenic 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, Suski, & Bazar, 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 inability to right oneself (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* increases when exposed to contaminated soil when compared to individuals from non-contaminated 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). Due to *P. cinereus*'s capacity 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 & 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, Pauley, & Butler, 2003).

VI. Is *Plethodon cinereus* an EEB Model Organism?

In completing the comprehensive review, it is clear that Duffy *et al.*'s (2021) requirement that a model system have been studied long enough to generate a "substantive body of knowledge" (pg. 55) has been met by the research to date on *P. cinereus*. In defining EEB model systems, Duffy *et al.* (2021) highlight Travis' (2006) related stipulations that "robust inference requires horizontal comparisons and vertical integration" (p. 307). 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). 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 Table S1 from Duffy *et al.*, 2021).

Thus, *P. cinereus* falls short of model organism status. This is due to many of the challenges around developing new model systems laid out in Duffy *et al.* (2021). In particular, the broader appeal of *P. cinereus* research and plethodontids as model organisms more generally has been hampered by a lack of infrastructure-building, historical gatekeeping, funding constraints, and other limitations imposed on both academic and non-academic scientists in the United States and Canada. Since *P. cinereus* is not a model organism yet, we have the rare opportunity to build the infrastructure required of successful model systems around *P. cinereus* and other plethodontid salamanders with a deliberate eye towards inclusive, coordinated collaboration and knowledge sharing. In this section, we first describe how although the EEB community clearly values data collected at both long temporal scales and large spatial scales for illuminating fundamental phenomena (Fig. 2; Hughes *et al.*, 2017), it can be challenging and risky for an individual scientist to structure their research program around such data generation (Duffy *et al.*, 2021); yet such structured approaches are essential for data quality control and quality assurance (Clutton-Brock & Sheldon, 2010). We then describe and recommend coordinated distributed experiments (CDEs; Fraser *et al.*, 2013) as a model experimental

design for generating data sets of long temporal and large spatial scales. Finally, we demonstrate how we have put a CDE into practice for *P. cinereus* with our collaborative research network, The Salamander Population and Adaptation Research Collaboration Network (SPARCnet). We hope that our experience provides a blueprint for other researchers to more confidently develop the diversity of model systems and scientists called for by Duffy *et al.* (2021).

(1) Go big or go home: Long-term studies over large spatial scales

The intellectual pursuits of EEB fields are deeply intertwined (Fig. 2), such that the fundamental phenomena which model systems are tasked with illuminating are often overlapping and difficult to isolate in both practice and theory (see, for example, Sutherland *et al.*, 2013). Illuminating these fundamental phenomena in EEB not only benefits from use of diverse model systems (Duffy *et al.*, 2021; Wale & Duffy, 2021), but also from long-term, individual-based data sets (Clutton-Brock & Sheldon, 2010), as many of the fundamental phenomena are best viewed from the perspective of tracking many individuals over long periods of time. Much like the perpetual discussions in the literature about what counts as a biomolecular model organism, there has been much discussion in EEB on what counts as long-term data, how best to initiate and maintain a long-term study, and the disproportionate value of long-term data sets for both basic research and applied policy, as evidenced by number of publications and citation indices (e.g., Clutton-Brock & Sheldon, 2010; Hughes *et al.*, 2017). In parallel to these discussions, globalization has proceeded at a rapid pace with high speed internet connections and smart devices invading our homes, workspaces and field sites, making possible large collaborative research networks which take advantage of the relative ease of modern communication to coordinate large scale experiments across time and space. Fraser *et al.* (2013) term these collaborative research efforts CDEs, and note their particular value to testing large spatial-scale hypotheses in EEB fields.

CDEs are, in part, an answer to the difficulties of synthesizing data across studies with disparate experimental designs, as is traditionally done in meta-analyses (Fraser *et al.*, 2013) or with museum specimens (Grant, 2015). Beginning in the late 20th century with the Long-Term Ecological Research (LTER) network (Hobbie *et al.*, 2003), there has been a steady proliferation of CDEs in the early decades of the 21st century. While coming up with an exhaustive list of these CDEs is beyond the scope of our paper, we note for example, that the faculty authors of this paper belong to EREN (The Ecological Research as Education Network; Gartner *et al.*, 2020), Snapshot USA (Cove *et al.*, 2021), and SPARCnet (Sutherland *et al.*, 2016; Munoz *et al.*, 2016b; Hernandez-Pacheco *et al.*, 2019), and we have used SquirrelNet (Dizney *et al.*, 2020), LTER, and NEON (National Ecological Observatory Network; Keller *et al.*, 2008) data in both our teaching and research.

CDEs like those listed above could be to EEB what databases and networks like FlyBase (Drysdale, Crosby, & The FlyBase Consortium, 2005) and The Jackson Laboratory (Dewsbury, 2012) are to the biomolecular and biomedical sciences: the infrastructure and community ethos needed to successfully develop a new EEB model system by using standard, simple methods across research groups, time, and space. Leonelli & Ankeny (2013) argue that both infrastructure and the community ethos are critical to the development and success of a model organism, and this argument is echoed by both Duffy *et al.* (2021) and Wale & Duffy (2021) for EEB, the latter of which explores models within the subfield of the ecology and evolution of infectious disease. Many of the 25 EEB model systems listed in Duffy *et al.*'s (2021) supplement have substantial infrastructure and a thriving research community, including established field sites and protocols (e.g., Barro Colorado Island Forest Census Plot; Kress *et al.*, 2009) and community-building events like subgroup meetings in tandem with national conferences (e.g., *Mimulus* meetings; Mimubase.org, 2021).

Fraser *et al.* (2013) and Borer *et al.* (2014) both argue that one important quality of successful CDEs is that they are not prohibitively expensive or prohibitively time consuming for participants. The majority of the authors on this paper are faculty and students at primarily undergraduate institutions (PUIs), and our ability to do research is more time and budget restricted than our peers at research-intensive (R1) institutions. Many of the CDEs we know of and participate in have both education and research as central

missions. In our experience, CDEs make it easier for PUI faculty and students to collaborate with R1 faculty and students and thus aid PUI faculty in maintaining active research programs while also teaching high contact-hour loads. This is achieved in part because CDEs make use of the *per capita* staffing potential of a PUIs' undergraduate classrooms. CDEs further help to include contingent, non-tenure track faculty and their students at both types of institutions in research activities. Simultaneous with the proliferation of CDEs over the last two decades, there has been a pedagogical pivot towards developing course-embedded undergraduate research experiences (CUREs) as a means to provide authentic research experiences to more students than faculty at PUIs and R1s alike could possibly individually mentor (e.g., Shortlidge, Bangera, & Brownell, 2017). This focus of most CDEs on both research and education is perhaps best embodied in EREN's mission statement (ERENweb.org, 2021):

"To create a model for collaborative ecological research that generates high-quality, publishable data involving undergraduate students and faculty at primarily undergraduate institutions (PUIs)."

The dual education and research missions of many CDEs also appeals to United States-based funding agencies, like the National Science Foundation (NSF), which scores proposals not just on intellectual merit, but also on broader impacts. By having education explicitly baked into the research proposal through CUREs and PUI collaborators, CDEs can make a broader impact argument for their proposed work. This is important because, as Clutton-Brock & Sheldon (2010) argue, the biggest challenge facing long-term studies in EEB is maintaining consistent funding. Hughes *et al.* (2017) also note this challenge, although the pair of papers disagree on what counts as a long-term study. Clutton-Brock & Sheldon (2010) use a minimum of 10 years, while Hughes *et al.* (2017) use a minimum of four years to define long-term. Hughes *et al.* (2017) directly connect their minimum to academic funding cycles: NSF typically funds short-term (four years or less) and long-term (> four years) proposals, and four years is the typical length of a graduate student's Ph.D. project, excluding coursework. The authors further demonstrate that the proportion of research dollars going toward short-term studies has steadily increased in the 21st century, while the proportion of research dollars going towards long-term studies steadily decreased, despite the disproportionate value placed on long-term studies (see their Fig. 2; Hughes *et al.*, 2017). This speaks in part to what Duffy *et al.* (2021) note as the one of the challenges to EEB model system development: that neither early career scientists nor funding agencies are willing to shoulder the risks inherent to starting a long-term or large spatial-scale study. To this we also note that there is a funding disconnect between NSF's short-term funding, long-term funding, and the minimums discussed by both Clutton-Brock & Sheldon (2010) and Hughes *et al.* (2017). NSF's Long Term Research in Environmental Biology program (LTREB; National Science Foundation, 2021) requires six years of continuous data at the full proposal stage in order to be eligible to apply for five years of funding with the potential to renew for an additional five years pending favorable review. This means a long-term study in the eyes of Clutton-Brock & Sheldon (2010; > 10 years) requires two consecutive short-term NSF grants in order to simply qualify for a LTREB that could cover the following 10 years.

(2) A Nascent Infrastructure for *Plethodon* salamanders in SPARCnet: 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.org, 2021). 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* (Fig. S4). SPARCnet methodology employs a simple and inexpensive, yet robust and spatially explicit mark-recapture design (Sutherland *et al.*, 2016; Munoz *et al.*, 2016b; Fleming *et al.*, 2020, 2021) using standardized ACO plots, arranged in pairs for potential experimental and control studies (e.g., snow removal, forest management). Despite the challenges of long-term individual based studies (i.e., consistency, quality, stable funding; Clutton-Brock & Sheldon, 2010), 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 & Sheldon, 2010). SPARCnet's framework is flexible, allowing individual researchers to design side projects that are site-specific or network-wide (i.e., collaborating on data collection with other research plots), which may focus on questions and topics as diverse as those reviewed in this paper. Additionally, the flexibility of SPARCnet structure allows for researchers to exploit observations and research questions that emerge in real time (i.e., emergence of disease or toxicology) and work together to rapidly study these phenomena across the geographic range in tandem.

CDEs generally, and SPARCnet in particular, provide a solution for consistent data collection methods and helps 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 the review above (Fig. 3). 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, as well as a unique educational framework for engaging students at all levels and community members. As we have highlighted in our review, there is much geographic variation in *P. cinereus* biology: puzzling aspects of *P. cinereus* physiology, behavior, roles in ecosystems, and potential roles as an indicator species (especially among color phenotypes; see Systematics and Geographic Variation, above). Some have criticized these inconsistencies (e.g., Moore & Ouellet, 2015), however in light of 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, is exactly what makes *P. cinereus* an ideal EEB model organism. SPARCnet is poised to address many of these inconsistencies (1) with existing standardized data collection, (2) minimal protocol changes disseminated throughout the network, and (3) with more substantial protocol pivots among a subset of willing network participants.

Unlike the other seven of the top eight most well-studied salamander species, *P. cinereus* is the only member of the Plethodontidae (Table 4; Table S2). As a direct-developing member of the largest family of salamanders, *P. cinereus* is also *more* representative of the majority of ecologically and evolutionarily successful salamander taxa than any of the other top seven species. What we learn about being a salamander 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*. 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, there is also a very healthy level of systematic interest in both Plethodontidae and the genus *Plethodon* (e.g., Wiens *et al.*, 2006; Fisher-Reid & Wiens, 2011; Fisher-Reid, Kozak, & Wiens, 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 Figure 1, we know, and demonstrate with our review, that *P. cinereus* is both highly lab tractable and field tractable, and research can be and has been done at all biological scales aside from global (Fig. 5). The one Achilles heel of *P. cinereus* as a model organism which we could come up with is that controlled laboratory breeding has not yet been possible (hence the lower vertical dimension representing lab tractability in Fig. 5). But females can be induced to lay fertilized eggs (e.g., Evans *et al.*, 2020), and courtship behaviors can be observed (Jaeger *et al.*, 2016), so perhaps one day we will crack the code for controlled breeding of *P. cinereus*, but, as we argue above, this requires infrastructure, community ethos, and investment from funding agencies.

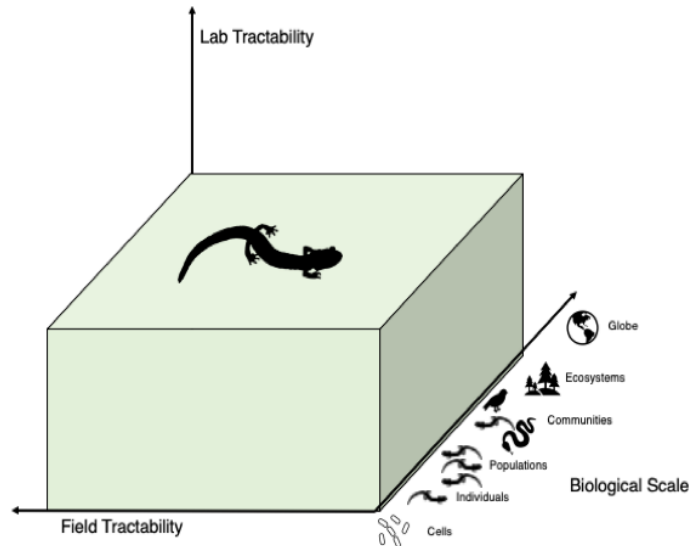


Figure 5. The versatility of *P. cinereus* as a model organism in EEB. Salamanders are highly tractable in both lab and field, and at all biological scales through ecosystems. Lab tractability is lower than field tractability because a protocol for controlled breeding in captivity has not been successfully developed yet. Figure modeled off of Figure 1 from Duffy *et al.* (2021).

VII. 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 stands out, *P. cinereus*, 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 family.
4. In just 22 years, over 400 papers on all aspects of *P. cinereus*' evolution, ecology, and behavior have been published in peer-reviewed journals. While studies are 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 which can be studied using *P. cinereus*.
5. *P. cinereus* falls short of model system status due to 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 coordinated distributed experiments to cohesively and repeatedly study *P. cinereus* populations 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.

VIII. Acknowledgements

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IX. Author Contributions

M.C.F.-R. conceived of the review, conducted the literature searches on salamander families, genera, and species, performed the GIS analyses, and prepared the *P. cinereus* article list for the group effort to categorize and summarize. All authors made substantial contributions to retrieving sources on *P. cinereus*, categorizing and summarizing these sources, planning and writing the manuscript. M.C.F.-R. combined the written summaries and cross-checked all sources prior to submission.

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XI. Supporting Information

- Table S1.xlsx.** List of number of source for each of 50 genera searched during genus-level search
- Table S2.xlsx.** List of number of source for each of 179 species searched during species-level search
- Table S3.xlsx – Table S10.xlsx.** List of sources for each of the top 8 most well-studied salamanders
- Table S11.xlsx.** Categorization & summaries of post-Petranka literature on *Plethodon cinereus*
- Table S12.xlsx.** Geographic range size data for all salamander species available from the IUCN
- Table S13.xlsx.** Categorization of sources cited by Petranka
- Table S14.xlsx.** Number of post-Petranka articles by state/province for *Plethodon cinereus*
- Supplemental Figures.docx.** Document of four supplemental figures and their captions
- Figure S1.** Natural tail fluorescence in *Plethodon cinereus* from Massachusetts
- Figure S2.** High density coverboards sharing in *Plethodon cinereus* from Virginia
- Figure S3.** An example of a bifurcated tail in *Plethodon cinereus* from Pennsylvania
- Figure S4.** Map of SPARCnet participants across the range of *Plethodon cinereus*