

# Discovery of Populations of the Eastern Red-Backed Salamander (*Plethodon cinereus*) with High Frequencies of the Lead-Backed Morph Beyond the Species' Northern Range Limit

Jean-David Moore<sup>1</sup> and Martin Ouellet<sup>2</sup>

**The Eastern Red-Backed Salamander (*Plethodon cinereus*) is one of the most abundant vertebrate species in the forests of eastern North America and is considered an important species for ecological processes. Two phenotypes most commonly coexist in most populations, but in different proportions: the red-backed (striped) and lead-backed (unstriped) morphs. Recent large-scale studies suggested that both color morphs of *P. cinereus* occur in and beyond the species' current northern range. The presence of lead-backed morphs in this area would contradict some previous studies that link the lead-backed morph with warmer conditions. To test this hypothesis, we conducted inventories in the boreal forest of northwestern Quebec (Canada), outside or at the edge of the species' known northern range, where temperatures are among the coldest encountered by this species. We documented 11 sites with the lead-backed morph, including five sites in the Parent area that fill a large gap in the species' known distribution. Among the latter, we found three distinct populations in which the lead-backed morph reached frequencies of 43–96%. These occurrences of *P. cinereus* are noteworthy given the harsh climatic conditions that prevail throughout the year and the recurrence of large-scale disturbances in these far-north forests. Although a previous study observed relatively high frequencies of the lead-backed morph in the northern part of the species' range, this is the first report of such high frequency findings so far north, outside of the known species' range. Our findings agree with the mounting evidence that variation in color morph frequency is not related only to temperature or shifts in climate.**

**I**N the forests of northeastern North America, the Eastern Red-Backed Salamander (*Plethodon cinereus*) is one of the most studied, widely distributed, and common amphibians (Petranka, 1998). Its range extends to the south from Missouri to North Carolina, and to the north from Minnesota to Nova Scotia, through Ontario and Quebec. It is considered as an important species for ecological processes (Burton and Likens, 1975; Walton, 2013). Being an ectotherm, this salamander depends on environmental heat sources to maintain its metabolic rate, and thus can be affected by temperature variables (Bobka et al., 1981; Homyack et al., 2011; Caruso et al., 2014). This species is also known to be sensitive to habitat disturbances (Homyack et al., 2011; Hocking et al., 2013). As a result, *P. cinereus* has the main qualities of a good bioindicator (Holt and Miller, 2010).

Eight color phenotypes and variants are known for this species (Moore and Ouellet, 2014; Ouellet and Moore, 2016). Two phenotypes are most common in most populations, but in different proportions: the red-backed (striped) and lead-backed (unstriped) morphs (Fig. 1). Over the last century, numerous studies have investigated the geographic variations in the proportions of *P. cinereus* color morphs. Many authors have suggested that the proportions of the two main morphs can vary either in space or time according to climate and have linked the lead-backed morph with warmer conditions (Lotter and Scott, 1977; Moreno, 1989; Gibbs and Karraker, 2006; Anthony et al., 2008). These studies, however, were performed at the local scale or did not cover the species' whole range; thus, their results cannot be extrapolated to the species' whole range. Consequently, no consensus has yet been reached regarding

the possible role of climatic variables in the distribution of color morphs of this species (Petrucci et al., 2006; Moore and Ouellet, 2015; Evans et al., 2018).

Recently, based on a large compilation of 236,109 observations compiled from 1880 to 2013 from 1,148 localities across the species' whole range, Moore and Ouellet (2015) showed that geographic variables do not influence the color morph proportions in populations of *P. cinereus*. They found low to high frequencies of the lead-backed morph in the northern part of the species' Canadian range. Even with this important demonstration, some doubts persist in the scientific community, probably because the idea that the lead-backed morph was linked to warmer conditions has been well established for decades.

Given that the northern part of northeastern North America was less inventoried, it is possible that some populations of *P. cinereus* exist further north. Based on meteorological data and a dataset of 400,090 observations, Moore et al. (2018) recently suggested that some populations of *P. cinereus* could have colonized some areas of the boreal forest at latitudes above 50°N, well beyond the species' current northern range limit.

In this context, we hypothesize that some populations with a high proportion of the lead-backed morphs could occur further north than what current knowledge suggests. We thus performed inventories in the boreal forest of northwestern Quebec (Canada), in areas at the border or outside of the species' known range, and where temperatures are among the coldest encountered by this species. We also tested for morph-specific differences in lengths and mass as a proxy of body condition, under the hypothesis that no difference should occur between red and lead-backed specimens.

<sup>1</sup> Ministère des Ressources naturelles et de la Faune, Direction de la recherche forestière, 2700 rue Einstein, Québec, Québec G1P 3W8 Canada; ORCID: 0000-0003-0957-0221; Email: jean-david.moore@mffp.gouv.qc.ca. Send correspondence to this address.

<sup>2</sup> Amphibia-Nature, 3380 rang Rochon, Rouyn-Noranda, Québec J0Z 2X0 Canada; ORCID: 0009-0007-0766-5143; Email: mouellet@amphibia-nature.org.

Submitted: 5 July 2023. Accepted: 17 December 2024. Associate Editor: W. L. Smith.

© 2025 by the American Society of Ichthyologists and Herpetologists DOI: 10.1643/h2023050 Published online: 13 February 2025



**Fig. 1.** The red-backed (striped) and lead-backed (unstriped) morphs of the Eastern Red-Backed Salamander (*Plethodon cinereus*). Photo by M. Ouellet.

Confirming these hypotheses by direct observations in very cold areas is important to resolve the issue about the use of morphs of *P. cinereus* as a climatic proxy.

## MATERIALS AND METHODS

**Salamander inventories and measurements.**—We conducted survey works during the summers of 2017–2019 (Table 1) in public forests where no inventory had been previously reported for *P. cinereus*, since snow cover in winter and low/cold temperatures in spring and fall preclude salamander inventory in these northern areas. In three distinct sites in the Parent area, our goal was to capture a maximum of specimens to evaluate relative morph frequencies. Additional observations were also made in eight other sites during other herpetological surveys. In all surveyed sites, we found specimens under fallen trees and tree bark in forests, or under rocks in rock outcrops. We recorded color morph, snout–vent length (SVL), and total length (TL) of individuals using electronic calipers (resolution: 0.1 mm), and mass using a digital balance (resolution: 0.1 g). Captured salamanders were released on-site immediately after measurements. All methods used were carried out in accordance with the Canadian Council of Animal Care.

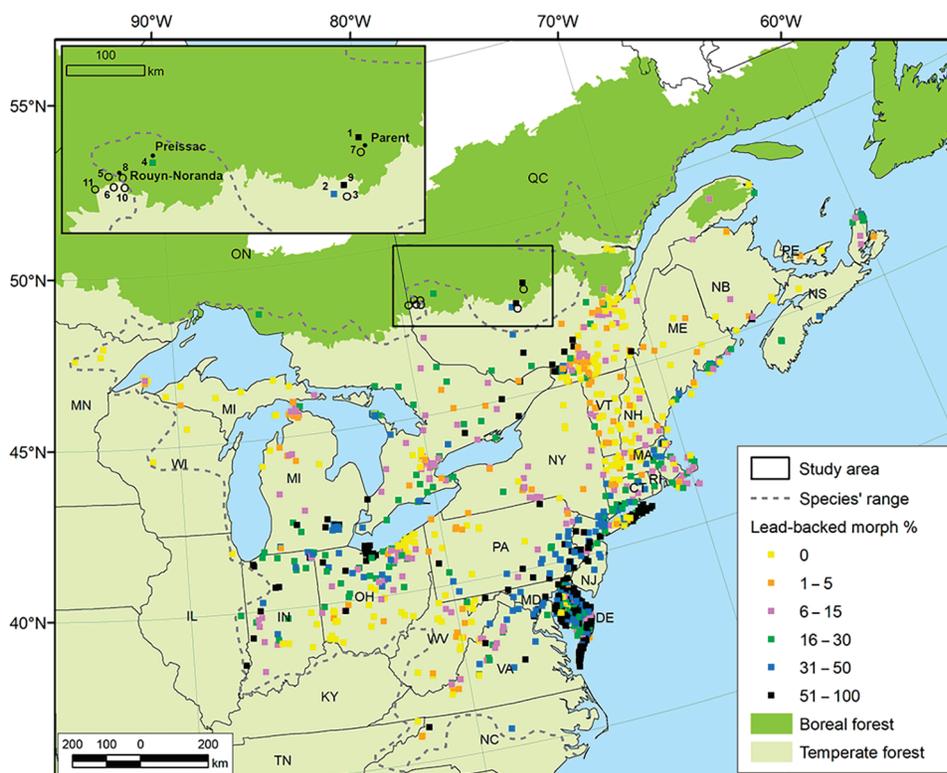
**Study area.**—The sites are located in the boreal forest zone of northwestern Quebec or at its edge (Fig. 2). One of the areas (site 1, approximately 20 hectares) was sampled three times, but never in the same part to avoid individual recapture. The encountered stand types were mainly even-aged (50 years old) or uneven-aged boreal shade intolerant hardwoods (Paper Birch, *Betula papyrifera*; Fig. 3) originating from forest fires or Spruce Budworm (*Choristoneura fumiferana*) outbreaks (Table 1). Annual mean temperature ranges from 1.2 to 2.8°C, daily mean temperature of the coldest month varies from –14.8 to –17.8°C, and lowest daily minimum temperature during the year ranges from –40.2 to –45.2°C (Table 1). Mean annual total precipitation varies from 893 to 1,060 mm, of which 240 to 314 mm (water equivalent) falls as snow. On average, the frost-free period lasts from 153 to 175 days. We estimated the average yearly climate conditions (2009–2019) of each site using BioSIM software (version 10.2.5.39,

**Table 1.** Summary information about populations of the Eastern Red-Backed Salamander (*Plethodon cinereus*) with high frequencies of the lead-backed morph at and beyond the species' known northern range.

Site	Location	Inventory date	Sample size	Number of lead-backed morph specimens	Elevation (m)	Stand composition <sup>1</sup>	Stand structure Age origin	Annual mean of daily mean temperature (°C)	Daily mean temperature of the coldest month (°C)	Lowest daily minimum temperature for the year (°C)	Mean annual total precipitation (snow) (mm)	Mean frost-free period (days) <sup>2</sup>
1	Parent (T-75)	2018-06-19 2019-09-10 2019-09-11	91	87	520	PB	Even-aged 50 years Burned (1929)	1.4	–15.6	–44.7	1012 (312)	156
2	Parent (T-26)	2018-06-19	21	9	454	PB	Uneven-aged 80 years Spruce Budworm	1.9	–15.7	–45.1	1060 (311)	153
3	Parent (T-20)	2018-06-19	16	15	482	YB-SM	Uneven-aged n.a.	1.9	–15.4	–45.2	1060 (310)	153
4	Preissac	2017-09-15	10	2	357	BF-PB	n.a. Burned (1950)	2.3	–15.4	–40.6	959 (286)	168
5	Rouyn-Noranda	2018-09-08	6	2	298	PB	n.a. Spruce Budworm	2.8	–14.9	–40.3	920 (257)	174
6	Rouyn-Noranda	2019-06-14	5	3	305	PB-BF	n.a.	2.8	–14.8	–40.5	925 (256)	175
7	Parent (Radar)	2019-09-12	2	2	598	PB-Po	n.a. Burned (1929)	1.2	–15.6	–44.6	1020 (314)	153
8	Rouyn-Noranda	2019-06-18	2	2	316	Po	n.a.	2.7	–14.9	–40.2	920 (262)	174
9	Parent (Patriotes outfit)	2018-06-19	1	1	432	PB	Even-aged 50 years n.a.	2.2	–17.8	–44.9	1060 (298)	158
10	Rouyn-Noranda	2017-09-19	1	1	314	Peatland	n.a. Burned (1944)	2.8	–14.8	–40.9	926 (256)	174
11	Rouyn-Noranda	2018-09-03	1	1	335	Po-PB	n.a. Burned (1930)	2.8	–14.9	–41.9	893 (240)	174

<sup>1</sup> BF = Balsam Fir (*Abies balsamea*), PB = Paper Birch (*Betula papyrifera*), Po = Populus spp., SM = Sugar Maple (*Acer saccharum*), YB = Yellow Birch (*Betula alleghaniensis*).

<sup>2</sup> Number of days in the year when the daily minimum temperature is >0°C. n.a.: not available.



**Fig. 2.** Site locations of the studied populations of *Plethodon cinereus* in northwestern Quebec, Canada, with frequencies of the lead-backed morph across the species' range (modified from Moore and Ouellet, 2015). The dotted line outlines the species' current known range (modified from Moore et al., 2018). In the study area, site numbers refer to Table 1, and open circles indicate occurrence of the lead-backed morph in sites where fewer than ten specimens of *P. cinereus* were found.

2013) developed by the Canadian Forest Service (Régnière and St-Amant, 2007). These estimates are based on climatic variables interpolated from eight nearby weather stations in Canada, adjusted for differences in elevation, latitude, and longitude.

**Statistical analysis.**—We conducted an analysis of variance (ANOVA) on individuals to test for differences in body variables (SVL, TL, and mass) between morphs. Also, we used a

linear regression to determine whether the relationship between salamander mass and SVL differed between the two color morphs. In this model, the response variable was mass. Analyses were performed using the SAS MIXED procedure (SAS Institute Inc., 2016) after checking for normality and heterogeneity of variance. The threshold used to determine significance was  $\alpha = 0.05$ .

## RESULTS AND DISCUSSION

**Range extension.**—Our survey revealed 11 sites that were at the limit or outside of the known range of *P. cinereus* (Fig. 2). The five sites in the Parent area fill a major gap in the known species' distribution. These findings complement a few other observations of *P. cinereus* in boreal forests (Fig. 2; Schueler and Karstad, 1975; Moore et al., 2018). The presence of *P. cinereus* in the Parent area is particularly noteworthy, given the harsh climatic conditions that prevail in early spring, late fall, and winter. This suggests that snow cover and the fossorial capacity of this salamander can mitigate the effect of extreme cold temperatures in these boreal forest ecosystems. *Plethodon cinereus* is intolerant to freezing and does not survive below  $-1.5^{\circ}\text{C}$  (Storey and Storey, 1986). Taub (1961) observed that *P. cinereus* burrow to protect themselves against adverse weather conditions, such as summer heat and winter cold, and that survival depends on winter severity and snow depth. Thus, in part of the species' range, snow cover may isolate and protect soils and salamanders from cold winter temperatures, provided that snowfall precedes periods of extreme cold, as soil



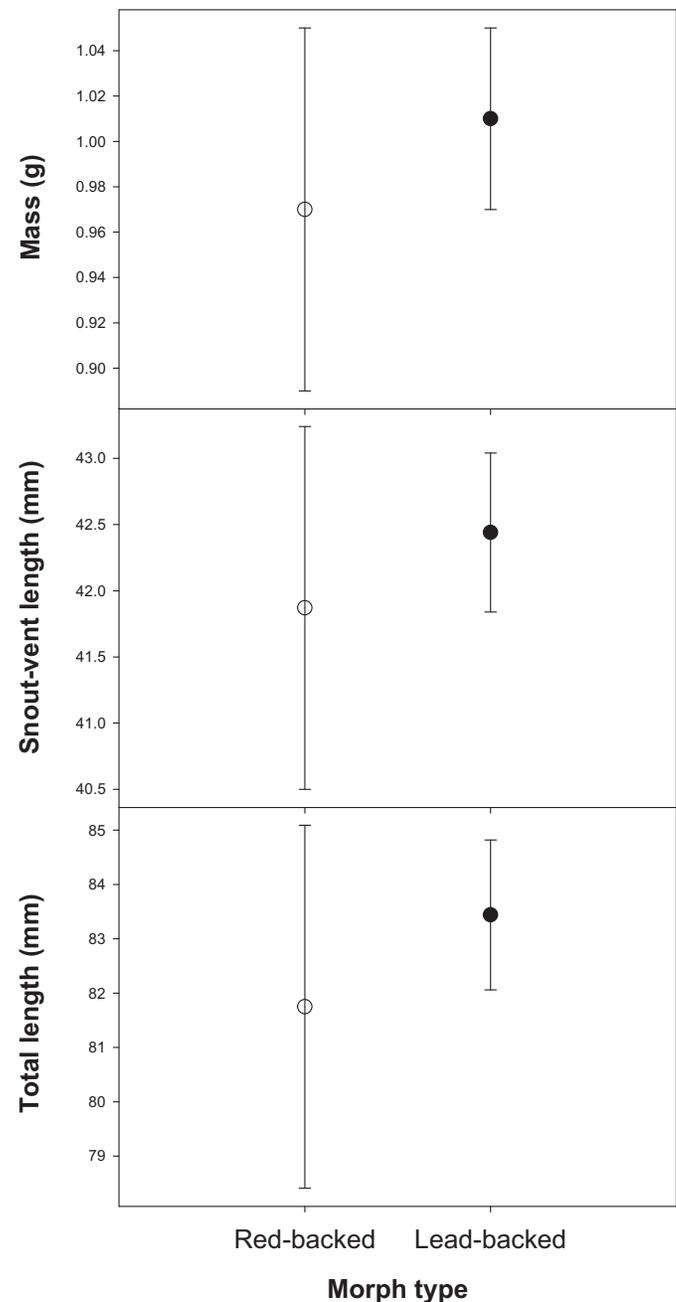
**Fig. 3.** Stand types at the study sites were mainly even-aged (50 years old) or uneven-aged boreal shade intolerant hardwoods (Paper Birch, *Betula papyrifera*) originating from forest fires or Spruce Budworm (*Choristoneura fumiferana*) outbreaks. Photo by M. Ouellet.

under snow cover is unlikely to get colder than 0°C (Houle et al., 2002).

**Lead-backed morph frequencies.**—We noted the presence of lead-backed specimens in all 11 sites (Table 1). Overall, 125 out of 156 *P. cinereus* were of the lead-backed morph. In particular, we discovered three distinct populations beyond the species' known range, in which lead-backed morph frequencies reached 43 to 96% (Table 1). In these areas, temperatures can be very cold (Table 1), with the daily mean temperature of the coldest month dropping as low as  $-17.8^{\circ}\text{C}$  and the lowest daily minimum temperature of the year reaching  $-45.2^{\circ}\text{C}$ . Although relatively high frequencies of the lead-backed morph were also observed in other areas in the northern part of the species' range (Fig. 2; Moore and Ouellet, 2015), this is the first report of finding such high frequencies of the lead-backed morph so far north, outside of the species' known range. Consequently, these results extend the conclusions of a previous study that high frequencies of the lead-backed morph of *P. cinereus* can occur in the northern part of the species' range (Moore and Ouellet, 2015). Moreover, these results also confirm the hypothesis that this species can also be found beyond its current known range (Moore et al., 2018). The presence of the lead-backed morph in these far-north forest ecosystems, especially that of populations with high frequencies of the lead-backed morph, contradict previous studies that associated a high prevalence of the lead-backed morph to warmer climates (Lotter and Scott, 1977; Moreno, 1989; Gibbs and Karraker, 2006; Anthony et al., 2008). After additional surveys of New England sites that had been originally sampled by Lotter and Scott (1977) in the early 1970s, Evans et al. (2018) found no evidence of the predicted shift in morph frequencies, despite substantial changes in climate. Moreover, Hantak et al. (2019) found that climate variables were not as important as geographic distance or waterway barriers in influencing color morph frequency in *P. cinereus*.

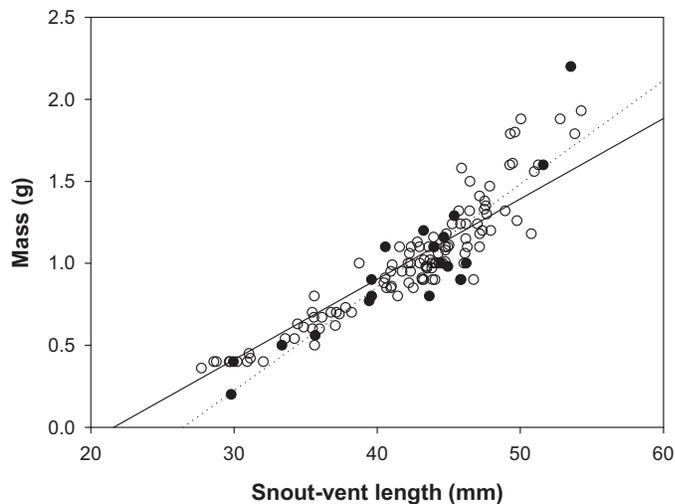
**Salamander size.**—The intercept, the linear effect of SVL, and the quadratic effect of SVL depended on the color morph. A difference in size between the lead-backed and the red-backed morphs could exist if their body condition was different. In our study, however, the size (SVL, TL, and mass) of both morphs was not significantly different within the three pooled populations of the Parent area ( $P \geq 0.641$ ; Fig. 4). Mass-length regressions were also not significant for either of the two color morphs ( $P \geq 0.578$ ; Fig. 5). Other studies have suggested using this regression technique to evaluate the body condition of populations of *P. cinereus* (Heatwole and Heatwole, 1962; Jaeger, 1981; Moore, 2020). These results indicate that body condition was similar for both morphs in these extreme northern ecosystems. In this context, it seems obvious that temperature alone does not govern the spatial distribution of the lead-backed morph in *P. cinereus* (Cosentino et al., 2017; Evans et al., 2018; Hantak et al., 2021).

**Forest disturbances versus color morph.**—The recurrence of large-scale natural (forest fire, Spruce Budworm outbreak, windthrow) and anthropogenic (clearcutting, forest fire) disturbances is also a characteristic factor of our studied forest ecosystems. Historical data revealed that these



**Fig. 4.** Mean body variables (mass, snout-vent length, and total length) of the red-backed and lead-backed morphs of *P. cinereus* within the three pooled populations of the Parent area. Error bars represent  $\pm$  SE.

forests originated from forest fires or Spruce Budworm outbreaks. These disturbances created canopy openings that could generate an increase of soil temperature (Moroni et al., 2009). Evans et al. (2020) found that eggs of *P. cinereus* incubated at warmer temperatures yielded a higher proportion of lead-backed morph individuals than those incubated at cooler temperatures; this result suggests that developmental temperature can influence coloration of *P. cinereus* and, thus, morph frequency distribution. In this context, it is possible that eggs of *P. cinereus* in the studied areas experienced above-normal habitat temperatures during their development, which caused an increased



**Fig. 5.** Linear regression showing the relationship between mass and snout-vent length for both the red-backed (white dots, dotted line) and lead-backed (black dots, solid line) morphs of *P. cinereus* for the three pooled populations of the Parent area.

frequency of the lead-backed morph. Nevertheless, our findings agree with the mounting evidence that variations in color morph frequency in *P. cinereus* are not related only to temperature or shifts in climate. Future works on color polymorphism are thus warranted in the Canadian boreal forest, both within and beyond the species' current northern range limit.

#### DATA ACCESSIBILITY

Unless an alternative copyright or statement noting that a figure is reprinted from a previous source is noted in a figure caption, the published images and illustrations in this article are licensed by the American Society of Ichthyologists and Herpetologists for use if the use includes a citation to the original source (American Society of Ichthyologists and Herpetologists, the DOI of the *Ichthyology & Herpetology* article, and any individual image credits listed in the figure caption) in accordance with the Creative Commons Attribution CC BY License.

#### AI STATEMENT

The authors declare that no AI-assisted technologies were used in the design and generation of this article.

#### ACKNOWLEDGMENTS

We are grateful to H. Tremblay (DRF) and È.-L. Grenier (Amphibia-Nature) for help in the field, J. Noël (DRF) for technical assistance, M.-C. Lambert (DRF) for meteorological data and statistical analyses, and D. Tousignant (DRF) for reviewing an earlier version of this manuscript.

#### LITERATURE CITED

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

**Bobka, M. S., R. G. Jaeger, and D. C. McNaught.** 1981. Temperature dependent assimilation efficiencies of two species of terrestrial salamanders. *Copeia* 1981:417–421.

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

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

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

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

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

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

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

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

**Heatwole, H., and A. Heatwole.** 1962. Weight-length curve of the salamander, *Plethodon cinereus*. *Journal of the Ohio Herpetological Society* 3:37–39.

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

**Holt, E. A., and S. W. Miller.** 2010. Bioindicators: using organisms to measure environmental impacts. *Nature Education Knowledge* 3:8.

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

**Houle, D., L. Duchesne, R. Ouimet, R. Paquin, F.-R. Meng, and P. A. Arp.** 2002. Evaluation of the FORHYM2 model for prediction of hydrologic fluxes and soil temperature at the Lake Clair watershed (Duchesnay, Quebec). *Forest Ecology and Management* 159:249–260.

**Jaeger, R. G.** 1981. Dear enemy recognition and the costs of aggression between salamanders. *The American Naturalist* 117:962–974.

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

**Moore, J.-D.** 2020. No effect of liming on the eastern red-backed salamander after 5 years. *Soil Organisms* 92:197–202.

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

- Moore, J.-D., and M. Ouellet.** 2015. Questioning the use of an amphibian colour morph as an indicator of climate change. *Global Change Biology* 21:566–571.
- Moore, J.-D., M. Ouellet, and M.-C. Lambert.** 2018. Potential change in the distribution of an abundant and wide-ranging forest salamander in a context of climate change. *Frontiers of Biogeography* 9.4:e33282.
- Moreno, G.** 1989. Behavioral and physiological differentiation between the color morphs of the salamander, *Plethodon cinereus*. *Journal of Herpetology* 23:335–341.
- Moroni, M. T., P. Q. Carter, and D. A. J. Ryan.** 2009. Harvesting and slash piling affects soil respiration, soil temperature, and soil moisture regimes in Newfoundland boreal forests. *Canadian Journal of Soil Science* 89:343–355.
- Ouellet, M., and J.-D. Moore.** 2016. Silver-white variants of the eastern red-backed salamander, *Plethodon cinereus*, from eastern Canada. *The Canadian Field-Naturalist* 130: 133–136.
- Petranka, J. W.** 1998. Salamanders of the United States and Canada. Smithsonian Institution Press, Washington, D.C.
- Petruzzi, E. E., P. H. Niewiarowski, and F. B.-G. Moore.** 2006. The role of thermal niche selection in maintenance of a colour polymorphism in redback salamanders (*Plethodon cinereus*). *Frontiers in Zoology* 3:10.
- Régnière, J., and R. St-Amant.** 2007. Stochastic simulation of daily air temperature and precipitation from monthly normals in North America north of Mexico. *International Journal of Biometeorology* 51:415–430.
- SAS Institute Inc.** 2016. SAS version 14.2. SAS Institute, Cary, North Carolina.
- Schueler, F. W., and A. R. Karstad.** 1975. Notes on the distribution and habitat of amphibians and turtles in northwestern Quebec. *The Canadian Field-Naturalist* 89:57–59.
- Storey, K. B., and J. M. Storey.** 1986. Freeze tolerance and intolerance as strategies of winter survival in terrestrially-hibernating amphibians. *Comparative Biochemistry and Physiology Part A: Physiology* 83:613–617.
- Taub, F. B.** 1961. The distribution of the red-backed salamander, *Plethodon c. cinereus*, within the soil. *Ecology* 42:681–698.
- Walton, B. M.** 2013. Top-down regulation of litter invertebrates by a terrestrial salamander. *Herpetologica* 69:127–146.