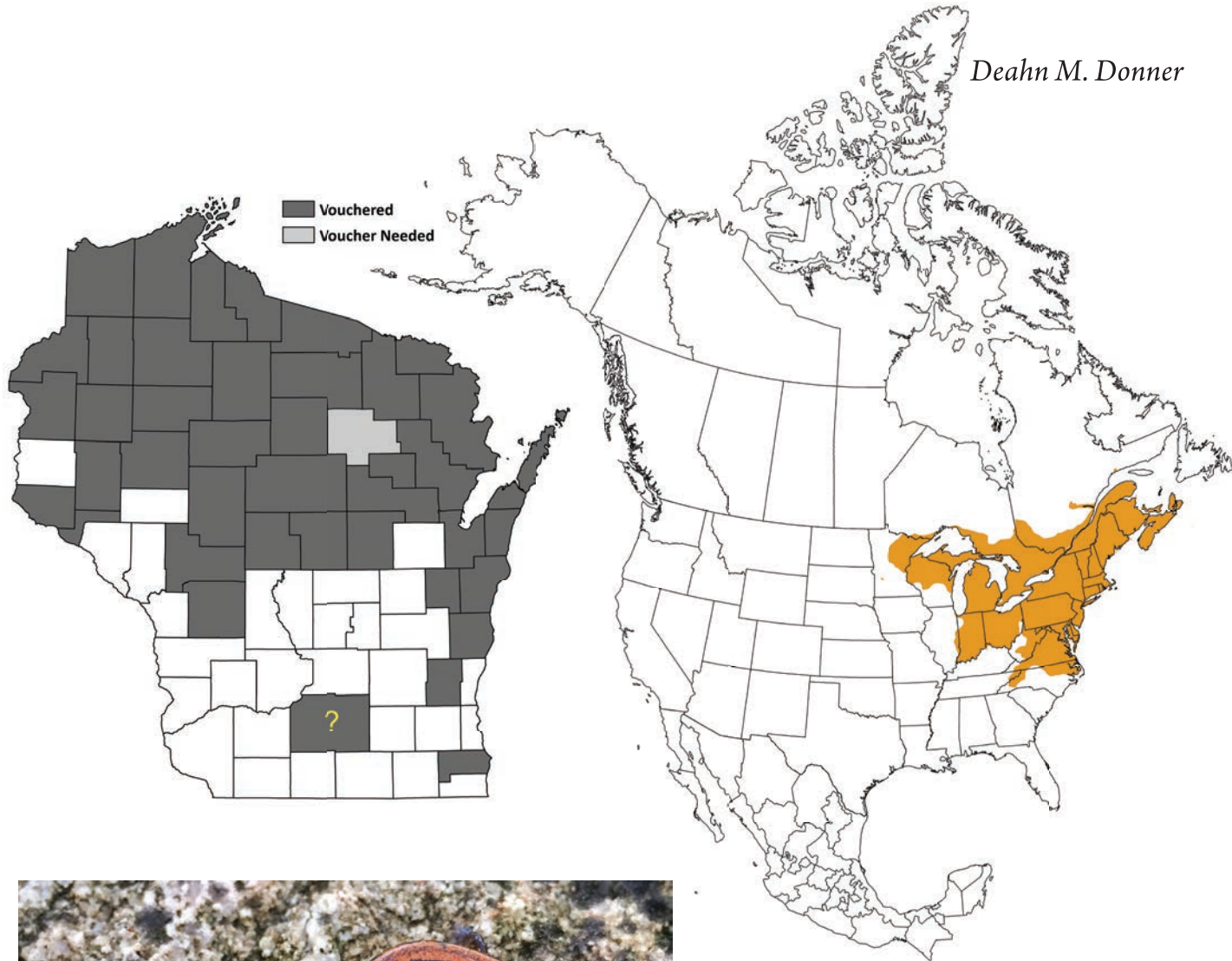


Eastern Red-backed Salamander

Plethodon cinereus (Green 1818)

Deahn M. Donner



Eastern Red-backed Salamander (Sheboygan County; photo by N. Melhorn).

AT A GLANCE

Eastern Red-backed Salamanders are a woodland species found primarily in northern Wisconsin, with isolated records from southeastern counties. This small slender salamander typically has a reddish dorsal stripe that extends from the head to the tail over a generally dark body, with light flecks on the belly, and five toes on the hind feet. Being lungless, they respire entirely through the skin and thus depend on moist conditions to breathe and are susceptible to desiccation. As such, they closely associate with forested habitats, particularly mesic to wet-mesic hardwoods, where they occur below ground debris. Eastern Red-backed Salamanders are active from April to mid-October. They have complex social systems and exhibit many interesting reproductive and territorial behaviors. Reproduction primarily occurs in autumn, and females store sperm internally, which is used to fertilize the eggs that are laid the following June. Females lay eggs on land in moist decaying logs, and they defend eggs from predators. Unlike other salamanders, there is no aquatic larval phase. Terrestrial hatchlings emerge in August, appearing similar to adults. Eastern Red-backed Salamanders consume a variety of small invertebrates and forage mostly at night by following chemical trails left by prey. This species is consumed by many birds, small mammals, and snakes. It is listed as a common species by the WDNR but is vulnerable to loss of suitable woodland habitat.

SYSTEMATICS

No subspecies of *Plethodon cinereus* (Eastern Red-backed Salamander) are currently recognized (Crother 2017). Highton (1995) reported 4 genetically differentiated geographic groups of the 35 species within the genus *Plethodon* across the eastern US, and 7 of these are part of the eastern *P. cinereus* clade. The majority of the seven species in this clade have highly restricted distributions (Highton 1999). Among these, *Plethodon serratus* (Southern Red-backed Salamander) is morphologically the most similar to *P. cinereus*, but *P. shenandoah* (Shenandoah Salamander) and *P. nettingi* (Cheat Mountain Salamander) are the most similar genetically (Highton 1999). Of the seven

species within this eastern clade, only *P. cinereus* is found in Wisconsin. Furthermore, only one other salamander species in Wisconsin is a member of the same family as *P. cinereus* (Plethodontidae): *Hemidactylium scutatum* (Four-toed Salamander).

DESCRIPTION

Adults: Eastern Red-backed Salamanders are so named because of the reddish dorsal stripe that typically extends from the head onto the tail (Figure 146). The rest of the body is generally dark gray or black, often with small light-colored speckles, with the base coloration becoming lighter on the white-flecked belly. They are slender with a long rounded tail (in cross section) and small legs that have four digits on the front feet and five slightly webbed digits on the back feet (Petranka 1998). The number of costal grooves ranges from 17 to 20, and the gular fold is prominent (Petranka 1998).

Eastern Red-backed Salamanders are one of Wisconsin's smaller salamanders, but their tail is long (i.e., nearly as long as the rest of their body). For example, the mean SVL of mature specimens from Wisconsin in the MPM and UWZM collections was 4.4 cm (1.7 in, $n = 145$; to ensure specimens were mature, only those with an SVL ≥ 3.7 cm



Figure 146. Dorsal view of an Eastern Red-backed Salamander showing the red stripe down the back from head to tail and the white flecking on the sides. The dorsal stripe can be salmon or dark brown in color as well (Sheboygan County; photo by N. Melhorn).

[1.5 in] were included). The mean intact tail length of mature specimens in these collections was 4.1 cm (1.6 in, $n = 102$). These measures are similar to those reported by Liebgold (2014), who determined that the mean SVL of adult males sampled in Michigan ($n = 76$) and Virginia ($n = 88$) was 4.5 cm (1.8 in, $SD = 0.3$ cm [0.1 in]). The largest Wisconsin specimen measured had an SVL of 5.3 cm and a tail length of 4.4 cm (2.1 in and 1.7 in, respectively, UWZM 9429, collected in 1903 from Iron County).

Preadult stages: The eggs are uniformly yellowish white and range in diameter from 0.3 to 0.4 cm (0.1 to 0.2 in). Eggs are laid in small clusters held together with a gel-like substance (Figure 147; reviewed by Petranka 1998). Unlike most Wisconsin amphibians, this species undergoes direct development, and there is no aquatic larval phase (see Reproduction and Development section). As such, hatchlings and juveniles are similar in appearance to adults. In Wisconsin, Vogt (1981) reported that hatchling TL was 2.2 cm (0.9 in), which was also the hatchling size reported in an Ohio population (Pfingsten 1989). The mean SVL from a small sample of Wisconsin hatchling specimens housed at MPM was 1.5 cm (0.6 in, $n = 8$), while mean tail length was 0.8 cm (0.3 in, $n = 8$). In Maryland, Sayler (1966) reported a mean SVL of 2.1 cm (0.8 in, $n = 47$) for hatchlings.



Figure 147. A clutch of Eastern Red-backed Salamander eggs (Door County; photo by C. Raimond).

Variation: There are several color variants of this species documented across its North American range (Moore and Ouellet 2014). For example, in some parts of its distribution, a “lead-back” phase commonly occurs that has no red stripe but often a dark and speckled back (Petranka 1998). The reasons for this color polymorphism have been attributed to differential predation, which influences dominance of the red-backed phase (Venesky and Anthony 2007, Fitzpatrick et al. 2009), and the genetics that control the presence of stripes along the back (Highton 1975). Detailed information on the prevalence of these variant color morphs in Wisconsin is sparse. Knudsen (1958b) anecdotally reported that the dorsal stripes of Wisconsin individuals ranged in color from “salmon-pink to brick-red, though sometimes . . . grayish-yellow, and more rarely dark, grayish-black.” Vogt (1981) stated that the lead-backed phase was not documented in Wisconsin and instead reported a “melanistic” population on Stockton Island in Lake Superior (Ashland County). Museum notes identify the specimen MPM 33208 as a “leadback” collected from Basswood Island (Ashland County). In addition, a dark-colored specimen collected from Forest County is listed as a “slate gray morph” (MPM 26484). Interestingly, Moore and Ouellet (2014) indicated the presence of lead-backed morphs in Wisconsin but did not report the source of their information. Although lead-backed morphs have been poorly documented in the state, it is reasonable that they exist in northern Wisconsin, considering Holman (2012) reported that they occurred (albeit infrequently) in the southern reaches of Michigan’s Upper Peninsula.

Further variation in appearance has been documented. Normal intact tails are round in cross section for the full length, but regenerated tails can be laterally compressed and dark gray, with the red stripe missing (Petranka 1998). Adult males are smaller than females, but the difference is minimal (reviewed by Petranka 1998). For example, in southwestern Michigan, Werner (1971) noted that the mean SVL of females was 4.5 cm (1.8 in) and that of males was 4.2 cm (1.7 in). In Maryland, Sayler (1966) reported that the mean SVL for adult males was 4.0 cm (1.6 in, $n = 262$) and 4.03 cm (1.6 in, $n = 85$) for females. During the breeding season, differences in external features can be used to distinguish males from females.



Figure 148. An adult male showing enlarged nasolabial grooves that extend below the nares on the front of the upper jaw (Oneida County; photo by C. Raimond).

For example, sexually active males possess a whitish area on the chin called a mental gland, as well as a whitish area lateral to the cloacal opening that is also slightly enlarged, and the snout becomes square due to enlarged premaxillary teeth (Gillette and Peterson 2001). Breeding males also possess a nasolabial groove that extends downward from each of the nares on the front of the upper jaw (Figure 148) and swollen hedonic glands at the base of the tail (reviewed by Petranka 1998). Sex of mature individuals can also be determined by shining a strong light behind the abdominal wall to show black testes in males; if they are absent, then the individual is female (Gillette and Peterson 2001, Jaeger et al. 2002). In gravid females, whitish circles (eggs as small as 0.1 cm [0.4 in]) can sometimes be seen through the skin along either side of the abdomen (Figure 149; Gillette and Peterson 2001).

Diagnosis: Eastern Red-backed Salamanders do not have tail fins that extend off the dorsal or ventral surface of the tail muscles. They do not have bushy external gills, the skin is not rough or granular in appearance, and there are no red dorsolateral spots bordered in black. Their body is long and thin, the tail and body coloration are normally similar (typically with a red dorsal stripe, but see Variation subsection), and there is no constriction at the base of the tail. The ventral surface is light gray (anteriorly) to dark



Figure 149. View of the abdominal cavity showing white eggs near the abdominal walls of a mature female. Also note the presence of five toes on the hind feet, a character used to distinguish this species from the Four-toed Salamander in Wisconsin (Bayfield County; photo by E. Wild).

gray or black (posteriorly), and there are five toes on each hind foot (Figure 149). Four-toed Salamanders have an orange-brown to red-brown dorsal stripe and could be confused with Eastern Red-backed Salamanders. However, the former has a constriction at the base of the tail and only four toes on the hind feet rather than five (Figure 149). Four-toed Salamanders also have a bright white belly with bold black spots or blotches (reviewed by Petranka 1998). Mole salamanders (*Ambystoma* spp.) are more stout-bodied, lack nasolabial grooves, and are generally larger as mature adults (reviewed by Petranka 1998).

Eastern Red-backed Salamander eggs look much different from those of other salamanders (uniformly yellowish or whitish in color as opposed to bicolored and encased in gelatinous envelopes). The eggs are also laid terrestrially rather than in the water or below moist *Sphagnum* moss as in other salamanders from Wisconsin. Juveniles should be easily distinguished from most other salamanders in Wisconsin because there is no aquatic larval phase, so they resemble smaller versions of the adults. Although members of the juvenile 'eft' stage in Eastern Newts (*Notophthalmus viridescens*) are small and reddish and could be mistaken for juvenile Eastern Red-backed Salamanders, the red in efts covers most of the body (it is not constrained to a stripe down the

middle of the back) and is not bright. Eastern Newts also do not possess costal grooves.

DISTRIBUTION AND HABITAT

Global distribution: Eastern Red-backed Salamanders range from southern Quebec and the Canadian Maritime Provinces, west to northeastern Minnesota, and south to northern and eastern North Carolina. Isolated populations occur in western Minnesota and southern North Carolina (Petranka 1998).

Distribution in Wisconsin: Eastern Red-backed Salamanders are mostly distributed in forested portions of the state north of the vegetative tension zone (Curtis 1959), including islands on the Door Peninsula (Long and Long 1976), although spotty records also occur in eastern to southeastern Wisconsin. The record from Racine County is based on an old specimen, and recent confirmation of Eastern Red-backed Salamanders in that county is desirable (see discussion in Kapfer et al. 2015). The species appears to be absent from counties with well-drained soils in central, south-central, and southwestern Wisconsin (Vogt 1981). Although a vouchered specimen exists for Dane County, this record remains questionable (see discussion in Kapfer et al. 2015). Of the published county records, a voucher could not be found for Langlade County (see the Appendix).

Localities of possible occurrence: This species is not currently documented in St. Croix, Eau Claire, and Outagamie Counties, but its presence in these locations seems likely due to confirmed records in surrounding counties. Given the historical distribution of mesic forests in Wisconsin, Fond du Lac and Winnebago Counties may also have areas of potentially suitable habitat for Eastern Red-backed Salamanders (Curtis 1959). Casper (1996) noted that Eastern Red-backed Salamanders could occur farther south along Lake Michigan in eastern Wisconsin than is currently recorded based on the historical presence of southern mesic forests in that region. Given the existence of old specimens from Racine County, recent confirmation in Washington County, and documentation of this species immediately across the Illinois border (Kapfer et al. 2015), all coupled

with the more extensive past distribution of mesic forests in southeastern Wisconsin, this species could also occur (or historically occurred) in Dodge, Jefferson, Ozaukee, Waukesha, Milwaukee, and Kenosha Counties (note that an old, unverified report from Waukesha County exists in Cahn [1929]). In addition, Eastern Red-backed Salamanders could have once been found in portions of Vernon, Crawford, Richland, and Sauk Counties where mesic forests were historically present, and perhaps remnant populations remain there in suitable locations. Vogt (1981) mapped a record from Sauk County that he had not confirmed but that he considered reliable; Casper (1993c) noted unconfirmed reports from the Baraboo Hills that further support its occurrence in Sauk County.

Habitat: Eastern Red-backed Salamanders are completely terrestrial and closely associated with forested habitats in Wisconsin such as mesic to wet-mesic northern forests (hardwood or mixed deciduous-coniferous forest) and conifer swamps (Vogt 1981, Petranka 1998; see Amphibians and Reptiles in Wisconsin Plant Communities chapter). They are lungless and respire entirely through the skin; thus, they rely on moist conditions to facilitate oxygen absorption and avoid desiccation. Therefore, Eastern Red-backed Salamanders in Wisconsin are frequently found in mature forests with dense tree canopies and well-developed moist ground litter (Vogt 1981). However, some sources report that they tolerate a broad range of moisture, temperature, and light levels (Wyman and Hawksley-Lescault 1987, Sugalski and Claussen 1997).

Given the probable importance of adequate moisture and humidity (Heatwole 1962), preferred microhabitats typically include the underside of damp ground cover objects such as old logs, bark, moss, leaf litter, humus substrates, and rocks. These provide a humid environment with a large supply of invertebrate prey and refugia from predators (Gergits and Jaeger 1990a). Accordingly, Bergeson (2001) determined that the volume of downed woody debris, particularly from Eastern Hemlock (*Tsuga canadensis*) and Sugar Maple (*Acer saccharum*), was positively correlated with Eastern Red-backed Salamander abundance at sites across northern Wisconsin (Vilas

and Forest Counties) and Michigan's Upper Peninsula (Gogebic County).

The type and texture of cover objects can further influence local abundance and distribution of this salamander. For example, Eastern Red-backed Salamanders at sites in northern Wisconsin and the Upper Peninsula of Michigan were found below logs on 96.9% of captures (385 of 397 total captures; Bergeson 2001). Bergeson (2001) also reported that salamander abundance was positively related to the presence of logs with diameters ranging from 51 to 107 cm (20 to 42 in) that were in advanced stages of decay. On the other hand, work in Vermont (Richmond and Trombulak 2009) and Pennsylvania (Moore et al. 2001) found that they were more common under rocks than woody branches, logs, or leaf litter in hardwood forests. Rocks further housed larger individuals (>3.47 cm SVL [1.37 in]), with smaller individuals more common under woody objects (Richmond and Trombulak 2009). The size of cover objects could also be correlated with the body size and mass of individual salamanders found beneath them (Mathis 1990, Moore et al. 2001), but some studies suggest that this could depend on season (Moore et al. 2001) or geography (Faragher and Jaeger 1997).

Eastern Red-backed Salamanders typically occupy fibrous woody substrates and humus ground layers, in part because they are moist but also because they provide easier movement through subsurface environments than do solid substrates (Heatwole 1962, Richmond and Trombulak 2009). When soil surface layers are dry, salamanders must move vertically below the soil surface to find adequate moisture (Vernberg 1953), which is more challenging in solid substrates. Heatwole (1960) reported that while this species is effective at penetrating loose layers of humus, it does not dig but rather "uses its head as a wedge and forces its body into cracks or small openings in the substrate by pushing with its feet, and in some instances, its tail." Kleeberger and Werner (1982) found 61% of all capture locations ($n=758$) were at the soil surface, primarily in litter layers and decaying logs in a northern hardwoods system of Michigan's Upper Peninsula, while the remaining locations were in the soil below humus and leaf litter associated with root systems of trees or in

raised mounds of soil, roots, and rocks. Eastern Red-backed Salamanders can enlarge existing burrows (Heatwole 1960) and will also often use earthworm (*Lumbricus terrestris*) burrows as refugia (Cáceres-Charneco and Ransom 2010, Ransom 2011).

Females lay eggs in moist locations, such as within or below decaying logs, beneath rocks, underground, or in other damp substrates (Vogt 1981). Because the eggs and larvae are not aquatic, habitat used for breeding and by hatchlings is similar to that occupied during the remainder of the year by adults. Specific data on overwintering habitat in Wisconsin are sparse, and most information comes from anecdotal observations in other states. Laboratory investigations support that Eastern Red-backed Salamanders do not tolerate freezing (Storey and Storey 1986), and studies from west-central Indiana found that they descend below the soil surface to avoid harsh winter conditions (Vernberg 1953). For example, they reportedly use root systems, animal tunnels, and natural crevices to avoid harsh conditions (Jaeger 1980b). Furthermore, Caldwell (1975) found 30 individuals during January in an ant mound (Formicidae) at depths of 31–75 cm (12.0–29.5 in) in Indiana. In Maryland, Grizzell (1949) uncovered a single individual overwintering at a soil depth of 88.9 cm (35 in).

REPRODUCTION AND DEVELOPMENT

In the Great Lakes region, mating typically occurs from October through December but can continue into the winter and early spring (Blanchard 1928). Males employ a "nose-tapping" behavior to detect chemical cues left on the ground by females and locate them for mating (Gergits and Jaeger 1990a). Once the male encounters a female, the male positions himself in front of her, blocking her movement, while arching his tail upward and wiggling it with the tip still on the ground (Gergits and Jaeger 1990a). As courtship progresses, the male approaches the female's side with his body in a low submissive posture. He then rubs glands located on his head and chin along her body until he reaches her snout, while she assumes a flat or submissive posture. The pair then walks forward with the female straddling the male's tail and pressing her head against the base of his tail

(Gergis and Jaeger 1990a). While she is in this posture, the female rubs her cloacal opening over the male's dorsum (Dyal 2006). The male next deposits a spermatophore on the substrate, and the female picks it up with her cloaca. Females store sperm internally, and eggs are fertilized during oviposition the following summer (reviewed by Sever 1997), which generally occurs from early to late June in Wisconsin (Vogt 1981, but see Bergeson 2001).

Eggs are laid in a cluster suspended by a gelatinous stalk attached to the undersurface of logs, rocks, or roots; in the absence of these larger cover objects, eggs are oviposited on the forest floor below ground litter or within small tunnels made by other animals (Test and Heatwole 1962). Reports of clutch size vary. Homyack and Haas (2009) found that the mean number of eggs per female ranged from 6.7 to 7.3 in central Appalachian oak forests ($n = 277$ females). The mean clutch size associated with 13 brooding females captured at sites in northern Wisconsin and adjacent Michigan was 7.8 (range = 4–12; Bergeson 2001). Leclair et al. (2008) found that the mean number of eggs per female was 9.4 (range = 4–15, $n = 21$ females) in Quebec. In Michigan, Blanchard (1928) reported 5–13 eggs per female ($n = 91$ females). In Ohio, the mean number of eggs across eight examined clutches was 7.9 (range = 4–10; Anthony and Pfingsten 2013). Several sources support that mature females do not produce eggs every year. In fact, due to the energy required to produce and subsequently guard eggs, females may only breed biennially (Sayler 1966, Ng and Wilbur 1995). At more northern latitudes, such as Canada, females may reproduce once every three years (LeClair et al. 2008).

Young undergo direct development, and females typically spend a significant amount of time in association with eggs (or 'brooding' the eggs) after they are laid. A brooding female wraps her body around the eggs to help them retain moisture and occasionally vibrates the eggs to maintain aeration and uniform distribution of eggs within clutches (Bachmann 1984, Tornick 2010). Females also guard eggs against invertebrate predators and other larger salamanders until the eggs hatch at six to nine weeks (often during August in Wisconsin; Vogt 1981), after which females remain with the young for up to three weeks until remnant gill buds are absorbed (Hard-

ing 1997). When an intruder approaches, the female adopts defensive behaviors such as nudging, chasing, and snapping at intruders and will exhibit heightened aggression when defending late-stage eggs (Tornick 2010). Brooding females do not actively forage while eggs develop, and they only eat opportunistically (Bachmann 1984).

Eastern Red-backed Salamanders, like many species with broad distributions, exhibit geographically variable growth rates due to differences in associated environmental conditions. Slower growth rates in northern latitudes translate to a more gradual increase in size until maturity and later age at first reproduction (Leclair et al. 2006). In Quebec, growth rates for the Eastern Red-backed Salamander were lower than those reported for populations at more southern latitudes in the US (Leclair et al. 2006). In this study, males reached sexual maturity at three to five years of age, and females reached sexual maturity at five to seven years of age; the minimum size at sexual maturity was 3.6 cm SVL (1.4 in) and 4.1 cm SVL (1.6 in) in males and females, respectively ($n = 775$ total salamanders assessed). In comparison, Sayler (1966) found that individuals from Maryland had matured by the end of their second year at a minimum SVL of 3.1 cm (1.2 in) in males and 3.4 cm (1.3 in) in females ($n = 1,272$ total salamanders assessed); mean adult SVL was 4.0 cm (1.6 in, range = 3.1–4.9 cm [1.2–1.9 in], $n = 347$). In Michigan, Blanchard (1928) documented sexual maturity at ca. two years old but noted that females did not successfully produce eggs until their fourth season ($n = 110$ females).

Annual growth rates decline with age. For example, estimates of growth during the first year was 1.5 cm (0.6 in), which declined to 0.8 cm (0.3 in) during year two, with greatly reduced growth rates after reaching sexual maturity (Nagel 1977). Within-year variation in growth also occurs. Sayler (1966) determined that individuals grew rapidly in April and May (0.4 cm [0.16 in], $n = 8$), and from September through December (1.0 cm [0.4 in], $n = 77$). Leclair et al. (2006) reported that female longevity in a Quebec population was eight years and male longevity was nine years but stated that most members of the population were two to four years old. Of these, adult males made up only 25% of captured male

three-year-olds, 57% of four-year-olds, and 100% of five-year-olds ($n=28$, 7, and 19, respectively); the oldest male was nine years old.

ACTIVITY

In Wisconsin, Eastern Red-backed Salamanders are typically active from April through October (Vogt 1981), but seasonal variation in activity apparently occurs. In Quebec, Leclair et al. (2008) captured 63.6% of 775 Eastern Red-backed Salamanders in drift fences during the first two weeks of October and <7.8% during spring and early summer (Leclair et al. 2008). Seasonal differences in activity are likely linked to seasonal variation in humidity. Eastern Red-backed Salamanders are nocturnal, and soil surface activity peaks during humid conditions (Keen 1984, Grover 1998, Grover and Wilbur 2002), which are often most prevalent at night in spring and autumn. Accordingly, surface activity declines during hot dry summer days, especially when humidity drops below 85% (Heatwole 1962, Jaeger 1980b). Leclair et al. (2008) captured far fewer individuals during mid-summer surveys in Quebec than during spring or autumn, which the authors linked to high air temperatures. Jaeger (1980b) found that this species modified its behavior during dry periods and moved from leaf litter to under rocks or logs, where conditions were presumably more favorable. Foraging activity also declines under dry conditions and can result in heightened intraspecific competition due to scarcity of prey (Jaeger 1980a, Jaeger et al. 2002).

Eastern Red-backed Salamanders are not particularly mobile, and studies of population genetics confirm that limited migration and gene flow occur among neighboring populations. For example, Cabe et al. (2007) reported that eight subpopulations separated by distances as little as 200 m (656 ft) in unfragmented habitat were genetically differentiated (suggesting that there is little movement between subpopulations). Similarly, Sites et al. (2004) found that populations separated by several kilometers were genetically distinct from each other. Accordingly, reported home range sizes and movement rates for this species are generally small. Mathis (1991) estimated home ranges of only 0.16–0.34 m² (1.7–3.7 ft²,

$n=25$) and found no difference in movement among adult males, adult females, and juveniles in a Virginia population. However, these findings are in contrast to other reports. For example, larger home range sizes were estimated from a mark-recapture study in Michigan that also found that males had slightly smaller home ranges than females ($\bar{x}$ male home range = 3.85 m² [41.4 ft²], $n=15$, $\bar{x}$ female home range = 4.82 m² [51.9 ft², $n=13$], modified MCP estimator; Kleeberger and Werner 1982). The authors further found that adult home ranges were larger than those of juveniles ($\bar{x}=2.87$ m² [30.9 ft²], $n=5$). Daily movement rates are also reportedly small and in a Michigan study averaged only 0.43 m/day (1.4 ft/day, $n=34$; Kleeberger and Werner 1982). In Virginia, recaptures between years indicated that adult dispersal movements were smaller, but not significantly (range = 0.85–0.88 m [2.8–2.9 ft], $n=85$), compared to juveniles (range = 1.14–1.22 m [3.7–4.0 ft], $n=83$; Ousterhout and Liebgold 2010).

Although they generally do not move great distances, Eastern Red-backed Salamanders are capable of larger mobility if required. Marsh et al. (2004) found that young adults moved up to 55 m (180 ft) to colonize experimental plots in open fields in Virginia. Migration during spring and autumn can also lead to larger bouts of movement. Woolbright and Martin (2014) observed adults moving uphill in autumn and downhill in the spring to wetland areas, most likely due to habitat availability for nesting; young salamanders remained near wetlands year-round.

Given Eastern Red-backed Salamanders do not typically move great distances, it is unsurprising that some authors have reported these salamanders exhibit high fidelity for specific locations. For example, Kleeberger and Werner (1982) indicated that individual bouts of movement were often restricted to beneath the same log or cover object. Furthermore, Gergits and Jaeger (1990b) marked individuals from Virginia and reported that 36% of recaptures occurred at nearly the original capture location, 35% of recaptures occurred within 50 cm (19.7 in), 20% occurred between 50 and 100 cm (19.7 and 39.4 in), and only 1% of recaptures occurred at greater distances ($n=90$ captures and 55 recaptures). Cabe

et al. (2007) found a mean intergenerational dispersal distance of 3.5 m (11.5 ft), with no difference detected between sexes, in Virginia. Liebgold et al. (2011) found that 44% of adult females in Virginia were recaptured within 1 m (3.3 ft) of natal locations, and 69% were recaptured within 2 m (6.6 ft). Homing ability is also documented in this species. Kleiber and Werner (1982) reported that 90% ($n=30$) of salamanders displaced 30 m (98 ft) from capture location returned and that 25% of individuals displaced up to 90 m (295 ft) also returned. Eastern Red-backed Salamanders exhibit complicated territorial behaviors related to reproduction and food acquisition, which influence their movement patterns (Natural History Box: Complex Behaviors).

PREY AND PREDATORS

Eastern Red-backed Salamanders eat a wide variety of small invertebrates that inhabit the forest leaf litter, such as insects and their larvae, earthworms, sow bugs, centipedes, springtails, mites, snails, slugs, and spiders (Jaeger et al. 1995, Lang and Jaeger 2000, Mitchell and Woolcott 1985). From October to November in New York, insects comprised 73.2% (total bulk) of all stomach contents assessed ($n=149$ stomachs assessed; Jameson 1944). Of the insects consumed, 20% were adult and larval beetles (order Coleoptera), 10.5% were true flies (order Diptera), and ca. 10% were hymenopterans, of which half were ants (Formicidae). Although comprising only 6.7% of total bulk consumed, earthworms were often the only food in the stomachs of some individuals, indicating their dietary importance to Eastern Red-backed Salamanders (Jameson 1944). In Indiana, ants were also a major part of their diet during December (18.2% by volume), although March Fly larvae (family Bibionidae) were the most abundant food items detected (38% by volume; Caldwell 1975). Gabor and Jaeger (1995) found that Eastern Red-backed Salamanders preferred termites to ants, likely because they were larger and had a softer and easier-to-digest exoskeleton. Furthermore, they are considered pulse feeders that also alter their preferred prey based on what is most readily available (Jaeger and Barnard 1981).

Eastern Red-backed Salamanders will forage throughout the day but most often hunt at night (Jaeger 1978). Yet they can modify foraging behavior with changing weather patterns. After rain, for example, prey are easier to obtain, and salamanders can forage for longer periods with little risk of desiccation, compared to drier periods, when they are restricted to moist patches of the forest floor and so encounter fewer prey items (Jaeger 1980a, Jaeger and Barnard 1981, Placyk and Graves 2001). Most active foraging occurs on the forest floor within the leaf litter and ground debris. They occasionally climb shrubs and tree trunks in search of prey (Jaeger 1978), although some authors suggest that this behavior is primarily adopted by satiated individuals that seek these higher locations to avoid predators that hunt on the ground (Roberts and Liebgold 2008). Chemoreception is the primary sensory modality used while hunting (David and Jaeger 1981), and Eastern Red-backed Salamanders reportedly tap their snout on substrates because it aids in detection of the chemical cues left by prey (reviewed by Jaeger 1984). Placyk and Graves (2001) found that salamanders lowered activity with increasing light intensity, suggesting they switched from active foraging with chemical cues to an ambush behavior via visual cues for prey detection with increasing light. Furthermore, Eastern Red-backed Salamanders are more likely to actively pursue food when prey densities are low, but they otherwise use ambush tactics (Jaeger and Barnard 1981).

Eastern Red-backed Salamanders are significant predators within forest floor communities and play a regulatory role within terrestrial detrital food webs (Davic and Welsh 2004, Walton 2013, Hickerson et al. 2017). During a six-year study in Ohio, Walton (2013) found the density of Eastern Red-backed Salamanders influenced forest floor invertebrate density and composition, especially for invertebrate taxa important to forest floor decomposition and nutrient cycling.

Eastern Red-backed Salamanders are important prey for many birds, small mammals (e.g., shrews), snakes (Brodie 1977, Brodie and Brodie 1980, Ducey and Brodie 1983), and larger salamanders such as the Spotted Salamander (*Ambystoma maculatum*;

NATURAL HISTORY BOX: Complex Behaviors

Eastern Red-backed Salamanders have a complex social system best documented by a series of natural behavioral studies conducted in Virginia (see Mathis 1991, Jaeger and Forester 1993, Gillette et al. 2000, Liebgold 2014). These studies determined that male-gravid female pairs of Eastern Red-backed Salamanders often cohabit and defend territories during both the noncourting and courting seasons. These pairings presumably occur because gravid females select males for reproduction based on male ‘quality,’ which is inferred through olfactory cues that indicate whether males have obtained high- or low-quality diets (Chouinard 2012), which in turn affects fecundity (Fraser 1980). Males, for their part, compete for and defend high-quality foraging areas that then attract females, who are allowed to share the male’s territory (Walls et al. 1989, Mathis 1991, Gabor 1995, Gabor and Jaeger 1995). Lang and Jaeger (2000) further found that males and females defend feeding areas under cover objects, and the paired residents were more aggressive to same-sex intruders. Kohn et al. (2005) determined that females spent more time in threat behavior with one male intruder but more time displaying escape behavior with more than one male.

Territory-holding adults not only engage in aggressive interactions with other adults but also act aggressively toward younger age classes. Presumably, this is because juveniles eventually represent a competitor to adults, as both age classes eat similar food. As such, juveniles and young adults are sometimes forced to modify their behavior or even vacate natal locations, moving long distances but still failing to breed in areas already near carrying capacity (Jaeger 1980a, Mathis 1991, Liebgold 2014). Juveniles are often found at the peripheries of adult home ranges (Liebgold and Jaeger 2007) but will sometimes co-occur with unrelated adults under rocks and logs (Jaeger et al. 1995, Liebgold and Cabe 2008). Jaeger et al. (1995) further found that juveniles were more likely to risk entering adult home ranges during dry conditions but typically left the area under wet conditions. Several studies also suggest that familiarity between young and mature Eastern Red-backed Salamanders can dictate the potential for aggressive interactions. Juveniles decreased nocturnal foraging activities when housed with unfamiliar adult females compared to familiar adults (Liebgold and Dibble 2011). Furthermore, juveniles forced to enter adult home ranges when conditions are dry experienced lower aggression from the resident adult if they had previously encountered each other (Jaeger et al. 1995). Accordingly, adults behaved more aggressively toward juveniles that they were unfamiliar with.

Territorial and aggressive behavior can take several forms in Eastern Red-backed Salamanders. For example, direct aggression usually involves threatening behavior and postures or physical attacks (Jaeger and Schwarz 1991). In a field setting, Gergits and Jaeger (1990a) documented the aggressive interactions between territorial residents and intruders. They determined that residents use ‘nose-tapping’ to investigate chemical cues left on substrates by intruders. Prior to employing aggressive postures or physical attacks, however, residents often threatened intruders by simply looking directly at them, which appeared to settle many territorial disputes. An encounter that escalates to a physical attack involved the resident biting the intruder’s snout, a behavior that continued until the intruder retreated. The bitten and retreating intruder then moved away using quick, jerky undulations of the body to ‘skip’ across the ground rather than crawling. The aggressor sometimes followed a short distance but eventually returned to the location of the initial interaction. Insight into territorial interactions can also be gleaned from the movement patterns and

spatial arrangement of salamanders on the forest floor. Although Mathis (1991) found no difference in home range size among adult males, adult females, and juveniles (which ranged from 0.16 to 0.34 m² [1.72 to 3.66 ft²], $n=25$, MCP estimator), she did determine that home ranges were spatially segregated within each sex. In other words, home ranges of adults of the same sex were farther apart than home ranges occupied by male and female pairs (based on nearest neighbor distances from center; Mathis 1991). A small number of different territories occupied by male-female pairs overlapped, but no same-sex territories overlapped. Liebgold et al. (2011) found that territorial females ($n=41$) were more closely related to females separated by 0–2 m (0–6.6 ft) than to females separated by 8–10 m (26.2–32.8 ft), while males were significantly more related to males separated by 6–8 m (19.7–26.2 ft).

Although male-female pairs often occur within a given area, a large proportion of resident males and females can also be nonterritorial ‘floaters’ that are found singly under cover objects (Mathis 1991). For example, Mathis (1990) found that only 4.6% of various-sized cover objects ($n=192$) contained cohabiting salamanders during summer and autumn months, with a maximum of three salamanders under a cover object. After transferring known pairs from the field into the laboratory, Gillette et al. (2000) further determined that two-thirds of the captured salamanders ($n=410$) were alone during the noncourtship period in summer. These individuals showed little interest in associating with their partners at this time, which suggests a socially monogamous system. Toll et al. (2000) reported that unoccupied cover objects and vacated cover objects were more quickly colonized by single females than males.

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Ducey et al. 1994, Grover and Wilbur 2002, Ransom and Jaeger 2006). If threatened, Eastern Red-backed Salamanders remain motionless when first detected (Brodie et al. 1974, Venesky and Anthony 2007), but once they have been touched by a perceived threat they will adopt a “swimming-running” motion to quickly escape into leaf litter and can apparently use their tail to jump (Harding 1997). If attacked, they release a sticky skin secretion that is distasteful to mammalian predators such as shrews (Brodie et al. 1979). Restrained Eastern Red-backed Salamanders writhe violently and may detach a portion of their tail (Jaeger et al. 1998). The dislocated tail continues to wiggle and distract the predator’s attention while the rest of the salamander escapes. Although the broken tail will regenerate, it does not grow as long or possess the same color pattern as the original. Eastern Red-backed Salamanders may also alter their behavior in response to predatory threats.

For example, Sullivan et al. (2002) found that they remained within refugia for up to two hours after exposure to Common Gartersnake (*Thamnophis sirtalis*) scent.

CONSERVATION

Status: Globally, the Eastern Red-backed Salamander is listed as a Least Concern species by the IUCN. It is considered a common species in Wisconsin by the WDNR.

Populations: Over 100 years ago, Cope (1889) stated that this was “the most abundant salamander in the northern and central eastern United States.” Despite this, it has appeared to experience substantial population losses across parts of its North American distribution. For example, long-term monitoring in the eastern US by Highton (2005) revealed that 79%

of 24 populations sampled prior to and after 1990 declined in abundance. Still, some studies suggest that Eastern Red-backed Salamanders can be one of the most abundant terrestrial vertebrates in eastern North American woodlands. Reported soil surface density (i.e., density of individuals not below ground) estimates for a Virginia population of this salamander ranged from 2.2 to 2.82/m² (0.20 to 0.26/ft²; Jaeger 1980b, Mathis 1991). Within the Hubbard Brooks Experimental Forest in New Hampshire, Eastern Red-backed Salamanders comprised 93.5% of total salamander biomass, with a soil surface density of 2,950/ha (1,200/ac), which was greater than the density of birds and mammals combined (Burton and Likens 1975). Bergeson (2001) estimated mean soil surface densities of 0.068/m² (0.006/ft²) and 680/ha (275.2/ac) at sites spread across Vilas and Forest Counties in northern Wisconsin and Gogebic County in Michigan's Upper Peninsula. Additional studies in Michigan calculated soil surface densities of 838/ha (339/ac; Werner 1975) and up to 0.89/m² (0.08/ft²; Heatwole 1962).

Several studies have investigated aspects of Eastern Red-backed Salamander populations beyond density. Leclair et al. (2008) reported an adult sex ratio of 1M:1.59F ($n=342$) and a juvenile sex ratio of 1M:2.28F ($n=154$) for a population in Quebec. Alternately, Test and Bingham (1948) found a sex ratio of 1M:0.36F ($n=284$) for a population in Michigan. Eastern Red-backed Salamander population growth is likely density-dependent (Bruce 2008), and the factors limiting population growth probably vary from population to population. Important limiting factors include density of suitable substrate and cover objects, food availability, and predation pressure.

Threats: Eastern Red-backed Salamanders are potentially susceptible to numerous conservation concerns that also threaten most Wisconsin amphibians, such as habitat loss, fragmentation, and degradation (see Introduction to Conservation and Management of Wisconsin's Amphibians and Reptiles chapter). Destruction of wooded landscapes has substantial impacts on many salamander species, including Eastern Red-backed Salamanders (e.g., Pough et al. 1987, MacNeil and Williams 2014). The loss of available downed woody debris in forests further affects this

species at various life stages. For example, adults seek refuge below damp fallen logs within woodlands, but these substrates are also important for egg deposition. Riedel et al. (2012) found fewer juveniles in disturbed habitats with less available ground cover than in undisturbed habitats (although adult abundances did not differ between disturbed and undisturbed locations) and suggested that lack of cover may specifically impact reproductive success or survival of juvenile age classes. Limited information on the specific effects of habitat loss in Wisconsin exists. Yet woodlands and forests have experienced dramatic declines in the state since the time of European settlement (see Past, Present, and Potential Future Landscapes of Wisconsin chapter), which have probably led to substantial undocumented population losses. Knudsen (1958b) even suggested that Eastern Red-backed Salamanders once occurred across much of Wisconsin but were extirpated from the intensively cultivated portions due to the concomitant degradation and loss of moist woodland habitats.

Eastern Red-backed Salamanders are not well adapted for long-distance movement (see Activity section), so it is doubtful that they will experience much success in crossing large disturbed areas while searching for suitable habitat in fragmented landscapes. Given this, habitat fragmentation that creates unnatural barriers to dispersal is of special concern, as it can limit gene flow and population viability. Key anthropogenic features that often result in habitat fragmentation are roads, which several studies have determined negatively impact Eastern Red-backed Salamanders. Marsh and Beckman (2004) found lower salamander abundance within 20 m (66 ft) of gravel roads that bisected mature forests in Virginia, and edge effects were detected out to 80 m (262 ft) from roads during a dry period. At large scales, Gibbs (1998c) used molecular genetic markers to detect greater genetic differentiation in fragmented populations than in contiguous forest populations from Connecticut ($n=319$ individuals and 17 populations). Despite this, the impacts that roads have on this species can apparently be influenced by road width. For example, individuals in populations that were fragmented by smaller two-lane paved roads were similar genetically (indicating a lack of isolation due to roads fragmenting the population),

but populations separated by a divided four-lane interstate highway existed in genetically distinct subgroups, supporting that these road systems presented a barrier to movement and gene flow (Marsh et al. 2008). Furthermore, whether or not roads are paved also apparently results in different impacts to this salamander. Marsh et al. (2005) found that wide unpaved logging roads and narrow paved roads presented partial barriers to migrating salamanders, leading to a 25%–75% reduction in movement.

Habitat can also be degraded by the presence of invasive species. For example, northern hardwood forests in Wisconsin are susceptible to invasion by exotic earthworms (Gundale et al. 2005). These exotics could alter forest floor trophic interactions and negatively impact Eastern Red-backed Salamander populations, although the magnitude of this threat remains largely unknown. Maerz et al. (2009) reported that abundance of Eastern Red-backed Salamanders was negatively related to earthworm abundance because earthworms decrease forest leaf litter, which serves as habitat for the small arthropods that Eastern Red-backed Salamanders consume. Yet additional research found that this interaction is complicated (Cáceres-Charneco and Ransom 2010). For example, Ransom (2011) reportedly encountered Eastern Red-backed Salamanders in earthworm burrows on 50% of their observations and further suggested that the refuges created by earthworms benefited the salamanders because they facilitated predator avoidance and winter survival.

There are other important threats to Eastern Red-backed Salamanders worthy of consideration, including the potential impacts of climate change. Habitat suitability for and the activity patterns of this species are linked to acceptable temperature and moisture levels. Current projections suggest that Wisconsin will become warmer and drier as climate change progresses (Janowiak et al. 2014), which could reduce the suitability of local habitats for Eastern Red-backed Salamanders. Muñoz et al. (2016) further reported evidence that higher summer temperatures would alter salamander activity patterns and reduce growth rates, prolonging time to maturity and thus lowering fecundity and reproductive success. Emerging amphibian diseases can also pose serious threats to many species, and several infectious agents are

of concern, including the fungi *Batrachochytrium dendrobatidis* (Bd) and *B. salamandrivorans* (Bsal), as well as ranaviruses. Yet infections by these agents and their associated diseases are rarely reported from *Plethodon* salamanders such as the Eastern Red-backed Salamander (Muletz et al. 2014). Evidence currently supports that the normal bacterial communities present on the skin of Eastern Red-backed Salamanders could help protect them against a variety of pathogenic infections (e.g., Becker and Harris 2010, Loudon et al. 2014). Despite this, Standish et al. (2018) found a ranavirus on the single individual they sampled from Wisconsin (but they did not detect Bd or Bsal).

Management: Given their reportedly high densities and influential role in forest floor trophic interactions (see Prey and Predators section), Eastern Red-backed Salamanders could be an important species to monitor when assessing the integrity of ecosystems in managed properties (Welsh and Droege 2001). Many general management considerations relevant to woodland habitats could apply to Eastern Red-backed Salamanders, particularly maintenance of the ground debris that this species uses as cover (see Introduction to Conservation and Management of Wisconsin's Amphibians and Reptiles chapter). Habitat modification due to timber harvest, such as clear-cutting, alters tree canopy density and thus forest floor climate. Such habitat alterations are a major concern for *Plethodon* salamanders due to increased risk of desiccation and soil compaction (Ash and Bruce 1994, deMaynadier and Hunter 1995). Bergeson (2001) reported that significantly more Eastern Red-backed Salamanders were captured in old-growth forests vs. even-aged and uneven-aged managed forests in northern Wisconsin and adjacent forests in the Upper Peninsula of Michigan. Macneil and Williams (2014) found that clear-cut areas within oak-hickory and beech-maple forest systems negatively affected the relative abundance of associated Eastern Red-backed Salamanders on the local scale during years immediately following harvest, but shelterwood method treatments that left forest canopies intact had no effect on abundance. Leaving some forest tree canopy cover intact and maintaining the structural complexity on the forest

floor (including the presence of downed woody debris) can help minimize impacts following forest harvesting (McKenny et al. 2006). Yet the duration of negative impacts due to timber harvest could be relatively short-lived if the impact area is small and woodlands are allowed to regenerate after disturbance. For example, Brooks and Kyker-Snowman (2008) found that forest clearing had little lasting impact on the forest floor microclimate conditions between cut and uncut northern hardwood forests undergoing regeneration in Massachusetts.

It is noteworthy that recent studies suggest that recreational hiking trails within Eastern Red-backed Salamander habitat can negatively influence abun-

dance of this species. For example, Burger et al. (2017) reported that Eastern Red-backed Salamanders in a recreational nature reserve in Ohio were more abundant near low-traffic trails than high-traffic trails or wooded control sites. Interestingly, Fleming et al. (2011) found more Eastern Red-backed Salamanders near trails than in wooded areas away from trails. It is possible that a higher salamander density near trails occurs because trees that fall across trails must be removed, and the woody debris generated from this removal is often deposited near trail margins (Davis 2007, Burger et al. 2017). Habitat managers should consider these possible outcomes during design and maintenance of trail systems on public land.