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Seasonal Migration by a Terrestrial Salamander, *Plethodon websteri* (Webster's Salamander)

Thomas M. Mann[1,3] and Debora L. Mann[2,3,4]

[1]Mississippi Natural Heritage Program, Mississippi Department of Wildlife, Fisheries and Parks, Mississippi Museum of Natural Science, 2148 Riverside Drive, Jackson, Mississippi 39202, USA
[2]Millsaps College, 1701 North State Street, Jackson, Mississippi 39210, USA
[3]Authors contributed equally
[4]Corresponding author, e-mail: manndl@millsaps.edu

***Abstract*.—We report seasonal, horizontal migration by a winter-active, terrestrial salamander, *Plethodon websteri*, away from a limestone outcrop upon their emergence in the fall and toward the outcrop in spring. We made 3,597 captures (including recaptures) using a series of three drift fences erected at 9 m, 65 m, and 84 m from the outcrop. Peak months for travel were November, when 98% of captures were on the sides of the fences facing the outcrop, and March, when 96% of captures were on the sides facing away from the outcrop, as expected if salamanders were moving away from the outcrop in fall and returning in spring. Recapture of salamanders that we marked with visual implant elastomer confirmed that animals move from the outcrop in fall and initiated movement toward the outcrop in spring from as much as 150 m. To our knowledge this is the third report of horizontal migration in a *Plethodon* species and the first to be confirmed by mark-recapture. We suggest that crevices in rocks provide refugia and oviposition sites deep enough to afford protection from heat and desiccation in summer for *P. websteri*, which is among the southernmost members of its genus. The requirement for rock outcrops for summer survival and nesting is relevant to management for *P. websteri*, which is ranked as imperiled or critically imperiled in four of five states in the USA in which it occurs. Effective conservation requires protection of forest habitat where salamanders forage, summer refugia, and migration routes between them.**

Key Words.—drift fence; mark-recapture; photo identification; rock outcrop; VIE; visual implant elastomer

Introduction

Terrestrial salamanders play important ecological roles in forest ecosystems, where they may constitute a large, if easily overlooked, component of the vertebrate fauna (Davic and Welsh 2004). As major predators of invertebrates of the forest floor (Burton and Likens 1975a, b; Hairston 1987), salamanders affect the rate of litter decomposition and nutrient cycling (Burton and Likens 1975b; Wyman 1998) while providing a rich food source to larger vertebrate predators (Burton and Likens 1975a; Davic and Welsh 2004). Despite their ecological significance, detailed information on the natural history and habitat requirements necessary to inform management decisions is lacking for many terrestrial salamanders (Wyman 2003; Halliday 2005).

Plethodon websteri (Webster's Salamander) is a small, terrestrial salamander that occurs in scattered locations across five southern states in the USA, where it is ranked as vulnerable in Alabama, imperiled in South Carolina, Georgia, and Mississippi, and critically imperiled in Louisiana (NatureServe. 2015. Available from http://explorer.natureserve.org [Accessed 1 August 2016]). As with many members of its genus, much remains unknown about the ecology and behavior of *P. websteri* (Petranka 1998; Lannoo 2005). *Plethodon websteri* forages in the litter layer of forested habitats between late October and May, disappearing beneath the surface during the warmer months. Oviposition has not been observed, but data on the reproductive condition of dissected specimens indicate that it occurs during the period when they are below the surface (Semlitsch and West 1983). The species is associated with rocky substrates (Petranka 1998: 409; Wyman 2003; Camp 2008), although the reasons for this association have not been addressed.

Members of the genus *Plethodon* lack an aquatic stage and do not migrate to ponds to breed (Dunn 1926). However, seasonal, horizontal migration has been reported for two members of the genus, the Ozark Zigzag Salamander, *P. angusticlavius* (Meshaka and Trauth 1995) and the Red-backed Salamander, *P. cinereus* (Woolbright and Martin 2014). We observed mass movements of *P. websteri* toward and away from a rock outcrop that suggested the possibility of horizontal migration in a third species of *Plethodon*. Further, these observations suggested a reason for the association of this species with rock outcrops: the use by salamanders of crevices in rocks to reach subterranean refugia and oviposition sites deep enough to afford protection from heat and desiccation in summer. Here we describe our investigation of these mass movements and the implications of our findings for the conservation of this species.

Between 13 and 15 March 2009 we noticed adult *P. websteri* of both sexes crossing an 80 m stretch of the Natchez Trace Parkway in Hinds County, Mississippi, USA. In slightly less than an hour on 15 March 2009 we observed 17 live *P. websteri*, most of which appeared to be traveling in the same direction, as well as six dead in the road. Similar movements occurred between 21 February and 9 March 2010 at the same location and with the same apparent directionality.

Initially we assumed that *P. websteri* in the road were probably foraging. However, another explanation for their movements presented itself in December 2010 when we discovered concentrations of first-year *P. websteri* under fallen limbs at several small limestone outcrops along a 1 km stretch of the Parkway. The closest of these outcrops was located about 70 m from the section of the road where adult *P. websteri* had been observed. Surveys for *P. websteri* under natural cover in the forest surrounding the outcrops revealed that adults and second-year juveniles could be found 100 m or more from the nearest rocks; whereas, young of the year were found only near the rock outcrops, often several together, suggesting that they were near the site where they had emerged. This raised the possibility that the outcrops serve as nest sites and that the adults we had observed crossing the road in the spring were on the return-trip to the outcrop where they would retreat for the summer. If so, then adult salamanders could be expected to cross the road in the opposite direction, outbound from the outcrop, upon their emergence in the fall.

We returned to this section of the road in both March and November of 2011 and observed adult *P. websteri* crossing the road. As predicted, individuals were oriented mainly toward the outcrop in spring and away from the outcrop in fall. However, vehicular traffic on the Parkway not only kills many animals but also complicates assessment of the direction of travel of survivors. Because a salamander may exhibit escape behavior in response to a near miss by a vehicle, it is not always possible to determine the direction it was heading when it first entered the road. Therefore, we erected a series of drift fences to intercept the salamanders to clarify the timing and direction of their movements in relation to the rock outcrop. Our hypothesis was that salamanders migrate away from the rock outcrop upon their emergence in the fall and return to it in late winter and spring. One prediction stemming from this hypothesis was that salamanders would be intercepted primarily at the sides of the fences facing the outcrop in the fall, and at the sides of the fences facing away from the outcrop in late winter and spring. A second prediction was that salamanders marked at the outcrop in the fall would be intercepted at the fences bordering the road, and that salamanders marked in late winter or spring on the opposite side of the road from the outcrop would be intercepted at the fence nearest the outcrop.

Materials and Methods

Study site.—The study took place along the Natchez Trace Parkway (a unit of the U.S. National Park Service), approximately 0.1 km north of milepost 86 and 0.2 km south of the Lindsey Creek Bridge in Hinds County, Mississippi, where we had previously observed adult *P. websteri* crossing the road. An exposure of Glendon limestone (Howe 1942) where we had found hatchling *P. websteri* is located about 70 m west of the road. Although largely obscured by leaf litter, the limestone is visible as scattered, small boulders embedded in the soil, and between which rock is at or near the surface. The area within which scattered rocks are present at the soil surface, herein referred to as the outcrop, is approximately 140 m^2 (Fig. 1).

The forest surrounding the outcrop is a patchwork of cover types reflecting different histories of disturbance. Water Oak (*Quercus nigra*), Loblolly Pine (*Pinus taeda*), Eastern Redcedar (*Juniperus virginiana*), and Chinese Privet (*Ligustrum sinense*) dominate an area to the northeast of the outcrop where faint remnants of furrows indicate past farming. Elsewhere, including the outcrop itself, the canopy includes White Oak (*Q. alba*), Shumard Oak (*Q. shumardii*), Southern Red Oak (*Q. falcata*), Cherrybark Oak (*Q. pagoda*), Chinquapin Oak (*Q. muehlenbergii*), Post Oak (*Q. stellata*), and Shortleaf Pine (*P. echinata*). To the south and east of the outcrop there are borrow-pits on both sides of the road, possibly created during the construction of the Parkway. The borrow-pits have since recovered a closed canopy and sufficient leaf litter to provide cover for salamanders. The forested area surrounding the outcrop is bordered to the northwest by Lindsey Creek and to the southwest by a treeless power-line corridor that supports a 1–2 m cover of grasses, forbs, and scattered shrubs (Fig. 1).

Drift fences.—In early October 2012, we installed three drift fences (DF1, DF2, and DF3) at approximately 9 m, 65 m, and 84 m from the eastern edge of the outcrop, respectively (Fig. 1). DF1 was 27.4 m long and formed a shallow arc partially surrounding the rock outcrop, between the outcrop and the Parkway (Fig. 2A). The other two fences were each 82.3 m long and

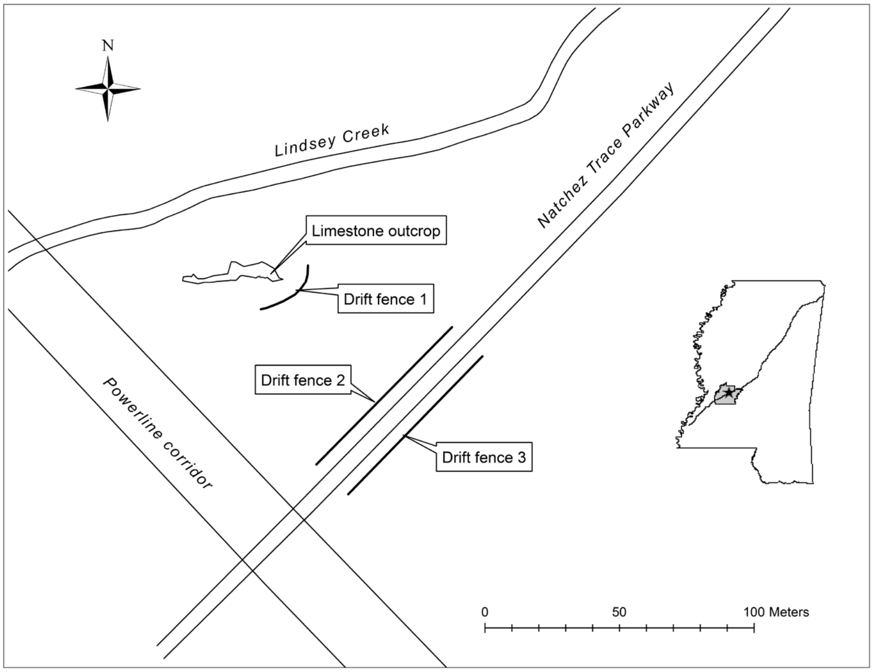

Figure 1. Map of the study site for *Plethodon websteri* (Webster's Salamanders) illustrating the position of three drift fences in relation to a limestone outcrop and the Natchez Trace Parkway. Inset shows the location of the site in Hinds County, Mississippi, USA, along the Parkway.

were installed at the forest edge bordering the mown strip on either side of the road where *P. websteri* had previously been observed (Fig. 2B).

The fences consisted of 61-cm tall, black, woven polypropylene silt-fencing (Forestry Suppliers, Inc., Jackson, Mississippi, USA) supported by wooden stakes at 2.74 m intervals (the fabric between posts hereafter referred to as panels). We extended the lower edge of the fabric flat along the ground and secured it with slender poles placed lengthwise along the base. We pinned the poles to the ground through the fabric with staples made of bent lengths of No. 9 galvanized wire, and covered the bottom edge with a shallow layer of leaf litter. After installation, the fences averaged 53 cm in height. They remained in place throughout the surface activity season and were removed in June 2013.

Because we found that most *P. websteri* climbed directly up the drift fences (Fig. 3), funnel traps installed at the bases proved ineffective for capturing this species and were removed after the first night that the salamanders appeared on the fences. Consequently, we monitored the fences at night when the salamanders were moving and captured them on or at the base of the fences. We were not able to monitor the fences at all times when salamanders were moving; however, we observed that salamanders that were not promptly captured leaped from the top of the fence or, occasionally, climbed down the opposite side. Thus, salamanders that encountered the fences when they were not monitored were able to continue on their chosen trajectory.

We released all captured salamanders immediately after recording and photographing them. We released those captured on DF1 on the opposite side of the fence about 1 m from the fence. We assumed the animals captured on the sides of DF2 or DF3 facing away from the road were heading toward the road. To reduce mortality from vehicular traffic, we carried them across the road and released them about 1 m from the far side of the fence on the opposite side.

When time permitted, we photographed the dorsum and venter of each salamander. For photographs of the venter, we used a 125 × 120 × 8 mm clear, plastic compact-disc case into which was taped an acetate photocopy of a ruler. We placed the salamander in the case aligned with the ruler, covered it with a folded, moist paper towel to secure the animal, closed the case, and inverted it. For photographing larger groups of salamanders on nights when there were too many to process individually, we used a clear, plastic picture frame in a similar manner but with a moistened, soft-foam backing cut to the dimensions of the frame to secure the salamanders before inverting. We estimated snout-vent lengths (SVL) from photographs of the venters and compared them with the SVL reported for *P. websteri* by Semlitsch and West (1983) as a guide to assign animals to one of three age classes: first-year juveniles, second-year juveniles, and adults. We could not assign all individuals to age classes by size alone because of overlap in SVL between age classes (Semlitsch and West 1983). For mature specimens, we

Figure 2. (A) Drift Fence 1 formed an arc partially surrounding and approximately 9 m away from the eastern edge of a limestone outcrop located about 70 m from the Natchez Trace Parkway in Hinds County, Mississippi, USA. The rocks are mostly covered by leaf litter; (B) Drift fences 2 (right) and 3 (left) bordered the Parkway where *Plethodon websteri* (Webster's Salamander) adults had been observed crossing the road and were located approximately 65 m and 84 m from the outcrop, respectively. (Photographed by Thomas M. Mann).

classified an animal as a male if the mental gland and/or yellowish cloacal glands were visible or as a female if ovarian follicles were visible through the translucent skin. Reproductive structures were discernable on most but not all individuals of adult size. The data recorded for each animal included the date, time, fence, fence-panel, side of the fence on which the animal was found, and, when they could be determined, the age class and sex. To analyze the directionality of movement of salamanders intercepted at a fence during a given month, we used chi-square goodness-of-fit with alpha set at 0.05 to test the null hypothesis that equal numbers were intercepted on opposite sides of the fence against the alternative hypothesis that unequal numbers were intercepted on opposite sides.

Each October from 2013 to 2016 we reinstalled DF2 in its previous location. We reinstalled DF3 in January 2014 and October 2014 to 2016. Additionally, in each October 2013 to 2015, we installed a shorter (5.49 m) version of DF1, which was lengthened to its original 27.4 m in March 2016 and remained in place for the fall of 2016. Otherwise, we removed fences at the end of each surface activity season in June. We monitored these fences as for the 2012–2013 surface activity season and, after marking salamanders (described below), checked captured animals for the presence of a mark.

Marking with visual implant elastomer.—To determine whether salamanders captured on the drift fences originated in the rock outcrop, we captured 40 *P. websteri* within the outcrop 9–21 November 2014, photographed and marked them on-site with fluorescent-orange visual implant elastomer (VIE; Northwest Marine Technology, Inc., Shaw Island, Washington). While marking, we restrained the salamander in a clear plastic bag fitted with a piece of moistened-foam backing and injected through the bag using a 29-gauge syringe. The VIE was injected shallowly under the relatively transparent skin of the ventral surface of the tail, along or near the midline posterior to the vent. We marked 18 adult males, 21 adult females, and one individual large enough to be an adult but of undetermined sex. Each animal was released at its exact point of capture.

To determine whether salamanders moved in the direction of the outcrop from the opposite side of the road in late winter and spring and to investigate the distances from which they initiated their hypothesized return trip, we searched for salamanders under fallen limbs in the forest east of DF3 between 24 January and 27 February 2016. We captured six adult females and five adult males located 25–68 m from DF3 (109–152 m from the outcrop), marked them with fluorescent-pink VIE, photographed each salamander, and released it at its exact point of capture. Although we recaptured several of these pink-marked animals on DF3, we did not capture any on DF1. On 13 March 2016, we extended DF1 to 30.2 m. On 24 March 2016, we captured one adult female and three second-year juveniles on the east side of DF3, marked them with pink VIE, photographed them, and released them 1 m west of DF2. For both orange- and pink-marked salamanders, we used a tape measure to measure distances from flagged release points to subsequent recapture points on the drift fences.

Results

Drift fence captures.—Between 3 November 2012 and 29 May 2013, we monitored the fences on all or part of 56 nights when salamanders were moving, which occurred when the leaf litter and upper soil layer were

Figure 3. *Plethodon websteri* (Webster's Salamander) at the top of Drift Fence 1 on 5 November 2012. The salamanders climbed drift fences readily. If not captured they leaped from the top or, occasionally, climbed down the opposite side. (Photographed by Thomas M. Mann).

moist and the air temperature was approximately 5–23° C; movement occurred on nights with and without rain. We recorded 3,597 captures of *P. websteri*, of which 3,064 were on DF1, 246 were on DF2, and 287 were on DF3. Because we released salamanders immediately after they were photographed, these data presumably include recaptures.

During the 2012–2013 season, the largest number of captures in a single night occurred on 5 November, when we captured 533 on DF1 and three on DF2 in 5 h under light rain with the air temperature at 11° C. The second largest number captured in a night occurred on 10–11 March when in slightly less than 11 h we captured 348, of which 219 were on DF1, 16 on DF2, and 113 on DF3, under conditions of moderate rain and air temperature declining from 14° C to 6° C.

For brevity, we refer to the sides of the drift fences facing the outcrop as the west sides, and the sides facing away from the outcrop as the east sides, although the precise aspect may differ from this shorthand. Accordingly, salamanders traveling away from the outcrop would encounter what we term the west sides of the fences and those traveling toward the outcrop would encounter the east sides. Here we report only the sides of the fences on which the salamanders were captured; these data may include a small number of animals that ascended the fences and began to climb down the opposite side before being captured.

The peak month for captures on DF1 was November when 99.1% of the salamanders were on the west side of the fence ($X^2 = 1156.40$, df = 1, $P < 0.001$, n = 1,200; Fig. 4A). A second but oppositely oriented peak occurred in late winter and spring when 96.0% of captures in March ($X^2 = 594.47$, df = 1, $P < 0.001$, n = 702) and 97.3% of captures in April ($X^2 = 473.48$, df = 1, $P < 0.001$, n = 528) on DF1 were on the east side of the fence (Fig. 4A). Total captures on DF1 included 926 adults, 452 second-year juveniles, 1,007 first-year juveniles, and 679 of undetermined age class or sex. Of the latter, 521 occurred during the first three nights of the study, when we were unprepared to photograph the large number of animals that ascended the fence; however, they were larger than hatchlings and were either adults or second-year juveniles.

Most of the captures on DF2 occurred in November or December with 95.0% in November ($X^2 = 64.80$, df = 1, $P < 0.001$, n = 80) and 89.3% in December ($X^2 = 74.59$, df = 1, $P < 0.001$, n = 121) captured on the west side of the fences (Fig. 4B). No first-year *P. websteri* were found on DF2. Of the captures on DF2 for the entire 2012–2013 season, we categorized 223 as adults, 14 as second-year juveniles, and nine were undetermined but of adult to second-year juvenile size.

On DF3, most of the captures occurred in February and March (Fig. 4C). In contrast to DF2, 92.3% captured in February ($X^2 = 46.53$, df = 1, $P < 0.001$, n = 65) and 98.5% captured in March ($X^2 = 192.18$, df = 1, $P < 0.001$, n = 204) were found on the east side of the fence. As with DF2, we found no first-year *P. websteri* on DF3. For the season as a whole, 271 *P. websteri*

Table 1. Recaptures on drift fences of *Plethodon websteri* (Webster's Salamander) marked with fluorescent visual implant elastomer (VIE) at the study site along the Natchez Trace Parkway in Hinds County, Mississippi, USA. Drift fences were located 9 m (DF1), 65 m (DF2), and 84 m (DF3) east of a limestone outcrop. DF1 partially surrounded the outcrop; DF2 and DF3 bordered the Parkway. The abbreviation DOPC is the distance from the original point of capture and DPR is the distance from point of release.

Age class/sex	Date released	Date recaptured	Fence	Side of fence	DOPC (m)	DPR (m)
A. Salamanders captured in the outcrop, marked with orange VIE, and released at their point of capture.						
Adult male	9 November 2014	28 March 2016	DF1	East	17	
Adult female	11 November 2014	31 October 2015	DF2	West	73	
Undetermined	16 November 2014	16 November 2014	DF1	West	12	
Adult male*	16 November 2014	23 December 2014	DF2	West	73	
		19 March 2015	DF3	East	91	
		9 March 2016	DF3	East	91	
Adult male	16 November 2014	22 March 2015	DF1	East	10	
Adult male	16 November 2014	3 December 2016	DF1	West	9	
Adult female	21 November 2014	29 November 2016	DF2	West	65	
B. Salamanders captured in the forest east of the Natchez Trace Parkway, marked with pink VIE, and released at their point of capture.						
Adult female	24 January 2016	9 March 2016	DF3	East	34	
Adult female	7 February 2016	2 March 2016	DF3	East	52	
Adult male	7 February 2016	4 March 2016	DF3	East	42	
Adult female†	7 February 2016	9 March 2016	DF3	East	68	
		28 November 2016	DF2	West	86	
Adult male	7 February 2016	11 March 2016	DF3	East	68	
Adult male	14 February 2016	10 March 2016	DF3	East	34	
Adult male	27 February 2016	12 March 2016	DF3	East	42	
Adult female	27 February 2016	9 March 2016	DF3	East	30	
C. Salamander captured on DF3, marked with pink VIE, and released 1 m west of DF2.						
Second-year juv.† ‡	24 March 2016	28 March 2016	DF1	East		53
		28 November 2016	DF2	West		55

*Recaptured three times, †Recaptured twice, ‡Adult male at second recapture

captured on DF3 were categorized as adults, 11 were second-year juveniles and five were undetermined but of adult to second-year juvenile size.

Young of the year emerged later than adults and second-year juveniles and over a longer period of time. Most of the adults and second-year juveniles that reached the west side of DF1 had arrived by late November, when large numbers of first-year juveniles were first beginning to arrive. First-years continued to arrive at the west side DF1 through early March. First-year juveniles also returned to the outcrop later in the spring. Most adults and second-year juveniles that reached the east side of DF1 arrived between February and early April, whereas most first-years arrived during April and May.

For the years following the 2012–2013 surface-activity season, we describe only those captures relevant to the mark-recapture study. However, we note that captures in subsequent years were similar to 2012–2013 with regard to seasonality and direction of travel. The total numbers of captures per year cannot be directly compared because DF1 differed in length between years. However, the number of captures on DF2 and DF3 increased each year, possibly because we saved many salamanders by transporting them across the road. For the most recently completed year, 2015–2016, we recorded 1,262 on DF2 and 1,261 on DF3.

Recapture of marked salamanders.—Of 40 salamanders marked at the outcrop with orange VIE in November 2014, we recaptured seven, one of which we recaptured three times over a period of more than a year (Table 1A). Although these were class marks (all the same color, all injected under the tail), we found that small differences in the placement of the mark as well as the pattern of iridophore patches on the venter, the dorsal coloration, and the sex made it possible to recognize individuals (Fig. 5). This enabled us to measure the distance from the point of release to the panel of the drift fence on which each individual was recaptured.

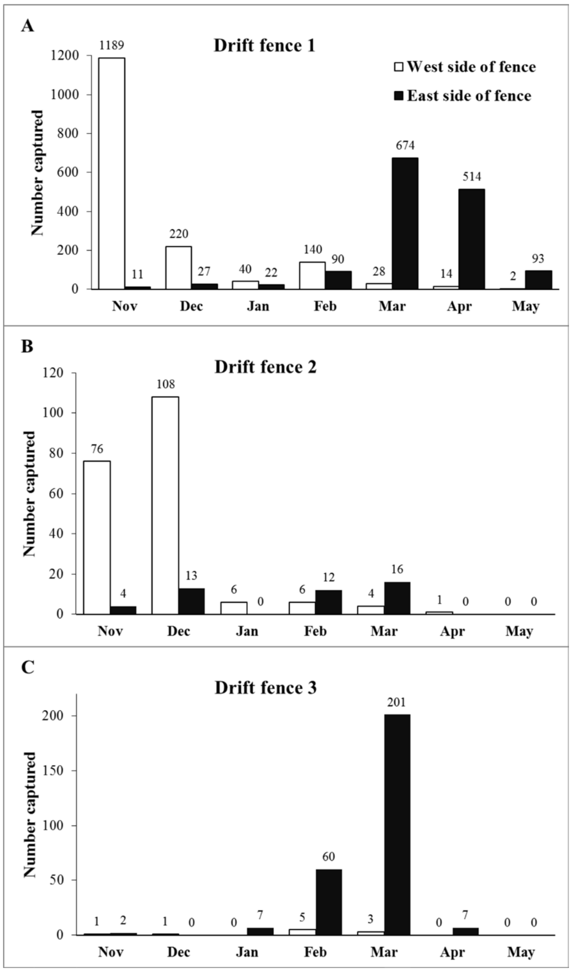

Figure 4. Monthly drift fence captures of *Plethodon websteri* (Webster's Salamander) at Natchez Trace Parkway in Hinds County, Mississippi, USA from November 2012 to May 2013. Captures on the west sides of the fences (facing the outcrop) are consistent with travel away from the limestone outcrop; captures on the east sides (facing away from the outcrop) are consistent with travel toward the outcrop: (A) Drift fence 1 was in the forest partially surrounding the outcrop. Salamanders captured on Drift Fence 1 were released on the opposite side 1 m from the fence; (B) Drift fence 2 (approximately 65 m from the outcrop) bordered the Natchez Trace Parkway. To reduce mortality from traffic, salamanders captured on the west side of Drift fence 2 were transported across the road and released 1 m east of Drift fence 3; (C) Drift fence 3 (approximately 84 m from the outcrop) bordered the Parkway on the far side of the road from the outcrop. Salamanders captured on the east side of Drift fence 3 were transported across the road and released 1 m west of Drift fence 2.

Recaptures in October, November, and December were on the west sides of the fences; recaptures in March were on the east sides (Table 1A). Of 11 salamanders from the forest east of the road marked with pink VIE in 2016, we recaptured eight on the east side of DF3 at distances of 30–68 m from their release points in the forest (Table 1B), which were approximately 114–152 m from the outcrop. Of four individuals captured on the east side of DF3, marked with pink VIE and released 1 m west of DF2, we recaptured a single second-year juvenile on DF1, 53 m from its release (Table 1C).

Discussion

Evidence for horizontal migration.—The timing and directionality of the movements of *P. websteri* captured on the drift fences are consistent with the hypothesis of seasonal, horizontal migration. The overwhelming majority were captured on the west sides of the fences in November and December, as expected if salamanders were traveling away from the outcrop. To a similarly striking degree, we captured salamanders on the east sides of the fences from February through May, as expected if animals were traveling toward the outcrop.

The asymmetry in captures on the east and west sides of the fences bordering the road is explained by the feature of our protocol that was designed to reduce mortality by vehicular traffic. During the times when we monitored the fences, few eastbound salamanders reached DF3 because we intercepted them on the west side of DF2 and carried them across the road; likewise, most westbound animals were intercepted at DF3 before reaching DF2. The recapture of VIE-marked salamanders confirmed that adult *P. websteri* travel substantial distances, and that they do so as expected of seasonal migration from and toward the outcrop. To our knowledge, this is the first confirmation by mark-recapture of horizontal migration in the genus *Plethodon*.

Although the presence of a mark was sufficient to confirm the seasonality and direction of travel by these salamanders, identification of individuals based on differences in natural pigmentation (particularly ventral iridophore patches), sex, and minor differences in the placement of the VIE enabled us to determine more precisely the distance traveled by recaptured salamanders and permitted recognition of multiple recaptures of the same individual. Two long-term recaptures indicated that natural pigmentation patterns in adults were stable for two years. This suggests that natural pigmentation could be used as a non-invasive means to identify individual adult *P. websteri* from photographs, as described by Trauth et al. (2006) for the Western Slimy Salamander, *P. albagula* and Bendik et al. (2013) for the Jollyville Plateau Salamander, *Eurycea tonkawae*.

The recapture on DF3 in March 2016 of eight salamanders marked in the forest on the opposite side of the road from the outcrop suggests that at least some individuals initiate travel in the direction of the outcrop from as much as 150 m from the outcrop. We did not recapture any of these animals on DF1. This may be explained partly by the fact that the short version of

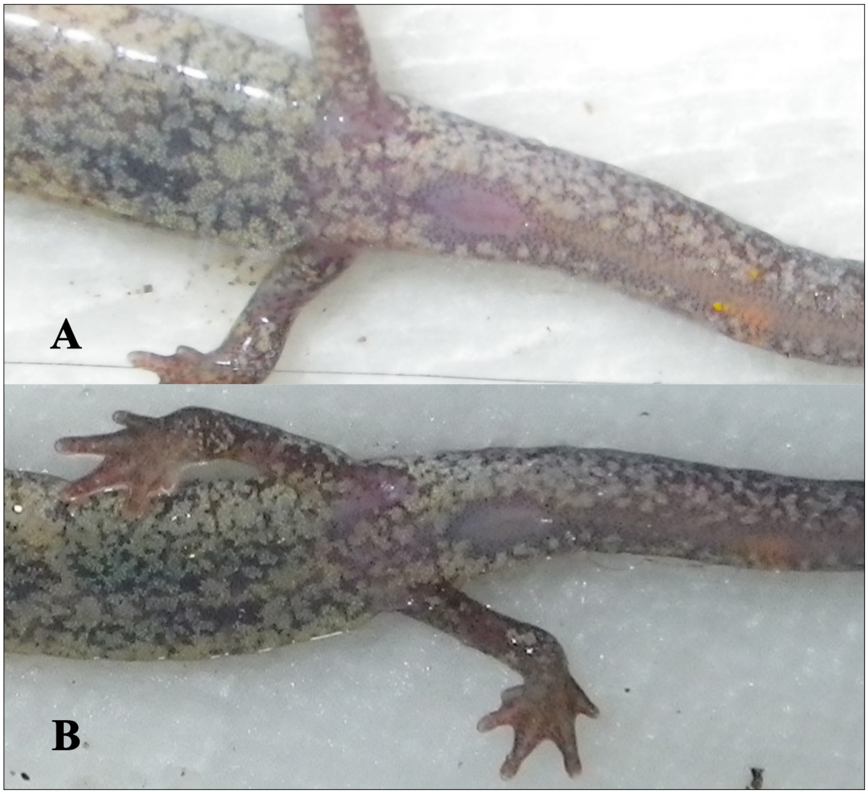

Figure 5. Ventral photographs of a female *Plethodon websteri* (Webster's Salamander). (A) on 16 November 2014 in the limestone outcrop where she was marked with fluorescent-orange visual implant elastomer; (B) on 31 October 2015 upon her recapture on Drift fence 2, 73 m from her release point in the outcrop. After nearly a year the VIE was discernible but less bright. Note the pattern of iridophore patches, which facilitated individual recognition of salamanders with class marks. (Photographed by Thomas M. Mann).

DF1 was only 5.49 m long, which presumably enabled many salamanders to by-pass the fence on their route to the outcrop. Additionally, because of the time it took to monitor DF2 and DF3 with much larger numbers of salamanders than in previous years, and because we underestimated the speed at which *P. websteri* travel under favorable conditions, we did not allot sufficient time to monitor DF1 when these pink-marked salamanders were most likely to arrive. From the recapture in mid-March of four unmarked but individually-recognizable salamanders, we learned that they can travel the distance from DF2 to DF1 (56 m) in about 12 h of darkness when the leaf litter is wet. By that time of year we were no longer able to find salamanders in the forest east of the road for another marking attempt. However, we were able to capture and mark four animals from the east side of DF3, one of which was subsequently recaptured on DF1, thus providing additional evidence of travel from the road toward the outcrop in spring.

Not all of the adults that migrate to and from the outcrop cross the road, as indicated by the larger number of adults captured on DF1 than on DF2 and DF3. Young of the year also migrated but not as far as adults and some second-year juveniles, as shown by the observation of large numbers of first-year juveniles on DF1 but none on DF2 or DF3. This is also consistent with our previous observations of animals found under natural cover in which we found adults and second-year juveniles within a much greater radius of rock outcrops than first-year juveniles.

Our data do not provide a comprehensive picture of the seasonal movements of *P. websteri*. We were unable to monitor the fences at all times when the salamanders were moving, and because they climb the fences readily, an unknown but potentially large number of salamanders crossed the fences undetected. The fences did not completely encircle the outcrop, and although we assume that neither the deforested powerline corridor nor the floodplain of Lindsey Creek provide favorable habitat for this species, there is forested habitat on both sides of the road (and on both sides of the powerline corridor) that could have been reached by salamanders without their having been intercepted by a fence.

Why migrate?—The selective advantage(s) for the horizontal migration of *P. websteri* is (are) not known. One possibility is that by migrating, salamanders avoid the depletion of food resources that might occur if all individuals remained near the site of their emergence from underground. The large number of animals we observed making the return trip to the outcrop in the spring indicates that the mass movement we have documented is primarily two-way migration (*sensu* Semlitsch 2007) rather than one-way dispersal. However, the tendency to travel substantial distances during migration may occasionally offer opportunities to mate with individuals that emerged from different outcrops, or may result in dispersal to different outcrops, facilitating the colonization of unused habitats or recolonization after disturbance. We suggest that migratory behavior may contribute, at least in part, to gene flow reported by Feist et al. (2017) between animals sampled at our study site and those from six other limestone outcrops at distances of 290–580 m.

Observations of *P. websteri* movements elsewhere are suggestive, although not clearly indicative, of horizontal migration. Near Chewacla State Park in Lee County, Alabama, USA, Craig Guyer (pers. comm.) observed numbers of *P. websteri* on a road cut through rock on one side and a flat forested area on the other side. At Legion State Park in Winston County, Mississippi, USA, Luke McDonald, Nicole Hodges, and Jeanne Jones (pers. comm.) erected drift fences on four sides of a laminated shale outcrop where one of us (TMM) had previously found concentrations of hatchling *P. websteri*. Monitoring the fences on several nights in March and April 2015, they observed more than 100 *P. websteri* on the fences, mostly on the sides of the fences indicating movement toward the outcrop.

We do not know whether the horizontal migration we have documented is characteristic of *P. websteri* throughout its range. In Mississippi, rock exposures are highly localized; therefore, access to summer refugia by way of rock crevices may be a limiting resource. In parts of the range where rock exposures are more abundant, access to summer shelters may be so readily available that seasonal migration is primarily vertical with only a minimal horizontal component. The migratory behavior of *P. websteri* in different parts of the range characterized by differences in the availability of rock outcrops warrants further study. The extent of seasonal movements by *P. websteri* may also depend on population density. Salamanders may need to migrate farther from their point of emergence to find sufficient prey when large numbers use the same refugium.

Significance of rock outcrops.—We have suggested that rock outcrops allow *P. websteri* to reach crevices deep underground where the temperature and moisture permit survival and nesting during the hot months of the year. Many members of the genus *Plethodon* are associated with rocky substrates (Petranka 1998 and references therein), and the role of rock crevices in facilitating vertical migration to habitable microclimates has been proposed for various *Plethodon* species. For example, Petranka (1979) noted the association of the Northern Zigzag Salamander, *P. dorsalis*, and the Southern Ravine Salamander, *P. richmondi*, with rock outcrops, talus areas, and caves, which he related to their poor burrowing ability. Neither *P. dorsalis* nor *P. richmondi* that he maintained in terraria were able to burrow through lightly compacted potting soil. He suggested that localized, rocky habitats provide passageways to underground retreats deep enough to afford protection from weather extremes in winter and summer and thus may harbor populations at higher densities than areas lacking such passageways. Although rocks may also serve as cover for salamanders during the season when they are active on the surface, this does not appear to be of importance at our study site, where most rocks are deeply and firmly embedded in the soil. Loose rocks are few, and we find salamanders almost entirely under fallen limbs and leaves at this site rather than under rocks.

We note that rock outcrops that harbor *P. websteri* are not necessarily obvious. At some sites where we have found *P. websteri*, rocks project conspicuously above the surface, but at others the surface rock is hidden under leaf litter and noticeable only upon close inspection. There are no obvious crevices at the surface of the outcrop at our study site, and we do not know precisely where salamanders enter and exit summer shelters. However, surveys for salamanders under natural cover early and late in the surface activity season suggest that they do not emerge and retreat throughout the entire area of the outcrop but rather at localized areas within it. Whereas the outcrop at our study site is limestone, *P. websteri* populations elsewhere in Mississippi are found in association with other types of rock (Appendix 1). Therefore, the physical structure provided by the rocks is relevant to the habitat requirements of this species rather than a secondary effect on soil pH or other chemical characteristics specific to limestone.

In geographic distribution, *P. websteri* is one of the southernmost members of its genus (Petranka 1998; Duellman 1999). Consequently, the ability to escape heat during the summer may be of particular importance to this species. It is smaller than members of the *P. glutinosus* complex that overlap its range: the total length of adult *P. websteri* is 69–82 mm (Petranka 1998:407) as compared with 115–205 mm for *P. glutinosus* (Petranka 1998:354). The small size and delicate build of *P. websteri* may not only make them more susceptible to desiccation but also less capable of digging though soil to reach cooler and more moist layers during the summer than their larger congener. We have no data on the burrowing ability of *P. websteri*, but they are similar in size to other small members of genus that in captivity have demonstrated little ability to burrow. These include *P. cinereus* (Heatwole1960) as well as *P.*

dorsalis and *P. richmondi* (Petranka 1979). Although apparently not an adept burrower, *P. cinereus* is reported to use burrows created by other small vertebrate and invertebrate animals (Test and Heatwole 1962; Caldwell and Jones 1973; Ransom 2012). We speculate that at our study site, and perhaps throughout much or all of the range of *P. websteri*, small animal burrows are not deep enough to provide reliable protection from summer heat.

***Migration in the genus* Plethodon**.—Literature on migration of amphibians often focuses on movements between terrestrial habitats and aquatic breeding sites (e.g., Semlitsch 2007), but viewed more broadly, animal migrations involve the exploitation of a variety of resource types that vary in time and space (Dingle and Drake 2007). Because *Plethodon* species forage, mate, shelter, and nest terrestrially, individuals can often meet their resource needs within a comparatively small area without extensive horizontal migrations, and small home ranges have been reported for several *Plethodon* species (Taub 1961; Stebbins and Cohen 1995 and references therein). Therefore, *Plethodon* salamanders are not generally thought to undertake extensive, horizontal migrations like those of aquatic-breeding salamanders (Lannoo 2005). Local horizontal movements by members of the genus to microhabitats with favorable conditions of moisture and temperature have long been known (e.g., Dumas 1956; Heatwole 1962); however, migrations reported more recently for *Plethodon* salamanders are comparable in distance to breeding migrations of aquatic-breeding salamanders (see Semlitsch 1998, for migration distances of pond-breeders). Meshaka and Trauth (1995) reported evidence of migration by adult *P. angusticlavius* between the base of rocky bluffs and sandstone cedar-glades 100–150 m away. Woolbright and Martin (2014) reported migration of adult *P. cinereus* between cover-board arrays installed in a low-lying, wet area and a rocky hilltop at a distance of approximately 65 m (Lawrence Woolbright, pers. comm.).

As with *P. websteri*, the reason for these migrations is not completely understood. Meshaka and Trauth (1995) suggested that sandstone cedar-glades may provide *P. angusticlavius* adults with favorable temperatures and/or a reduced risk of predation during courtship. In the case of migrating *P. cinereus*, Woolbright and Martin (2014) suggested that boulders at their uphill site might enable salamanders to reach warmer shelters underground where they are better able to remain active during the winter, yolking eggs and mating.

Our data add to the growing evidence that at least some populations of *Plethodon* species undertake extensive horizontal migrations. Considering the secretive nature of these small animals, and that neither the reasons for their travel nor their destinations are entirely obvious, migratory behavior in *Plethodon* salamanders can easily go unnoticed. Woolbright and Martin (2014) raised the possibility that some (but not all) other populations of *P. cinereus* may be found to migrate, citing examples of observations made elsewhere in the range that are consistent with, although not necessarily indicative of, migration. To this we add the possibility that examples of seasonal, horizontal migration may be discovered in other populations of *P. websteri* and perhaps in other species of the genus.

Conservation implications.—The recognition that some populations of *Plethodon* species migrate has implications for the conservation of these salamanders because it indicates that resources they require as well as the connecting corridor(s) must be protected on both wings of their annual journey. It also presents the challenge to better understand the nature of those resources and the ways in which local differences in resource availability affect the extent to which populations migrate, if at all. Reports of widespread declines of North American amphibians (Grant et al. 2016) and eastern *Plethodon* populations specifically (Highton 2005) indicate the need for effective conservation measures for *Plethodon* salamanders. Because much remains unknown about the behavior and habitat requirements of many of these salamanders, recommendations for the management of poorly known species or populations are sometimes based on what is known about their better studied relatives. For *P. websteri*, this has led to an emphasis on the protection of closed-canopy forests, as well as an assertion that these salamanders have small home ranges and can exist in smaller areas of habitat than many other amphibians (Beamer and Lannoo 2005). While we agree that the protection of forest habitat is necessary for the conservation of this species, our data highlight the importance of rock outcrops in providing summer shelter and nest sites for *P. websteri*, and indicate that many individuals travel farther than previously suspected between underground retreats and the locations where they forage at the surface.

To the currently recognized threats to *P. websteri* posed by deforestation and conversion of deciduous forest to intensively harvested pine monocultures (Petranka 1998), our study suggests additional threats that have not previously been addressed. These include destruction of subterranean nest sites by mining, mortality on heavily trafficked roads that cross migration routes, and destruction of leaf litter during the surface activity season by prescribed burns at rock outcrops and the surrounding areas occupied or traversed by *P. websteri*. Our observation that first-year juveniles do not migrate as far as older animals suggests that the presence of the youngest age class may be useful in identifying critical areas that require protection to maintain access to summer shelters and nest sites for this species.

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Thomas M. Mann (on right) is the Zoologist for the Mississippi Natural Heritage Program at the Mississippi Museum of Natural Science, Mississippi Department of Wildlife, Fisheries, and Parks. Tom received his B.S. degree at the University of Miami and M.S. degree at Florida Atlantic University, where he studied the impact of developed shoreline in Southeast Florida on nesting and hatchling sea turtles. As Natural Heritage Program Zoologist, Tom has been involved in surveys of many of the state's fauna, including the Gopher Tortoise, Diamond-backed Terrapin, Gulf Saltmarsh Snake, Alabama Red-bellied Cooter, Florida Harvester Ant and, of course, Webster's Salamander. **Debora L. Mann** (on left) is an Assistant Professor of Biology and Director of Environmental Studies at Millsaps College, where she teaches introductory biology, ecology, field biology, and environmental studies. She received her B.S. degree at the University of Miami, M.S. at Vanderbilt University and her Ph.D. at Clemson University. (Photographed by Victor Mendia).

Appendix 1. Mississippi Museum of Natural Science specimens of Webster's Salamander, *Plethodon websteri*, from Mississippi by county with associated geology. Rock types are listed only for localities where we have found first-year juveniles, which serve as an indicator of proximity to nest sites.

Catalog number*	County*	Date collected*	Collectors*	Geology**
3166	Claiborne	2/14/1993	T.M. Mann	Catahoula sandstone
3170, 3171	Claiborne	2/7/1987	D.D. Dickerson	Catahoula sandstone
16306, 16307	Claiborne	2/26/1993	T.M. Mann	Catahoula sandstone
16731	Claiborne	3/23/2010	T.M. Mann	Catahoula sandstone
3159	Copiah	3/14/1992	T.M. Mann	Catahoula sandstone
3161–3163	Hinds	2/1/1992	T.M. Mann	Catahoula sandstone
3167–3169	Hinds	2/19/1984	R.L. Jones, T.L. Vandeventer	Catahoula sandstone
16070, 16071	Hinds	2/16/2009	T.M. Mann	Glendon limestone
17199	Jefferson	4/2/2010	T.M. Mann, D.L. Mann	opaline silica cemented siltstones/claystone
16072	Madison	3/11/2009	T.M. Mann	Glendon limestone
16733	Wilkinson	3/12/2010	T.M. Mann	opaline silica cemented siltstone
16734	Winston	3/16/2010	T.M. Mann	laminated shales
16732	Yazoo	3/16/2010	D.L. Mann, S.B. Surrette, M.A. Stegall	Glendon limestone

*Collections data courtesy of the Mississippi Museum of Natural Science. Locality data may be requested from the Curator, Mississippi Museum of Natural Science, 2148 Riverside Drive, Jackson, Mississippi 39202.
** Geological identifications courtesy of James Starnes, Surface Geology Division, Office of Geology, Mississippi Department of Environmental Quality