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## WITHIN-SPRING MOVEMENT OF THE GEORGETOWN SALAMANDER (*EURYCEA NAUFRAGIA*)

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**Abstract.**—Movement is a critical ecological and evolutionary factor for many species, and understanding patterns of movement is important in conservation planning and management. Faced with increasing urbanization, aquifer depletion, and pollution, spring- and cave-dwelling salamanders of the genus *Eurycea* on the Edwards Plateau of Texas are of conservation concern, yet relatively little is known about their patterns of movements within and between habitats. We studied movement of the Georgetown Salamander (*Eurycea naufragia*) within two spring sites in central Texas over 32 mo. Using capture-recapture methods, we tracked the movement of individual salamanders and found limited movement at both sites: only 23% of recaptured salamanders at Swinbank Spring and only 17% of recaptured salamanders at Twin Springs moved beyond their 5 m section of original capture. A higher proportion of gravid salamanders than nongravid salamanders moved, and gravid salamanders exhibited a higher rate of movement. Salamanders that moved had larger body size, and there was a positive correlation between rate of movement and body size. Body condition, as measured by initial relative tail width, was not significantly different between salamanders that moved and those that did not move, and was not correlated with rate of movement. We found no differences in body condition or body size between salamanders that moved upstream and those that moved downstream. These findings are consistent with other studies of headwater and spring salamanders that found limited dispersal. Our findings suggest that *Eurycea naufragia* exhibits limited movement within surface springs.

**Key Words.**—body condition; Edwards Plateau; gravid; karst; salamander movement

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### INTRODUCTION

Movement of individuals is an important ecological and evolutionary factor that affects growth, survival, reproduction, gene flow, population persistence, metapopulation dynamics, competition, speciation, and species ranges (Dieckmann et al. 1999; Clobert et al. 2001; Nathan et al. 2008). In addition, understanding patterns of movement is critical for conservation management of many organisms because movement determines effective population size, genetic connectivity, subpopulation diversification, and potential recolonization, all of which affect the risk of extinction (Mills and Allendorf 1996; Hanski and Gilpin 1997; Trakhtenbrot et al. 2005). Data on movement can be used to guide the scale and type of conservation management (Allen and Singh 2016), and movement may be important in the design of protected areas (Thirgood et al. 2004) and designation of critical habitat (Bendik et al. 2016).

Because many amphibians use fragmented and ephemeral habitats, movement is particularly important for understanding their biology, as well as for understanding the nature of recent amphibian declines (Stuart et al. 2004; Wake and Vredenburg 2008), and for developing more effective conservation strategies for these animals (Pittman et al. 2014; Bendik et al.

2016). Amphibians have traditionally been viewed as organisms with low rates of movement and high site fidelity (Wells 2007), but this notion has been challenged (Smith and Green 2006). Movement has been widely studied in pond-breeding amphibians (see Pittman et al. 2014 for a review) and to a lesser extent in some headwater stream salamanders (Lowe 2003; Lowe et al. 2006a, 2006b, 2008; Cecala et al. 2009; Lowe 2010). Only a few studies (Pierce et al. 2014; Bendik et al. 2016) have examined movement in permanently aquatic (paedomorphic) salamanders that occupy isolated springs and caves.

Fifteen described and several undescribed species of *Eurycea* salamanders occur in springs and caves on the Edwards Plateau (Chippindale et al. 2000; Bendik et al. 2013a), a large uplifted region of karst limestone in central Texas. All of these species are permanently aquatic and have limited geographic ranges and many are threatened or endangered (Chippindale and Price 2005). Although widely recognized as important for conservation planning, the extent and patterns of movement within and between populations have not been studied for many of these species.

We focused on within-spring movement of the Georgetown Salamander (*Eurycea naufragia*, Fig. 1), an endemic spring- and cave-dwelling salamander known



FIGURE 1. The Georgetown Salamander, *Eurycea naufragia*. (Photographed by Benjamin Pierce).

only from 15 sites on the Edwards Plateau (Pierce et al. 2010, 2014). All of the known sites are found within a small area in Williamson County, Texas, USA; the furthest distance between known sites is only about 21 km. All populations occur in an area undergoing rapid urbanization, and they depend critically on the Edwards Aquifer, a shallow-ground aquifer that is threatened by groundwater pumping, reduced recharge, and pollution (Chippindale and Price 2005). The species was federally listed as threatened in 2014 (U.S. Fish and Wildlife Service [USFWS] 2014). *Eurycea naufragia* is paedomorphic, forgoing metamorphosis to reproduce as aquatic, gilled, adults (Chippindale et al. 2000). No overland dispersal occurs; movement is therefore limited to the aquatic habitat (Chippindale et al. 2000).

Because most individuals are found in close proximity to spring outlets (Sweet 1978; Pierce et al. 2010; but see Bendik et al. 2016), surface movement among populations is assumed to be limited. The extent of subsurface movement through the aquifer is unknown. We studied within-spring movement of *E. naufragia* at two sites in central Texas over a 32-mo period, using capture-recapture methods that allowed us to recognize unique individuals. Our objectives were to determine the proportion of salamanders that moved and their rates of movement and associations of movement with body size, reproduction, and body condition.

## MATERIALS AND METHODS

**Study sites.**—We studied within-spring movement of *Eurycea naufragia* at Swinbank Spring and Twin Springs, two permanent spring sites located in Williamson County, Texas, USA (see Pierce et al. 2014 for more detailed information about these sites). Each site consists of a primary spring outlet and a downstream spring run approximately 1 m in width, with pools and riffles and water depth ranging from a few cm to 0.5 m. These two sites are located 7.8 km apart and are separated by a large reservoir. Each population is estimated to

consist of several hundred adult salamanders (Pierce et al. 2014), which are active throughout the year.

At each spring, we captured salamanders monthly from October 2012 to June 2015 along a transect starting at the primary spring outlet and extending downstream 24 m at Swinbank Spring and 36 m at Twin Springs. We conducted additional surveys further downstream but found few salamanders below these transects (salamanders below the transects were not included in this study of movement). We divided each transect into approximately 5 m length sections, with a total of five sections at Swinbank Spring and six sections at Twin Springs. During a survey, we carefully searched the entire wetted surface from bank to bank of each section of the transect for the presence of salamanders by slowly wading through the spring run, and searching underneath potential cover objects, such as rocks, leaf litter, and other objects. We captured salamanders with small aquarium nets. We recorded the 5 m section from which an animal was captured, and temporarily placed captured salamanders in mesh boxes within the spring run to maintain them at ambient temperature, with one box for each 5-m section. Following the survey, we examined each captured salamander in the field for the presence of eggs by placing it in a water-filled petri dish and holding it up to sunlight or using a small flashlight. When present, eggs were visible through the abdominal wall, appearing as distinct, white masses. We then photographed each salamander against a  $0.635 \times 0.635$  cm grid for later size measurements. Following photography, we returned all salamanders from each 5 m section to a single, arbitrarily selected location within the 5 m section from which they were originally captured.

**Measurements.**—We used ImageJ software (vers. 1.48, <https://imagej.nih.gov/ij/>) to measure salamanders from the digital photographs taken in the field. Head-trunk length (HTL) was measured as the distance from the tip of the snout to the middle of a line drawn through

the anterior-most insertion of the hind limbs. We used HTL as a measure of overall body size instead of snout-vent length because we were unable to determine the location of the vent from the dorsal photographs of the animals. We measured tail width as the width of the tail at the posterior most insertion of the hind limbs. To standardize tail width for body size, we computed relative tail width (RTW) as tail width divided by HTL. We used RTW as a measure of body condition because salamanders often deposit lipids in the tail, and tail width has been used as a measure of body condition in other studies (Bendik and Gluesenkamp 2012). Also, tail width is less likely than other measures to be influenced by short-term increases in mass resulting from a recent meal or the presence of eggs. We measured HTL and RTW on photographs from the first capture of each salamander.

**Identification of salamanders.**—Using a unique pattern of melanophores on the head, we identified individual salamanders from photographs (cropped images of each head) and Wild-ID (vers. 1.0; Bolger et al. 2012), a pattern-recognition software. Bendik et al. (2013b) and our own pilot studies demonstrated that this method can reliably identify individual *Eurycea* salamanders, at least over the time-frame of this study. This identification system allowed us to determine if we had captured a salamander previously.

**Data analysis.**—We based all analyses only on salamanders that were recaptured at least once, as we had no way to determine movement of individual salamanders that were not recaptured. We based our analyses of HTL and RTW on measurements taken at the initial capture of a salamander. We identified salamanders as gravid if they were observed with eggs at initial capture or any subsequent recapture. We designated salamanders to have moved if they were recaptured outside of the 5 m section of their original capture.

We measured distance between sections as the distance in meters from the center of one section to the center of another section. To calculate rate of movement, we first determined all the movements of a salamander as revealed by all of its recaptures, and then summed the total distance between sections for these movements. We calculated rate of movement (m/day) as the total distance a salamander moved during all of its recaptures divided by the total number of days from the day of first capture to the day of the last recapture during the 32-mo study period.

We used chi-square tests of independence to compare the proportion of animals that moved in the two populations, and between gravid and nongravid individuals. Because movement distances were not normally distributed, we used nonparametric Mann-

Whitney U tests to compare rates of movement of salamanders from different populations, and between gravid and nongravid salamanders. We also used Mann-Whitney U tests to compare HTL and RTW of salamanders that moved and those that did not move. We used Spearman's nonparametric correlation to examine the association of HTL and rate of movement, and RTW and rate of movement. We calculated chi-square values by hand, but used IBM SPSS Statistics (Version 24 Armonk, New York; <https://www.ibm.com/us-en/marketplace/statistical-analysis-and-reporting>) to perform Mann Whitney U tests and correlations. We set our alpha level for all statistical tests at 0.05.

## RESULTS

During the 32 mo of our study, we captured 691 unique salamanders at Swinbank Spring. Of these, we recaptured 242 (35.0%) at least once. We captured 204 unique salamanders at Twin Springs, of which we recaptured 80 at least once (39.2%). There was no difference in the proportion of recaptures between the two populations ( $\chi^2 = 1.203$ ,  $df = 1$ ,  $P = 0.27$ ).

Among those salamanders that were recaptured, only 23.9% moved one or more times at Swinbank Spring, and 17.5% moved one or more times at Twin Springs, a difference that was not significant ( $\chi^2 = 1.45$ ,  $df = 1$ ,  $P = 0.229$ , Fig. 2). The average rate of movement at Swinbank Spring was  $0.0128 \pm (SE) 0.00227$  m/d and at Twin Springs it was  $0.0130 \pm 0.00723$  m/d; these differences were not significantly different (Mann Whitney  $U = 9003$ ,  $P = 0.199$ ). There was no obvious directionality to the movement of salamanders (Fig. 3). The average total distance moved by individual salamanders during the 32-mo study (including those that moved and did not move; both sites combined) was only  $3.035 \pm 0.413$  m (range, 0–55.3 m, Fig. 4).

To compare movement of gravid and nongravid salamanders, we combined the two populations because of the small number of recaptured salamanders that were gravid in each population (46 at Swinbank and 21 at

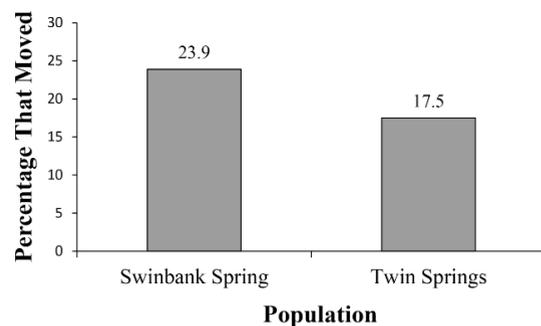


FIGURE 2. Percentage of Georgetown Salamanders (*Eurycea naufragia*) that moved at least once during the 32 mo study at Swinbank Spring and Twin Springs, in Williamson County, Texas, USA.

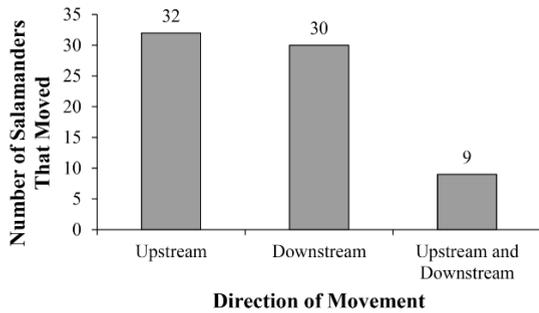


FIGURE 3. Numbers of Georgetown Salamanders (*Eurycea naufragia*) that moved upstream, downstream, or both upstream and downstream (Swinbank Spring and Twin Springs combined) during the 32 mo study in Williamson County, Texas, USA.

Twin Springs). Significantly more gravid salamanders moved than nongravid salamanders ( $\chi^2 = 18.40$ ,  $df = 1$ ,  $P < 0.001$ ). There was also a higher rate of movement among gravid salamanders than among nongravid salamanders ( $U = 6438.5$ ,  $P < 0.001$ ; Fig. 5). Only considering salamanders that were, at first capture,  $\leq 25$  mm HTL (the minimum size of gravid females reported in Pierce et al. 2014), there was still a higher proportion of gravid salamanders that moved than nongravid salamanders ( $\chi^2 = 13.85$ ,  $df = 1$ ,  $P < 0.001$ ,  $n = 264$ ), and the rate of movement of gravid salamanders exceeded that of nongravid salamanders ( $U = 4722$ ,  $P < 0.001$ ). Although gravid individuals moved more than nongravid individuals, there was no obvious direction to the movement of gravid salamanders: 11 moved upstream and 13 moved downstream, which was not significantly different from the direction of movement of nongravid salamanders ( $\chi^2 = 0.524$ ,  $df = 1$ ,  $P = 0.469$ ).

The HTL of salamanders at Swinbank Spring that moved ( $28.60 \pm 0.40$  mm) was significantly longer than the HTL of salamanders that did not move ( $27.40 \pm 0.27$  mm;  $U = 4241.0$ ,  $P = 0.018$ ). There was also a significant, but weak, positive correlation between HTL and rate of movement (Spearman  $r_s = 0.14$ ,  $P =$

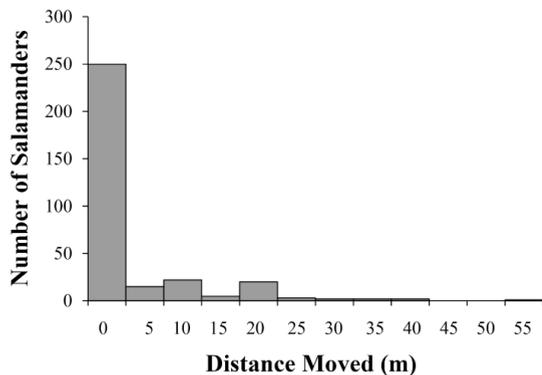


FIGURE 4. Total distance moved (in m) by individual Georgetown Salamanders (*Eurycea naufragia*) during the 32 mo study (Swinbank Spring and Twin Springs combined) in Williamson County, Texas, USA.

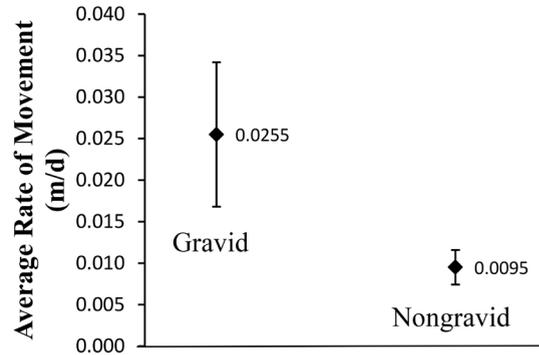


FIGURE 5. Average rate of movement of gravid and nongravid Georgetown Salamanders (*Eurycea naufragia*) (Swinbank Spring and Twin Springs combined) in Williamson County, Texas, USA.

0.029) at Swinbank Spring. At Twin Springs, the HTL of salamanders that moved ( $29.66 \pm 0.69$  mm) was not significantly different from the HTL of salamanders that did not move ( $28.29 \pm 0.40$  mm;  $U = 334.5$ ,  $P = 0.106$ ). There was no significant correlation between HTL and rate of movement at Twin Springs ( $P = 0.109$ ). The larger size of individuals that moved was not strictly due to greater movement in gravid individuals, because even among nongravid individuals, body size was larger for individuals that moved than those that did not move ( $U = 5536.5$ ,  $P = 0.044$ ,  $n = 255$ , both populations combined).

Body condition, as measured by RTW, was not significantly different between salamanders that moved ( $0.1142 \pm 0.00139$ ) and those that did not move ( $0.1143 \pm 0.00074$ ) at Swinbank Spring ( $U = 5188.5$ ,  $P = 0.751$ ). There also was no difference in RTW of salamanders that moved ( $0.1033 \pm 0.00190$ ) and did not move ( $0.1042 \pm 0.00112$ ) at Twin Springs ( $U = 440.0$ ,  $P = 0.781$ ). There was no significant correlation between RTW and rate of movement at either Swinbank Spring ( $P = 0.860$ ) or Twin Springs ( $P = 0.654$ ).

We also compared size and body condition of salamanders that moved upstream and salamanders that moved downstream. For this analysis we combined the populations and excluded salamanders that moved both up and down. The HTL of salamanders that moved upstream ( $28.04 \pm 0.64$  mm,  $n = 32$ ) was not significantly different from the HTL of salamanders that moved downstream ( $29.19 \pm 0.44$  mm,  $n = 30$ ;  $U = 527$ ,  $P = 0.508$ ). Relative tail width (our measure of body condition) of salamanders that moved upstream ( $0.1125 \pm 0.0018$ ,  $n = 32$ ) was also not significantly different from the RTW of salamanders that moved downstream ( $0.1103 \pm 0.0020$ ,  $n = 30$ ;  $U = 429$ ,  $P = 0.473$ ).

## DISCUSSION

The extent of movement within and among populations is an important factor that affects many ecological and evolutionary characteristics (Dieckmann

et al. 1999; Clobert et al. 2001; Nathan et al. 2008) and understanding patterns of movement is critical for management of threatened and endangered species (Thirgood et al. 2004; Pittman et al. 2014; Allen and Singh 2016; Bendik et al. 2016). Many species of *Eurycea* salamanders that occupy the Edwards Plateau occur at a limited number of sites and are threatened by habitat loss, pollution, groundwater pumping, and reduced groundwater recharge (Chippindale and Price 2005). Information about movement within and between populations of these salamanders is important for developing effective conservation management strategies.

Our study found limited movement of Georgetown Salamanders within individual springs, a conclusion that corroborates the findings of an earlier study (Pierce et al. 2014). In this earlier study, salamanders were marked with visual implant elastomers and recaptured over a 24-mo period. The number of unique salamanders observed in that earlier study was considerably less than in the present study (at Swinbank Spring a total of 90 salamanders in the earlier study vs 691 in the current study; at Twin Springs 63 in the earlier study vs 204 in the current study). Although the duration of the current study was longer than that of the previous study (34 mo and 24 mo, respectively), the proportion of salamanders that moved was similar at Swinbank (24%) and less at Twin Springs (17.5%). The current study, based on a completely independent set of salamanders, also allowed us to examine the effects of size, reproduction, and body condition on the probability of movement and rate of movement, insights not provided by the Pierce et al. (2014) study.

Other studies of aquatic stream salamanders also found limited movement within headwater streams. Cosentino et al. (2009) observed low levels of movement of the Spring Salamander, *Gyrinophilus porphyriticus*, with only 12% of the salamanders moving more than 1 m during a four-week period. Over a 2-y period, Lowe (2003) found that 54% of recaptured *G. porphyriticus* moved less than 1 m from their initial point of capture, and most of those that did move dispersed 10 m or less. Even over a 6-y period, 25% of the recaptured *G. porphyriticus* moved less than 1 m. Similarly, Cecala et al. (2009) found that 51% of the Red Salamander, *Pseudotriton ruber*, larvae never moved more than 5 m between captures in a 1-y study.

Although differences in study design and analysis make direct comparisons difficult, Bendik et al. (2016) observed that 26% of *E. tonkawae* moved greater than 15 m during just 4 mo of their study, a rate of movement that was considerably higher than that which we observed in *E. naufragia*. The reason for the higher rate of movement observed in *E. tonkawae* is not

known, but could reflect species specific differences in movement. Alternatively, there may be more suitable habitat downstream of springs in the watershed studied by Bendik et al. (2016).

We detected no directional bias to salamander movement, with almost equal numbers of salamanders moving upstream and downstream. Similarly, Bendik et al. (2016) observed no directionality to movement of *E. tonkawae*. In contrast, some headwater stream salamanders show a strong directional bias (Bruce 1986; Lowe 2003).

We found that gravid individuals are more likely to move and exhibit higher rates of movement than nongravid individuals. The higher rate of movement in gravid females might reflect their movement to specific habitats for egg laying. Eggs of this and other central Texas *Eurycea* are rarely observed in the field (Pierce et al. 2014; Bendik 2017), suggesting that eggs are deposited in subsurface or subterranean habitats (Bendik 2017). The higher rates of movement we observed in gravid females may reflect their movement to and from these selected habitats. Information on seasonality of movement would be useful in evaluating this hypothesis, but we are unable to determine seasonal patterns of movement with our data because of the frequently long and irregular intervals between recaptures.

We also found evidence that larger salamanders at Swinbank Spring were more likely to move and that they moved further than smaller salamanders. However, the effect was small: salamanders that moved were, on average, only 1.2 mm longer (4% of HTL) than those that did not move. Bendik et al. (2016) also found that larger *E. tonkawae* moved further distances; they also observed that juveniles were more likely to occupy downstream habitat. In contrast, Lowe (2003) found no relationship between size of *G. porphyriticus* salamanders and the distance they moved. Cecala et al. (2009) found that larger *P. ruber* were more likely to move upstream than smaller individuals.

We found no relationship between the initial body condition and movement: recaptured salamanders that moved did not differ in relative tail width from those that did not move, and there was no significant correlation between relative tail width and rate of movement. Similarly, Lowe (2010) found no relationship between dispersal distance and initial body condition in *G. porphyriticus*. However, in the same species, Lowe et al. (2006a) found an association between body condition and direction of movement: salamanders with high body condition were more likely to move upstream and salamanders with low body condition were more likely to move downstream. We found no difference in the body condition of salamanders that moved upstream and those that moved downstream, although our sample

size is limited because relatively few salamanders in our study moved at all.

We recognize several limitations of our study. First, we only have information about the movement of salamanders that were recaptured. Salamanders that were not recaptured may have died, moved out of the study area, or were present but not recaptured. We have no way of assessing whether the movement behavior of the recaptured salamanders differs from that of salamanders that were not recaptured and therefore the conclusions of this study apply to salamanders that were recaptured at least once.

Another limitation is that our conclusions apply only to movement of larger juveniles and adults. In our surveys, we found relatively few salamanders < 25 mm total length. Movement behaviors of small *Eurycea* larvae may differ from those of larger juveniles and adults (McEntire and Pierce 2015; Bendik et al. 2016) and therefore the results we obtained on larger juveniles and adults should not be extrapolated to small larvae. An additional limitation is that we only surveyed the upper reaches of the spring run at each site: 24 m downstream of the spring origin at Swinbank Spring and 36 m downstream of the spring origin at Twin Springs. We also have no information on underground movement through the aquifer, although some genetic studies of differentiation among central Texas *Eurycea* suggest that it is limited (Lucas et al. 2009).

After capture, we released salamanders at an arbitrarily selected location within the 5 m section of their original capture. We recognize that displacing the animals from their point of capture, although by at most a few meters, could have artificially increased subsequent movement after release, causing us to overestimate natural rates of movement. Also, our detection of movement is restricted to movement beyond the 5 m length of the sections we sampled. With our present design, we have no way of detecting movement within each 5 m section, which certainly occurs. However, more fine-scaled determination of distances moved would be unlikely to alter the major conclusions of the study.

The limited movement of salamanders that we observed within these two springs has implications for conservation planning and management of *Eurycea naufragia*. Limited movement typically results in population fragmentation and reduced gene flow, increasing the risk of population extirpation. Although we have no information about long-range surface or underground movement, the limited movement within our sites suggests that this species is not highly mobile. Coupled with the limited number of populations, extremely restricted surface habitat at each known site, and low population numbers (Pierce et al. 2014), these

data reinforce the suggestion of long-term vulnerability of this species.

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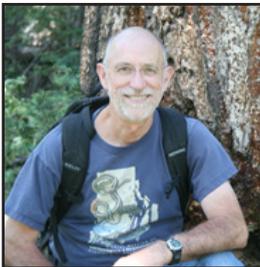
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