Pond pH, Acid Tolerance, and Water Preference in Newts of Vermont

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Abstract - *Notophthalmus viridescens* (Red-spotted Newt) collected from 3 low-pH ponds (ca. 4.8) and 3 high-pH ponds (ca. 8.1) in Vermont varied in pH tolerance and water preference. While newts from all ponds survived in pH values as low as 4.4, the mean 10-day survival of newts in pH = 3.2 was 69% for newts from the low-pH Green Mountain ponds compared to 33% for newts from the high-pH Taconic Mountain ponds. Taconic Mountain newts selected water from Taconic ponds 73% of the time, while Green Mountain newts exhibited no preference for pond water from either mountain range. In order to isolate the effect of pH on water choice, we conducted an experiment in which newts chose between reconstituted soft water (RSW) that had been adjusted to either high pH (8.0) or low pH (4.5). Taconic Mountain newts selected high-pH RSW 72% of the time. Although Green Mountain newts exhibited no preference for pond water having high or low pH, they selected the high-pH RSW 70% of the time. These differences in pH tolerance and water preference between Green and Taconic Mountain newts may represent local adaptation shaping population distribution and divergence.

Introduction

Acidic habitats, both anthropogenic and naturally occurring, have been implicated in limiting the distribution and abundance of amphibians around the world (Barth and Wilson 2010, Merilä et al. 2004, Vatnick et al. 2006). Amphibians are particularly vulnerable to acidic environments due to their aquatic breeding habits and permeable skin. Low pH has been linked to problems in immune function (Brodkin et al. 2003, Vatnick et al. 2006), embryonic development and hatching (Barth and Wilson 2010, Merilä et al. 2004, Persson et al. 2007, Pierce and Harvey 1987, Räsänen et al. 2003), larval growth and performance (Barth and Wilson 2010, Brady and Griffiths 1995, Gerlanc and Kaufman 2005, Pierce and Wooten 1992), and ion regulation (Meyer et al. 2010, Robinson 1993). We have observed *Notophthalmus viridescens* Rafinesque (Red-spotted Newt) living and reproducing in ponds of very different pH in two mountain ranges in southern Vermont. The ponds of the Taconic Mountains (which form the western boundary of the Vermont Valley) are underlain by extensive limestone deposits (Merwin 1993), and we have measured pH values there over 8. Conversely, ponds in the Green Mountains (bounding the eastern edge of the Vermont Valley) have a granitic base with little buffering capacity (Van Diver 1987), and these ponds have been influenced by atmospheric acid deposition (Driscoll et al. 2001). We have recorded pH values as low as 4.0 in the ponds of the Green Mountains. The Green Mountain ponds and Taconic Mountain ponds from which the newts used

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in our study originated are separated by roughly 30 km and two main highways. Both the distance and presence of roads make migration between the ponds of the two mountain ranges unlikely (Rinehart et al. 2009). However, ponds within the same mountain ranges (having roughly the same pH) are within distances over which both terrestrial efts and adult newts could migrate (Rinehart et al. 2009). Nevertheless, adult newts exhibit fidelity to their natal ponds (Gill 1978, Hairston 1987). Even if there is some migration between neighboring ponds, it is likely that different populations of newts have been isolated in ponds of different pH for many generations (Semlitsch 2008).

We addressed two sets of questions in our research. First, do adult newts from ponds of different pH exhibit differences in pH tolerance? Geographic variation in acidic pH tolerance has been reported for a number of anuran species, suggesting local adaptation to low pH (Persson et al. 2007, Pierce and Harvey 1987, Pierce and Wooten, 1992, Räsänen et al. 2003). These studies involved pH tolerance in embryos and larvae from different geographic ranges. However, studies on geographic variation in acid tolerance for adult urodeles are lacking. The Red-spotted Newt is widespread in eastern North America and is a keystone predator in many of the ponds in which it is found (Kurzava and Morin 1994, Smith 2006). Thus, the presence of newts has a significant effect on the assemblage of the organisms in the ponds they inhabit. Moreover, Biek et al. (2002) argued that studies on embryonic and larval amphibians do not accommodate the important role played by post-metamorphic animals in the persistence of amphibian populations.

The second set of questions we addressed concern water preferences of newts from different ponds. The homing ability of Red-spotted Newts is well documented (Sinsch 2006). Newts use an array of sensory information, including olfaction, in order to orient to their home ponds (Hershey and Forester 1980). The different chemical cues used by amphibians for orientation are not completely known (Sinsch 2006), but likely include chemicals from vegetation, algae, bottom sediments, and predators (Ferrari et al. 2010, Hershey and Forester 1980). Moreover, acidic environments have been reported to interfere with chemosensory processing in fish (Leduc et al. 2007). A diversity of chemical cues, including but not necessarily limited to pH, could provide differing information about ponds in the Taconic Mountains and Green Mountains. We assessed whether newts distinguish between water from the two different mountain ranges, assuming greater similarity of chemical cues from ponds within a mountain range than between ranges. We also tested whether newts can distinguish between water from their home pond and that of another pond from the same mountain range. The presence of newts in ponds of different pH and their preference for breeding in the same ponds year after year present a unique opportunity to experiment with potentially competing factors in water preference. For example, do newts from the Green Mountains (low pH) prefer water from their home pond or the higher pH, and thus possibly less stressful, water from the Taconic Mountains? Finally, we isolated the effect of pH by permitting newts from both mountain ranges to choose between reconstituted soft water (RSW) treatments that differed primarily in pH.

Field-site Description

We studied adult male newts from three high-pH Taconic Mountain ponds (Wood Pond, Birch Hill Pond, Powderhorn Pond) and three low-pH Green Mountain ponds (Branch Pond, Beebe Pond, Grout Pond). The three Taconic ponds are within 2 km of one another (approximately 43°10'30"N, 73°5'W) with areas of roughly 1 ha each. All three are at an elevation of about 250 m and are surrounded by meadow and cattail marsh. The Green Mountain ponds are both larger (roughly 15 ha) and at higher elevations than the Taconic ponds (approximately 700 m). The Green Mountain ponds are surrounded by forest to the shoreline. Grout Pond (43°2'30"N, 72°57'40"W) is 7 km east of Branch Pond and Beebe Pond (approximately 43°5'0"N, 73°2'0’"W). As noted above, the Taconic Mountain ponds and the Green Mountain ponds are roughly 30 km apart and are separated by two major highways.

The Taconic and Green Mountain Ponds differ dramatically in at least two important chemical measures, pH and conductivity. Since 1998, we have measured both pH and conductivity of the ponds in these two mountain ranges at many times through the spring, summer, and fall (including times of newt collection). We have roughly 100 separate measurements of the pH of the six ponds, and our data are in agreement with prior work (Kellogg et al. 1994). Fifty-ml water samples were collected 5 cm below the surface in clean polyethylene bottles at sites near where newts were found on collection days and at indiscriminately chosen sites on other days. The pH of these samples was determined immediately on site with a Sper Scientific Portable pH meter and later in the laboratory with a Beckman 34 bench pH meter within 2 h of collection. There was good agreement among these readings (within 0.2 pH units), and we report only the laboratory measurements. We measured conductivity in the field with a Corning Checkmate 90 meter. The pH of the 3 Green Mountain ponds ranged from 4.0 to 5.6 (average = 4.8), and conductivities ranged from 12 to 28 $\mu S\ cm^{-1}$ (average = 22 $\mu S\ cm^{-1}$). The pH of the 3 Taconic Mountain ponds ranged from 7.1 to 8.5 (average = 8.1), and conductivities ranged from 296 to 437 $\mu S\ cm^{-1}$ (average = 387 $\mu S\ cm^{-1}$). Unlike the ponds of the Taconic Mountains, the water in the ponds of the Green Mountains is tea-colored, suggesting the presence of organic (humic) acids (Barth and Wilson 2010). Thus, the chemical characteristics of the ponds of the two mountain ranges are very distinct.

Methods

Adult male newts in apparently good health were collected from the study ponds from June through August 2007, and transported to the laboratory in their home pond water. Newts were maintained in 38-liter aquaria in their own pond water (no more than 10 newts per aquarium) and were fed *Enchytraeus* sp.

(white worms) on alternate days. All experiments were conducted within three days of collection. Under all experimental regimes, newts were maintained and tested at room temperature (22 ± 1 °C) in a natural (14:10) LD cycle. We collected pond water regularly, and newts were always exposed to pond water that had been collected no more than 3 days prior. Individual newts were used in experiments only once.

pH tolerance experiments

We tested pH tolerance among adult newts from the 6 ponds at the following average pH values: 9.4, 8.0, 4.4, 3.2, and 2.9. We used RSW (Pierce and Harvey 1987) adjusted to a particular pH with dilute NaOH or dilute sulfuric acid. For each replicate pH tolerance experiment, 5 to 8 newts from each pond were placed in 15 liters of RSW at a particular pH and their survival was noted for 10 days. The pH of the water was tested twice daily and adjusted as necessary, never varying more than ± 0.3 pH units. Roughly one third of the water in each tank was replaced every third day. We performed from 3–5 replicate pH-tolerance experiments on newts from each pond with the exception of pH 2.9. The survival of newts in pH 2.9 was so low that we discontinued exposing the newts to that pH after testing only 8 newts each from 3 different ponds (8 from a Taconic Mountain pond and 16 from 2 Green Mountain ponds). We compared the mean % survival of newts from the 3 Green Mountain ponds and the 3 Taconic Mountain ponds after 10 days, using an ANOVA model with the individual ponds nested within each range.

Pond-water preference

The arena in which pond water preference was studied had four plastic containers each connected to one side of a square central plastic platform (15 cm x 15 cm). The walls of the arena were 6 cm high, which prevented the newts from escaping. Each container (15 cm x 18 cm x 5.5 cm) held 500 ml of pond water. Before an experiment, each newt was placed on the central platform, which was about 1 cm above the water, and allowed to adjust to the apparatus for 15 minutes under an inverted cylindrical mesh cup (diameter = 8.5 cm) that permitted the newt to turn around and sense chemical cues from the different pond water containers. Once the cup was removed, the newt could enter and leave any of the four pond water containers by walking into them on a sloped, gravel covered plate leading from each of the four sides of the central platform into each of the 500 ml containers. One of the containers held water from the newt's "home" pond. Another of the containers held water from a randomly chosen different pond from the same mountain range. The other two containers held water randomly chosen from among the three ponds of the different mountain range. Thus, each newt chose among two ponds from its home mountain range (one being its home pond) and two ponds from the foreign mountain range. The assignment of the 4 different pond waters to the four different containers was random. Newts were tested one at a time, and the arena was washed and dried between trials.

After the 15-minute adjustment period, the position of the newt was noted every five minutes for 180 minutes. If a newt remained on the central platform for the first hour, the experiment was discontinued. We recorded the total amount of time that each newt spent in each of the four different pond water containers, with the position of the newt at the end of each 5-minute period taken as the newt having selected that pond water for the entire 5 minutes. We only considered time spent in the pond-water containers. If a newt returned to the central platform during the experiment, that time was not counted. We used from 6–9 newts from each pond.

We assessed the effect of "home" (source) pond on pond-water choice, comparing the time that newts from each pond spent in water from the same mountain range (pooling the time spent in water from the home pond and the different pond from the same mountain range) to the time that newts from each pond spent in water from the foreign mountain range (pooling the time spent in water from both foreign range ponds). We performed separate two-way ANOVAs for newts from ponds of each mountain range (Taconic and Green), with home-pond and pond-water options (home range or foreign range) as independent variables and time spent by the newts in Green Mountain and Taconic Mountain pond water as the dependent variable. In a separate analysis, we assessed the effect of source pond on pond-water choice within the same mountain range, comparing the time that newts from each pond spent in water from their home pond to that of the different pond from the same mountain range. Thus, we performed separate two-way ANOVAs for newts from each mountain range, with home-pond and pond-water options (this time, home pond or different pond from the same mountain range) as independent variables and time in the different water as the dependent variable.

pH preference

We tested the preference of newts for RSW with a pH of 4.5 (± 0.3), similar to the pH of Green Mountain ponds, or 8.0 (± 0.4), similar to the pH of Taconic Mountain ponds. The pH of the RSW was adjusted with NaOH or sulfuric acid as noted above. The test arena was a modified version of the pond-water preference arena, with only two containers on opposite sides of the central platform. Again, the different pHs were assigned to the two containers randomly, and the containers were washed and dried between experiments. The experiments were conducted as described for the pond-water preference experiments. We used from 7–13 newts from each pond.

We assessed the effect of source pond on pH of RSW choice, comparing the time that newts from each pond spent in either high- or low-pH RSW. For newts from ponds of each mountain range (Taconic and Green), we performed separate two-way ANOVAs with home pond and RSW water pH options (high pH = 8.0, low pH = 4.5) as independent variables and time in the different pH RSW as the dependent variable.

Results

pH tolerance

There was no difference in survival among newts from the low-pH Green Mountain ponds and the high-pH Taconic Mountain ponds until pH values of 3.2 or lower. All newts from the three Taconic Ponds and the three Green Mountain ponds survived 10 days in water at pH values of 9.4, 8.0, and 4.4. However, Green Mountain newts had higher survival than Taconic Mountain newts in pH of 3.2 (range: $F_{1, 17} = 95.05$, $P < 0.0001$; Fig. 1). There was also significant variation in mean % survival among newts from ponds within the same range (ponds: $F_{2, 17} = 7.584$, $P = 0.004$; Fig. 1), but no range x pond interaction ($P = 0.816$). Overall, the mean % 10-day survival at pH 3.2 was 69% for Green

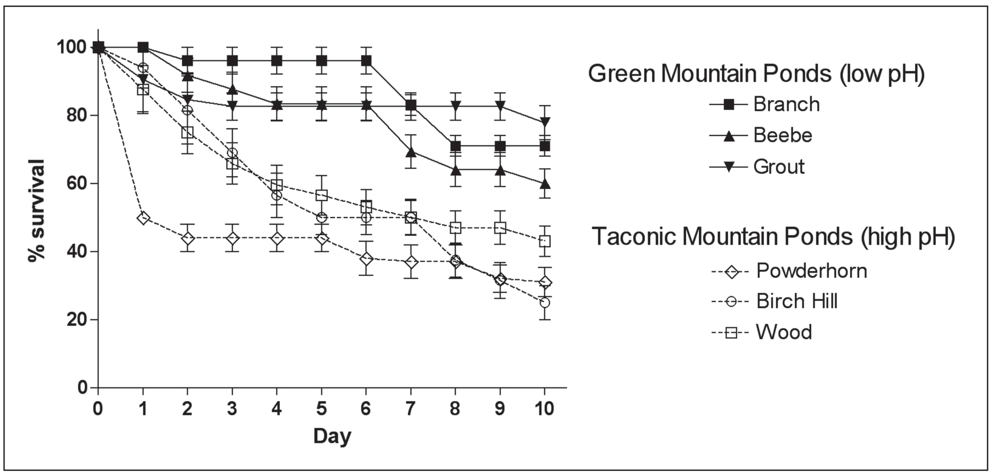

Figure 1. Mean percent survival (± SE) of newts from Green Mountain ponds (closed symbols) and Taconic Mountain ponds (open symbols) at pH = 3.2.

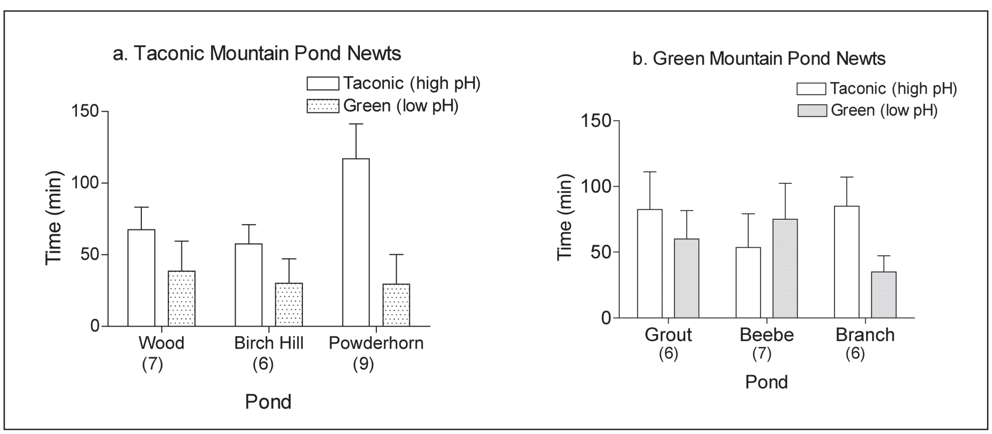

Figure 2. Mean time (± SE) that newts selected Taconic Mountain pond water (open bars) and Green Mountain pond water (shaded bars). Numbers in parentheses indicate sample size. a) Taconic Mountain newts: only the preference for Taconic Range water is significant ($P = 0.007$). b) Green Mountain newts: no significant preference for water from either range ($P = 0.393$).

Mountain newts compared to 33% for Taconic Mountain newts. At a pH of 2.9, although we discontinued the experiments before testing newts from all ponds, all of the Taconic newts tested were dead after 3 days, while 20% of the Green newts survived for 10 days. Thus, Green Mountain newts were more tolerant of very low pH than were Taconic Mountain newts.

Pond-water preference

Newts from the 3 Taconic ponds showed a preference for Taconic Mountain water compared to Green Mountain water (range: $F_{1, 38} = 8.016$, $P = 0.0074$; neither pond [$F_{2, 38} = 1.054$, $P = 0.359$] nor pond x range interaction [$F_{2, 38} = 1.369$, $P = 0.267$] was significant; Fig. 2a). Taconic newts selected Taconic water 73% of the time (Table 1). Green Mountain newts, on the other hand, exhibited no preference for either Green Mountain water or Taconic Mountain water (no significant effects; range: $F_{1, 32} = 0.7485$, $P = 0.3934$; pond: $F_{2, 32} = 1.1108$, $P = 0.895$; pond x range interaction: $F_{2, 32} = 1.115$, $P = 0.34$; Fig. 2b). They selected Taconic Mountain water 56% of the time (Table 1).

Among Taconic newts, there was no preference for pond water from the home pond compared to water from a different pond within the Taconics (neither water

Table 1. Total time (min) in water and percent time in water that newts from Taconic Mountain ponds (n = 22) and Green Mountain ponds (n = 19) selected pond water from the Taconic (high pH) range and Green (low pH) range.

	Taconic Mountain newts	Green Mountain newts
Time (min) in Taconic (high pH) water	1895	1380
Time (min) in Green (low pH) water	685	1095
Total time (min) in water	2580	2475
% time in Taconic (high pH) water	73	56
% time in Green (low pH) water	27	44

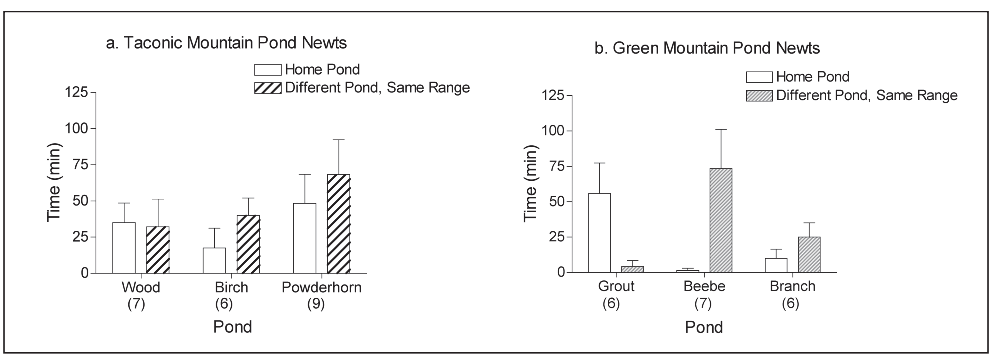

Figure 3. Mean time (± SE) that newts selected water from their home pond (open bars) and pond water from a different pond from the same mountain range (shaded bars). Numbers in parentheses indicate sample size. a) Taconic Mountain newts: no significant preference for water from either newt home pond or different pond from the same range (P = 0.414) b) Green Mountain newts: only significant effect is interaction of water source (home pond or different pond in same range) x pond (P = 0.002).

source [$F_{1, 38}$ = 0.2555, P = 0.4142], pond [$F_{2, 38}$ = 1.314, P = 0.281], nor their interaction [$F_{2,38}$ = 0.2555, P = 0.776] was significant; Fig. 3a). However, newts from Green Mountain ponds responded differently from one another. Grout Pond newts preferred water from their home pond, while newts from Beebe and Branch Ponds exhibited a preference for water from a different pond within the same range (water source: $F_{1,32}$ = 0.832, P = 0.367; pond: $F_{2, 32}$ = 0.807, P = 0.455; water source x pond choice: $F_{2, 32}$ = 7.577, P = 0.002; Fig. 3b).

pH preference

Newts from Taconic ponds preferred high-pH RSW to low-pH RSW (pH: $F_{1,46}$ = 10.01, P = 0.0028; Fig. 4a), with pH accounting for over 14% of the variation in time spent in the different water. However, both the source pond ($F_{2,46}$ = 3.491, P = 0.039) and the interaction of source pond x pH ($F_{2,46}$ = 3.873, P = 0.028) contributed significantly to the variation in time spent in the different water, accounting for 9.9% and 11% of the variation, respectively. Moreover, Wood Pond newts spent less time in water altogether than newts from either of the other Taconic ponds. Among Green Mountain newts, Beebe and Branch Pond newts selected the higher pH water, while Grout Pond newts did not appear to have a preference. Nevertheless, pH was the only factor that contributed significantly to the variation in time spent in the different water (pH: $F_{1,54}$ = 6.606, P = 0.01; pond: $F_{2,54}$ = 1.491, P = 0.234; pond x pH: $F_{2,54}$ = 1.792, P = 0.1763; Fig 4b).

Discussion

Our study revealed geographic variation in both pH tolerance and water preference among newts from ponds of different pH. Newts from the low-pH Green Mountain ponds were more tolerant of low pH = 3.2 compared to newts from the higher-pH Taconic Mountain ponds (69% survival compared to 33%

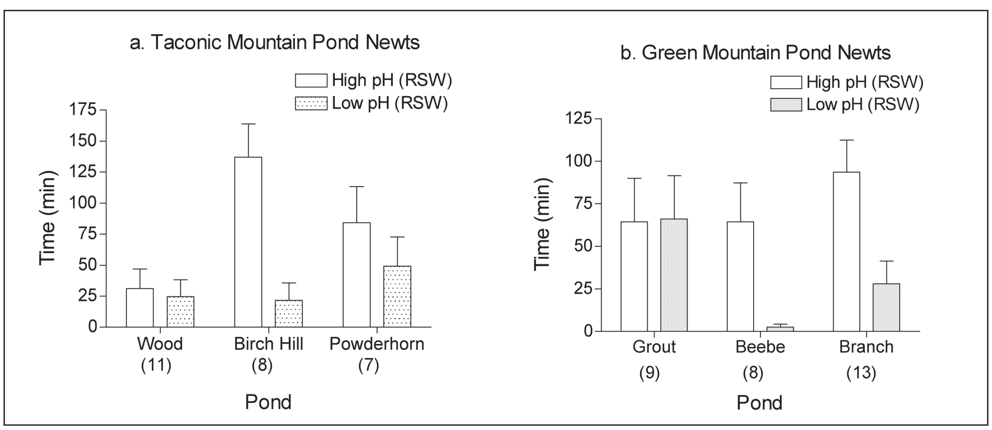

Figure 4. Mean time (± SE) that newts selected high-pH reconstituted soft water (RSW), (open bars) or low-pH RSW (shaded bars). Numbers in parentheses indicate sample size. a) Taconic Mountain newts: pH (P = 0.0028), pond (P = 0.0388) and their interaction (P = 0.0279) were all significant. b) Green Mountain newts: only pH was significant (P = 0.013).

survival, respectively; Fig. 1). Freshwater vertebrates experience a deleterious loss of Na^+ ions in low-pH water, which can sometimes lead to death (Meyer et al. 2010, Robinson 1993). Among amphibians, these effects can occur in water that is only moderately acidic, i.e., pH of 5 (Frisbie and Wyman 1992). Robinson (1993) reported that Red-spotted Newts are comparatively tolerant of low pH and exhibit compensatory changes in Na^+ balance such that original rates of Na^+ transport are restored after a few days exposure to low pH. However, Frisbie and Wyman (1992) reported that newts were unable to compensate for net Na^+ loss at a pH of 3 (during a 48-h exposure). Our results are consistent with these data in that 100% of our newts, regardless of the pH of the pond of origin, were able to survive in pH of 4.4 for 10 days. Only when the pH was dropped to 3.2 or lower was there greater survival among the low-pH Green Mountain newts compared to the higher-pH Taconic Mountain newts.

Newts from Taconic ponds were consistent in their preference for the high-pH Taconic Mountain water over low-pH Green Mountain water (Fig. 2a), but revealed no preference for water from their source pond compared to water from another Taconic pond (Fig 3a). These results in concert with the preference of Taconic mountain newts for high-pH RSW compared to low-pH RSW (Fig. 4a) suggest that pH is an important characteristic of pond water for Taconic newts. The absence of a preference for their natal water may simply be an inability of the newts to distinguish among ponds within the observed range of chemical properties.

Unlike the newts from the high-pH Taconic Mountains, the newts from the low-pH Green Mountains did not exhibit a preference for either Green Mountain or Taconic Mountain pond water (Fig. 2b). Thus, newts from low-pH ponds may be less stressed by exposure to different pHs than newts from high-pH ponds. However, while pH was an important characteristic of a pond for Taconic newts from all three ponds, there was striking variation among newts from the different Green Mountain ponds with regard to response to both home pond vs. home-range water (Fig. 3b) and high- or low-pH RSW (Fig. 4b). Grout Pond newts (the newts with the greatest survival at low pH) preferred their home-pond water to water from other Green Mountain ponds, Beebe newts preferred other Green Mountain pond water to their home-pond water, and newts from Branch Pond exhibited no preference (Fig. 3b). By contrast, Grout Pond newts exhibited no preference for either low- or high-pH RSW, while newts from both Beebe and Branch Ponds preferred high-pH RSW (Fig. 4b). It is unclear if newts from the different ponds in the Green Mountains represent distinct populations. However, Branch Pond and Beebe pond are separated by only 2 km, within documented migration distances for newts (Gill 1978, Marsh and Trenham 2001), whereas Grout Pond is 7 km east of the other two. Given their proximity, newts of Branch and Beebe Ponds might represent a single population or a metapopulation, within which there is significant migration (Smith and Green 2005), isolated and distinct from the newts in Grout Pond. However, neither elevation nor measured chemical properties (pH, conductivity) vary significantly among the three ponds.

Overall, Taconic newts spent more time in high-pH water, whether Taconic pond water or high-pH RSW (roughly 70% of the time), and while Green Mountain newts spent more time in high-pH than low-pH RSW (again, roughly 70% of the time), they exhibited no such preference when choosing between their home-range pond water and Taconic Mountain pond water. Barth and Wilson (2010) have reported that the presence of large organic acids found in low-pH ponds may have beneficial effects on the amphibians found in those ponds. It is likely that Green Mountain Ponds, having characteristic tea-colored water, contain such organic acids, rendering the pond water tolerable to the newts, while low-pH reconstituted soft water has no such mitigating chemicals. Finally, the ponds from the Taconic Mountains are adjacent to human habitation and are probably exposed to fertilizer runoff, road salt, and other chemicals that would be rare in the more isolated Green Mountain ponds. Thus, pH may not be the only important chemical characteristic of ponds that can affect newt distribution.

Conclusions

The variation in pH tolerance and water preference between Green and Taconic Mountain newts may shape newt distribution and evolution. It remains to be seen if the differences in pH tolerance and water preference between Green and Taconic Mountain newts are due to local adaptation to ponds of different pH. Genetic differences among populations of amphibians, which vary in tolerance to low pH, have been reported in anuran amphibians (Pierce and Harvey 1987, Pierce and Wooten 1992). However, some of the reported phenotypic variation in acid tolerance may be due to non-genetic effects such as acclimatization and maternal effects (Merilä et al. 2004, Pierce 1993). We are unaware of studies on the genetic basis of variation in acid tolerance among urodeles. Finally, the nature of chemical qualities of water in addition to pH, their interaction with pH, and their effect on amphibian distribution deserve attention.

Acknowledgments

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