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Abstract.—Prior studies have shown that macrogeographic gradients in temperature associated with latitude and altitude can lead to countergradient patterns of variation in a number of taxa: individuals from colder environments are known to grow or develop faster than their conspecifics from warmer environments when placed in a common setting. In this study, I hypothesized that countergradient variation also is important at microgeographic scales. The wood frog, *Rana sylvatica*, breeds in open-canopied, temporary wetlands as well as those heavily shaded by vegetation. Shading leads to cooler thermal environments that are associated with embryonic development rates as much as 50% slower than those in unshaded wetlands. Wetlands with contrasting canopy environments are often found within tens or hundreds of meters of each other. In a common garden experiment, embryos from nearby natural wetlands displayed countergradient variation: individuals collected from shaded wetlands developed up to 12% faster than those collected from relatively unshaded wetlands. The results of this study suggest that the concept of countergradient variation may be extended to small scales of space. In addition, the rate and scale of vegetation dynamics (the agent of wetland shading) imply that divergence in development among residents of nearby wetlands may be relatively rapid, on the order of decades.

Key words.—Amphibian, development, divergence, embryos, light, local adaptation, temperature.

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When genotypes are distributed such that genetic and environmental influences are in opposition, a trait is said to display countergradient variation (Levins 1969; Conover and Schultz 1995). Mounting evidence suggests that countergradient variation is an important contributor to the distribution of phenotypes in space for a diversity of taxa (e.g., Berven et al. 1979; Schultz et al. 1996; Parsons 1997; Arendt and Wilson 1999; Trussell 2000; Carroll et al. 2001). To date, countergradient variation has generally been described as a macrogeographic phenomenon (e.g., Futuyma 1998). Most studies have centered on latitudinal or altitudinal clines in growth or developmental rates of ectotherms. In these cases, individuals from colder environments within a species' range grow or develop more slowly in situ, but are able to grow or develop more rapidly than conspecifics from warmer parts of the range when compared within a common garden setting. This effect is expected to diminish observed phenotypic variation across space. Because it represents a situation in which natural selection can homogenize phenotypes, countergradient variation can be an important consideration even when observed phenotypic gradients are small or not apparent.

The purpose of this study is to evaluate the importance of countergradient variation at microgeographic scales. There may be good reasons to discount the existence of countergradient patterns across small distances. Countergradient variation may not be important at small spatial scales because relevant environmental gradients are not strong enough or consistent enough to influence the distribution of genotypes. Equally important, individuals may be able to easily move across microgeographic gradients. Movement among sites with different environmental characteristics could overwhelm localized selection (Lenormand 2002). Against these arguments is the frequent observation of cogradient variation (when genotypic and phenotypic gradients in space are aligned) at small spatial scales. This form of local adaptation is an important, widely described form of evolution (Stearns 1983; Taylor 1991; DeMeester 1996; Van Zandt and Mopper 1998; Hendry and Kinnison 1999; Reznick and Ghalambor 2001). In some cases, these genotypic gradients exist at extremely small scales easily traversed by the movements of individuals.

In this study, I have chosen to focus on a system for which localized countergradient variation is unknown, but might be expected. The wood frog, *Rana sylvatica*, breeds in small, discrete temporary wetlands (Skelly et al. 1999). Its range encompasses much of North America, stretching from Georgia to Hudson Bay to Northern Alaska, and is abundant in both coastal lowlands and montane environments (Conant and Collins 1998). Wood frogs lay their eggs in early spring and larvae develop to metamorphosis within two to three months after hatching (Berven 1995). Catastrophic failure of cohorts due to premature drying of the wetland is commonly observed (Berven 1995).

Prior studies have established that larval development of the wood frog displays countergradient variation across both latitudinal and altitudinal clines within its geographic range (Berven 1982a,b, 1987; Riha and Berven 1991). This pattern may reflect strong selection for wood frogs from colder parts of the range to develop rapidly in the face of severe time constraints imposed on premetamorphic individuals.

Thermal gradients similar in magnitude to those seen across macrogeographic scales also can occur among nearby wetlands. Shading by vegetation rooted near the shoreline and within the basin of small wetlands can dramatically alter light and thermal environments (Skelly and Freidenburg 2000; Skelly et al. 2002; Halverson et al. 2003). Insolated and shaded wetlands are often located within meters of each other (Skelly et al. 1999; Halverson et al. 2003).

Wood frogs also show evidence of local adaptation. As an example, wood frog larvae from wetlands with high densities
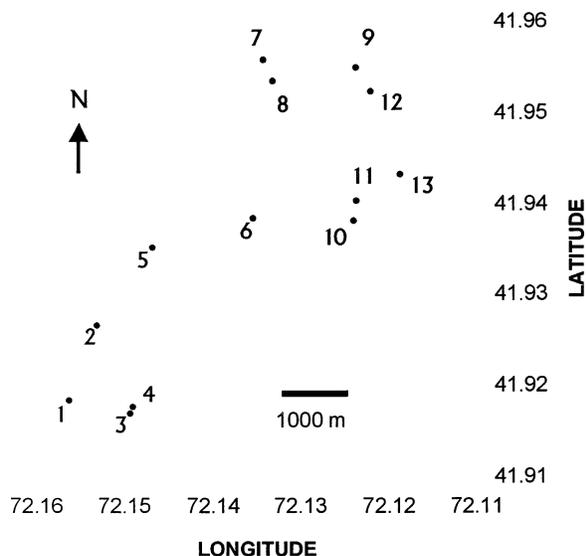
FIG. 1. Locations of study wetlands at the Yale-Myers Forest (3800 ha) in northeastern Connecticut, U.S. Land cover at Yale-Myers Forest is dominated by mixed deciduous and coniferous forest with very few barriers to amphibian movement. The locations of 13 wetlands are presented in terms of longitude (degrees W) and latitude (degrees N).

of predators tend to have larger, deeper tails than those from wetlands with few predators (Relyea 2002). These morphological attributes are associated with lower rates of capture by predators and are maintained when larvae are reared in a common garden setting (Relyea 2001, 2002). This documentation of microgeographic, cogradient variation suggests that countergradient variation also could exist on small spatial scales.

This study includes both observational and experimental components. I used observations of in situ embryonic development across wetlands to show that eggs in shaded wetlands develop much slower than eggs in insolated wetlands. Based on this pattern, I predicted that wood frog embryos will display countergradient variation, that is, recently laid eggs collected from deeply shaded wetlands will develop more rapidly than eggs collected from sunlit wetlands when placed in the same incubator. By using two incubators set at temperatures that span much of the range in average in situ temperatures, I was also able to evaluate the alternative possibility that embryos from different wetlands are adapted to maximize development rates at different temperatures (Yamahira and Conover 2002). Because maternal effects could influence patterns among wetlands, I also evaluated the role of egg size on development patterns.

METHODS

I studied embryonic development of wood frogs from natural wetlands located at the Yale-Myers Forest (3800 ha) in northeastern Connecticut, U.S. (Fig. 1). In this region, wood frogs lay their eggs in late March or early April when wetlands are flooded and well before deciduous plants leaf out. The light environment within wetlands was measured using hemispherical photos of the vegetation canopy (Halverson et al. 2003). Canopy photographs are widely used by plant ecol-

ogists; important advantages of the method include the lack of dependence on weather conditions and the ability to use multiple photographs to scale estimates across space and time (Chazdon and Field 1987). In this study, photographs were taken while deciduous trees were without their leaves and within the boundary formed by the springtime shoreline according to a cartesian grid aligned to true North and spaced every 5 m. These photographs were used to estimate light intensity (as global site factor) using the HemiView software package (methods detailed in Halverson et al. 2003). Global site factor ranges from 1.0 if a location receives full, unobstructed sunlight, to 0.0 if it is entirely obstructed and receives no light. I used two global site factor values in statistical analyses. Because oviposition site can vary among years and among breeding pairs (D. K. Skelly, unpubl. data), a wetland-wide average global site factor was used in analyses evaluating the role of natal wetland origin on development in a common garden experiment. In order to evaluate the relationship between global site factor and in situ development rate of embryos, I used global site factor calculated from the single photograph closest to the point of the monitored egg aggregation.

During 2000, embryonic duration of wood frogs was measured at six natural wetlands at the Yale-Myers Forest (wetland name followed by wetland number in parentheses: Blacksmith (9), Clearcut (7), Dentist (11), Kealoha's (2), Laurel (8), Morse Bog (12)). For each wetland, embryonic duration was estimated as the number of days between the date on which eggs were first found and the date on which hatchlings were first seen. I estimated the relationship between field embryonic development rate and global site factor using linear regression. Estimates of global site factor for the egg laying sites ranged from 0.574 to 0.934 across the six wetlands.

During 2001, I conducted a common garden experiment in order to estimate variation associated with the light environment of the natal wetland. I collected embryos from 12 different wetlands: Blacksmith (9), Boulder (3), Centre Pike (13), Clearcut (7), Dentist (11), Greenbriar (4), Kealoha's (2), Little Thing (10), Mill (5), Morse Bog (12), Shrub (6), and Westford (1); range of wetland-wide global site factors: 0.476–0.910, and subjected them to two different temperature treatments. All wetlands are fishless, temporary, located between 20 and 4800 m of each other, and are within a 60 m altitudinal range. Temperature treatments (high: 13.4 ± 0.06; low: 11.3 ± 0.04) were imposed by maintaining embryos in incubators (Precision Model 818). The experimental temperatures are within the ranges observed in situ and the 2.1°C difference between treatments reflects a substantial fraction of the range in average temperatures measured at wood frog egg laying sites (e.g., 3.2°C across 12 wetlands in 2001; D. K. Skelly, unpubl. data). Embryos were exposed to a 14:10 L:D cycle.

Egg laying took place and eggs were collected during five days between 9 and 13 April 2001. At each wetland, up to six wood frog egg masses were collected from the aggregation less than 24 hours after they had been laid, placed on ice, and immediately returned to the laboratory where individual eggs were dissected from each mass while carefully preserving the vitelline membrane. An individual egg was
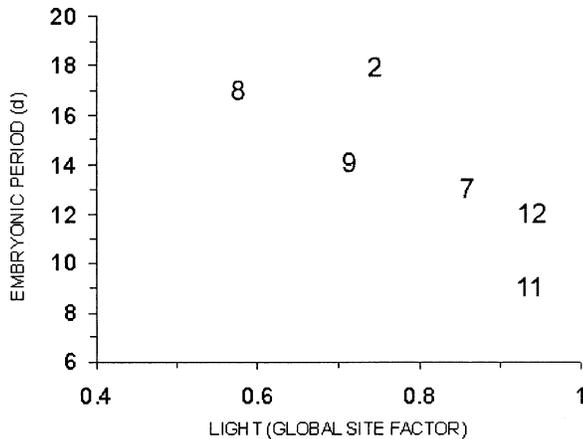
FIG. 2. Duration of embryonic development by *Rana sylvatica* at six wetlands as a function of light environment. Embryonic period was measured as the number of days between egg laying and the first observation of hatched larvae at the egg masses. Light environment (global site factor) was measured using hemispherical photos of the canopy above each wetland basin. The response of embryos in each wetland is marked by a number according to the wetland numbers presented in Figure 1.

then placed into the well of a tissue culture plate holding 17 ml of aged tap water. Each plate was allocated six eggs from a single mass. Each mass was used to fill two plates, and one was assigned to each temperature treatment. In three of the wetlands, low breeding effort precluded collecting six masses; in these wetlands four (two cases) or three (one case) egg masses were collected. A total of 780 embryos from 65 egg masses were stocked into the experiment.

Upon stocking, each embryo was staged according to Gosner (1960) and photographed using a digital camera attached to a dissecting microscope. This photograph was used to measure egg diameter with digitization software (TPSDig, Stonybrook, NY). I estimated the relationship between wetland-wide global site factor and egg size using linear regression. Embryos were then staged at two to four day intervals. For each treatment, I calculated the average Gosner stage for each date. Specifically, I averaged stages across the six embryos from a given egg mass. I then averaged stages across the egg masses from a given natal pond-incubator treatment combination.

I used logarithmic regression (Gosner Stage = $m \times \ln(\text{day}) + b$; where m is slope and b is the y-intercept) to capture the nonlinear relationship between Gosner Stage and time for each of the 24 treatments. Fits were excellent (average $R^2 = 0.98$). Relationships from logarithmic regressions were used to estimate the time elapsed between Gosner stages 1 (laying) and 20 (hatching).

I used analysis of covariance to estimate the effects of temperature (high or low, a categorical variable) and light environment of the natal wetland (global site factor, a continuous variable) on the estimated embryonic period. An ANCOVA including the interaction term (temperature $\times$ light) showed that slopes were equivalent between temperature treatments ($P = 0.402$). Consequently, the ANCOVA presented here includes just the main effects of temperature and light level. Prior to this analysis, the data were screened for
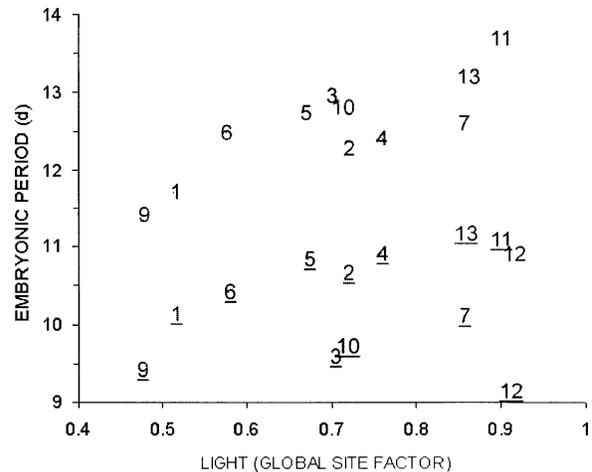

FIG. 3. Estimated embryonic period for wood frogs collected from 12 different wetlands and reared in low or high temperature incubators. Embryonic period is plotted against global site factor of the natal wetland. Global site factor is a measure of the light environment ranging from zero in total darkness to one in unobstructed, full sunlight. The response of embryos from each wetland is marked with a plain (low temperature) or underlined (high temperature) number that refers to the wetland numbers presented in Figure 1. Wetland no. 12 (Morse Bog) was identified as an outlier and excluded from statistical analyses except where indicated otherwise.

outliers by calculating studentized residuals from linear regressions for both warm and cold temperature treatments. One wetland (Morse Bog) was found to be an outlier in both of these regressions (studentized residuals: $t > 2.72$ and $P < 0.02$ in both cases). No other wetlands were identified as outliers. Based on these results, Morse Bog was excluded from the analysis.

RESULTS

Across six natural wetlands that varied from relatively open to heavily shaded, an index of the light environment (global site factor) was a strong predictor of in situ embryonic development rate (linear regression: $n = 6$ wetlands, $R^2 = 0.65$, $P < 0.05$; Fig. 2). Embryos in the darkest wetlands took up to twice as long to hatch compared with embryos in the lightest wetlands (18 vs. 9 days).

Of 780 embryos stocked into the common garden experiment, 722 (93%) survived to hatching. Both incubator temperature (ANCOVA: df = 1, 19; mean square = 27.2; $F = 122.4$; $P < 0.001$) and light environment of the natal wetland (ANCOVA: df = 1, 19; mean square = 4.0; $F = 18.1$; $P < 0.001$) influenced wood frog development in a common environment (Fig. 3). Across the 11 wetlands included in the analysis, embryos from the high temperature treatment developed more rapidly than those in the low temperature treatment, reaching hatching stage an average of 18% faster. Global site factor in the natal wetland was strongly associated with estimated embryonic period. Individuals from the darkest wetlands developed up to 12% faster than those from the lightest wetlands.

Finally, there was no evidence across the 11 wetlands that egg size was associated with global site factor (linear re-

gression: $n = 11$, $t = 0.700$, $P = 0.501$). This result was unchanged when Morse Bog was included in the analysis (linear regression: $n = 12$, $t = 0.665$, $P = 0.521$).

DISCUSSION

This study shows that countergradient variation occurs at microgeographic scales. Although localized, cogradient variation has long been described; nearly all prior studies have focused on countergradient variation as a macrogeographic phenomenon (for an exception, see Arendt and Wilson 1999). In part, this situation may reflect a continuation of the focus by initial studies on countergradient patterns associated with latitudinal and altitudinal clines in temperature (Levins 1969; Berven et al. 1979).

The motivation for this study was the discovery that microgeographic variation in thermal conditions among nearby wetlands can rival differences associated with macrogeographic clines (Riha and Berven 1991; Skelly and Freidenburg 2000; Halverson et al. 2003). Shading of wetland basins by vegetation is associated with up to twofold increases in embryonic period for wood frogs in Connecticut. Because shaded wetlands tend to dry as early, or earlier, than unshaded wetlands (Skelly et al. 1999), an increase in the premetamorphic period by up to nine days in shaded wetlands could mean the difference between successful metamorphosis or death.

Strong countergradient variation among wetlands separated by tens to hundreds of meters suggests that differences in environmental conditions distributed across small spatial scales are capable of influencing the distribution of genotypes. Although the pattern observed in this study could result from maternal effects, there was no evidence that egg size (an important transmitter of maternal effects to wood frog offspring; Berven 1988; Berven and Chadra 1988) was related to wetland light environment. A genotypic mechanism for the countergradient pattern is consistent with rapid divergence among wood frogs breeding in nearby wetlands. The light environment within wetlands can darken dramatically in as little as two decades as red maple (*Acer rubrum*) and other wetland associated plant species invade and then spread their crowns above the basin (Skelly et al. 1999). Disturbances such as clearing by humans or beavers (*Castor canadensis*) can immediately increase light levels within wetland basins (Skelly and Freidenburg 2000). Recent study of the canopy above wetlands suggests that it is a dynamic and critical agent of change for wetland dwellers such as wood frogs (reviewed by Skelly 2001). The results of this study imply that evolutionary responses to changes in the light and thermal environment within nearby wetlands may be both substantial and rapid. That these responses occur despite the ease with which wood frogs could move from one wetland to another suggests that philopatry is very high (Berven and Grudzien 1990), selection against invaders is extremely strong (Schluter 2000; Rundle and Whitlock 2001), or that emigrating wood frogs select new wetlands for breeding accounting for light and thermal conditions.

Although this study provides strong evidence for microgeographic countergradient variation, one wetland (Morse Bog) was an outlier in the common garden experiment. Morse Bog was the least shaded wetland, but embryos collected from Morse Bog developed as fast as any in the study under common garden conditions. The portion of Morse Bog used by wood frogs is a small flooded meadow that is about 200 m from the most heavily shaded wetland in the study (Blacksmith Pond). Embryos from Blacksmith Pond and Morse Bog had nearly identical developmental rates in the common garden experiment. While there is frequent successful recruitment from Blacksmith Pond, in many years Morse Bog ''dries'' prematurely when the vegetation mat lifts off the pond bottom and floats to the surface exposing aquatic organisms (D. K. Skelly, unpubl. data). It is possible that Morse Bog is a reproductive sink dominated by immigrants from other wetlands such as adjacent Blacksmith Pond. Comparable source-sink demographic patterns have been described in other amphibian systems (e.g., Tarkhnishvili and Gokhelashvili 1999; Trenham et al. 2000; Hels 2002). Alternatively, extremely rapid embryonic development in Morse Bog may be an evolved response to the shorter duration between egg laying and the timing of wetland drying.

As with all cases of countergradient variation, this study provokes an important question (Yamahira and Conover 2002). Why do wood frog embryos from unshaded wetlands develop at rates less than the physiological capacity demonstrated by conspecifics from shaded wetlands? Prior authors have invoked trade-offs to explain countergradient patterns (Conover and Schultz 1995; Arendt and Wilson 1999). In the case of anuran embryos, it is possible that decreases in embryonic period lead to hatchling phenotypes that are less capable at swimming or feeding or are less successful at dealing with predators (Warkentin 1995, 1999). An alternative to this trade-off hypothesis, that wood frogs from different wetlands have evolved to optimize development at different temperatures (Yamahira and Conover 2002), was not supported by the results of this experiment: embryos from the most heavily shaded wetlands tended to experience the most rapid development when reared in both low and high temperature treatments.

The results of this study have implications for the study of countergradient variation generally. Prior studies have focused on latitudinal or altitudinal temperature clines as agents of selection on development or growth. This study shows that local heterogeneity in thermal environments also can be critical to understanding countergradient variation. This means that researchers exploring macrogeographic patterns may need to carefully select study sites for which macrogeographic trends in climate are not confounded by the influence of local environmental variation. As an example, wetlands at higher altitudes are more likely to be relatively unshaded compared with those at lower elevations. In that case, local canopy conditions may be as important in understanding the strength of countergradient patterns as the influence of altitude on climate. More importantly, researchers interested in how a factor such as temperature may influence the evolution of a species will need to closely consider how geographic clines interact with local variation. Whereas research interests often sort by scale, the influence of temperature and other critical ecological agents may not.

The patterns uncovered in wood frogs highlight the potential for concurrence of countergradient and cogradient ef-

fects on the distribution of phenotypes across small scales of space. Wood frogs exhibit local cogradient variation in response to variation in the abundance of predators and potential competitors among wetlands (Relyea 2001, 2002). This study shows local countergradient variation in the same species at the same scale. As a consequence, developmental rate and other phenotypic traits of wood frogs may undergo simultaneous selection in opposite directions over very small scales of space and time. As Levins (1969) pointed out, limited variation in phenotypes across space may indicate selection just as strong variation does. For wood frogs, and probably for other species, a complete understanding of phenotypic variation will require explicit consideration of both countergradient and cogradient mechanisms.

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