Can natural phenotypic variances be estimated reliably under homogeneous laboratory conditions?

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Introduction

The phenotype is a major determinant of individual fitness, often mediated through associated variation in behaviour or performance (Arnold, 1983; Kingsolver & Huey, 2003), and is usually the foundation of evolutionary quantitative genetic analyses (Falconer & Mackay, 1996; Roff, 1997; Lynch & Walsh, 1998). Experimentalists seeking to illuminate links between phenotype, performance and fitness and to estimate essential quantitative genetic parameters have often turned to laboratory (or greenhouse) settings in an effort to control factors that complicate many field studies of the same questions. The results of these laboratory studies are then usually interpreted as providing meaningful insights into natural systems. But how environmentally realistic are the outcomes of these microevolutionary experiments?

Genes, environmental factors (including nongenetic parental effects), and genotype–environment interactions control the phenotypes of quantitative traits (Roff, 1997; Schlichting & Pigliucci, 1998). Abiotic environmental factors may play a reduced role in determining phenotypic variation in traits subject to substantial family (parental or genetic) effects, yielding similar phenotypes under diverse environmental conditions (but see West-Eberhard, 2003). In contrast, traits with environmentally induced phenotypic plasticity are commonly assumed to exhibit the greatest degree of plastic response in variable environments, whereas less variation is expected in constant environments (e.g. Bull et al., 1982; Mitchell-Olids & Rutledge, 1986; Janzen, 1992). If so, then difficulties arise in estimating meaningful quantitative genetic parameters of traits measured in usually less variable environmental conditions of the laboratory (but see Riska et al., 1989). In particular, heritability estimates (but not evolvabilities; see Houle, 1992) are fundamentally calculated from variance components, including the phenotypic variance (Falconer & Mackay, 1996; Roff, 1997; Lynch & Walsh, 1998).

To address this concern over environmentally induced phenotypic variance, Weigensberg & Roff (1996) reviewed the literature on wild animals and found eight...
studies that compared the heritability of traits in matched field and laboratory populations. These heritabilities did not differ significantly ($n = 22$ paired comparisons). Moreover, the phenotypic variances of traits (all of which pertained to insects) in the laboratory averaged 82% of those found in the corresponding field populations. These results suggest that, counter to common assumption, variance components of quantitative traits may not diverge greatly between the laboratory and the field. However, this conclusion is controversial and has been challenged on various grounds (e.g. Hoffmann, 2000; Hermida et al., 2002). Beyond differing environmental conditions and the taxonomic bias noted by Weigensberg & Roff (1996), a confounding statistical factor underlying such extrapolations is that the sibships (e.g. clutches, litters, seed sets, clones and lines) used in matched laboratory and field studies may not be the same. When using different sibships, genetic and parental effects that might influence phenotypic variation cannot be controlled explicitly, foisting additional inference onto interpreting the results. Instead, split-family or reciprocal transplant designs can better account for the phenotypic effects of environment and parentage (e.g. Gustafsson & Merila, 1994; Simons & Roff, 1994; Lynch & Walsh, 1998; Packard et al., 1999).

The thermal and hydric environments to which developing reptile embryos are exposed can substantially influence phenotypic traits of the resulting neonates (reviewed in Ewert, 1985; Deeming & Ferguson, 1991; Packard, 1999; Arnold & Peterson, 2002), which can have substantial fitness consequences (e.g. Janzen et al., 2000). Incubation experiments in this active field of inquiry are usually conducted under constant conditions in the laboratory, even though it is well known that the environment typically fluctuates extensively in natural nests (e.g. Plummer et al., 1994; Shine & Harlow, 1996; Packard et al., 1999). How fluctuating temperatures in particular influence development of embryos relative to constant conditions is increasingly recognized to be of some importance (Georges et al., 1994; Shine & Harlow, 1996; Shine et al., 1997; Andrews et al., 2000; Ashmore & Janzen, 2003). Even so, extrapolating laboratory results to the field occurs frequently (but usually with an awareness of the assumptions) in incubation experiments involving reptile eggs and embryos. Whether we can reasonably infer that conditions in the laboratory yield similar phenotypes of offspring (and clutches) as circumstances in the field thus remains a subject of controversy (e.g. Packard et al., 1999 vs. Rimkus et al., 2002).

Our study evaluates this controversy and helps redress the taxonomic bias and design shortcoming of nearly every prior microevolutionary analysis of this issue. We report an experimental assessment of variation in the means and variances of key phenotypic traits of hatchling common snapping turtles (Chelydra serpentina Linnaeus, 1758) deriving from clutches of eggs split between a constant common-garden setting in the laboratory and a naturally highly heterogeneous environment in the natal nest. The advantage of this split-family design is control of clutch effects that could otherwise complicate the applicability of laboratory results to the field. We examine body mass, carapace length, carapace width, plastron length and incubation time, traits that are influenced greatly by environmental factors and that have substantial fitness consequences as described above. We first compare the phenotypic means and variances of these traits between groups of siblings in the laboratory and field settings. We also explore whether increased variability in nest temperature in the field induces greater variation in hatching phenotypes. Our goal was not, and cannot be, to calculate quantitative genetic parameters in this study for reasons discussed below.

**Methods**

**Study organism and field methods**

The common snapping turtle, *C. serpentina*, is widespread throughout the eastern two-thirds of North America (Ernst et al., 1994), and ranges as far south as Ecuador. As in most species of turtles, eggs in a single *Chelydra* clutch are ovulated simultaneously (White & Murphy, 1973) and are oviposited with embryos all in a late gastrula stage (Ewert, 1985). Females (at least in the northern temperate zone) nest once per year at most (Ernst et al., 1994; Iverson et al., 1997).

We conducted field research in the Upper Mississippi River National Wildlife and Fish Refuge in Carroll and Whiteside Cos., IL, USA. The field site is mainly sand prairie with a riparian zone near the river, providing a diversity of nesting habitat. We patrolled the field site daily from 1 to 30 June 2001; nesting activity ($n = 48$) occurred between 7 and 27 June.

We employed a split-family design in which 12 eggs were removed from the top of each of 15 targeted nests for laboratory study ($n = 180$) (two eggs per nest were frozen for use in another study (St Juliana et al., 2004)). All other eggs ($n = 24–65$ per nest) remained to incubate in their natal nests. This sampling procedure is unlikely to have influenced our results because eggs of other freshwater turtles do not vary systematically in size in relation to order of oviposition (Tucker & Janzen, 1998). We placed the eggs extracted from the nests into chicken egg cartons containing damp sand and stored the cartons in shaded Styrofoam coolers for 1–4 days before transporting them to Iowa State University.

We protected most of the 15 focal nests with a cage containing a 3-cm grid of white, plastic-coated wire. Each cage was centred over the nest and secured with gardening rebar. The grid minimized disturbance to a nest site, allowing natural vegetation to persist through its openings. Several nests constructed in a sand road did not receive a cage for practical reasons. We briefly
re-opened 14 nests between 27 and 30 June to insert an external probe into the middle to record temperature. We then buried a logger (HOBO Temp; Onset Corp., Pocasset, MA, USA) adjacent to a given nest and connected it to the probe. Loggers recorded temperature every 45 min for about 7 weeks (~60–80% of development). We excavated all nests on 12 August to remove loggers and nearly hatched eggs \( (n = 609) \) for transport to Iowa State University. The unhatched eggs completed incubation in the laboratory (see below for details).

**Laboratory methods**

We placed the 10 unfrozen eggs from each clutch into a constant-temperature chamber that averaged \( 28.37 \pm 0.18 \, ^\circ \text{C} \) during incubation and \(-150 \, \text{kPa} \) water potential of the vermiculite incubation substrate (detailed in St Juliana et al., 2004). This thermal regime reflects mean temperatures recorded in *Chelydra* nests at the field site during the middle portion of incubation (Table 1, see also Kolbe & Janzen, 2002), a period of embryonic development that encompasses substantial organ differentiation and growth (Yntema, 1968, 1979; Ewert, 1985; Janzen, 2007). The experimental hydric environment is also representative of soil moisture availability recorded in *Chelydra* nests laid in sandy soils like those found at the field site (Packard et al., 1985). We incubated nearly hatched eggs retrieved from nests on 12 August in the same thermal and hydric conditions used for their laboratory-incubated siblings.

We checked all boxes two to three times day for hatchlings beginning 12 August and recorded incubation time as the number of days elapsed from oviposition until hatching. Upon hatching, we placed a turtle in a cup with a moist paper towel for 2 days to permit solidification of the carapace and absorption of the yolk sac and then scored the targeted phenotypic traits for all surviving hatchlings from laboratory-incubated \( (n = 137) \) and field-incubated \( (n = 564) \) eggs. We recorded body mass to the nearest 0.01 g and carapace length along the dorsal midline, carapace width at the widest point, and plastron length along the ventral midline to the nearest 0.01 mm. We released all surviving hatchlings at the field site on 16 September (St Juliana et al., 2004).

**Statistical analysis**

We used JMP version 5.1.1 (SAS Institute, Inc., 2004) for all statistical analyses, most of which employed means and variances of traits at the level of clutch. We examined relationships among nest and offspring characteristics in the laboratory and in the field with linear regression and correlation analyses and with analyses of variance. We also explored trait variation between laboratory- and field-incubated eggs using paired \( t \)-tests. We did not calculate any detailed quantitative genetic parameters (e.g. additive genetic variance) in this study because both the relatively small number of families \( (n = 15 \text{ clutches}) \) and the lack of information on parental phenotypes would probably yield wide standard errors (e.g. Simons & Roff, 1994). Furthermore, any estimate of heritability or genotype–environment interaction is likely to be inflated, and therefore relatively useless, because we cannot account for the important maternal effect of egg mass on offspring body size for the field-incubated eggs. Hence, we have focused conservatively on interpreting only phenotypic means and variances of the offspring.

**Table 1** Characteristics of 15 nests of common snapping turtles (*Chelydra serpentina*).

<table>
<thead>
<tr>
<th>Clutch</th>
<th>Date laid</th>
<th>Clutch size</th>
<th>Incubation temperature (°C)</th>
<th>Laboratory hatching success (proportion)</th>
<th>Field hatching success (proportion)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>8 June</td>
<td>63</td>
<td>31.36 ± 2.67</td>
<td>1</td>
<td>0.96</td>
</tr>
<tr>
<td>2</td>
<td>10 June</td>
<td>36</td>
<td>28.12 ± 2.33</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>3</td>
<td>10 June</td>
<td>49</td>
<td>28.86 ± 2.82</td>
<td>1</td>
<td>0.97</td>
</tr>
<tr>
<td>4</td>
<td>11 June</td>
<td>54</td>
<td>27.97 ± 1.84</td>
<td>1</td>
<td>0.95</td>
</tr>
<tr>
<td>5</td>
<td>11 June</td>
<td>73</td>
<td>26.08 ± 1.71</td>
<td>0.90</td>
<td>0.80</td>
</tr>
<tr>
<td>6</td>
<td>12 June</td>
<td>51</td>
<td>26.13 ± 1.80</td>
<td>0.90</td>
<td>1</td>
</tr>
<tr>
<td>7</td>
<td>12 June</td>
<td>50</td>
<td>N/A</td>
<td>0.80</td>
<td>0.53</td>
</tr>
<tr>
<td>8</td>
<td>12 June</td>
<td>33</td>
<td>N/A</td>
<td>0.80</td>
<td>0.95</td>
</tr>
<tr>
<td>9</td>
<td>12 June</td>
<td>75</td>
<td>N/A</td>
<td>1</td>
<td>0.90</td>
</tr>
<tr>
<td>10</td>
<td>12 June</td>
<td>35</td>
<td>N/A</td>
<td>0.90</td>
<td>1</td>
</tr>
<tr>
<td>11</td>
<td>12 June</td>
<td>38</td>
<td>27.68 ± 1.99</td>
<td>0.90</td>
<td>0.92</td>
</tr>
<tr>
<td>12</td>
<td>12 June</td>
<td>77</td>
<td>24.20 ± 1.88</td>
<td>0.90</td>
<td>0.97</td>
</tr>
<tr>
<td>13</td>
<td>14 June</td>
<td>53</td>
<td>28.59 ± 2.71</td>
<td>0.90</td>
<td>0.95</td>
</tr>
<tr>
<td>14</td>
<td>15 June</td>
<td>40</td>
<td>28.38 ± 2.48</td>
<td>0.90</td>
<td>0.82</td>
</tr>
<tr>
<td>15</td>
<td>20 June</td>
<td>73</td>
<td>27.24 ± 1.87</td>
<td>0.90</td>
<td>0.95</td>
</tr>
<tr>
<td>Mean</td>
<td>12 June</td>
<td>53.3 ± 15.6</td>
<td>27.69 ± 1.84</td>
<td>0.91 ± 0.07</td>
<td>0.91 ± 0.12</td>
</tr>
</tbody>
</table>

Incubation temperature is the mean (± 1 SD) recorded during the majority of embryonic development.
Phenotypic means and variances

As expected from numerous prior laboratory and field studies of this species, incubation time in the field was inversely correlated with nest temperature (|\(r| = 0.23, P = 0.0019, n = 11\)). Consequently, some eggs spent more time in the laboratory than others before hatching (mean ± 1 SD = 20.42 ± 0.88 days). Mean incubation time; |\(r| = 0.37, P < 0.0001\) for mean incubation length; |\(r| = 0.23, P = 0.0017\) for mean incubation temperature; |\(r| = 0.17, P > 0.10\) in all pairwise comparisons.

The clutch means of the four morphological traits, body mass, carapace length, carapace width, and plastron length, were all individually affected by the site of hatching (mean ± 1 SD = 29.02 ± 0.79 g, 11.90 ± 0.62 mm, 9.05 ± 0.41 mm, 31.64 ± 1.14 mm, respectively). Consequently, our sampling scheme included a negligible impact on the results of the study. As expected from numerous prior laboratory and field studies of this species, incubation time in the field was inversely correlated with nest temperature (|\(r| = 0.23, P = 0.0019, n = 11\)). Consequently, some eggs spent more time in the laboratory than others before hatching (mean ± 1 SD = 20.42 ± 0.88 days). Mean incubation time; |\(r| = 0.37, P < 0.0001\) for mean incubation length; |\(r| = 0.23, P = 0.0017\) for mean incubation temperature; |\(r| = 0.17, P > 0.10\) in all pairwise comparisons.
Fig. 1 Reaction norms for fitness-related traits of embryonic and neonatal common snapping turtles (*Chelydra serpentina*) deriving from 15 clutches. Eggs from each clutch were split between a constant incubation environment in the laboratory and the fluctuating incubation environment of the natal nest. Each line connects the laboratory and field means for a given clutch.

Table 3 Paired comparisons of means and variances of phenotypic traits for embryos and offspring from 15 clutches of common snapping turtle (*Chelydra serpentina*) eggs reared in a split-family design.

<table>
<thead>
<tr>
<th>Trait</th>
<th>Means</th>
<th>Variances</th>
<th>Variance ratios</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Correlations, ( r ) (( P ))</td>
<td>Paired t-tests, ( t ) (( P ))</td>
<td>Correlations, ( r ) (( P ))</td>
</tr>
<tr>
<td>Incubation time</td>
<td>+0.35 (0.1944)</td>
<td>2.71 (0.0169)*</td>
<td>+0.36 (0.1867)</td>
</tr>
<tr>
<td>Body mass</td>
<td>+0.92 (0.0001)</td>
<td>1.18 (0.2574)</td>
<td>–0.10 (0.7251)</td>
</tr>
<tr>
<td>Carapace length</td>
<td>+0.65 (0.0084)</td>
<td>0.67 (0.5136)</td>
<td>+0.06 (0.8322)</td>
</tr>
<tr>
<td>Carapace width</td>
<td>+0.79 (0.0005)</td>
<td>1.06 (0.3077)</td>
<td>–0.02 (0.9393)</td>
</tr>
<tr>
<td>Plastron length</td>
<td>+0.70 (0.0034)</td>
<td>0.34 (0.7417)</td>
<td>+0.17 (0.5443)</td>
</tr>
</tbody>
</table>

*P*-values for all comparisons are two-tailed. Variance ratios are the ratios of phenotypic variance in the field to phenotypic variance in the laboratory, calculated over all individuals.

*Mean incubation time was systematically longer in field-reared vs. laboratory-reared embryos.*
higher constant incubation temperature employed in the laboratory part of the experiment (i.e. 28.37 °C).

In contrast to the results from the comparisons of means, the variances of offspring traits from laboratory-incubated eggs were uncorrelated with the corresponding variances for traits of offspring derived from field-incubated eggs (Table 3). Similar to the examination of means, though, there was no tendency for the variance of any morphological trait for a given clutch to be larger in the field relative to its laboratory counterpart (Table 3). The variances in incubation time for field-incubated eggs were systematically greater than for their laboratory-incubated counterparts, however (Table 3). Because mean incubation times differed substantially between the laboratory and field settings (\( F_{1,28} = 6.04, P = 0.0205 \)), we also statistically compared the coefficients of variation for this trait and found no significant difference (paired \( t = 1.21, P = 0.2466 \)). Paired \( t \)-tests of the coefficients of variation for the morphological variables revealed no significant comparisons as well (paired \( t \leq 1.59, P \geq 0.13 \) in all four cases).

Neither the mean nor the variance in nest temperature was implicated as a cause of the observed among-nest differences in means and variances of offspring morphology. All 16 possible correlations between temperature and morphology variables were small and far from statistical significance (\(| r | \leq 0.44, P \geq 0.11 \)). In contrast, mean incubation time declined with increases in both the mean and the variance of nest temperature (\( r = -0.62, P = 0.0019 \) and \( r = -0.46, P = 0.0305 \) respectively); the variance in incubation time was not related to either measure of nest temperature, however (\( r = -0.10, P = 0.7672 \) and \( r = -0.09, P = 0.7962 \) respectively). To further explore the potential impact of temperature on phenotypic variation, we compared the mean and variance of nest temperature with the ratio of the field to laboratory phenotypic variances for each of the five traits of interest. In none of the 10 analyses was the correlation statistically significant (\(| r | \leq 0.37, P \geq 0.26 \)), indicating that neither measure of nest temperature was important in influencing phenotypic variation in the nest when controlling for phenotypic variation in the laboratory.

**Discussion**

A primary requirement of adaptive microevolution is additive genetic variance for the trait(s) of interest (Falconer & Mackay, 1996; Lynch & Walsh, 1998). This genetic parameter is usually estimated through breeding designs conducted under controlled conditions and reported in terms of heritability (but see Houle, 1992). Because these conditions are typically artificial, the investigator must assume that the genetic estimates are representative of those operative in natural systems. Yet quantitative traits can be heavily influenced by environmental conditions (Roff, 1997; Schlichting & Pigliucci, 1998), thus this assumption is debatable. Moreover, changes in global climate are predicted to derive primarily from greater environmental variance through increases in extreme meteorological events (Karl & Trenberth, 2003). Thus, from a practical perspective as well, it is critical that we understand how increases in environmental heterogeneity affect organismal phenotypes. We explicitly addressed these issues by examining key phenotypic traits of offspring with a split-family design that incorporated both typical constant conditions in the laboratory and heterogeneous environments of natural nests.

The primary result of our study is that the phenotypic variances of the focal traits did not differ consistently or significantly on a clutch-by-clutch basis between offspring from eggs reared either in the laboratory or in the field (Table 3). In other words, the phenotypic variances obtained in the laboratory for a given clutch were essentially representative of those obtained in the natal nest. Importantly, offspring sex ratios were similar in the laboratory and in the field (St Juliana et al., 2004), thus this result cannot be attributed to any aspects of temperature-dependent sex determination (Janzen, 2007).

These findings are important because the phenotypic variance is a fundamental component of the heritability of a trait (i.e. narrow sense heritability is the ratio of the additive genetic variance to the phenotypic variance, Falconer & Mackay, 1996; Lynch & Walsh, 1998). Thus, if the additive genetic variances are similar in both laboratory and field settings (likely a reasonable assumption in this study as families were split between the two settings; but see, e.g. Simons & Roff, 1994), the heritabilities of the traits examined should be comparable in both conditions as well. This conclusion from our experiment on a vertebrate accords with the important review by Weigensberg & Roff (1996), which documented little difference in phenotypic variances between laboratory- and field-reared insects for various traits (but see Hoffmann, 2000; Hermida et al., 2002; Conner et al., 2003).

Besides comparing phenotypic variances for eight matched laboratory–field studies, Weigensberg & Roff (1996) also assessed the relationship between heritability estimates from hundreds of different laboratory and field studies across a diversity of animal species, obtaining essentially the same result. This finding is encouraging, but the potential for publication bias, particularly against field studies that are more likely to estimate nonsignificant heritabilities because of smaller sample sizes than laboratory studies, cannot be ignored (e.g. Palmer, 2000). Thus, we emphasize again that one of the strengths of our experiment (see also Simons & Roff, 1994) is the split-family design, which overcomes potentially confounding genetic and parental effects and can minimize the need for prohibitively large sample sizes.

The phenotypic traits that we considered in this study possess at least two characteristics that render them...
especially effective candidates for testing the comparability of laboratory and field estimates in microevolutionary analyses. First, development time and body size have been linked to individual fitness in Chelydra and other organisms (e.g., Ultsch, 1989; Janzen, 1993; Bernardo, 1996; Janzen et al., 2000; but see Kolbe & Janzen, 2001). Because these traits are often under selection, estimates of their quantitative genetic parameters are particularly valuable for exploring microevolutionary dynamics (Grant & Grant, 1995; Sinervo & Doughty, 1996; Reznick et al., 1997). Second, prior laboratory (reviewed in Deeming & Ferguson, 1991; Packard, 1999; Arnold & Peterson, 2002) and field (Packard et al., 1993, 1999; Kolbe & Janzen, 2002; St Juliana et al., 2004) studies have linked phenotypic variation in these and other traits in reptiles to environmental variables, particularly temperature and substrate moisture during embryonic development. Thus, to the extent that these environmental factors varied in nature relative to the laboratory during this study, our experiment was ideally situated to document their impact on phenotypic differentiation and variation.

The near absence of differences in phenotypic means and variances between the laboratory and the natural nests was somewhat unexpected because we focused on traits known to be affected by thermal and hydric environments in the laboratory (Deeming & Ferguson, 1991; Packard, 1999). Although egg size is a major determinant of offspring size in Chelydra (Packard & Packard, 1993), cool, moist incubation conditions slow embryonic development and produce relatively larger neonatal common snapping turtles than warm, dry incubation environments (e.g., Packard et al., 1987). Of course, most of this prior research has centred on differences in trait means, rather than in trait variances, among (usually constant) incubation treatments. One notable exception explored the effects of controlled variation in incubation temperature (substrate moisture was held constant) on means and variances of offspring traits in smooth softshell turtles (Apalone mutica Lesueur, 1827). Of particular note, the phenotypic variances of all measures of body size (the same as those included in the present study) declined with increasing thermal variance (Ashmore & Janzen, 2003). Similarly, in the present experiment, the greater environmental heterogeneity inherent in natural nests generally did not translate into higher phenotypic variances than in the laboratory, as indicated by variance ratios less than one (Table 3).

The similarity of trait means and variances between the laboratory and the field indicates that we did not monitor soil moisture, prior research on Chelydra elsewhere has documented substantial and phenotypically meaningful levels of variation in water potential among nests constructed in similar soils (Packard et al., 1985, 1999). In sum, the ample variation in thermal (and likely hydric) conditions within and among nests did not consistently elicit correspondingly higher phenotypic variances in hatching turtles arising from eggs incubated in those nests compared with their siblings reared in the laboratory.

Our study is not without its limitations, however. We focused primarily on morphological traits, but other classes of traits (physiology, behaviour, life history, etc.) or phenotypes measured at different life stages could potentially yield different results. Also, we recorded temperatures during a limited, albeit important, fraction of the incubation period and only monitored temperatures in the centre of the nests. The contribution of temperatures at other times in development (especially during the first 2 weeks of incubation) to phenotypic variation is, thus, not known. Similarly, we removed eggs from the tops of nests, yet temperatures vary somewhat between the top and bottom of Chelydra nests (Wilhoft et al., 1983); this thermal variation could contribute to the phenotypic variation within and among nests. Finally, multiple paternity has been described in Chelydra clutches (Galbraith et al., 1993), which could contribute to errors in this study if paternity were distributed unevenly between eggs incubated in the laboratory and those that developed in the nests. Even so, the critical point is that we did not detect regular differences in phenotypic variances between the laboratory and the natural nests. To better address the possibility of nest matching by females and to quantify genotype–environment interactions in nature, our split-family design could be extended to a cross-fostering approach among nests. In this way, eggs from various clutches could experience multiple natural incubation environments, in addition to their natal nest environment and one or more homogeneous laboratory conditions.

Despite shortcomings, our experiment nonetheless showed that substantial levels of natural environmental heterogeneity did not have a great effect on phenotypic variances of key offspring traits in common snapping turtles. We also noted that phenotypic variances observed in the laboratory were generally representative of those detected in the field. Even so, we recognize that more research is required to determine whether our observations hold more broadly in vertebrates and in other taxa. Because experts predict forthcoming climate change to be characterized by increases in environmental heterogeneity (Karl & Trenberth, 2003), this issue holds implications as well for conservation research with a microevolutionary perspective. At the same time, field studies are not always practical for certain organisms. Consequently, extrapolating results from the laboratory or greenhouse to the field will likely always be a staple of
biological inquiry. Our work adds some confidence beyond the important review of Weigensberg & Roff (1996) that such extrapolations in microevolutionary experiments can be environmentally relevant and, thus, biologically meaningful.

Acknowledgments

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