The roles of phylogeny and climate in shaping variation in life-history traits of the newt genus *Triturus* (Caudata, Salamandridae)

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Assessing the origin of trait variation during evolutionary history is an important first step in understanding evolutionary diversification. Here, we tested the influence of shared ancestry and climate, and the interplay of both, on the variation of ten life history traits in *Triturus* newts. We showed that (1) climate alone has driven the evolution of variation in five life history traits, (2) phylogenetic signal partly explains the variation in two traits (vitellus diameter and snout–vent length of larvae at metamorphosis), and (3) the interplay of shared ancestry and climate explains the variation in one trait (snout–vent length of larvae at metamorphosis). This study highlights the coarse-grained influence of shared ancestry and climate on the structure of phenotypic trait variation in *Triturus* and provides a handle for more detailed, fine-grained studies on the evolution of phenotypic trait variation.

**Introduction**

Determining the role of environmental selection pressures in the evolution of phenotypic trait variation in related species is a major challenge for evolutionary ecologists. Constraints, defined as “any limitation on phenotypic evolution that results from past evolutionary change in a particular lineage” (Schwenk 1995) and often referred to as phylogenetic or intrinsic constraints, are important factors in shaping the effects of environmental selection pressures. Phylogenetic signal (or phylogenetic effect) means that closely related species tend to be phenotypically similar and is an outcome of constrained phenotypic evolution (Revell et al. 2008).

Many studies (in morphology, life history, behaviour, physiology and ecology) have focussed on elucidating patterns of trait variation across species driven by environmental selection pressures, while taking phylogenetic signal into account (e.g. Freckleton et al. 2002, Blomberg et al. 2003, Desveges et al. 2003). However, the majority of “phylogenetic correction” methods
attributes most of the explained variation in a trait to phylogeny and considers only the residual as explained by ecology (Westoby et al. 1995). Westoby et al. (1995) pointed out that part of the variation of a trait may not be related only to phylogeny or to ecology, but to both phylogeny and ecology “at the same time” as a potential outcome of phylogenetic niche conservatism. Phylogenetic niche conservatism is a tendency of lineages to retain their niche-related traits through speciation events (Wiens et al. 2010). For example, sister species could independently develop adaptive phenotypes, but, as they tend to inhabit the same kind of environment as their ancestors, they develop the same plesiomorphic trait.

To summarize, the drivers behind trait variation across species can be partitioned into three main components: (1) purely phylogenetic (intrinsic), where species traits evolve under constraints, (2) purely ecological (extrinsic), where species traits evolve in response to ecological drivers alone, and (3) phylogenetically structured environmental variation, where species traits related to niches are retained after speciation (Desdevises et al. 2003, Diniz & Bini 2008). Although life history traits are closely related to fitness and therefore tightly connected to ecological factors, many papers confirmed correlation of different life history traits and species’ phylogenetic history in different animal groups (e.g. Stearns 1983, 1984, Gotelli & Pyron 1991, Miles and Dunham 1992, Freckleton et al. 2002, Blomberg et al. 2003). Here, we focus on the role of climate and phylogeny in shaping life history traits in the genus Triturus (Amphibia, Caudata, Salamandridae), which is a well-recognized model system for evolutionary studies (e.g. Amtzen et al. 2007, Ivanović et al. 2012). For the genus Triturus, variation in life history traits has been studied in detail (see Appendix), and the phylogeny is well understood (Wielstra & Amtzen 2011). However, the life history traits of Triturus have never been analysed in a framework of the interplay of evolutionary history and climate.

The genus Triturus is a monophyletic clade divided into two coherent groups (Fig. 1), marbled newts (T. marmoratus, T. pygmaeus) and crested newts (T. carnifex, T. cristatus, T. dobrogicus, T. macedonicus, T. karelinii). It should be noted that T. karelinii comprises more than one species but as the taxonomy is currently not yet settled (see Wielstra et al. 2013a, 2013b) we treat it as a single unit; this should not affect our conclusions as there are as yet no known differences among the potential species involved (Amtzen 2003). The Triturus species show species-specific ecological demands (e.g. duration of the annual aquatic period being one of the most pronounced difference, Amtzen 2003, Amtzen et al. 2007, Ivanović et al. 2012) which is reflected in differences in many life history traits among Triturus species (see Fig. 1). We include the Pyrenean brook newt (Calotriton asper) as an outgroup. Despite its sister relationship to Triturus, C. asper has a completely different ecology, being adapted to a benthic life in mountain streams (Griffiths 1996), in contrast to Triturus newts, which congregate in stagnant water bodies to court, mate and lay eggs.

The aim of this study is to trace life history traits over a phylogeny and explore the drivers behind life history trait variation, which is a crucial step in providing important insights into whether the evolution of life history traits had an important role in the radiation of Triturus species. In order to do so, we explore the structure of life history trait variation in the genus Triturus by testing for (1) variation explained by shared ancestry, (2) variation explained by climate, and (3) variation explained by both, shared ancestry and climate.

**Material and methods**

**Phylogeny, climate and life history data**

The phylogeny of the Triturus species used in this study (Fig. 1) was obtained from Wielstra and Amtzen (2011). Phylogeny was expressed in the form of principal coordinates via a Principal Coordinate Analysis (PCoA: Gower 1966) computed from the patristic distance matrix. Then, following Desdevises et al. (2003), principal coordinates (PCs) were subjected to a forward selection procedure to select PCs that significantly contributed to the explanation of the dependent variable (life history trait). PCs selection procedure was performed for each life
history trait independently. Significant PCs were used as independent variables in a variation partitioning model. Patristic distances, PCoA and significance of PCs were calculated using the functions cophenetic, pcoa, and lmorig in the ape library (Paradis et al. 2004) of the R statistical package (R Development Core Team 2006).

As climatic data we used biomeclimatic variables available from the WorldClim database ver. 1.4 (http://www.worldclim.org, Hijmans et al. 2005). Data values were extracted from these data layers for 4480 Tiritus newt occurrences [311 T. karelinii, 139 T. macedonicus, 120 T. carnifex, 1695 T. cristatus, 136 T. dobrogicus, 1529 T. marmoratus, and 559 T. pygmaeus, locality data from Wielstra et al. (2012) and 491 Pyrenean brook salamander (C. asper) occurrences (GBIF)]. GBIF refers to the data obtained via the GBIF Data Portal (http://www.gbif.org/) originally supplied by the following: (1) Ministerio de MedioAmbiente, y Medio Rural y Marino. Dirección General de Medio Natural y Política Forestal. Inventario Nacional de Bio-

Fig. 1. The phylogeny of the genus Triturus according to Wielstra and Amtzen 2011 (left); numbers next to the species names represent the duration of the annual aquatic period (in months) and cartoons represent body shape (based on Vukov et al. 2011). Relative variation of life history traits is presented with horizontal bars (right). Early life history traits: black = length of egg (mm), grey = vitellus diameter (mm), white = duration of embryonic period (days), vertical lines = length of larvae immediately after hatching (mm), horizontal lines = snout–vent length (SVL) at metamorphosis. Late life history traits (average for both sexes): black = average age, grey = longevity, white = age at maturation, vertical lines = average SVL (from tip of the snout to the posterior end of the cloaca), horizontal lines = sexual size dimorphism (SSD) index.

diversidad 2007, Anfibios; (2) Museum of Vertebrate Zoology Berkeley; (3) Service du Patrimoine naturel, Muséum national d’Histoire naturelle, Paris; (4) Centre d’etudes de la neuf de la muntanyad’Andorra (CENMA), Institut d’Estudis Andorrans; (5) Smithsonian National Museum of Natural History; (6) University of Navarra, Museum of Zoology. Considering recommendations to use only biologically meaningful data based on life history knowledge of the model system (Austin 2007, Guisan & Thuiller 2005), we selected several uncorrelated (Pearson’s r < 0.7) climatic variables for further analyses (sensu Wielstra & Amtzen 2012): bio11 = mean temperature of the coldest quarter, bio16 = precipitation of the wettest quarter, bio17 = precipitation of the driest quarter. The median values of climate variables for each species were used as independent variables in a variation partitioning method.

Life history data of the Triturus newt species and C. asper were obtained from the published literature (see Appendix). If the data were
Variation partitioning method

In order to estimate what proportion of the life history traits are correlated with climate alone, phylogeny alone, and jointly with climate and phylogeny, we calculated several fractions (Fig. 2): (1) \([a + b]\), (2) \([b + c]\) and (3) \([a + b + c]\) (Deserves et al. 2003). The first fraction was defined as the regression of each life history trait to each climatic variable. The second fraction was defined as the regression of each life history trait to the PCs (represents phylogeny). The third fraction was defined as the regression of each life history trait to the significant PCs and climatic variables. Factors \([a]\) ("pure" climatic component) and \([c]\) ("pure" historical component) were found by two partial regression equations. Fraction \([a]\) was found by regressing climate to PCs and computing residuals. The partial regression was obtained by regressing life history traits on these residuals. Fraction \([c]\) was found by calculating residuals from the regression of each individual PC on each climate variable. Next, life history trait was regressed on those residuals via multiple linear regressions. As an unbiased estimator of the contribution of the fractions of variation in the variation partitioning model, the adjusted coefficient of determination \((r^2)\) was used (Peres-Neto et al. 2006). Variation partitioning and the tests of significance of the fractions were computed using the function `Imorigin` in the `ape` library (Paradis et al. 2004) of R (R Development Core Team 2006). All tests were performed through a permutation procedure using 9999 permutations.

Variation partitioning was performed for each life history trait separately by using each of the three climatic variables as an exploratory variable separately (10 life history traits × 3 climate variables = 30 variance partitioning procedures). PCs, a second set of exploratory variables, were used according to the results of the PC selection procedure described above.

Results

Mean values of the dependent variables (life history traits) and median values of the independent exploratory variables (climatic variables) are

![Variation partitioning method diagram](image_url)
shown in Tables 1 and 2. Results for the life history traits where all fractions are non-significant were not presented in the result section and are available upon request.

The phylogenetic (historical) component

The phylogeny of newts is expressed as principal coordinates, and PC1 and PC3 are selected as coordinates that contribute to the explanation of the life history traits. PC1 and PC3 represent 58.1% and 12.2%, respectively, of the total variance of the PCoA-transformed patristic distance matrix. PC3 contributes to the explanation of most of the life history traits while PC1 contributes to SVL at metamorphosis and age at maturation (Table 3). PC1 presents differences between *C. asper* + marbled newts and crested newts, while PC3 presents differences between *C. asper* and *Triturus* newts (Fig. 3).

After strict permutation procedures, only the variation of vitellus diameter and snout–vent length at metamorphosis contained a significant

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Table 1. Mean values of early life history traits and median values of climatic variables.

<table>
<thead>
<tr>
<th>Species</th>
<th>Length of egg (mm)</th>
<th>Vitellus diameter (mm)</th>
<th>Duration of EP (days)</th>
<th>Length of hatched larvae (mm)</th>
<th>SVL at metamorphosis (mm)</th>
<th>bio11 (°C)</th>
<th>bio16 (mm)</th>
<th>bio17 (mm)</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Triturus dobrogicus</em></td>
<td>3.75</td>
<td>1.74</td>
<td>19.97</td>
<td>9.18</td>
<td>37.10</td>
<td>0.24</td>
<td>219</td>
<td>114.5</td>
</tr>
<tr>
<td><em>T. cristatus</em></td>
<td>4.78</td>
<td>1.95</td>
<td>16.84</td>
<td>10.34</td>
<td>35.59</td>
<td>-2.35</td>
<td>223</td>
<td>112</td>
</tr>
<tr>
<td><em>T. carnifex</em></td>
<td>4.38</td>
<td>1.75</td>
<td>13.65</td>
<td>9.25</td>
<td>31.50</td>
<td>3.06</td>
<td>300.5</td>
<td>151</td>
</tr>
<tr>
<td><em>T. macedonicus</em></td>
<td>3.89</td>
<td>2.28</td>
<td>19.89</td>
<td>10.14</td>
<td>34.28</td>
<td>1.68</td>
<td>292</td>
<td>129</td>
</tr>
<tr>
<td><em>T. karelinii</em></td>
<td>4.29</td>
<td>1.99</td>
<td>14.89</td>
<td>9.65</td>
<td>33.25</td>
<td>1.62</td>
<td>237</td>
<td>110</td>
</tr>
<tr>
<td><em>T. pygmaeus</em></td>
<td>3.75</td>
<td>1.75</td>
<td>12.50</td>
<td>10.00</td>
<td>25.88</td>
<td>8.57</td>
<td>224</td>
<td>32</td>
</tr>
<tr>
<td><em>T. marmoratus</em></td>
<td>4.25</td>
<td>1.88</td>
<td>20.00</td>
<td>9.25</td>
<td>28.74</td>
<td>5.07</td>
<td>256</td>
<td>110</td>
</tr>
<tr>
<td><em>Calotriton asper</em></td>
<td>5.00</td>
<td>4.08</td>
<td>24.33</td>
<td>12.93</td>
<td>34.38</td>
<td>0.53</td>
<td>311.5</td>
<td>229.5</td>
</tr>
</tbody>
</table>

EP = embryonic period, SVL = snout–vent length, bio11 = mean temperature of the coldest quarter, bio16 = precipitation of the wettest quarter, bio17 = precipitation of the driest quarter.
phylogenetic signal (fraction \([b + c]\), Table 3 and Fig. 2). However, the “pure” phylogenetic component (fraction \([c]\)) was not significant (Table 3), which means that the phylogenetic component for these life history trait variations overlaps to a great extent (fraction \([b]\)) with the climatic component. Only for snout–vent length at metamorphosis variation, when the precipitation of the wettest quarter was used in a full model \((a + b + c)\), a “pure” historical component was extracted \((r^2 = 0.582, p = 0.007\); Table 3). Although tests show that fractions \([a]\), \([b]\) and \([c]\) were not significant for all traits for which a signal was confirmed, we noticed a potentially important role of fraction \([b]\) in the phylogenetic signal \((b + c)\). The phylogenetic signal in the variation of vitellus diameter is a consequence of the large vitellus in _C. asper_ as compared with that in _Triturus_ newts, while the signal in snout–vent length at metamorphosis is a consequence of smaller size at metamorphosis of marbled newts as compared with other newts.

The climatic component

A significant portion of the snout–vent length at metamorphosis variation was explained by the mean temperature of the coldest quarter (fraction \([a + b]\), \(r^2 = 0.788\); see Table 3). Precipitation of the wettest quarter explained a significant portion of the variation of average age in males \((r^2 = 0.606)\) and females \((r^2 = 0.603)\) and age at maturation for males \((r^2 = 0.483)\) (fraction \([a + b]; \text{see Table 3}\). The portion of duration of embryonic period variation was explained by the precipitation of the driest quarter (fraction \([a + b]\), \(r^2 = 0.370\); see Table 3). However, the “pure” climatic component (fraction \([a]\)) was significant only for age at maturation for both males and females (Table 3).

**Discussion**

The variation in five out of ten tested life history traits among _Triturus_ species can be explained by climate or phylogeny (vitellus diameter, duration of embryonic period, snout–vent length at metamorphosis, age at maturation and average age). Only two of these five life history traits (snout–vent length at metamorphosis and vitellus diameter) showed a phylogenetic signal.

Differentiation within life history traits is likely to have been driven by natural selection considering their tight link to the environment. Temperature has a profound impact on life history traits of newts, where higher temperatures cause smaller egg size and vitellus diameter, a shorter embryonic period, a smaller size of hatched larvae, a shorter life span (i.e. the mean population age is lower) and earlier maturation (e.g. Griffiths & de Wijer 1994). Precipitation, together with temperature, also has a strong influence on life histories of newts. Under more unstable precipitation seasonality and at a higher temperature of the coldest quarter, larvae are smaller at metamorphosis. In general, individu-

**Table 2.** Mean values of late life history traits.

<table>
<thead>
<tr>
<th>Species</th>
<th>Average age (years)</th>
<th>Longevity (years)</th>
<th>Age at maturation (years)</th>
<th>SVL (mm)</th>
<th>SSD</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>males</td>
<td>females</td>
<td>males</td>
<td>females</td>
<td>males</td>
</tr>
<tr>
<td><em>Triturus dobrogicus</em></td>
<td>3.58</td>
<td>3.69</td>
<td>6.50</td>
<td>7.00</td>
<td>2.00</td>
</tr>
<tr>
<td><em>T. cristatus</em></td>
<td>6.12</td>
<td>6.00</td>
<td>15.75</td>
<td>13.25</td>
<td>3.00</td>
</tr>
<tr>
<td><em>T. carnifex</em></td>
<td>6.65</td>
<td>6.85</td>
<td>11.50</td>
<td>13.50</td>
<td>3.50</td>
</tr>
<tr>
<td><em>T. macedonicus</em></td>
<td>8.80</td>
<td>8.30</td>
<td>14.00</td>
<td>13.00</td>
<td>3.80</td>
</tr>
<tr>
<td><em>T. karelinii</em></td>
<td>5.50</td>
<td>5.63</td>
<td>9.00</td>
<td>9.00</td>
<td>3.25</td>
</tr>
<tr>
<td><em>T. pygmaeus</em></td>
<td>5.86</td>
<td>5.94</td>
<td>12.00</td>
<td>10.00</td>
<td>3.50</td>
</tr>
<tr>
<td><em>T. marmoratus</em></td>
<td>6.64</td>
<td>7.38</td>
<td>12.00</td>
<td>12.33</td>
<td>3.75</td>
</tr>
<tr>
<td><em>Calotriton asper</em></td>
<td>11.98</td>
<td>13.78</td>
<td>22.00</td>
<td>24.00</td>
<td>6.15</td>
</tr>
</tbody>
</table>

SVL = snout–vent length, SSD = sexual size dimorphism, m = males, f = females.
Table 3. Results of variation partitioning of life history traits between phylogenetic and climatic component. p values indicating significance are set in boldface. SVL = snout-vent length.

<table>
<thead>
<tr>
<th></th>
<th>[a + b + c]</th>
<th>[a + b]</th>
<th>[b + c]</th>
<th>[a]</th>
<th>[b]</th>
<th>[c]</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Mean temperature of the coldest quarter (bio11)</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Vitellus diameter (PC3)</td>
<td>0.739</td>
<td>0.0488</td>
<td>0.080</td>
<td>0.5128</td>
<td>0.735</td>
<td>0.0296</td>
</tr>
<tr>
<td>SVL at metamorphosis (PC1 &amp; PC3)</td>
<td>0.825</td>
<td>0.0165</td>
<td>0.788</td>
<td>0.0010</td>
<td>0.717</td>
<td>0.0291</td>
</tr>
<tr>
<td><strong>Precipitation of the wettest quarter (bio16)</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Average age (females) (PC3)</td>
<td>0.575</td>
<td>0.0443</td>
<td>0.603</td>
<td>0.0021</td>
<td>0.242</td>
<td>0.2792</td>
</tr>
<tr>
<td>Average age (males) (PC3)</td>
<td>0.560</td>
<td>0.0360</td>
<td>0.606</td>
<td>0.0017</td>
<td>0.188</td>
<td>0.1495</td>
</tr>
<tr>
<td>Age at maturation (females) (PC1 &amp; PC3)</td>
<td>0.652</td>
<td>0.0206</td>
<td>0.339</td>
<td>0.0758</td>
<td>0.705</td>
<td>0.0528</td>
</tr>
<tr>
<td>Age at maturation (males) (PC1)</td>
<td>0.774</td>
<td>0.0010</td>
<td>0.483</td>
<td>0.0051</td>
<td>0.192</td>
<td>0.1541</td>
</tr>
<tr>
<td>Vitellus diameter (PC3)</td>
<td>0.728</td>
<td>0.0263</td>
<td>0.276</td>
<td>0.1040</td>
<td>0.735</td>
<td>0.0296</td>
</tr>
<tr>
<td>SVL at metamorphosis (PC1 &amp; PC3)</td>
<td>0.753</td>
<td>0.0423</td>
<td>0.161</td>
<td>0.8715</td>
<td>0.717</td>
<td>0.0291</td>
</tr>
<tr>
<td><strong>Precipitation of the driest quarter (bio17)</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Vitellus diameter (PC3)</td>
<td>0.689</td>
<td>0.1300</td>
<td>0.240</td>
<td>0.1232</td>
<td>0.735</td>
<td>0.0296</td>
</tr>
<tr>
<td>Duration of embryonic period (PC3)</td>
<td>0.253</td>
<td>0.1890</td>
<td>0.370</td>
<td>0.0489</td>
<td>0.183</td>
<td>0.1601</td>
</tr>
<tr>
<td>SVL at metamorphosis (PC1 &amp; PC3)</td>
<td>0.673</td>
<td>0.0791</td>
<td>0.405</td>
<td>0.0683</td>
<td>0.717</td>
<td>0.0291</td>
</tr>
</tbody>
</table>

*p values not available because r²[b] was calculated as r²[b + c] - r²[c].
traits among *Triturus* species. Precipitation of the wettest quarter had a strong positive effect on the average age and age at maturation, suggesting that newt species that live in regions with high precipitation (usually during winter) are older and mature later. Regarding *Triturus* species, *T. dobrogicus* has the “youngest” populations, with individuals that mature early, while *T. macedonicus* has the “oldest” populations, with individuals that mature late. *Calotriton asper* has much older individuals in populations that mature later in comparison with *Triturus*. Seasonal temperature regimes have a major impact on growth and sexual maturation, as amphibians in colder climates (high altitudes and latitudes) grow more slowly and reach maturity later than amphibians in warmer climates (e.g. Liao & Lu 2012). Our analysis did not show a direct connection between mean temperature of the coldest quarter and age and maturation for *Triturus* species, but higher precipitation is usually present at higher altitudes and therefore could be treated, cautiously, as a proxy for seasonal temperature regimes. Precipitation of the driest quarter had a strong positive effect on duration of the embryonic period, suggesting that newt species that live in drier regions have a shorter embryonic period (such as *T. pygmaeus*). *Calotriton asper* has a much longer embryonic period in comparison with *Triturus*. Again, this prolonged embryonic period is best explained in the literature by low temperatures during embryonic development at high altitudes (Griffiths & de Wijer 1994). Precipitation of the driest quarter can be used as a proxy, again cautiously, for such seasonal temperature regimes.

Although life history traits are under strong influence of the environment, their variation patterns could be shaped by shared ancestry, which we detect as a phylogenetic signal in trait variation. We detected a phylogenetic signal in the variation of vitellus diameter and snout–vent length at metamorphosis. Phylogenetic signal in the variation of vitellus diameter is detected at the node between *C. asper* and *Triturus*, where *C. asper* has a larger vitellus. Phylogenetic signal of variation in snout–vent length at metamorphosis is detected at the node that separates marbled newts from *C. asper* on one side and crested newt on the other side, where marbled newts have a smaller snout–vent length at metamorphosis.

Since life history traits show a connection with climate, the variation patterns in life history traits found in *Triturus* could be a consequence of niche evolution. Given the ecological variation in *Triturus* observed today, climatic niche differentiation probably has an important role during the evolution of *Triturus* (Wielstra et al. 2012). We tried to quantify the shared influence of climate and phylogeny on life history trait variation patterns in *Triturus*, which represent the potential effects of niche evolution on life history traits. Only for snout–vent length at metamorphosis did we detect a significant influence of both fractions; climate (mean temperature of the coldest quarter) \(a + b\), and phylogeny \(b + c\). However, we failed to extract a “pure” climatic \(a\) and a “pure” historical \(c\) component and their overlap \(b\) (see Fig. 2), which means there could be a large overlap between climate and phylogeny. This result implies that phylogenetic signal in the pattern of variation of snout–vent length at metamorphosis could potentially be a consequence of niche change along the marbled newt branch, where marbled newts have become adapted to warmer climate. Regarding phylogenetic signal in variation of the vitellus diameter, we detected a significant influence of phylogeny \(b + c\) but failed to extract a “pure” historical component. This means that the variation pattern of vitellus diameter is under the influence of phylogeny but we still have to elucidate if there is a shared influence of climate and phylogeny.

Our analyses of the influence of climate and a shared history on life history trait variation among *Triturus* confirmed the presence of a phylogenetic signal for two life history traits. However, we cannot rule out the presence of signals in the other eight life history traits. Besides climatic influences on life histories, other factors like differences in biotic interactions, and the abundance of natural enemies, competitors and food resources can influence variation in life history traits. We have to keep in mind that phenotypic plasticity also influences the variation in life histories. A study on environment–life history traits variation in the light of phylogeny for a wider set of species (e.g. the whole Sala-
mandridae family) is a logical next step to better understand the evolution of life history traits.

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43 Maletzky, A., Pesta, J., Schabetsberger, R., Jelše, R., Sztatecsny M. & Goldschmidt, A. 2004: Age structure and size of the synoptic populations of Triturus carnifex (Laurenti, 1768), Triturus vulgaris (Linnaeus, 1758) and Triturus alpestris (Laurenti, 1768) in the lake Ameise-see (1282 m a.s.l.). — Herpetozoa 17: 7–82.


50 Miles, D. B. & Dunham, A. E. 1992: Comparative analysis of phylogenetic effects in the life history patterns of...
**Appendix.** List of data sources used in this study to obtain life history traits. Numbers correspond to those in the references list.

<table>
<thead>
<tr>
<th>Species</th>
<th>Length of egg</th>
<th>Vitellus diameter</th>
<th>Duration of EP</th>
<th>Length of hatched larvae</th>
<th>SVL at metamorphosis</th>
<th>Average age</th>
<th>Longevity</th>
<th>Age at maturation</th>
<th>SVL</th>
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