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Life history variation in North American freshwater minnows: effects of latitude and phylogeny

Nicholas J. Gotelli and Mark Pyron

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We examined the relationship between latitude, phylogeny, and interspecific variation in life history traits of 21 species of North American minnows with a well-resolved phylogeny. Only one life history trait was significantly correlated with latitude: species at higher latitudes had shorter spawning seasons than did species at lower latitudes. Two measures of body size showed evidence of a phylogenetic correlate. Total female body length at maturity and maximum total female body length were more similar for closely related species pairs than for distantly related species pairs. Moreover, total female body length at maturity was correlated with the position of each species in Mayden's cladogram of cyprinid fishes: species close to the root of the cladogram had relatively small body sizes compared with species that were more distant from the cladogram root. This pattern is reminiscent of Cope's Law of phyletic increase in body size within a lineage. Although phylogenetic correlates are most common at high taxonomic levels (the "taxon-level effect" of Pagel and Harvey), phylogeny was a significant predictor of body size in this closely related group of minnows. Both historical factors, such as phylogenetic relationships, and ecological factors, such as latitude, probably contribute to interspecific variation in life history traits of minnows.

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Ecological factors such as environmental stability play a key role in the evolution of life history traits (Dobzhansky 1950, MacArthur and Wilson 1967, Schaeffer 1974, Stearns 1976). For example, the r-K selection model (MacArthur and Wilson 1967, Pianka 1970) and the bet-hedging model (Murphy 1968, Schaeffer 1974) each predict a different suite of life history traits, depending on whether mortality is variable in the adult (r-K selection) or juvenile (bet-hedging) stages. Thermal gradients may also impose energetic constraints on organisms that ultimately affect the evolution of life history traits (Levinton 1983, Conover and Present 1990).

Modern tropical environments are relatively warmer and less seasonal than temperate environments (Stevens 1989), and life history traits in many taxa vary systematically along a latitudinal gradient, both within (Lonsdale and Levinton 1985) and between (Thorson 1950) species. Latitudinal variation in life history traits may result from genetic differentiation of local populations (Berven and Gill 1983) and/or phenotypic plasticity of individuals living in different environments (Mann et al. 1984).

These approaches to understanding life history traits emphasize ecological factors, such as the temperature or seasonality of tropical and temperate environments, as important selective forces (Partridge and Harvey 1988). Thus, latitudinal gradients in life history traits may reflect gradients in life history tactics, "a set of co-adapted traits designed, by natural selection, to solve particular ecological problems" (Stearns 1976).

An alternative viewpoint is that the features of an organism – including its life history traits – do not necessarily represent a "solution" to a current ecological problem (Gould and Lewontin 1979). Rather, organisms may exhibit certain properties because of histor-

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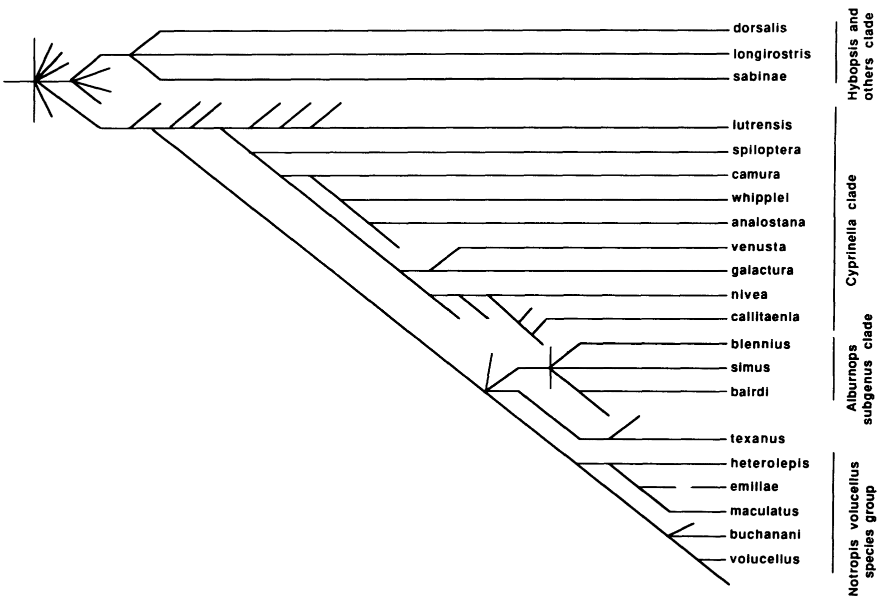

Fig. 1. Cladogram derived from Mayden's (1989) phylogenetic analysis of *Notropis*. This composite cladogram is constructed from Figures 1, 4, 5, 6, and 85 in Mayden (1989). Only the 21 species used in this analysis are illustrated. All interior nodes of the cladogram are also displayed.

ical legacy (Brooks 1985). Thus, a particular life history trait may not represent an adaptation to a current environment, but may be present simply because it was inherited from an ancestral population or taxon (Coddington 1988). Interspecific differences in life history traits could reflect different phylogenetic pathways rather than adaptations to different ecological conditions. A phylogenetic perspective has proven useful for understanding the evolution of life history and behavioral traits in a variety of taxa (Dobson 1985, Sillén-Tullberg 1988, Carpenter 1989, Murphy 1989). Kochmer and Handel (1986) suggest that phylogeny should be used as a "null hypothesis" for testing ecological models.

Patterns of variation in life history traits are often sensitive to the taxonomic level of comparison (Stearns 1976). At higher taxonomic levels, differences between species in life history traits are often pronounced (Pianka 1970), whereas, at lower taxonomic levels, patterns of variation may be less clear-cut (Murphy 1989). For example, 70% of the interspecific variation in mammalian life history traits occurs at the level of order, but only 18% at the level of family (Stearns 1983). This "taxon-level effect" may itself have an adaptive basis if ecological conditions are more similar among closely related species than among distantly related ones (Pagel and Harvey 1989). Thus, phylogeny and current ecology do not represent mutually exclusive hypotheses, but provide alternative perspectives from which to view life history variation.

In this study, we compare life history traits among 21 species of freshwater North American minnows which already have a well-resolved phylogeny (Mayden 1989). We ask whether life history traits are more closely associated with phylogeny, as measured by each species' position within a cladogram, or by current ecological conditions, as measured by the latitude of the collection site for each species.

Materials and methods

Data sources. We compiled data on 6 life-history traits of 21 species of freshwater North American minnows. These species are morphologically rather similar and were all classified in the genus *Notropis* until recently. They have been the subject of a recent detailed systematic revision (Mayden 1989). Fig. 1 is a composite cladogram derived from Mayden's (1989) phylogenetic analyses of North American minnows. Only the cladogram branch tips with the 21 species used in this study are shown, although all interior nodes in the cladogram are also illustrated.

For each species, we gathered from the literature information on six life history traits: length of spawning season, age at maturity, total body length at maturity, mean diameter of mature ova, and maximum age and maximum total body length of individuals in the population (see Appendix 1 for data and sources). Length of spawning season was measured in weeks and was based on observations of a population through at least one spawning season and often through an entire year. These data must be considered cautiously because spawning season of cyprinids is possibly confounded by multiple clutching in some species (Heins and Rabito 1986). Age and size at maturity were measured as the age in years and the total body length in millimeters at which females were reported to first have the ability to spawn. For each species, we used the mean diameter of mature ova in millimeters or the midpoint of the reported range of mature ova diameters. Maximum age was defined as the oldest year-class present in a population. Because sexual dimorphism in body size of fishes is common (Nikolsky 1963: 163), only female body size data were used.

When replicate measures of a trait were available from different studies (11 species), we used the mean value of the trait, and the mean latitude of collection. With one exception, replicate populations differed by less than 4 degrees latitude, so the averages were not greatly distorted by measurements from widely separated populations.

Statistical analyses. To compare life history traits at different latitudes, we used a simple linear regression of each life history trait on the latitude of the collection site. Although we are describing interspecific variation in life history traits, intraspecific variation may represent a potential source of bias, especially if life history traits within a species vary latitudinally among populations (Berven and Gill 1983). Thus, our results could be affected by the latitude of the population from which the life history trait was measured. However, we obtained very similar correlations of life history traits with latitude by using the midpoint of the species' latitudinal range rather than the latitude of the collection site. This finding suggests that intraspecific variation is probably not so large as to completely obscure interspecific correlations, although intraspecific variation is probably an important source of "noise" in these analyses.

The comparison of life history traits with phylogeny is less straightforward, as it is difficult to assign a single phylogenetic "value" to each species that could be used as a predictor of life history traits in a simple regression analysis. Recently, a variety of new methodologies for analyzing comparative data have been proposed (Ridley 1983, Pagel and Harvey 1988), including nested analyses of variance (Stearns 1983) and phylogenetic regressions (Felsenstein 1985). Unfortunately, many of these methods require large sample sizes and/or unrealistic assumptions, which limit their usefulness. Moreover, some of these techniques merely assign species according to taxonomic rank and do not make direct use of phylogenetic information in cladograms (Wanntorp et al. 1990).

For this analysis, we used two tests of association between life history and phylogeny. Both tests treat each life history trait as a continuous dependent variable. The independent variable is a measure of phylogenetic distance based on the structure of the interior nodes of the cladogram in Fig. 1.

Our first test was a simple correlation between the life history trait and the number of nodes separating each species from the root of the cladogram. This measure, a modification of the "cladistic distance" of Farris (1969), describes the "primitiveness" of each species. Species close to the root of the cladogram are characterized by a suite of relatively primitive or ancestral morphological traits. In contrast, species far removed from the cladogram root are characterized by more derived morphological character states. Thus, the number of nodes separating each species from the cladogram root can be taken as a simple index of primitiveness and used in a standard regression analysis with life history traits. If there are no phylogenetic effects, there should be no association between life history traits and the primitiveness index.

An alternative approach would treat life history variables as cladistic characters and then constructs parsimonious cladograms that may reveal phylogenetic patterns (e.g., Coddington 1988, McLennan et al. 1989). We see two problems with this approach in our study. First, continuous life history traits would have to be gap-coded (Thorpe 1984, Archie 1985), i.e., arbitrarily split into discrete traits for cladistic analysis. The existing gap-coding algorithms may generate conflicting results (Chappill 1990), and gap-coding always results in a loss of information from the original continuous variable (Pagel and Harvey 1988). Second, a cladistic analysis would necessitate polarizing life history characters. For example, even if body size were gap-coded, it would still be necessary to decide whether small body size represents the ancestral or derived character state. It is difficult to polarize life-history traits without a specific evolutionary hypothesis in mind (e.g., Carpenter 1989). Indeed, one of the goals of this study is to let the true polarity of each character identify itself, i.e., to reveal suites of life-history traits that are relatively primitive or derived. For these reasons, we have chosen to treat the life history traits as dependent response variables, and the phylogenetic information in the cladogram as the independent predictor variable.

For our second test of phylogenetic association, we adapted the Mantel test (Mantel 1967) to assess the degree of the association between phylogeny and life history. For a set of n species, the Mantel test is a measure of association between two symmetric $n \times n$ difference matrices (Schnell et al. 1985): here, one matrix was used for phylogeny and the other for life history. The entries in the phylogeny matrix represented the phylogenetic distance between all unique pairs of species. As in the primitiveness test, we used the number of nodes between each species pair in the cladogram as a simple measure of distance. The entries in the life history matrix were the pairwise differences in the measured life history trait between all unique pairs of species. For the purposes of the Mantel test, we treated polychotomous branches in the cladogram of Fig. 1 as separate nodes, because a dichotomous tree would result from a fully resolved phylogeny (Wiley 1981).

The Mantel test assesses the hypothesis that there is no relationship between phylogenetic distance and life history differences among species. A positive correlation between phylogeny and life history differences would suggest a phylogenetic association: the more

Table 1. Correlations between life history traits of North American minnows, latitude and phylogeny. Each entry is the product moment correlation between two variables. Two-tailed probability values are given in parentheses, and the sample size for each association is given in brackets. The first column lists the six life history variables, and the remaining three columns give the predictor variables. Latitude is the latitude of the collection site. The Mantel test measures the association between the pairwise differences in life history traits and the number of nodes separating each species pair on the cladogram in Fig. 1. – The primitiveness test measures the correlation between life history traits and the number of nodes separating each species from the root of the cladogram in Fig. 1. See text for details.

Life history trait	Latitude	Phylogeny	
		Mantel test	Primitiveness test
Length of Spawning season [18]	-0.696 (0.001)	0.296 (0.991)	-0.254 (0.308)
Age at maturity [12]	0.240 (0.452)	0.092 (0.777)	-0.081 (0.800)
Total female body length at maturity [11]	-0.081 (0.812)	0.523 (0.0008)	0.676 (0.022)
Mature ova diameter [11]	0.121 (0.724)	0.171 (0.106)	0.210 (0.534)
Maximum age [12]	0.283 (0.373)	0.141 (0.170)	0.580 (0.048)
Maximum total female body length [18]	0.185 (0.463)	0.191 (0.046)	0.286 (0.250)

closely related two species are, the more similar their life history traits should be from inheritance per se (Moore and Gotelli 1990). The scattergram of species-pair points can be evaluated with the product-moment correlation coefficient (Pearson's *r*), although the Mantel test of significance takes into account the fact that the pairwise points are not independent of one another.

Results of the primitiveness test and the Mantel test are not independent of one another, although they do test for slightly different patterns. The Mantel test will reveal any association between life history traits and phylogeny, whereas the primitiveness test examines the more specific hypothesis that between-species variation in life history traits is proportional to the number of nodes separating each species from the cladogram root.

Cheverud et al. (1989) discuss three limitations of the Mantel test. First, the test is sensitive to skewness and non-linearity of the data (Dietz 1983, Faust and Romney 1985). We found that results of the Mantel test were sensitive to whether or not the difference measures were transformed to absolute values. In most cases only the untransformed distance data gave significant correlations, which we report here. Second, the test cannot incorporate "missing" data. We calculated associations only between species pairs for which both the life history trait and the midpoint of the geographic range were available. Conseguently, slightly different sets of species (and sample sizes) were used to calculate associations with different life history traits. Finally, the test is sensitive to small sample sizes. Cheverud et al. (1989) recommend a Monte Carlo simulation, but we used the large-sample approximation to the Mantel test. The large sample approximation compares favorably with Monte Carlo results for sample sizes as small as 10 (Moore and Gotelli 1990). Note that the large-sample approximation is usually a conservative test: it decreases the probability of incorrectly rejecting the null hypothesis.

To insure that the tests for phylogeny and latitude effects were equally powerful, we also conducted the Mantel test for associations between life history traits and latitude. The results were qualitatively similar to the simple regressions, although the Mantel test usually generated lower probability values. These findings suggest that it is appropriate to compare associations using the Mantel test and ordinary least-squares regressions. For both the simple regressions and the Mantel tests, we used two-tailed tests of significance.

In theory, both latitude and phylogeny could be simultaneously incorporated into a multiple regression analog to the Mantel test (Smouse et al. 1986). However, small sample sizes precluded such an analysis, so we have used only univariate tests.

Simple correlations may be confounded if both of the predictor variables (latitude and phylogeny) are themselves intercorrelated. However, the Mantel test between phylogeny and the midpoint of each species' geographic range was not significant ($r = 0.144$, $p = 0.457$). This does not imply that there is no relationship between phylogeny and biogeography; indeed some clades within *Notropis* (sensu lato) do appear to follow generalized tracks (Mayden 1988). Rather, the non-significant association suggests there is no simple linear relationship between phylogeny and the midpoint of the latitude of a species' geographic range.. Thus, it is appropriate to consider latitude and phylogeny as independent predictors of life history traits.

We recognize that an analysis of several probability tests does not control for the "family-wide" error rate for the set of comparisons (Day and Quinn 1989), although this is somewhat balanced by the weaker power of the Mantel test for modest sample sizes. However, we are primarily interested in the distribution of significant associations with latitude and phylogeny rather than the exact probability associated with any particular test.

Results

Only one life history trait was significantly correlated with latitude (Table 1). At higher latitudes, spawning season decreased (Fig. 2). Length and age at maturity, maximum age, maximum length, and mean ova diameter were not significantly correlated with latitude. Two

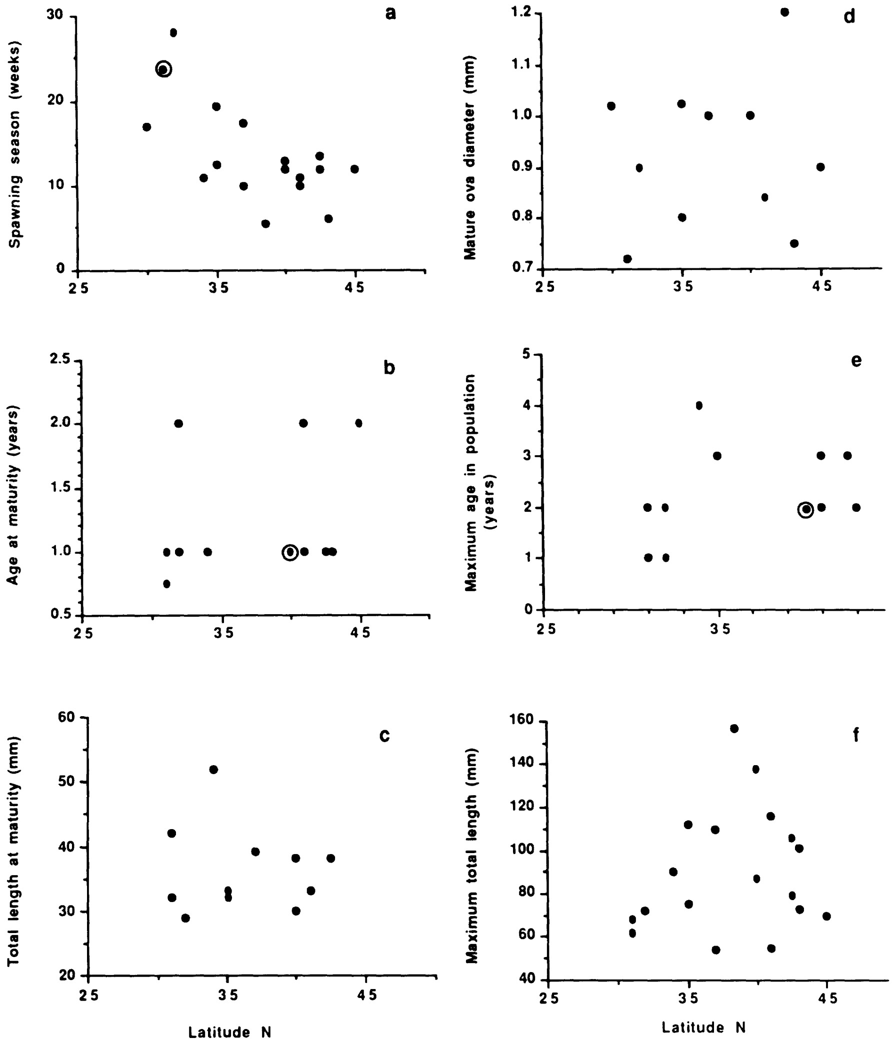

Fig. 2. Relationships between life history parameters and latitude. Each point represents a different species. Open circles represent multiple points. The y axis is the life history trait and the x axis is the latitude of the collection site. a. spawning season; b. age at maturity; c. total female body length at maturity; d. mean mature ova diameter; e. maximum age in population; f. maximum total female body length.

measures of body size were correlated with phylogeny: body length at maturity and maximum body length. For each of these variables, species that were more closely related tended to be more similar in body size than species that were distantly related (Table 1), although there was considerable variation for individual pairs of species (Figs 3c and 3f). The primitiveness test gave a significant correlation for body length at maturity and maximum age in the population. This test must be interpreted cautiously, because the results hinge on the presence of the largest species in the analysis, *Cyprinella nivea* (total length 58 mm; maximum age 4 yr; 18 nodes from the cladogram root). If *C. nivea* is deleted, neither pattern is statistically significant (total length: $r = 0.411$, $p = 0.475$, $n = 10$; maximum age: $r = 0.375$, $p = 0.256$, $n = 11$). Species with more derived morphological traits were characterized by relatively large body sizes (Fig. 4c) and older individuals (Fig. 4e). Mature ova diameter and age at maturity of each species were correlated with neither latitude nor phylogeny (Table 1).

Discussion

Latitude. For North American minnows, length of the spawning season decreased at higher latitudes. Similar correlations have been demonstrated for other groups of fishes, although usually at the intraspecific level of variation. For example, Hubbs (1985) found that southern populations of 29 species of darters have longer breeding intervals than northern populations. Both photoperiod and temperature vary latitudinally, and Hubbs suggested that photoperiod probably influences the initiation of reproduction, whereas temperature influences the termination. Nikolsky (1963: 159) sug-

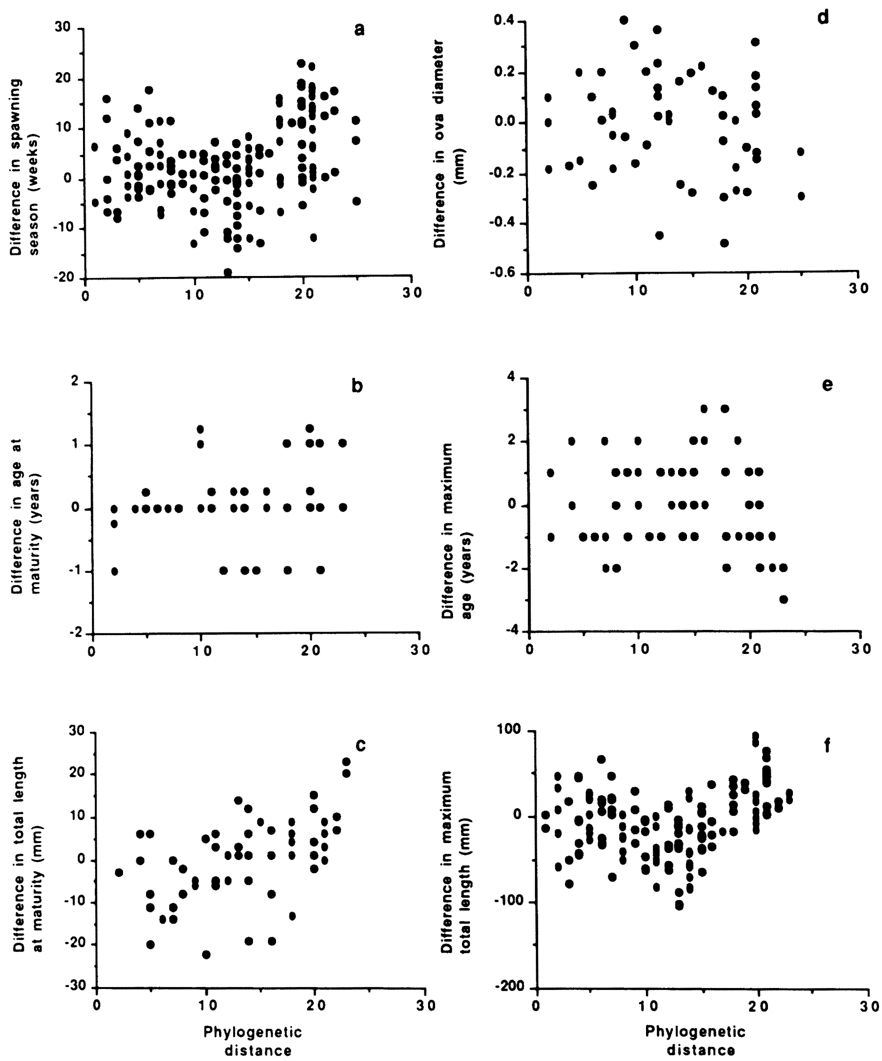

Fig. 3. Relationship between life history parameters and phylogenetic distance. Each point represents a different pair of species. The y axis is the pairwise difference in the life history trait, and the x axis is the number of nodes separating the pair of species in the cladogram in Fig. 1.

gested, as a general rule, that widely-distributed species mature later at high latitudes.

Other fish life history traits also vary with latitude, both within and between species (Table 2). The underlying environmental gradients associated with these latitudinal clines are not always apparent. In addition to latitude, life history traits of freshwater fishes are often correlated with river thermal regime (Leggett and Carscadden 1976, L'Abee-Lund et al. 1989), runoff (Heins and Baker 1987) and productivity (Mann et al. 1987). Without controlled transplant experiments (e.g., Conover and Present 1990), it is difficult to know how much of the interspecific variation represents genetic differences between species (Mitton and Lewis 1989) and how much represents phenotypic plasticity of populations living at different latitudes.

Other studies suggest phylogenetic affinities with life history variation in fishes. Wootton (1984) performed a phenetic cluster analysis on seven life history traits measured for 162 species of Canadian fishes. One of the resulting clusters contained only salmonid species. Other clusters, however, did not segregate neatly along taxonomic lines and contained genera and species from different clades that were united by similar life history traits. Within the Salmonidae, Hutchings and Morris (1985) used similar methods and identified three higher-level clusters that corresponded to the three subfamilies of the Salmonidae. Winemiller (1989) measured ten life history traits for 71 freshwater fish species in Venezuela and identified three major clusters of species that differed in life history tactics. As in Wootton's (1984) study, there were taxonomic patterns in Winemiller's clusters, although there was not a simple mapping of phylogeny onto life history.

The studies of Wootton (1984), Winemiller (1989), and Thresher (1988) illustrate the "taxon-level effect", the idea that phylogenetic patterns are most apparent at higher taxonomic levels (families and subfamilies of

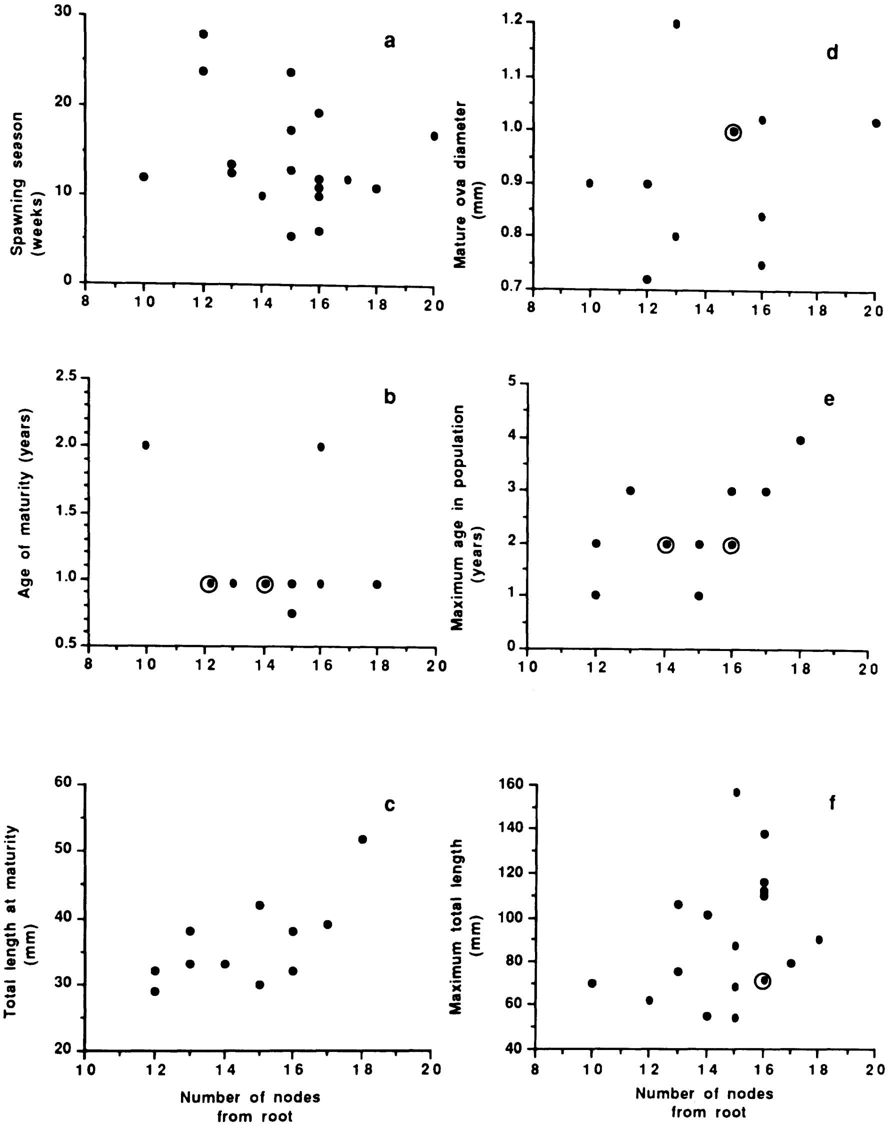

Fig. 4. Relationship between life history parameters and primitiveness. Each point is a different species. The y axis is the life history trait and the x axis is the number of nodes separating the species from the root of the cladogram in Fig. 1. Life history variables as in Fig. 2.

fishes) (Stearns 1983, Pagel and Harvey 1989). In a study of taxonomic differences in the scaling of brain and body weight among mammals, Pagel and Harvey (1989) suggested that the taxon-level effect may be a reflection of the tendency for closely related species to live in ecologically similar conditions. If Pagel and Harvey's hypothesis is correct, it will be difficult to distinguish historical effects from ecological influences on life history patterns.

However, most studies of phylogenetic constraints have been conducted at relatively high taxonomic levels. Taxonomic status is often used as a nesting variable, and variation within a taxonomic level is simply averaged (Wanntorp et al. 1990). In this study, we have taken a different approach by analyzing a single family of closely related species and genera and using information present in the cladogram to measure phylogenetic effects. Even at this relatively low taxonomic level, we find a number of correlations of life history with phylogeny that do not seem to be confounded with a simple measure of current ecology.

Although sample sizes were limited, the data in Table 1 form an interesting mosaic with respect to predictor variables: life history traits show an association with phylogeny or with latitude, but not with both. Thus, some life history traits, such as length of the spawning season, can be understood as a function of the current environment in which species are living. Other traits, such as maximum body size, are not associated with latitude, but do seem to reflect a strong historical component.

It is interesting to note that two of the variables that did show phylogenetic effects were related to some measure of body size: total female body length at matu-

Table 2. Life history correlates with latitude. A "+" means the trait increased significantly with latitude. A "−" means the trait decreased significantly with increasing latitude. "NS" means a non-significant correlation with latitude.

Source	Taxa	Life history trait	Correlation with latitude
Intraspecific variation with latitude:			
Hubbs (1985)	darters	spawning season	−
Nikolsky (1963)	fish	age at maturity	+
Mann et al. (1984)	sculpin, loach, and gudgeon	maximum age	+
		age at maturity	+
		clutches/year	−
		growth rate	−
L'Abee-Lund et al. (1989)	sea-run brown trout	growth rate	−
		smolt age	+
		size at maturity	+
		age at maturity	+
Leggett and Carscadden (1989)	American shad	repeat spawning	+
		age at maturity	NS
Conover and Present (1991)	Atlantic silversides	growth rate	+
Edwards (1984)	temperate vs tropical fishes	growth rate	NS
Thresher (1988)	demersal spawning marine fishes	egg size	+
	pelagic spawning marine fishes	egg size	NS

rity and maximum female body length in the population. The primitiveness test suggests that length at maturity was larger for taxa that are relatively more derived.

This pattern is reminiscent of Cope's Law of phyletic increase in body size (Simpson 1944). The reasons for Cope's Law have been debated, but one explanation for poikilotherms is that natural selection leads to an increase in body size because it allows females to carry more eggs (Rensch 1980). Another explanation is that large-bodied taxa are relatively vulnerable to extinction. Consequently, the ancestors of most clades (following a major environmental perturbation) tend to be small-bodied taxa. Any further evolutionary change in body size is likely to be an increase (Stanley 1979).

Although body size is larger for more derived species of minnows (Fig. 4c), the analogy with Cope's Law cannot be carried too far because it is usually inappropriate to assign a temporal scale to the branching pattern in a cladogram (Wiley 1981). Nevertheless, the results do suggest that large body size of minnows is often associated with clusters of relatively derived morphological traits. This finding contrasts with the situation in darters, in which evolutionary progression is accompanied by a decrease in body size (Page 1983: 179).

Our study can be added to a growing list of examples (Wanntorp et al. 1990) in which a phylogenetic perspective provides insight into ecological associations. Our results should be interpreted cautiously because of the modest sample sizes, and because diverse data from the literature on life history traits, geographic ranges, and phylogenetic relationships have been combined. None of these studies were originally addressing the questions we have posed, and the results may be sensitive to errors in any of the original measurements (Pagel and Harvey 1988).

For example, Stearns (1984) found that patterns of covariation in life history traits of squamate reptiles were influenced by classwide correlations with body size. However, there were errors of classification and measurement in the original data set (Vitt and Seigel 1985). A reanalysis of the corrected data did not yield all of the same conclusions (Dunham and Miles 1985). These problems may be common in any analysis of comparative data, although an explicit hypothesis of phylogenetic relationships expressed in a cladogram (Fig. 1) should at least minimize taxonomic ambiguities.

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Appendix 1. Life history data and literature sources for 21 species of North American minnows. Numbers in parentheses give sample sizes when life history traits for more than one population were averaged.

Species	Mean latitude of collection	Length of spawning season (wk)	Female age at maturity (yr)	Total female body length at maturity (mm)	Mature ova diameter (mm)
Cyprinella analostana	42.5	12			
Notropis bairdi	37			39	
Notropis blennius	41	11 (2)	2		0.84
Notropis buchanani	41	10 (3)	1	33	
Cyprinella callitaenia	30	17			1.02
Cyprinella camura	38.5	5.5 (2)			
Notropis dorsalis	45	12	2		0.90
Notropis emiliae	37	17.5 (2)			1.00
Cyprinella galactura	37	10			
Notropis heterolepis	43		1		
Notropis longirostris	32	28	1	29	0.90
Cyprinella lutrensis	40	13 (4)	1 (2)	30	1.0*
Notropis maculatus	31	24 (3)	0.75 (2)	42	
Cyprinella nivea	34	11	1	52	
Notropis sabinae	31	24	1	32	0.72
Notropis simus	32		2		
Cyprinella spiloptera	42.5	13.5 (2)	1 (2)	38	1.2
Notropis texanus	35	12.5 (2)		33	0.80
Cyprinella venusta	35	19.5 (2)		32	1.025*
Notropis volucellus	43	6 (4)			0.75
Cyprinella whipplei	40	12 (2)	1	38	

Species	Maximum age in population (yr)	Maximum total body length (mm)	Source
Cyprinella analostana	3	79	Gale and Buynak (1978), Lee et al. (1980)
Notropis bairdi			Cross et al. (1983)
Notropis blennius	3	116 (2)	Pflieger (1975), Becker (1983)
Notropis buchanani	2	55 (3)	Pflieger (1975), Becker (1983), Cross (1967), Trautman (1981)
Cyprinella callitaenia			Wallace and Ramsey (1981)
Cyprinella camura		157	Cross (1967)
Notropis dorsalis		70	Becker (1983)
Notropis emiliae		54	Gilbert and Bailey (1972), Becker (1983)
Cyprinella galactura		110	Pflieger (1975)
Notropis heterolepis	2	101	Emery and Wallace (1974), Becker (1983)
Notropis longirostris	1		Heins and Clemmer (1976)
Cyprinella lutrensis	2	87	Forbes and Richardson (1920), Laser and Carlander (1971), Pflieger (1975), Farringer et al. (1979)
Notropis maculatus	1	68	Beach (1974), Cowell and Barnett (1974), Burr and Page (1975)
Cyprinella nivea	4	90	Cloutman and Harrell (1987)
Notropis sabinae	2	62	Heins (1981)
Notropis simus	2	72.5	Hatch et al. (1985)
Cyprinella spiloptera		106 (2)	Pflieger (1975), Becker (1983)
Notropis texanus	3	75	Bresnick and Heins (1977), Becker (1983), Heins and Davis (1984), Heins and Rabito (1988)
Cyprinella venusta		112	Becker (1983), Heins and Dorsett (1986)
Notropis volucellus		73	Moyle (1973), Pflieger (1975), Becker (1983)
Cyprinella whipplei	2 (2)	138	Forbes and Richardson (1920), Lewis and Gunning (1959), Pflieger (1965), Pflieger (1975)

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