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PISCIVORY LIMITS DIVERSIFICATION OF FEEDING MORPHOLOGY IN CENTRARCHID FISHES

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Proximity to an adaptive peak influences a lineage's potential to diversify. We tested whether piscivory, a high quality but functionally demanding trophic strategy, represents an adaptive peak that limits morphological diversification in the teleost fish clade, Centrarchidae. We synthesized published diet data and applied a well-resolved, multilocus and time-calibrated phylogeny to reconstruct ancestral piscivory. We measured functional features of the skull and performed principal components analysis on species' values for these variables. To assess the role of piscivory on morphological diversification, we compared the fit of several models of evolution for each principal component (PC), where model parameters were allowed to vary between lineages that differed in degree of piscivory. According to the best-fitting model, two adaptive peaks influenced PC 1 evolution, one peak shared between highly and moderately piscivorous lineages and another for nonpiscivores. Brownian motion better fit PCs 2, 3, and 4, but the best Brownian models infer a slow rate of PC 2 evolution shared among all piscivores and a uniquely slow rate of PC 4 evolution in highly piscivorous lineages. These results suggest that piscivory limits feeding morphology diversification, but this effect is most severe in lineages that exhibit an extreme form of this diet.

KEY WORDS: Brownian motion, diet, functional morphology, Ornstein–Uhlenbeck process, rate of morphological evolution, suction-feeding.

What factors limit morphological diversity? Although some lineages have diversified into an extraordinary variety of head and body shapes, others show surprising conservation of form. Intrinsic properties of organismal design, like genetic variance (Houle 1992; Schluter 1996) or body plan complexity (Vermeij 1973; Lauder 1990), affect the capacity for form to evolve in a lineage, but ecological factors shape opportunities to diversify. For example, the presence of resource competitors throughout a clade's history may constrain divergence in resource use and thus limit the evolution of form (Erwin et al. 1987; Harmon et al. 2003), or conversely, invasion of a competitor-free geographic region may provide opportunities for a lineage to radiate into a variety

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of available niches (Simpson 1953; Grant 1972; Schluter 1988). Here, we apply the adaptive landscape model (Simpson 1944, 1953) to jointly account for intrinsic and ecological factors that determine the mode of natural selection a lineage has experienced during its evolutionary history.

The adaptive landscape model describes the fitness consequences of morphological variation, where the positions of fitness peaks in morphospace are partly determined by the quality and availability of resources as well as morphology's effect on procuring those resources (Simpson 1944, 1953; Lande 1976, 1979; Arnold 1983; Arnold et al. 2001). The position of a lineage in this landscape has consequences for its capacity to diversify phenotypically (Hansen and Martins 1996). For a lineage near an adaptive peak, selection limits morphological variation because fitness decreases with distance from the optimum character values. As the lineage splits, the adaptive peak constrains morphological divergence between daughter lineages, slowing the accumulation of diversity within a clade (Hansen and Martins 1996; Hansen 1997; Butler and King 2004). Here, we ask whether piscivory, a high quality but functionally demanding trophic strategy, represents an adaptive peak that has limited morphological diversification in a radiation of North American endemic freshwater teleost fishes, the Centrarchidae.

Although our work focuses on the consequences for phenotypic diversity, the plausibility of piscivory as an adaptive peak is supported by several ecological and functional studies involving centrarchid fishes. First, fish are a highly profitable food resource, providing a source of both lipid and protein (Weatherly and Gill 1987). In fact, the ontogenetic diet switch to piscivory in the largemouth bass, *Micropterus salmoides*, is concurrent with an increase in growth rate, and individuals of this species that switch to piscivory earlier in life have higher relative fitness (Post 2003). Second, fish impose stringent functional requirements for their capture because they are relatively large freshwater prey and employ a fast-start escape response to elude striking predators. The demanding nature of piscivory is evident in the correlation between performance when feeding on fish prey and head and body form among centrarchid species. Werner (1977) found that the large mouthed, slender bodied *M. salmoides* exhibit lower handling times and higher success rates when feeding on fish than either the small mouthed, deep bodied bluegill sunfish, *Lepomis macrochirus*, or the intermediate shaped green sunfish, *Lepomis cyanellus*, but *L. cyanellus* performed better than *L. macrochirus*. These differences among species suggest that mouth size and body shape are related to the energetic and foraging time costs of piscivory. Moreover, Werner's (1977) feeding trial results are consistent with mechanical measures of feeding performance. Higham et al. (2006) showed that, relative to *L. macrochirus*, *M. salmoides* ingest a larger volume of water per unit time (i.e., higher volumetric flow rate), which is necessary to engulf a large prey in the open water before it can escape. Finally, these functional studies also demonstrated that a performance trade-off exists between piscivory and other trophic strategies. The costs of foraging for *M. salmoides*, *L. cyanellus*, and *L. macrochirus* are reversed when feeding on nonevasive, open water planktonic prey (Werner 1977). This performance difference is likely due in part to *L. macrochirus*'s capacity to generate higher suction-induced flow velocities and accelerations (Higham et al. 2006), which translate into stronger hydrodynamic forces exerted on prey (Holzman et al. 2008a). Taken together, these studies suggest that piscivory is a profitable but functionally demanding diet, and that a fitness valley likely separates the adaptive peak for piscivory from adaptive peaks corresponding to other trophic strategies.

Much of the evidence to support piscivory as an adaptive peak in centrarchids is derived from the high performance capabilities of the species, *M. salmoides*. Indeed, *Micropterus* (Black Bass) species may be the highest performing and most specialized centrarchid piscivores (Mittelbach and Persson 1998). Nevertheless, several non-*Micropterus* centrarchid species are also known to become piscivorous at some life stage (Keast 1985; Mittelbach and Persson 1998; Liao et al. 2002). Therefore, we asked whether piscivory has limited morphological diversification across all centrarchid lineages that have evolved this diet. But, we also assessed whether extreme piscivory, which characterizes at least some *Micorpterus* species, has a uniquely limiting effect on morphological diversification.

In this study, we measured functional features of the skull, synthesized published diet studies, and applied a well-resolved and time-calibrated phylogeny for Centrarchidae (Near et al. 2005) to reconstruct the evolutionary history of piscivory and to compare the fit of several models of character evolution to our morphological data. We examined Ornstein–Uhlenbeck (OU) models, which explicitly incorporate selection due to adaptive peaks (Hansen and Martins 1996; Hansen 1997; Butler and King 2004), as well as Brownian motion models because adaptive character evolution can resemble Brownian motion under some conditions (Hansen and Martins 1996; Revell et al. 2008). To assess the role of piscivory on feeding mechanism diversification, we compared OU models that differ in the number of adaptive peaks, where separate peaks are assigned to lineages with different inferred degrees of piscivory, and Brownian models that differ in the number of rates (the model's time-independent variance parameter, σ^2). These models describe different processes of morphological evolution on a phylogenetic tree and provide different predictions for the distribution of species in morphospace (Hansen and Martins 1996; Butler and King 2004; Collar et al. 2005; O'Meara et al. 2006). Therefore, comparisons of model fit to species character values and a time-calibrated phylogeny allowed us to detect the effects of piscivory on morphological diversification across centrarchid lineages and to differentiate these general effects from those that are specific to the highly piscivorous *Micropterus* lineages.

Materials and Methods

RECONSTRUCTING PISCIVORY IN CENTRARCHIDAE

The contribution of fish to the diets of centrarchid species was quantified through a synthesis of published gut content analyses. We collected data from studies that reported piscivory as the percent frequency of occurrence of a food item in individual fish guts (percent frequency of occurrence, % FO), the contribution of fish as the percent of the total number of prey in the gut (percent numerical contribution, % N), and the contribution of fish as the percent of the total volume of prey (percent volumetric contribution, % V). For each of these metrics, the contribution of fish to species' diets was averaged over seasons, localities, and size classes above adult body size. We transformed these quantitative variables (% FO,% N, and% V) into a discrete variable that describes each species' degree of piscivory as one of three states: "not piscivorous" indicates that the species included fish in its diet with less than 5% FO,% N, or% V, "moderately piscivorous" describes species whose% FO,% N, or% V of fish is greater than 5 but less than 50, and "highly piscivorous" describes species that include fish with greater than 50% FO,% N or% V. Admittedly, this character coding is simplistic, but the distribution of piscivory among centrarchid species conforms well to this three state framework (see Table 1), and use of this discrete variable allowed us to combine data on piscivory from the three metrics and thus maximize the number of species to which we were able to assign a degree of piscivory. Moreover, this character-coding scheme led to a general agreement between quantitative metrics with regard to the degree of piscivory assigned to species.

To infer piscivory in ancestral centrarchid lineages, we applied stochastic character mapping (Nielson 2002; Huelsenbeck et al. 2003; Bollback 2006). We used the computer program SIMMAP (Bollback 2006) to implement stochastic mapping of the degree of piscivory based on an ordered model of character change and Near et al.'s (2005) phylogeny for Centrarchidae (Fig. 1). We sampled 500 character histories and performed model-fitting analyses on each of these reconstructions (see below). Rather than base all subsequent analyses on a single ancestral state reconstruction inferred by maximum likelihood (Schluter et al. 1997; Pagel 1999) or parsimony (Maddison 1990), we chose this method because it incorporates uncertainty in the evolutionary history of the degree of piscivory (Huelsenbeck et al. 2003).

MORPHOLOGICAL MEASUREMENTS

We obtained species' values for a suite of morphological features of the skull and jaws as means from at least three specimens for 29 centrarchid species. Specimens were either field collected by the authors or borrowed from museum collections. Information regarding collection localities and museum lot numbers for the species included in this dataset is in Supporting Table S1. After dissection of relevant cranial muscles (see below), all specimens were cleared using trypsin and double-stained with alcian blue cartilage stain and alizirin red bone stain (Taylor 1967), and morphological measurements were made on cleared and stained specimens.

We focused on morphological features of the skull and jaws that contribute to prey capture and processing. We measured gape width; premaxilla (PMX) protrusion; the lower jaw opening and closing in-levers (Open L_{in} and Close L_{in}, respectively); the lower jaw out-lever (L_{out}); mass of the primary oral jaws closing muscle, the adductor mandibulae (AM); and mass of the primary pharyngeal jaw adductor muscle, the levator posterior (LP). In addition, because many aspects of feeding performance scale with body size, we used values of species' maximum total length (TL) reported in Page and Burr (1991) to reflect differences in adult body size.

To account for differences between species' character values that were due to differences in sizes of specimens, we regressed log-transformed species' means for each morphological variable against the log-transformed means of standard lengths (a standard ichthyological measure of fish body size-–the distance along the mid-line of the fish from the anterior tip of the upper jaw to the anterior-most point of the caudal fin rays) of the specimens from which measurements were made. To account for the potentially confounding effects of phylogeny, regression slopes were estimated using standardized independent contrasts of the log-transformed morphological variables and standard lengths (Felsenstein 1985; Garland et al. 1992). Then, these slopes were imposed on regressions involving species' values, and the residuals of these regressions were taken as size-corrected species' values for the seven morphological variables (Blomberg et al. 2003). Standardized contrasts were calculated using the computer program CAIC (Purvis and Rambaut 1995) and the phylogenetic topology and branch lengths for Centrarchidae reported in Near et al. (2005).

To reduce dimensionality and account for correlations among morphological variables, we performed principal components analysis (PCA) on the correlation matrix for the seven size-corrected morphological variables and species maximum TL. We also estimated sampling error for species' principal component scores using the following procedure. We obtained size-corrected character values for individuals as the residuals from regressions of log-transformed character values on log-transformed standard length, where the slopes were constrained to be equal to their estimates from the regressions involving independent contrasts as described above. We then transformed these size-corrected

Table 1. Piscivory in centrarchid fishes based on a synthesis of published diet studies. *Diet variable abbreviations: % FO, percent frequency of occurrence; % N, percent numerical contribution; % V, percent volumetric contribution. **In cases in which diet variables disagree with regard to most common prey type, we report the most common prey from the metric based on the largest sample size in terms of individuals; this metric is noted in parentheses. Otherwise, the most common prey type is consistent across diet variables.

Species	Sample size		Contribution of fish prey to diet*			Piscivory state	Most common prey type**	References[1]
	Localities	Individuals	% FO	% N	% V			
Acantharchus pomotis	1	150	8.7	7.2	22.4	moderate	amphipods	[37]
Ambloplites cavifrons	1	63	–	14.3	18.5	moderate	crayfish	[38]
Ambloplites rupestris	3	382	18.9	2.7	6.7	moderate	odonates (% V)	[2, 12, 22, 24]
Archoplites interruptus	7	449	16.7	0.0	19.6	moderate	dipterans	[1, 20]
Centrarchus macropterus	1	4	–	0.0	–	not/mod.	copepods	[34]
Enneacanthus chaetodon	1	150	0.0	–	0.0	not	dipterans	[43]
Enneacanthus gloriosus	2	43	0.0	0.0	–	not	copepods (% N)	[13, 34]
Enneacanthus obesus	1	11	–	0.0	–	not	dipterans	[34]
Lepomis auritus	5	2138	3.1	0.1	2.2	not	dipterans	[3, 8, 13, 34]
Lepomis cyanellus	3	710	0.0	0.0	15.8	moderate	dipterans	[36, 39]
Lepomis gibbosus	8	2477	1.0	0.0	0.0	not	snails (% V)	[13, 18, 24, 25, 27, 39, 40, 45]
Lepomis gulosus	7	382	20.3	14.6	25.5	moderate	crayfish	[10, 13, 14, 26, 31, 40]
Lepomis humilis	1	52	1.9	0.0	–	not	dipterans	[7]
Lepomis macrochirus	13	3290	0.1	0.0	5.0	not	dipterans	[2, 10, 13, 19, 24, 31, 36, 39, 45, 47]
Lepomis marginatus	1	42	0.0	0.0	–	not	dipterans	[34]
Lepomis megalotis	7	1356	–	0.0	4.5	not	dipterans (% V)	[2, 27, 36]
Lepomis microlophus	4	164	0.0	0.0	0.0	not	snails	[10, 18, 19, 31]
Lepomis miniatus	1	9	–	0.0	–	not/mod.	dipterans	[47]
Lepomis punctatus	2	117	1.5	0.0	0.0	not	amphipods (% N)	[10, 34]
Lepomis symmetricus	1	29	0.0	0.0	–	not	cladocerans (% N)	[5]
Micropterus cataractae	1	156	–	–	55.0	high	fish	[48]
Micropterus coosae	2	78	–	14.2	–	moderate	crayfish	[15]
Micropterus dolomieu	11	2019	50.0	55.9	53.5	high	fish	[2, 11, 16, 17, 36, 44]
Micropterus floridanus	2	429	88.3	81.6	–	high	fish	[21, 28, 32, 33]
Micropterus notius	4	263	9.2	45.1	–	moderate	crayfish	[6, 42]
Micropterus punctulatus	8	780	61.5	–	58.1	high	fish	[4, 9, 36, 41, 44, 46]
Micropterus salmoides	14	2326	89.4	63.0	60.6	high	fish	[7, 9, 16, 17, 22, 24, 28, 31, 36, 40, 41, 42, 45, 48]
Pomoxis annularis	2	1095	21.3	0.0	46.5	moderate	dipterans (% FO)	[7, 29, 30]
Pomoxis nigromaculatus	8	1944	25.0	0.7	21.6	moderate	dipterans (% V)	[7, 9, 19, 22, 23, 24, 28, 31, 45]

[1] Reference key: [1] Aceituno and Vanicek (1976); [2] Angermeier (1985); [3] Bass and Hitt (1974); [4] Bohn (1975); [5] Burr (1977); [6] Cailteux et al. (2002); [7] Clark (1943); [8] Coomer et al. (1977); [9] Dendy (1946); [10] Desselle et al. (1978); [11] Doan (1940); [12] Elrod et al. (1981); [13] Flemer and Woolcott (1966); [14] Germann et al. (1974); [15] Gwinner et al. (1975); [16] Hodgson et al. (1997); [17] Hubert (1977); [18] Huckins (1997); [19] Huish (1957); [20] Imler et al. (1975); [21] Johnson and Hale (1977); [22] Keast (1965); [23] Keast (1968); [24] Keast (1978a); [25] Keast (1978b); [26] Larimore (1957); [27] Laughlin and Werner (1980); [28] Liao et al. (2002); [29] Mathur and Robbins (1971); [30] Mathur (1972); [31] McCormick (1940); [32] McLane (1948); [33] McLane (1950); [34] McLane (1955); [35] Moyle et al. (1974); [36] Mullan and Applegate (1967); [37] Pardue (1993); [38] Petrimoulx (1983); [39] Sadzikowski and Wallace (1976); [40] Savitz [1981]; [41] Scalet (1977); [42] Schramm and Maceina (1986); [43] Schwartz (1961); [44] Scott and Angermeier (1998); [45] Seaburg and Moyle (1964); [46] Smith and Page (1969); [47] VanderKooy et al. (2000); [48] Wheeler and Allen (2003).

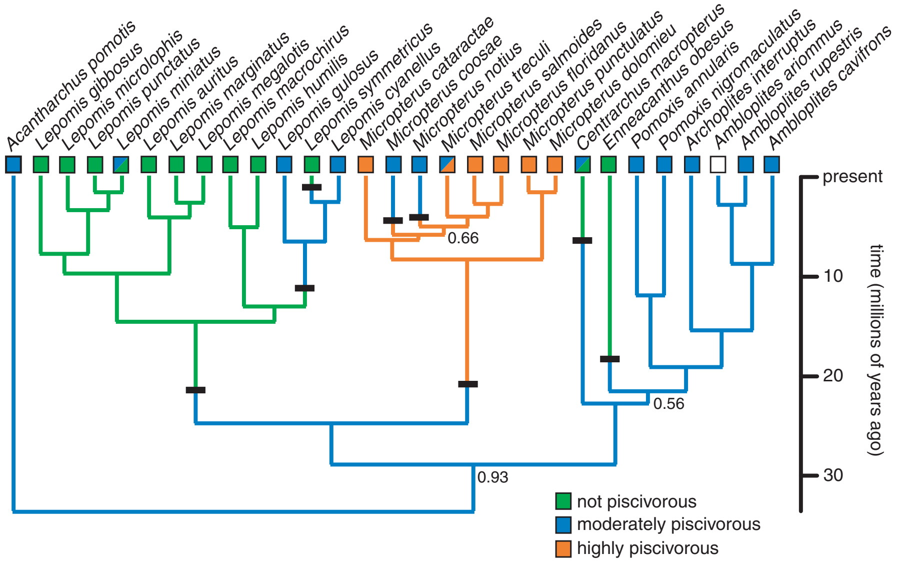

Figure 1. Reconstruction of piscivory in centrarchid lineages. Phylogenetic relationships and fossil-calibrated divergence time estimates are based on Near et al. (2005); nodes are supported by greater than 0.95 Bayesian posterior probabilities unless indicated. The 29 recognized centrarchid species (out of 33 total) shown here are those for which we obtained morphological data; colored boxes next to species' names denote piscivory states based on our diet synthesis (see Table 1); green is not piscivorous, blue is moderately piscivorous, orange is highly piscivorous, white is unknown, and boxes with two colors indicate uncertainty between piscivory states in that species. This ancestral reconstruction of piscivory represents a single character history from the 500 character histories we obtained by stochastic mapping of piscivory states in SIMMAP (Bollback 2006) and illustrates the modal number of state changes, the most common ancestral state for Centrarchidae, and the most common ancestral state for the *Micropterus* clade. Colors of branches indicate inferred piscivory state and black bars show transitions between states. We used this reconstruction and the other 499 sampled character histories as the basis for evaluating the fit of multiple-peak OU and multiple-rate Brownian motion models in which model parameters were allowed to differ between lineages inferred to have different piscivory states.

character values to PC scores for individuals using the eigenvalues and eigenvectors from the PCA on species' means. For each PC, we calculated variance within each species and estimated an overall sampling error as the pooled within-species variances. These values for sampling error were incorporated into model fitting analyses described in the next section.

COMPARING THE FIT OF MODELS OF CHARACTER EVOLUTION

We assessed fit of several models of character evolution to the morphological PCs. We compared four OU models to test the effects of adaptive peaks on diversification of skull morphology. The OU model describes Brownian motion character evolution under an elastic restraining force toward some optimum character value, where the strength of the restraining force is an increasing function of distance to the optimum (Felsenstein 1988; Garland et al. 1993; Martins 1994; Hansen and Martins 1996; Hansen 1997; Blomberg et al. 2003; Butler and King 2004). The parameters of this model are the ancestral character state, θ_0; the time-independent variance parameter for the Brownian process, σ^2; the strength of selection, α; and at least one phenotypic optimum, θ (Hansen 1997; Butler and King 2004). We evaluated the fit of OU models that differed in the number of optima, where optima are assigned to lineages according to their inferred degree of piscivory—highly (θ_{HP}), moderately (θ_{MP}), or not piscivorous (θ_{NP}) (see above). The simplest OU model included only a single adaptive peak for all centrarchid lineages regardless of diet state (OU1: $\theta_{HP} = \theta_{MP} = \theta_{NP}$). The most complex OU model included three peaks, one for each degree of piscivory (OU3: $\theta_{HP}, \theta_{MP}, \theta_{NP}$). We also examined the fit of two OU models that had two adaptive peaks. One of the two-peak models included an optimum for nonpiscivorous lineages and a second optimum shared between lineages that were moderately or highly piscivorous (OU2a: $\theta_{NP}, \theta_{HP} = \theta_{MP}$); this model describes a general effect of piscivory. The other two-peak model included one optimum shared between moderately and nonpiscivorous lineages and a separate optimum for highly piscivorous lineages (OU2b: $\theta_{HP}, \theta_{MP} = \theta_{NP}$); this model represents a unique effect of extreme piscivory. We assessed model fit using AICc, a modification of Akaike Information Criterion that accounts for small sample size (Burnhan and Anderson 2002), where sample size is the number of taxa, as in Butler and King (2004) and O'Meara et al. (2006). We used the program Brownie 2.1 (O'Meara et al. 2006; O'Meara 2008) to obtain parameter estimates and AICc for each of the OU models. This program modifies the method described and developed by Hansen (1997) and Butler and King (2004) to incorporate stochastic mapping of piscivory states by assigning different optima to segments of branches mapped with different discrete states (O'Meara 2008). The program also incorporates empirical estimates of the sample variance in estimation of species means, as suggested by Martins and Hansen (1997) and O'Meara et al. (2006).

Under some conditions, adaptive evolution can be well represented by Brownian motion (Hansen and Martins 1996; Revell et al. 2008), and we also compared the fit of four Brownian motion models that differed in the number of rates of character evolution—defined as the time-independent variance parameter, σ^2, of the Brownian model—assigned to lineages with different degrees of piscivory (σ^2_{HP} for highly, σ^2_{MP} for moderately, and σ^2_{NP} for nonpiscivorous). These multiple-rate Brownian models parallel the multiple-peak OU models described above. Accordingly, we examined the fit of a three-rate Brownian model that allows rates to vary between lineages inferred to be highly, moderately, and not piscivorous (BM3: σ^2_{HP}, σ^2_{MP}, σ^2_{NP}), a single-rate model (BM1: $\sigma^2_{\mathrm{HP}} = \sigma^2_{\mathrm{MP}} = \sigma^2_{\mathrm{NP}}$), and two two-rate models. The first two-rate model assigns one rate to nonpiscivorous lineages and a second rate to both highly and moderately piscivorous lineages (BM2a: σ^2_{NP}, $\sigma^2_{\mathrm{HP}} = \sigma^2_{\mathrm{MP}}$). The other two-rate model assigns one rate to highly piscivorous lineages and a second rate to both moderately and nonpiscivorous lineages (BM2b: σ^2_{HP}, $\sigma^2_{\mathrm{MP}} = \sigma^2_{\mathrm{NP}}$). Similar to the two-peak OU models described above, comparisons of these two-rate Brownian models allowed us to detect a general effect of piscivory (BM2a) as well as a unique effect of an extreme form of this diet (BM2b) on morphological diversification. Parameter estimation and model fitting for all Brownian models were performed in Brownie 2.1 (O'Meara et al. 2006; O'Meara 2008), which uses a method that is similar to the one developed by Thomas et al. (2006) and the noncensored rate test developed by O'Meara et al. (2006) except that it incorporates stochastic mapping of piscivory state output from SIMMAP (Bollback 2006) and empirical estimates of variance in the estimates of species means.

To assess the best-fitting evolutionary model for each morphological PC, we calculated AICc scores of the OU and Brownian models for each of the 500 character histories reconstructed using stochastic mapping and compared mean AICc scores among models. Because SIMMAP samples character histories in proportion to their posterior probability (Bollback 2006), the mean AICc is weighted by the probability of each character history given the data and phylogeny. In this way, our comparisons of model fit account for uncertainty in the evolutionary history of piscivory in Centrarchidae. We chose to assess model fit using AICc rather than likelihood-ratio tests because AICc allowed us to compare fit of multiple-peak OU to multiple-rate Brownian motion models even though these models are not nested.

Results

Synthesis of published gut content studies allowed us to assess the degree of piscivory in 29 of the 33 recognized centrarchid species. For each species included in our diet synthesis, Table 1 reports sample sizes, values for the contribution of fish to centrarchid diets (as% FO, % N, and % V), the inferred degree of piscivory, the most common prey item, and citations for the original studies. We found that 12 species could be unambiguously classified as not piscivorous, nine of these are in the *Lepomis* clade (the sunfishes) and the other three are the recognized *Enneacanthus* species. Sample sizes were too small to confidently classify *Centrarchus macropterus* or *Lepomis miniatus* as nonpiscivorous even though we did not find reports of fish in their diets; we treated these species' degrees of piscivory as uncertain between moderately and nonpiscivorous. Of the moderately piscivorous species, only *L. cyanellus*'s degree of piscivory is unclear because its values for % FO and % N indicate that this species does not feed on fish, but its value for % V classifies it as moderately piscivorous. Nevertheless, we considered this species to be moderately piscivorous because% V ($n_{individuals} = 710$, $n_{localities} = 3$) is based on a much larger sample size than either % FO or% N ($n_{individuals} = 12$, $n_{localities} = 1$). We found that five of the seven sampled *Micropterus* species are highly piscivorous, and this diet is unique to these lineages. Two *Micropterus* species were found to exhibit only moderate piscivory, *M. coosae* (Schramm and Maceina 1986; Cailteux et al. 2002) and *M. notius* (Gwinner et al. 1975). We were unable to find quantitative diet information for *Ambloplites ariommus*, *Ambloplites constellatus*, *Micropterus treculi*, and *Lepomis peltastes*. *Ambloplites constellatus* and *L. peltastes* were not included in our analyses. The degree of piscivory in *M. treculi* was treated as uncertain between moderately and highly piscivorous and unknown in *A. ariommus*.

We sampled 500 reconstructions of the degree of piscivory produced by SIMMAP (Bollback 2006). In this sample, the total number of transitions in piscivory state varied between 7 and 16 with a mode of 8. Figure 1 illustrates one of these eight-transition character histories. The most frequent transition was from moderately to not piscivorous (mode = 3, minimum = 0, maximum = 7 transitions), and transitions were also inferred for the following state changes: from not to moderately piscivorous (mode = 2, minimum = 0, maximum = 8 transitions), from moderately to highly piscivorous (mode = 2, minimum = 0, maximum = 5 transitions), and from highly to moderately piscivorous (mode = 1, minimum = 0, maximum = 5 transitions). Transitions between highly and nonpiscivorous states were never inferred. The ancestral degree of piscivory for Centrarchidae was moderately

Table 2. Eigenvectors and descriptive statistics resulting from principal components analysis on the correlation matrix for log-transformed and body size corrected cranial morphological variables. Bold values denote loadings considered strong (|loading| > 0.30).

Variable	PC 1	PC 2	PC 3	PC 4
max. TL	**−0.38**	−0.01	**0.35**	**−0.60**
gape width	**−0.40**	0.27	−0.30	**0.50**
PMX protrusion	**0.38**	−0.30	0.00	**0.35**
close L_{in}	0.05	**0.40**	**0.80**	**0.37**
open L_{in}	**0.32**	**0.49**	−0.13	−0.01
L_{out}	**−0.46**	0.25	−0.27	0.07
AM mass	0.16	**0.60**	−0.14	−0.28
LP mass	**0.46**	0.12	−0.19	−0.22
Eigenvalue	3.31	2.10	0.86	0.63
% total variation	41.4	26.3	10.8	7.9

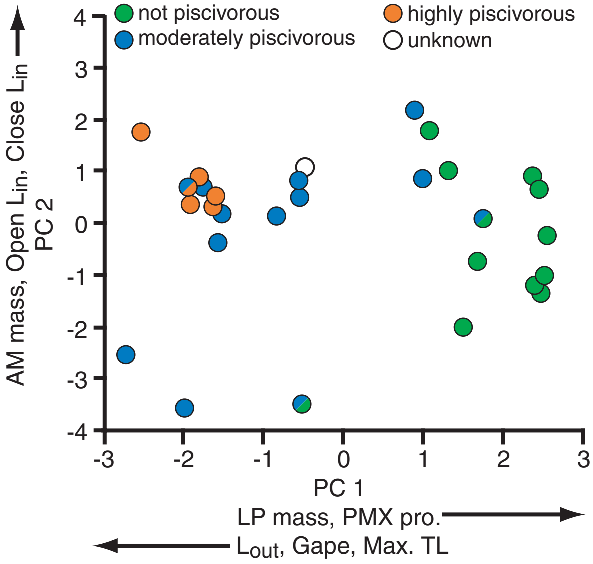

Figure 2. Scatterplot of 29 centrarchid species' scores on morphological PCs 1 and 2. Principal component 1 accounts for 41% of the morphological variation among species and loads strongly and positively with LP muscle mass and premaxilla protrusion (PMX pro.) and negatively with lower jaw out-lever length (L_{out}), gape width, and maximum total length (max. TL). Morphological PC 2 explains 26% of the morphological variation and loads strongly with AM muscle mass and the lengths of the lower jaw opening and closing in-levers (Open L_{in} and Close L_{in}, respectively). Colors indicate species' piscivory states; green is not piscivorous, blue is moderately piscivorous, orange is highly piscivorous, open circles have unknown state, and points with two colors indicate uncertainty between those states.

piscivorous in 84% of the reconstructions, not piscivorous in 15%, and highly piscivorous in only 1%. In 87% of the reconstructions, the highly piscivorous diet state was unique to the *Micropterus* clade. In addition, the most recent common ancestor of *Micropterus* was inferred to be highly piscivorous in 66% of the character histories and moderately piscivorous in the remaining 34%.

The PCA of morphological variables provided four axes that together explained 86% of the total variation among species. Principal component (PC) 1 loads positively with LP muscle mass and PMX protrusion and negatively with L_{out}, gape, and maximum TL (Table 2). Notably, PC 1 separates species that feed on fish from species that do not: all but two (*L. cyanellus* and *Lepomis gulosus*) of the 15 (moderately or highly) piscivorous species have negative scores on PC 1 (Fig. 2). Principal component 2 loads with AM muscle mass, open L_{in} and close L_{in} (Table 2), and accounts for much of the variation between species classified as moderate or nonpiscivores (Fig. 2).

Results from model fitting are summarized in Tables 3 and 4, which provide parameter estimates and fit (−ln likelihood and AICc) for the four OU models and four Brownian models, respectively. All parameter estimates and model fit scores are shown as means and standard errors taken over the 500 reconstructions of the degree of piscivory obtained from SIMMAP. Table 3 also includes parameter estimates and model fit scores for the single-rate Brownian model to facilitate comparisons between Tables 3 and 4.

An OU model with two adaptive peaks, one shared between highly and moderately piscivorous lineages and another for nonpiscivores, provided the best fit for the evolution of PC 1 (Tables 3 and 4). This model was substantially favored over all four Brownian models (ΔAICc > 5.0), the single-peak model (ΔAICc (OU1–OU2a) = 11.00 ± 4.62 (mean difference ± standard error calculated over the 500 sampled piscivory reconstructions)), and the alternative two-peak model (ΔAICc (OU2b–OU2a) = 11.30 ± 4.85) and somewhat favored over the three-peak OU model (ΔAICc (OU3–OU2a) = 1.66 ± 1.28). In addition, this preferred two-peak OU model provided the best fit across 83% of the stochastic piscivory reconstructions; no other model provided the best fit for more than 5% of the reconstructions.

For PCs 2, 3, and 4, Brownian motion was favored over all OU models. The single-rate Brownian model provided a substantially better fit than the single- or multiple-peak OU models (Table 3), and the total Akaike weights for all Brownian motion models were 0.96, 0.83, and 0.79 for PCs 2, 3, and 4, respectively. Below we describe comparisons among single- and multiple-rate Brownian models. To highlight differences in Brownian rates of PC evolution, Figure 3 shows the model-averaged rate estimates in highly, moderately, and nonpiscivorous lineages, where the rate estimates are weighted by the Akaike weights of the four Brownian models (Burnham and Anderson 2002; O'Meara 2008).

Table 3. Parameter estimates and fit of one-rate Brownian and OU models to morphological PCs. Means and standard errors are calculated over the 500 sampled piscivory reconstructions (note that these are not calculated for the one-rate Brownian or one-peak OU models because parameter estimation and fit of these models do not depend on piscivory reconstructions). θ_{NP}=optimum for nonpiscivorous lineages; θ_{MP}=optimum for moderately piscivorous lineages; θ_{HP}=optimum for highly piscivorous lineages; BM1=Brownian motion with one rate, σ^2, and ancestral state, θ_0; OU1=OU with rate, σ^2, ancestral state, θ_0, strength of selection, α, and one optimum: $\theta_{NP}=\theta_{MP}=\theta_{HP}$; OU2a=OU ($\sigma^2$, θ_0, α) with two optima: θ_{NP}, $\theta_{MP}=\theta_{HP}$; OU2b=OU (σ^2, θ_0, α) with two optima: $\theta_{NP}=\theta_{MP}$, θ_{HP}; OU3=OU (σ^2, θ_0, α) with three optima: θ_{NP}, θ_{MP}, θ_{HP}. Bold values denote best-fitting model.

Character	Model	θ_0	σ^2 (My^{-1})	α (My^{-1})	θ_{NP}	θ_{MP}	θ_{HP}	−ln L	AICc
PC 1	BM1	−0.297	0.056	—	—	—	—	36.756	77.975
	OU1	−0.298	0.056	1.059×10^{5}	-1.064×10^{-4}	-1.064×10^{-4}	-1.064×10^{-4}	36.757	83.181
	OU2a	**0.498±0.910**	**0.051±0.006**	**0.053±0.011**	**11.498±2.969**	**−10.143±3.378**	**−10.143±3.378**	**29.785±2.308**	**72.178±4.617**
	OU2b	−1.923±0.642	0.050±0.005	$1.059\times10^{-5}\pm$ 2.791×10^{-6}	$5.532\times10^{3}\pm$ 2.773×10^{3}	$5.532\times10^{3}\pm$ 2.773×10^{3}	$-5.532\times10^{3}\pm$ 2.773×10^{3}	35.436±0.829	83.480±1.659
	OU3	−0.206±0.916	0.036±0.005	0.060±0.013	7.754±2.877	−2.537±0.984	−6.314±2.425	29.009±2.307	73.836±4.614
PC 2	**BM1**	**−0.315**	**0.142**	**—**	**—**	**—**	**—**	**49.983**	**104.428**
	OU1	−0.151	0.228	0.041	−0.459	−0.459	−0.459	49.075	107.817
	OU2a	−0.376±0.200	0.223±0.018	0.040±0.004	−0.800±0.692	−0.219±0.388	−0.219±0.388	48.915±0.283	110.438±0.567
	OU2b	0.339±0.241	0.239±0.015	0.049±0.005	−0.737±0.107	−0.737±0.107	2.154±0.930	48.568±0.251	109.744±0.503
	OU3	0.168±0.265	0.241±0.025	0.051±0.009	−0.727±0.681	−0.658±0.351	2.166±0.959	48.419±0.333	112.657±0.667
PC 3	**BM1**	**−0.389**	**0.028**	**—**	**—**	**—**	**—**	**28.922**	**62.305**
	OU1	−0.447	0.033	0.009	−0.150	−0.150	−0.150	28.867	67.401
	OU2a	−0.120±0.221	0.035±0.003	0.018±0.006	1.081±0.321	−1.152±0.273	−1.152±0.273	28.167±0.546	68.943±1.093
	OU2b	1.462±0.881	0.031±0.004	0.016±0.006	−20.292±239.760	−20.292±239.760	21.140±239.705	27.150±0.481	66.908±0.962
	OU3	0.647±0.683	0.042±0.014	0.054±0.033	0.124±1.217	−1.674±1.620	3.196±2.814	25.090±1.187	65.997±2.374
PC 4	**BM1**	**0.208**	**0.047**	**—**	**—**	**—**	**—**	**35.427**	**75.315**
	OU1	0.002	0.135	0.113	0.089	0.089	0.089	33.409	76.484
	OU2a	0.002±0.006	0.194±0.060	0.179±0.064	−0.111±0.204	0.133±0.088	0.133±0.088	33.095±0.227	78.800±0.454
	OU2b	−0.009±0.011	0.130±0.010	0.110±0.008	0.130±0.023	0.130±0.023	−0.454±0.364	33.226±0.235	79.060±0.471
	OU3	−0.004±0.012	0.198±0.060	0.189±0.066	−0.124±0.200	0.220±0.106	−0.366±0.312	32.741±0.418	81.300±0.835

Table 4. Parameter estimates and fit of single- and multiple-rate Brownian motion models to morphological PCs. Means and standard errors are calculated over the 500 sampled piscivory reconstructions (note that these are not calculated for one-rate Brownian motion because parameter estimation and fit of this model does not depend on piscivory reconstructions). σ^2_{NP}=rate for nonpiscivorous lineages. σ^2_{MP}=rate for moderately piscivorous lineages; σ^2_{HP}=rate for highly piscvorous lineages; BM1=Brownian motion with ancestral state, θ_0, and one rate: $\sigma^2_{NP}=\sigma^2_{MP}=\sigma^2_{HP}$; BM2a=Brownian motion ($\theta_0$) with two rates: σ^2_{NP}, $\sigma^2_{MP}=\sigma^2_{HP}$; BM2b=Brownian motion ($\theta_0$) with two rates: $\sigma^2_{NP}=\sigma^2_{MP}$, σ^2_{HP}; BM 3=Brownian motion (θ_0) with three rates: σ^2_{NP}, σ^2_{MP}, σ^2_{HP}. Bold values denote best-fitting model.

Character	Model	θ_0	σ^2_{NP} (My^{-1})	σ^2_{MP} (My^{-1})	σ^2_{HP} (My^{-1})	−ln L	AICc
PC 1	BM1	−0.297	0.056	0.056	0.056	36.756	77.975
	BM2a	**−0.821±0.281**	**0.148±0.060**	**0.028±0.015**	**0.028±0.015**	**35.378±0.993**	**77.716±1.986**
	BM2b	−0.389±0.089	0.065±0.005	0.065±0.005	0.013±0.014	35.856±0.517	78.672±1.035
	BM3	−0.767±0.312	0.132±0.063	0.039±0.025	0.010±0.009	34.910±0.839	79.487±1.679
PC 2	BM1	−0.315	0.142	0.142	0.142	49.983	104.428
	BM2a	**−0.310±0.136**	**0.271±0.026**	**0.076±0.008**	**0.076±0.008**	**47.609±0.408**	**102.178±0.815**
	BM2b	−0.228±0.099	0.165±0.011	0.165±0.011	0.021±0.016	48.498±0.468	103.956±0.937
	BM3	−0.245±0.145	0.270±0.026	0.091±0.011	0.024±0.017	46.968±0.524	103.602±1.048
PC 3	**BM1**	**−0.389**	**0.028**	**0.028**	**0.028**	**28.922**	**62.305**
	BM2a	−0.350±0.040	0.020±0.002	0.032±0.002	0.032±0.002	28.767±0.090	64.494±0.180
	BM2b	−0.414±0.019	0.026±0.002	0.026±0.002	0.054±0.019	28.684±0.195	64.329±0.390
	BM3	−0.380±0.042	0.021±0.003	0.028±0.003	0.053±0.019	28.603±0.183	66.873±0.366
PC 4	BM1	0.208	0.047	0.047	0.047	35.427	75.315
	BM2a	0.195±0.021	0.060±0.008	0.040±0.004	0.040±0.004	35.230±0.171	77.420±0.343
	BM2b	**0.177±0.035**	**0.055±0.004**	**0.055±0.004**	**0.003±0.003**	**33.623±0.471**	**74.207±0.943**
	BM3	0.174±0.038	0.058±0.008	0.054±0.009	0.003±0.006	33.559±0.472	76.784±0.944

Principal component 2 was best fit by the two-rate model that infers a shared rate of evolution in moderately and highly piscivorous lineages and a different rate in nonpiscivores (Table 4). This preferred two-rate model was substantially supported over single-rate Brownian motion (ΔAICc (BM1–BM2a) = 2.25 ± 0.82) but only somewhat supported over the alternative two-rate model (ΔAICc (BM2b–BM2a) = 1.78 ± 1.24) or the three-rate model (ΔAICc (BM3–BM2a) = 1.42 ± 0.85). The preferred two-rate model provided the best fit across 91% of the stochastic piscivory reconstructions. The model-averaged rates of PC 2 evolution differ strongly between highly and nonpiscivorous lineages, with the former inferred to have a slower rate; the intermediate rate in moderate piscivores is more similar to the highly piscivorous state (Fig. 3).

The single-rate Brownian motion model best fits the evolution of PC 3 (Tables 3 and 4). This model is substantially preferred over all other Brownian models (ΔAICc > 2.0) and was the best-fitting model in 94% of the piscivory reconstructions. This result suggests that the evolutionary process underlying PC 3 does not vary systematically with piscivory state (Fig. 3).

The favored model for PC 4 evolution was Brownian motion with two rates, one shared between moderate and nonpiscivores and a second slower rate for highly piscivorous lineages (Table 4; Fig. 3). The model inferring a slower rate in highly piscivorous lineages is strongly preferred over the other two-rate (ΔAICc (BM2a–BM2b) = 3.21 ± 0.98) and three-rate Brownian models (ΔAICc (BM3–BM2b) = 2.58 ± 0.20) and somewhat preferred over the single-rate model (ΔAICc (BM1–BM2b) = 1.11 ± 0.94). The favored two-rate model provided the best fit for 95% of the stochastic reconstructions of piscivory.

Discussion

Piscivory constrains diversification of feeding morphology in Centrarchidae, but this effect is most pronounced in the highly piscivorous lineages of *Micropterus*. The best-fitting model of evolution for PC 1 infers an adaptive peak shared by all piscivorous lineages and a separate peak for nonpiscivores (Table 3). This result suggests that a diet that includes fish imposes functional demands that have a strong influence on the diversification of feeding morphology and that these demands are distinct from those experienced by lineages that exclude fish and eat other types of prey. The demanding nature of piscivory is also evident in the relatively slow rates of evolution of PCs 2 and 4 in piscivores versus nonpiscivores. The preferred model for PC 2 evolution is a two-rate Brownian model that infers a slow rate of diversification shared between moderately and highly piscivorous lineages (Table 4). This relatively slow rate suggests that an adaptive peak for piscivory has further constrained these lineages from diversifying along this morphological axis to the extent seen in centrarchid

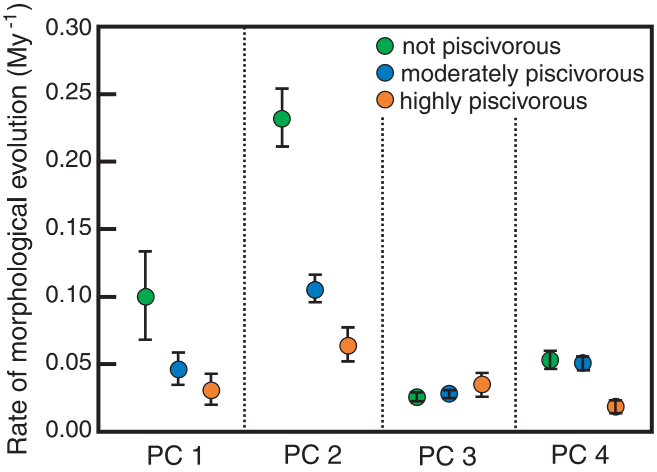

Figure 3. Model-averaged estimates for the rates of evolution of PCs 1, 2, 3, and 4 in highly (orange), moderately (blue), and not (green) piscivorous lineages. Parameter estimates were averaged across the four Brownian motion models and weighted by their Akaike weights. Error bars represent the standard errors calculated across the 500 sampled reconstructions of piscivory and weighted by Akaike weights. Piscivory slows diversification of PCs 1, 2, and 4. Moderately and highly piscivorous lineages have similarly slow rates of PC 1 and PC 2 evolution, and highly piscivorous lineages are inferred to have a substantially slower rate of PC 4 evolution. Note that differences in rates of PC 1 evolution should be interpreted with caution because the best-fitting model for PC 1 was a two-peak OU model. Rates of PC 3 evolution do not vary substantially across piscivory states.

lineages that feed on other prey types. This effect is particularly severe in the highly piscivorous lineages of *Micropterus*, which exhibit the slowest model-averaged rate of PC 2 evolution (Fig. 3) and have experienced a uniquely slow rate of PC 4 evolution (Table 4; Fig. 3). Altogether our findings demonstrate that piscivory represents an adaptive peak that limits morphological diversity in centrarchid lineages.

These results contribute to accumulating evidence that the constraining effects of adaptive peaks are important factors in accounting for the uneven distribution of morphological and ecological diversity among evolutionary lineages. Stabilizing selection is commonly cited to explain phenotypic stasis in the face of ample genetic variance and time to diversify (Charlesworth et al. 1982; Lynch 1990; Hansen 1997). Additionally, in a large-scale study of paleontological data, Estes and Arnold (2007) found that evolutionary models that explicitly incorporate adaptation to optimal character values best explain divergence in a variety of phenotypic character types over a wide range of time scales, suggesting that selection due to adaptive peaks has far-reaching consequences for the distribution of morphological diversity. Our study highlights the role of ecologically imposed selection in shaping the adaptive landscape; adaptation to a highly profitable but functionally demanding resource may be a common way that lineages approach adaptive peaks. Furthermore, our analyses demonstrate phylogenetically explicit methods for further tests of the importance of adaptive peaks in diversification. Comparisons of the fit of OU and Brownian motion models that allow parameters to vary between lineages that differ in ecological state provide insights into the evolutionary processes that influence the diversification of form.

Piscivory has a strong effect on the evolution of feeding morphology in spite of heterogeneity in trophic strategies exhibited among piscivorous centrarchids. The piscivores are comprised of species that feed primarily on fish (highly piscivorous species) as well as species that include fish in their diets but feed primarily on other types of prey (moderate piscivores). Even within the moderate piscivores there is substantial diet variation, including some species that feed primarily on the same prey items that comprise the majority of the diets of nonpiscivorous centrarchids (Table 1; Collar et al. 2005). Yet, our model-fitting results provide evidence that moderate and extreme piscivores share an adaptive peak for PC 1 (Table 3) and have a similarly slow rate of evolution of PC 2 (Tables 3 and 4; Fig. 3). These results suggest that selection imposed by the functional demands of feeding on fish has outweighed selection imposed by other prey types in moderately piscivorous centrarchids. The heterogeneity in trophic strategies of piscivorous centrarchids does, however, manifest itself as an elevated rate of PC 4 evolution in moderate piscivores relative to extreme piscivores (Table 4; Fig. 3). In the following paragraphs, we elaborate on our interpretation of the model-fitting results for each of these PCs.

ADAPTIVE PEAKS FOR PISCIVORY AND NONPISCIVORY INFLUENCE PC 1 EVOLUTION

Two adaptive peaks have influenced diversification along PC 1, the primary axis of feeding morphology variation in centrarchids—one for lineages that include at least a moderate amount of fish in their diets and one for lineages that do not. This two-peak OU model infers the positions of these optima to be beyond the values realized for any centrarchid species; the optimum PC 1 score for moderate and highly piscivorous lineages ($\theta_{MP} = \theta_{HP}$) is -10.14 ± 3.38 (standard error calculated across alternative piscivory reconstructions) even though no centrarchid species has a PC 1 score less than -3.0, and the optimum PC 1 score for nonpiscivores is 11.50 ± 2.97 even though no species has a score greater than 3.0 (Fig. 2). These parameter estimates suggest that centrarchid species have not reached the optima for piscivory and nonpiscivory but are instead interspersed between them, having experienced the pull of directional selection toward one of the two peaks. The distance between the inferred optima and observed species values suggests these lineages have been slow in their approaches to their adaptive peaks. This is partly a consequence of the relatively low estimate for the strength of selection ($\alpha = 0.053 \pm 0.022$ million years [My^{-1}]). Using Hansen's (1997) phylogenetic half-life ($t_{1/2} = \ln(2)/\alpha$), defined as the time required to traverse half the morphological distance from the ancestral state to the optimum, this estimate for the strength of selection corresponds to a phylogenetic half-life of 13.1 My. This value is nearly 40% of the age of the most recent common ancestor of all Centrarchidae and thus represents a relatively long time to reach the optima. We explore this two-peak model to more thoroughly interpret our hypothesis in light of the inference that piscivorous and nonpiscivorous lineages are evolving slowly toward optima they have not yet reached.

According to the multiple-peak OU model specified in Hansen (1997), species are not expected to be at the inferred optimum character value because the process of adaptation in a species is not only a function of the focal selective regimes (here, piscivory vs. nonpiscivory) but also unconsidered lineage-specific background effects—differences in environment, genetics, and other selective factors. These background effects prevent lineages from adapting perfectly to the selective factor under study, and the magnitude of this resistance to adaptation is reflected in phylogenetic half-life. Our estimate for this parameter (half-life = 13.1 My) provides evidence that lineage-specific effects have had a strong influence on the process of PC 1 evolution in centrarchids. The goal of fitting the multiple-peak OU model is to evaluate the effect of a selective factor across lineage-specific background effects (Hansen 1997), and indeed, we find support that selection due to piscivory and nonpiscivory have influenced PC 1 diversification even though other unconsidered factors have constrained adaptation to these trophic strategies.

Inference of optima beyond the range of observed values warrants some additional consideration. Given the distribution of piscivory states among centrarchid lineages, piscivores and nonpiscivores are each polyphyletic, and lineages have spent different amounts of their evolutionary history as piscivores or nonpiscivores. According to the piscivory reconstruction depicted in Figure 1, there are two different types of histories leading to piscivorous species (one for *L. gulosus* and *L. cyanellus* and another for all other piscivores) and four different types of histories leading to nonpiscivorous species (one that is unique to *L. symmetricus*, another for all other nonpiscivorous *Lepomis* species, and separate histories for *C. macropterus* and *Enneacanthus obesus*). These piscivory histories represent variation among lineages in their opportunities to evolve toward the adaptive peaks and allow for the inference of optima beyond the observed species values. According to Hansen's (1997) formulation of the two-peak OU model, the expected character value for a species is a function of the age and character value of the ancestor, the positions of the optima, the selection parameter, and the amount of time spent in each selective regime (Hansen 1997, equations 3 and 4; also see equation A4 in Butler and King 2004). Therefore, the expected PC 1 scores will be the same for species characterized by the same type of piscivory history (e.g., *Acantharchus pomotis* and *Archoplites interruptus*) but different for species that have experienced different histories even if they are presently in the same state (e.g., *L. macrochirus* and *E. obesus*; see Fig. 1 and Supporting Appendix S1).

Following Hansen (1997), we used our parameter estimates for the two-peak (piscivory vs. nonpiscivory) OU model (Table 3) and the piscivory reconstruction in Figure 1 to calculate the expected PC 1 scores for both types of histories leading to piscivorous species and each of the four types of histories leading to nonpiscivorous species. We found that no species is expected to have reached its optimum (see Supporting Appendix S1). This occurs in part because selection for piscivory and nonpiscivory is relatively weak and movement toward the optima is relatively slow. Even for species that have experienced only one selective regime during the entire history of the Centrarchidae, selection is not strong enough to move them from their estimated ancestral value to the optimum. In addition, other centrarchid species have experienced transitions between selective regimes during their evolutionary history. These species will be further from the optimum for their present selective regime because they have spent portions of their history evolving toward the alternative optimum (see Supporting Appendix S1). For example, centrarchid species that have spent their entire evolutionary history (at least since the origin of Centrarchidae) as piscivores have expected PC 1 scores that are 83% due to adaptation to the piscivory peak and 17% due to slowness of movement away from the ancestral value. In contrast, the expected PC 1 scores for the piscivorous species, *L. gulosus* and *L. cyanellus*, are 62% due to selection for piscivory, 21% due to ancestral selection for nonpiscivory, and 17% due to the ancestral value. Therefore, a species that has spent all of its centrarchid history as a piscivore is expected to be closer to the optimum than *L. gulosus* or *L. cyanellus*, and in fact, species' positions on PC 1 reflect this expectation (Fig. 2).

Given an inference of weak selection toward optima that have not been reached, Hansen (1997) suggests this scenario may be better modeled as Brownian motion with opposing trends. This model posits that selection is too weak or the optima are too distant for any species to reach the peaks (Hansen 1997). It thus predicts that lineages subject to different selective regimes will tend to evolve in opposite directions indefinitely. The two-peak OU model inferred herein differs from this opposing trend model in that it predicts lineages will eventually reach the optimum (unless they switch to other selective regimes), resulting in a deceleration of character evolution during the approach and resistance to evolution away from the peak once it has been reached (Hansen and Martins 1996). When lineages are far from their optima and selection is weak, however, the two-peak OU model predicts a pattern of character evolution that is practically indistinguishable from that of the opposing trend model. Although the opposing trend model may provide an even better fit to PC 1 because it is less parameterized (though we do not test this), its long-term prediction of limitless cranial evolution seems less biologically realistic than movement toward an optimum that no species has yet reached. Nevertheless, the inferred effect of piscivory on PC 1 evolution in Centrarchidae is similar under both the opposing trend and two-peak OU models.

Differences in positions of the optimal PC 1 scores highlight variables that confer differential performance for feeding on fish. The position of the adaptive peak shared by highly and moderately piscivorous lineages implies that selection has favored larger body sizes, wider gapes, longer lower jaw out-levers, smaller LP muscles, and less extensive PMX protrusion. This result indicates that capturing and processing fish prey require large body and mouth size, gracile pharyngeal jaws, and little jaw protrusion. The position of this peak is readily interpretable in terms of function; large body and mouth size enable the fish to engulf a volume of water that encapsulates the prey (Werner 1977; Keast 1985; Wainwright and Richard 1995), slight pharyngeal jaws allow the passage of large-bodied prey into the esophagus (Wainwright 1988), and jaw protrusion makes little contribution to closing the distance to the prey because these piscivores accelerate their bodies to overtake escaping prey (Norton and Brainerd 1993; Higham 2007a). The adaptive peak shared by nonpiscivorous lineages pulls these characters in the opposite direction. Nonpiscivorous centrarchid species feed primarily on aquatic insect larvae, small crustaceans, or snails (Table 1). The functional requirements of capturing and processing these prey have likely favored smaller mouth sizes to generate greater suction-induced flow speeds (Muller et al. 1982; Carroll et al. 2004), more robust pharyngeal jaws to break down or crush hard-shelled prey (Lauder 1983; Galis and Drucker 1996), and greater jaw protrusion to close the distance between predator and prey (Waltzek and Wainwright 2003) and to augment hydrodynamic forces exerted on prey that cling to substrates (Holzman et al. 2008b).

TWO-RATE BROWNIAN MOTION INDICATES SLOW EVOLUTION OF PCs 2 AND 4 IN PISCIVORES

The constraining effects of piscivory are also apparent in diversification of PC 2. Moderately and highly piscivorous lineages share a relatively slow rate of evolution along this axis, suggesting that nonpiscivorous lineages have experienced an increase in the rate of PC 2 evolution. The elevated rate in these lineages is likely due to diversifying selection associated with diet differentiation. Indeed, species classified as nonpiscivores have divergent diets, ranging from molluscivorous to insectivorous and planktivorous species (Table 1; Collar et al. 2005), and PC 2 is an axis reflecting variation in mechanical properties of lower jaw opening and closing (Table 2), which affect feeding performance on these prey types. However, moderately piscivorous species also feed extensively on prey that are included in nonpiscivore diets (Table 1; Collar et al. 2005). Therefore, the contrast between the rates of PC 2 evolution in moderately and nonpiscivorous lineages suggests that the functional demands of capturing and processing fish prey have constrained morphological diversification in lineages that feed even moderately on fish. This result underscores that morphological and ecological specialization do not necessarily correspond to one another because selection on feeding morphology may be driven by prey that impose the strictest functional demands for capture, which may not be the most common diet items (Robinson and Wilson 1998).

The association between the origin of an extreme form of piscivory and a slow down in the rate of feeding mechanism evolution further supports the hypothesis that piscivory constrains diversification. PC 4 has evolved more slowly in highly piscivorous lineages than in moderately or nonpiscivorous centrarchid lineages. But, for this axis the causal factor is specialization on fish rather than the general functional demands of capturing these prey. The effect of specialization is also seen in the relatively low model-averaged estimate for the rate of PC 2 evolution in highly piscivorous lineages. Selection due to an adaptive peak for extreme piscivory has likely limited the opportunities of highly piscivorous lineages to diversify along these morphological axes relative to lineages that feed on wider varieties of prey.

We attribute the slow down in rates of evolution of PCs 2 and 4 to the constraining effects of an adaptive peak even though the Brownian models were preferred over the OU models. This conclusion is not incompatible with these results. Although the OU model predicts that an adaptive peak steadily decreases accumulation of within-clade variance for a single, stationary peak (Hansen and Martins 1996; Hansen 1997; Butler and King 2004), several processes have been identified for which Brownian-like character evolution occurs in spite of selection toward a phenotypic optimum. These include evolution toward an optimum that moves in a Brownian way due to environmental change over time (Hansen and Martins 1996), or lineage-specific factors, such as environmental differences or selection for other functions, that cause the strength of selection to be low relative to the Brownian rate (Hansen 1997). Some combination of these processes may explain why morphological evolution is Brownian-like in piscivorous lineages in spite of the action of selection. The adaptive peak for piscivory for PCs 2 and 4 may not have been stationary throughout the history of centrarchid evolution; fish prey species may have turned over as community compositions changed over time, or prey species' escape performance and behaviors may have evolved in response to predation. In addition, diet and feeding morphology in these lineages may have evolved partly in response to selective demands for other functions resulting in divergence from the primary adaptive peak. The cranial features examined here perform other important functions and are likely to be correlated with features that perform other functions, and lineage-specific selective factors could have resulted in separate, realized optima that move in a Brownian way around the primary optimum (sensu Hansen 1997) for high performance piscivory.

CONSIDERATION OF POSSIBLE ROLES FOR ALTERNATIVE FACTORS

We implicate the adaptive peak for piscivory as a diversity-limiting factor in the Centrarchidae but note that our approach is limited to detecting the best of several plausible models of character evolution, which may not fully describe the true evolutionary process. Therefore, our model fitting results cannot exclude the possibility that alternative factors have underlain morphological diversification in centrarchid lineages. This is especially true for any factor that would generate patterns of diversification that are similar to those predicted by the hypothesis of an adaptive peak for piscivory. Below we present several additional factors that may have contributed to the observed patterns of diversification. Although these alternatives are not exclusive to the hypothesis presented here, we argue for the primacy of piscivory as an explanation for the patterns we document.

First, some ecological trait other than trophic strategy may be responsible for the adaptive peaks that have shaped diversification of PC 1. Because both piscivores and nonpiscivores are polyphyletic groups (Fig. 1), the number of possible confounding ecological traits with similar evolutionary histories is somewhat reduced. However, any aspect of ecology that is correlated with degree of piscivory will have a similar distribution among species and thus will be reconstructed to have a similar history. One such ecological feature is habitat use; centrarchid species differentially use highly vegetated areas versus the open water (Savino and Stein 1989). These habitats differ in structural complexity, ambient flow speeds, and threat of predation and thus impose different demands on a fish's ability to maneuver, accelerate, and swim steadily (Webb 1984). Moreover, patterns of habitat use may be associated with diet because fish predators must swim during the search for and pursuit of prey (Higham 2007b). Although the functional requirements imposed by different habitats will likely exert selection pressures on overall head shape, we have attempted to circumvent the confounding influences of such correlated variables by focusing on features of the feeding apparatus that have known consequences for feeding performance. Indeed, the positions of the adaptive peaks that we detected are consistent with biomechanical predictions about morphological differences that affect the capacity to capture and process fish and other types of prey.

In addition to piscivory-imposed selection, several factors could have contributed to the documented heterogeneity in the rates of evolution of PCs 2 and 4. Because the group of nonpiscivores is comprised primarily of most *Lepomis* species (but also includes *Enneacanthus* species) and the group of extreme piscivores is comprised of five of the eight *Micropterus* species, any factor that would cause the rate of skull evolution to increase in *Lepomis* or decrease in *Micropterus* would contribute to the observed pattern. One possibility is that genetic variation underlying these traits has increased in *Lepomis* or decreased in *Micropterus*. This difference could arise by nonadaptive means if mutation rates or effective population sizes have changed during these lineages' histories. This explanation seems unlikely, however, because these lineages exhibit rates of genetic divergence that are similar to each other and to other centrarchid lineages across several mitochondrial and nuclear loci (Near et al. 2004, 2005). Moreover, we are unaware of any factor unique to *Lepomis* or *Micropterus* that would have altered mutation rates or effective population sizes throughout these clades, though we were unable to find published data on these parameters for any centrarchid species. The adaptive peak hypothesis, however, does not exclude genetic variation as a factor because persistent selection toward an adaptive peak can lower genetic variation over time and increase the steepness of the peak, though fluctuations in the position of the optimum weaken this effect (Lande 1976). Therefore, limited genetic variation may have also led to the slow rate of evolution in piscivorous centrarchids.

Another potential explanation for the differences in rates of evolution of PCs 2 and 4 is that ecological opportunities have varied across centrarchid lineages. However, both *Lepomis* and *Micropterus* lineages arose early in the history of Centrarchidae (Fig. 1; Near et al. 2005) and each likely had access to the same trophic resources as other centrarchids during their histories; throughout their ranges *Lepomis* and *Micropterus* species co-occur frequently with one another and with other centrarchid species (Lee et al. 1980). Although all centrarchid lineages likely encountered similar prey types during their histories, competitive interactions among centrarchids may have precluded some *Micropterus* species from feeding on prey types other than fish. This scenario, however, is compatible with the adaptive peak hypothesis. Piscivory-induced selection may slow diversification in highly piscivorous lineages because of the high quality of fish as a food resource as well as the diminished competitive abilities of these species on alternative food. The comparative approach taken in this study is incapable of distinguishing between these scenarios.

A final factor that we consider is that some structural or behavioral innovation arose in *Lepomis* or *Micropterus*. If an unmeasured feature of the skull or aspect of behavior led some centrarchid species to feed in a fundamentally different way than others, then comparisons of rates of evolution of the characters measured here would be misleading. However, functional studies suggest that *Lepomis* and *Micropterus* species differ from each other and from other centrarchids only in the extent of modifications of cranial elements and behaviors that are shared throughout Centrarchidae. In fact, *Lepomis* and *Micropterus* and other centrarchid species use the same basic pattern of skull movements during suction-feeding (Lauder 1980; Wainwright & Lauder 1986; Richard & Wainwright 1995) and generate suction-induced flows using the same mechanism (Carroll et al. 2004; Higham et al. 2006). In terms of behavior, *Micropterus* species tend to swim fast to increase the speed with which they close on potential prey (so-called ram-feeding), whereas *Lepomis* species and other centrarchids use greater suction-induced water flows to carry prey into the mouth (Norton and Brainerd 1993; Carroll et al. 2004; Higham et al. 2006; Higham 2007a). However, species from all major centrarchid clades are known to vary swimming speeds from strike to strike and use different contributions from suction-induced flows and swimming speeds to successfully capture prey (Norton and Brainerd 1993; Higham et al. 2005). *Lepomis* and *Micropterus* differ from each other and from other centrarchids in their tendency to generate strong suction-induced flows or swim fast during a strike, but these behaviors are not novel in Centrarchidae.

We conclude that the evolution of piscivory had a strong effect on morphological evolution in Centrarchidae. As we note above, our evolutionary model-fitting approach does not rule out the role of some additional factors, but the best-fitting models support the hypothesis that an adaptive peak for piscivory has limited diversification of the feeding mechanism in centrarchid lineages.

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Supporting Information

The following supporting information is available for this article:

Appendix S1: Details for procedure used to determine the expected PC 1 scores for piscivorous and nonpiscivorous lineages based on the best fitting two-peak OU model.
Table S1: Species' values and standard errors for morphological features of the skull and collection localities or museum lot numbers for the specimens on which measurements were made.

Supporting Information may be found in the online version of this article.
(This link will take you to the article abstract).