

Ontogenic diet shifts and scale-eating in *Roeboides dayi*, a Neotropical characid

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Synopsis

Scale feeding (lepidophagy) has been documented for a variety of Neotropical fish taxa, including the characid genus *Roeboides*. Ontogenetic differentiation of jaws and snout teeth allow larger *Roeboides* to remove scales, however, the less specialized tooth/jaw structure in *Roeboides dayi*, indicates that it may be a facultative scale feeder. Population dynamics and diets of *R. dayi* in a Venezuelan lowland swamp/creek and a piedmont stream were compared over an annual cycle. Juvenile *R. dayi* consumed aquatic insect larvae and microcrustacea, and although spawning was year-round at both sites, most reproduction occurred during the wet season when the availability of these resources was greatest for juveniles. At both sites, larger *R. dayi* fed on a combination of invertebrate prey and fish scales, the former being more important at the piedmont site, and the latter being especially important during initial low water conditions at both sites. In the lowland stream, the reduction of aquatic habitat during the early dry season created higher fish densities and a more profitable environment for scale-feeders. Insectivory probably was less profitable during this early low water period due to interspecific competition for reduced aquatic insect stocks.

Introduction

The consumption of various fish parts is a significant component of the trophic niche of several fish taxa. Among those body parts consumed, scales are probably the most common (Sazima 1983), and at least five freshwater families and seven marine families contain lepidophagous (scale-eating) species. Tropical freshwater fishes in the following genera of the family Characidae (Characiformes) are known to be specialized scale-eaters: *Catoprion*, *Serrasalminus*, *Exodon*, *Roebroexodon*, *Roeboides*, *Probolodus*, and *Bryconexodon*. Of these genera, *Roeboides* is found throughout the Neotropics (Argentina to Mexico), whereas the other lepidophagous genera have more restricted ranges (Roberts 1970, Goulding 1980, Sazima 1983, Vari 1986).

Scales can be present in a fish's stomach for reasons other than lepidophagy. Piscivores that swallow their prey whole or that remove pieces of flesh can have scales in their stomachs after softer tissues have been digested. Scavengers and detritivores sometimes consume dislodged fish scales along with substrate. Truly lepidophagous species generally have scales in their stomachs without fish bones or flesh. Many lepidophagous fishes of the Neotropics have been directly observed removing scales in the laboratory or field (Sazima 1977, 1983, Sazima & Machado 1990, K. Winemiller personal observations).

Although lepidophagous fishes share no universal set of morphological attributes, most possess some specialization in dentition and jaw structure, especially those species that are obligate scale-eat-

ers. Most lepidophagous species have anterior teeth directed outwards from the mouth that are used for scale removal. Tooth position, tooth morphology, and the length of the jaws provide some insight into attack methods. Bilateral displacement of teeth and even tooth wear can show the tendency of an individual to attack from the right or left (Sazima 1983, Vari 1986). Sazima (1983) suggested that jaw structure and tooth placement determine the degree of lepidophagy. For example, *Roeboides prognathus* feeds almost entirely on scales, and has the most specialized tooth/jaw structure within this genus (protruding snout with external snout teeth used for dislodging scales). *Roeboides bonariensis* has less modified jaws than *R. prognathus*, and its diet is more variable consisting of insects in about the same proportion as scales (Sazima 1983).

Some species eat scales as juveniles and cease consumption of scales as they grow. This diet shift is usually accompanied by changes in dentition with growth (Major 1973, Smith-Vaniz & Staiger 1973, Sazima & Uieda 1980, Sazima 1983). Body size also plays a role in food consumption. Winemiller (1989a) found that the proportion of fishes consumed was strongly associated with predator length for nine dominant piscivores of a Venezuelan savanna stream. Aquatic microcrustacea, aquatic insects, and finally fishes were the major prey consumed as fishes progressed from larval to adult size classes over the course of the flood season. The scale-feeder, *Catoprion mento*, shifts from a broad diet of insects and plants as juveniles to a narrow diet of mostly scales as adults (Vleira & Géry 1979; Nico & Taphorn 1988). Several *Roeboides* species increase scale consumption as they grown (Roberts 1970, Sazima 1980, Sazima & Machado 1982).

Here we examine ontogenetic and seasonal diet trends for two Venezuelan populations of *Roeboides dayi* studied in 1984. The two populations occupy sites only 75 km apart, but one occurs in a llanos (savanna) swamp-creek with over 80 fish species, and the other inhabits a piedmont stream with about 20 fish species.

Materials and methods

During 1984, fishes were collected every month from two streams in the state of Portuguesa, Venezuela. One site, Caño Maraca, is a swamp-creek of the Rio Apure-Orinoco drainage in the western llanos (savannas) of Venezuela, and the other site, Caño Volcán, is a stream in the Andean piedmont. Caño Maraca lies in flat, sparsely wooded terrain that floods heavily during the wet season (May–August). The sheet flooding causes a large region bordering the creek channel to be converted from parched soil and thorn-scrub habitat into a productive marsh with an abundance of aquatic vegetation. When the dry season returns (January–April), the marsh created by the flooding returns to a network of mud bottom pools. Caño Volcán has heterogeneous substrates (e.g., sand, leaf litter, gravel, cobble), slow water velocity (0–0.07 m s⁻¹ at normal discharge), and contains pool, riffle, and run habitats. Because it drains a more forested watershed with greater topographical relief, Volcán has a more stable discharge than Maraca. Volcán has only 20 species, whereas Maraca has 88 species [see Winemiller (1990) for further descriptions of these sites].

Fishes were collected with seines of two sizes (2.5 m × 2 m, 3.2 mm mesh; 20 m × 2 m, 12.7 mm mesh). Gill nets and cast nets occasionally were used to supplement seine samples. Attempts were made to sample the entire fish assemblage without excluding any rare taxa, and so that the sample of each species approximated its relative abundance in the local community. Duration of field sampling was approximately equal among months for each site (but not between-sites), with the exception of the first three months of the wet season at Maraca. Due to the comparative inefficiency of fish captures in the flooded habitat at Maraca, more total time was spent collecting during the wet season. All obvious aquatic habitats were extensively sampled at the two sites (e.g., open water, vegetation, shallow/edge, deep/midpool). The December sample at Volcán included a rotenone sample from a single stream pool, so that absolute abundances of most species were larger for December relative to the other 11 months. Because pool habitats were much more prevalent than riffles and runs, relative abun-

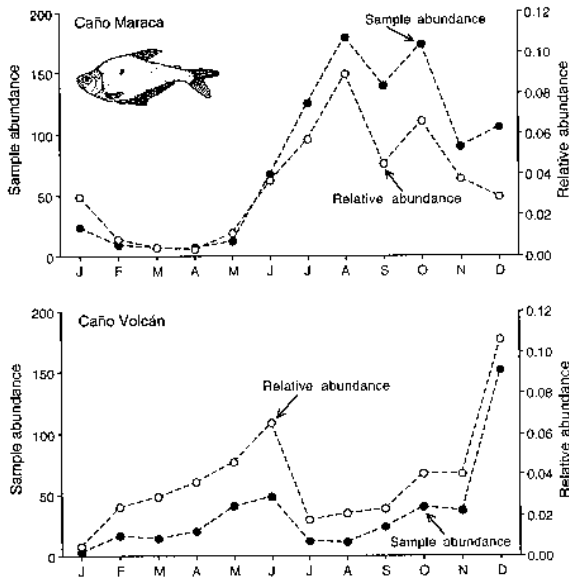


Figure 1. Monthly variation in sample abundance and relative abundance of *Roeboides dayi* in a lowland swamp-creek (Maraca) and piedmont stream (Volcán) in Venezuela during 1984.

dances of species should not have been greatly affected. Relative abundances of species were computed as the number of individuals of each species divided by the total number of fishes collected from all habitats for the site and period considered.

Specimens were preserved in 15% formalin, and returned to the laboratory to be identified, measured for standard length (SL), and analyzed for stomach contents. Each month, up to 50 *R. dayi* specimens from each site were dissected and examined for stomach contents. The total number of *R. dayi* examined for stomach contents was 353 for Maraca, and 323 for Volcán. All food items in the stomach chamber were removed, examined under a dissecting microscope, and identified to order (invertebrates), species (fishes), or general category (e.g., ctenoid, cycloid, and unidentified scales). Prey items were then sorted, blotted dry on a paper towel, and their volumes measured by water displacement in graduated cylinders according to methods described by Winemiller (1990). Resolution for the smallest items was 5 μ l. The percentage of juvenile *R. dayi* was estimated for each month/site sample. Juvenile was defined as a fish with a SL less than the minimum SL recorded for individuals with ripe

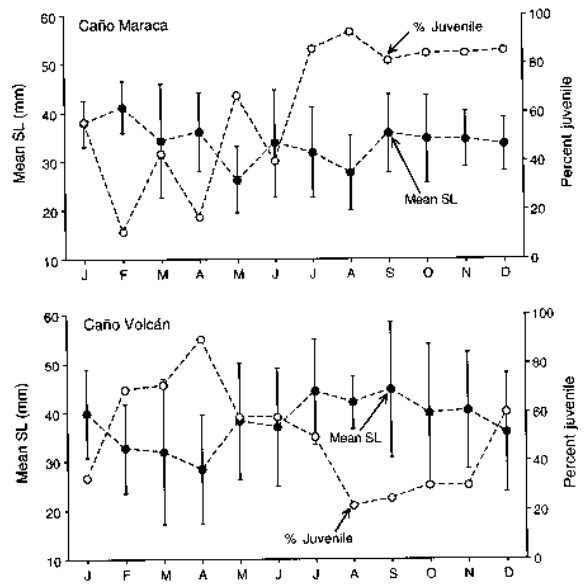


Figure 2. Monthly variation in the mean standard length (SL) and percentage of juvenile *R. dayi* at Maraca and Volcán during 1984 (bars are \pm 1 SD, monthly sample sizes ranged from 6 to 74).

gonads. The minimum adult SL for *R. dayi* was 27.9 mm at Maraca and 28.2 mm at Volcán.

Results

Population dynamics

The abundance of *R. dayi* in samples varied from 7 to 179 at Maraca, and from 3 to 152 at Volcán (Figure 1). Abundances were lowest at Maraca during the dry season, when fishes were concentrated at high densities in the isolated pools of warm (30–34°C), shallow, hypoxic (0.4–5.0 mg l⁻¹ DO) water. Both the absolute and relative sample abundance of *R. dayi* increased and peaked during the early period of transition to dry conditions (August to December) at Maraca (Figure 1), and this was a result of continuous reproduction and recruitment with high survivorship in the expanded aquatic habitat. In all monthly samples from both sites, virtually all *R. dayi* of both sexes that were > 28 mm SL contained ripe gonads (Winemiller 1989b). Ovaries always contained multiple oocyte cohorts and juveniles were encountered in every sample, a strong in-

dication of multiple spawning year round. At Maraca, juvenile *R. dayi* were least abundant during the dry season, and increased throughout the wet season reaching a peak in August (Figure 2). The mean standard length of the Maraca population was lowest during the wet season (May–August) and standard deviations were greatest during June and July, both of these parameters reflecting a greater representation of juveniles. Juveniles continued to dominate the Maraca population throughout the transition season (September–December; Figure 2), despite the fact that fish densities per unit area were at their highest levels.

The Volcán population had greatest sample abundances during the early wet and late transition seasons (Figure 1). If the December rotenone sample is excluded from consideration, the Volcán population showed much less seasonal variation in sample abundance than the Maraca population. In terms of water volume, Volcán is a more stable habitat than Maraca, and the primary disturbance at Volcán is scouring flash floods during wet season spates. These floods are of short duration (a few hours to a few days) and appear not to displace fishes greatly, as illustrated by the low variation in wet season sample abundance (Figure 1). *Roeboides dayi* sample abundances tended to track relative abundances at both sites, an indication that *R. dayi* tended to be one of the dominant species at each site. Juveniles comprised a larger percentage of the Volcán population during the late dry season (February–April), and were least common during the late wet and transition seasons (August–January; Figure 2). Temporal variation in mean lengths reflected this pattern of juvenile abundance, however standard deviations for length were relatively high during most months. Ripe gonads and juveniles were encountered year round, so the lower recruitment of juveniles during the transition season could result from predation within the hydrologically stable pool habitats. The primary piscivore at Maraca was *Hoplias malabaricus* (Hoplerythrinidae, Characiformes), but omnivorous characids (*Astyanax* spp., *Bryconamericus* spp.) also are abundant and probably consume fish larvae.

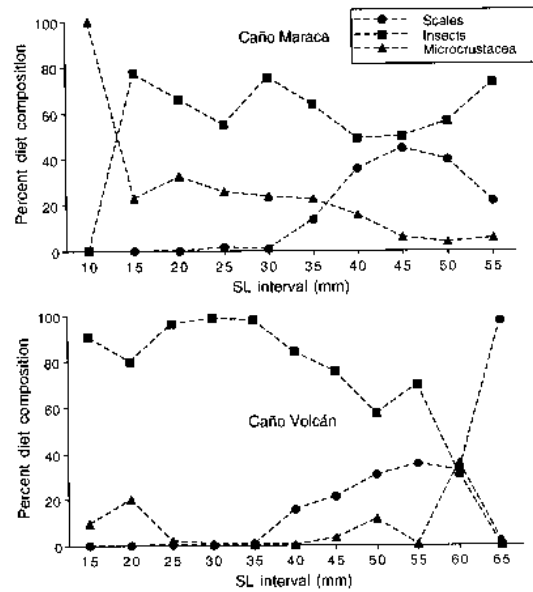


Figure 3. Changes in the volumetric percentages of three major diet categories according to SL interval of *R. dayi* at two sites during 1984 (total stomach sample N for Maraca = 353 and Volcán = 323).

Diet

Microcrustacea were the sole component of the diet of *R. dayi* < 10 mm SL at Maraca (Figure 3). At 11–15 mm, *R. dayi* switched to aquatic insects, although microcrustacea remained a minor diet component and gradually declined among fish in larger size classes. Aquatic insects were the dominant diet item for all *R. dayi* > 15 mm at Maraca. The most important insect orders were Ephemeroptera, Odonata, Coleoptera, Hemiptera (especially Corixidae), and Diptera (especially Chironomidae). Chironomid larvae comprised 32% of the diet volume during the wet season, but declined to 2.3 and 1.2% during the transition and dry season, respectively. Consumption of insects declined gradually for 26–40 mm *R. dayi*, but then gradually increased for larger fish. At Maraca, scale eating began at 25 mm, and scales comprised approximately 30–45% of the diet between 34–55 mm (Figure 3). The percentage of scales consumed actually dropped somewhat for fish > 45 mm, as consumption of aquatic insects increased, but this pattern could be biased by small samples (N = 6) for the largest size class. The corre-

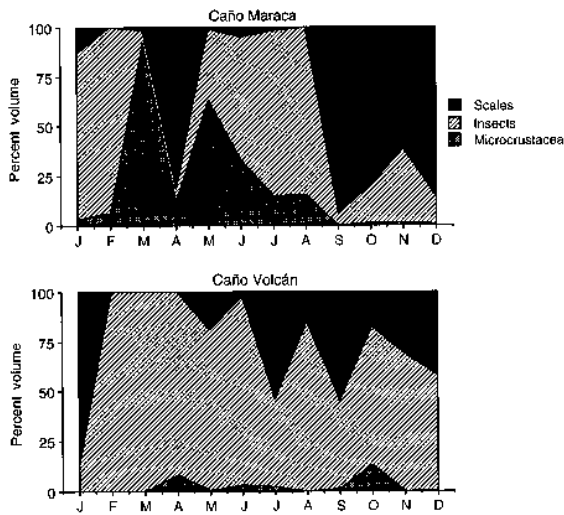


Figure 4. Monthly variation in volumetric percentages of three diet categories for *R. dayi* in two sites during 1984.

lation between SL and the volume of scales in the diet was 0.80 ($df = 9$, $p < 0.01$), and the correlation between SL and volumetric percentage of scales was 0.81 ($df = 9$, $p < 0.01$) at Maraca. Plant tissues and detritus were encountered infrequently, in trace amounts ($< 1\%$ volume), in stomachs of *R. dayi* from Maraca.

At Volcán, consumption of microcrustacea was only documented in the diets of juveniles < 25 mm, and attained maximum consumption at 20% of the diet for 14–20 mm fish (Figure 3). Insects were the primary food resource for all *R. dayi* between 15–55 mm SL, and insect consumption peaked among fish 21–35 mm. Ephemeroptera (41.1% – wet season, 26.3% – dry season) and chironomid Diptera (3.7% – wet, 10.6% – dry) were the major insect categories consumed at Volcán. Scale consumption peaked at 100% for the 61–65 mm size class at Volcán. At Volcán, SL was correlated with the volume of scales ($r = 0.86$, $df = 10$, $p < 0.01$) and the volumetric percentage of scales in the diet ($r = 0.79$, $df = 10$, $p < 0.01$). Consumption of plant tissues and detritus was negligible at Volcán ($< 1\%$ volume).

Seasonal shifts in the utilization of the three diet categories were greater for the Maraca population than the Volcán population (Figure 4). At Maraca, insects dominated diets during the early dry season and the entire wet season, and scales dominated the

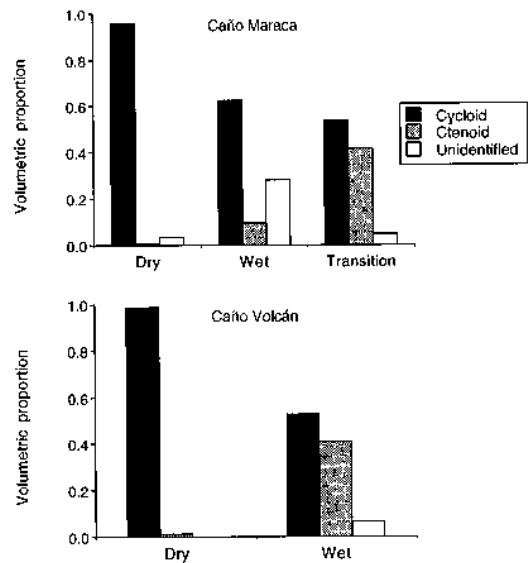


Figure 5. Volumetric proportions of cycloid, ctenoid, and unidentified fish scales consumed by *R. dayi* during different seasons at two sites during 1984 (sample N for Maraca[dry] = 49, M[wet] = 183, M[transition] = 121, Volcán[dry] = 162, V[wet] = 161).

April dry season sample and the entire transition season. Microcrustacea dominated the diet of Maraca *R. dayi* during May, when the initial state of wet season flooding was accompanied by rapid build up of copepods, cladocerans, and eubranchiopods from resting eggs in sediments. At Volcán, insects were the dominant diet component during every month except January, the initial survey that contained an unusually small sample of *R. dayi* ($N = 3$). Scales generally increased in the diets of Volcán *R. dayi* during the period June–December.

Of those scales consumed by the *R. dayi* populations at the two sites, cycloid scales were more abundant than ctenoid scales (Figure 5). Cycloid scales tended to be more abundant in diets at both sites during the dry season, but the association between scale type and season was not statistically significant at either site (Chi square goodness of fit test, $p > 0.05$). The scales from stomach contents could not be matched to individual species, but cycloid scales are assumed to be from diurnal characiform fishes (i.e., Anostomidae, Characidae, Curimatidae, Erythrinidae, Gasteropelecidae, Lebiasinidae, Prochilodontidae) and ctenoid scales were

from cichlids and the less abundant cyprinodontiforms (Poeciliidae, Rivulidae). Only characids, erythrinids, lebiasinids, prochilodontids, and cichlids were present at Volcán.

Discussion

Fish scales can provide a nutritious, abundant, renewable resource. Scales contain mostly protein, but also smaller concentrations of lipids and carbohydrates (Van Oosten 1957, Whitear 1986, Nico & De Morales 1994). On a per unit dry mass basis, the energy content of fish scales from several small llanos fishes is approximately two-thirds that of whole fish (Nico & De Morales 1994). In both piedmont and lowland streams, *R. dayi* showed greater scale consumption with increasing size, but the transition from a juvenile diet comprised of insects and microcrustacea to an adult diet comprised of insects and scales was more distinct in the lowland (Maraca) population. Adult *Roeboides* have more specialized tooth and jaw morphology than juveniles, and thus are able to supplement their diets with scales. Juveniles lack the snout teeth and the steep concave dorsal head profile of adults. Yet adult *Roeboides dayi* are not so specialized that they are unable to feed on other resources when available (i.e., aquatic insects and microcrustacea). Diets of adult size classes of *R. dayi* averaged approximately 45% scales by volume. When compared to several congeners (e.g., *R. affinis*, *R. prognathus*, *R. thurni*), *R. dayi* appears to possess a relatively unspecialized morphology. *Roeboides prognathus* from the Cuiabá River in Brazil consumed virtually 100% scales compared with about even amounts of scales and insects consumed by sympatric *R. bonariensis*, a species with less modified jaws and teeth (Sazima 1983).

Predator and prey recruitment dynamics, seasonal changes in resource supply/demand, and morphological changes during ontogeny interact to produce the shifts in diet composition observed at the two Venezuelan sites. At Maraca, high densities of aquatic insect and microcrustacean coincide with wet season flooding and provide a rich food resource for both juvenile and adult *R. dayi*. Insect

and microcrustacean availability was higher during the wet season than both the transition and dry seasons at Maraca (Winemiller 1990). Both primary production and the availability of invertebrates declines rapidly with the onset of peak dry conditions at Maraca (Winemiller 1989a, 1990). During the transition and dry seasons, dense schools of characiform fishes provide a food resource for those *R. dayi* that hatched and subsequently grew during the wet season. A potential major source of scales for *R. dayi* is *Ctenobrycon spilurus*, one of the most abundant small characids at Maraca. Except for the May sample, *Ctenobrycon* had consistently high relative abundance at the species-rich Maraca site (0.09–0.40). Other common small characiforms at Maraca (e.g., *Astyanax bimaculatus*, *Gephyrocharax valenciae*, *Steindachnerina argentea*) showed similar abundance patterns. The most abundant cichlid at Maraca, *Aequidens pulcher* (relative abundance 0.01–0.05), increased in both absolute sample abundance and relative abundance during the late wet-early transition seasons (July–August) and peaked during the early dry season (January).

At Volcán, aquatic insect availability changed little between the wet and dry seasons, but terrestrial insects were more abundant during the wet season (Winemiller 1990). Scales are probably easier to acquire during the dry season at Volcán when fish densities are higher within pools of reduced volume. The most abundant small species of characid (*Bryconamericus beta*, relative abundance 0.23–0.37) and cichlid (*Aequidens pulcher*, relative abundance 0.02–0.12) were available for scale feeding *R. dayi* throughout the year at Volcán. Both species showed early wet season (May–June) abundance peaks associated with a pulse of reproduction. Many of the fishes recruited from the wet season cohorts probably attained sizes that made them appropriate as prey for *R. dayi* during the late wet-transition to dry seasons (July–December), the period when scales were most abundant in the diet (Figure 4).

Fish body size and mouth gape limit the sizes and types of food particles that can be consumed (Werner & Gilliam 1984, Keast 1985a, b, Winemiller 1989a). Only larger individuals are powerful enough to dislodge and consume scales from fishes,

some of which may be larger than the scale-feeder. We have observed *R. dayi* feeding on a variety of natural prey in aquaria, and the attacker frequently used ambush tactics to get close enough to the prey to initiate the actual attack. Sazima (1983) gave a detailed account of the attack behavior of *Roeboides*, in which the attacker dashes toward the prey's flank, rams the flank with its snout teeth, and scrapes several scales loose with a rapid raking action. The free scales are intercepted as they sink in the water column then engulfed. *R. dayi* must attain a sufficient size to permit not only the ingestion of scales, but also flight from retaliatory actions by prey that, in many cases, are larger than the attacker (Breder 1927, Curio 1976, Sazima 1980, 1983). Despite the fact that the transition season *R. dayi* population at Maraca was dominated by juvenile size classes (Figure 2), scales were the major diet component (Figure 4). Adult *R. dayi* were present during the transition season (Figure 2), and larger stomach volumes of adults caused their diet to dominate the percentage volumes of the major food categories calculated for the overall sample. At Volcán, adults dominated the late wet and early dry season samples (August–November), so that the corresponding increase in scale feeding during this period (Figure 4) resulted from both adult domination of the sample and their greater stomach capacity.

Large variation in aquatic habitats and the resources contained therein provides Neotropical fishes with many avenues for interspecific niche diversification through resource specialization. In areas like the llanos, strong seasonality selects for broad niches, because organisms may not be able to specialize on limited subsets of unstable resources. Species may adapt to this challenge of temporal variation by either of two means. First, the life cycle can evolve, so that energy and nutrients acquired during periods of resource abundance can be stored during periods of resource scarcity to permit spawning during the return of favorable environmental conditions. Second, the trophic niche can evolve, so that a greater array of resources can be used when resources are plentiful, yet specialization on a stable subset of resources permits some reproduction even during periods of resource shortage. Our data

indicate that *R. dayi* is facultative scale feeder, and this is consistent with the lower degree of specialization in tooth/jaw structure relative to certain other *Roeboides* species. A comparative analysis of diet and morphology that included both facultative and obligate scale feeders (e.g., *R. affinis*, *R. thurni*) could provide a model for the evolution of niche specialization in fishes.

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