Spawning habitat, behavior, and morphology as isolating mechanisms of the golden redhorse, *Moxostoma erythrurum*, and the black redhorse, *M. duquesnei*, two syntopic fishes

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Synopsis

Golden redhorse, *Moxostoma erythrurum*, and black redhorse, *M. duquesnei*, were observed spawning during the springs of 1984 through 1987 in Stony Creek, Illinois, at water temperatures ranging from 15–21°C. Both species spawned simultaneously within the same stream reach in 1987. Male golden redhorse aggressively defended territories on shoals and were joined by females from an adjacent pool. Black redhorse also spawned in riffles and displayed no agonistic behavior. Both species spawned throughout daylight hours in groups of two to five, and golden redhorse also spawned at night. Habitat utilization curves indicate that black redhorse spawned in habitat that was slightly deeper, much swifter, and over coarser substrate than that of the golden redhorse. Males of both species exhibited nuptial body color and breeding tubercles on anal and caudal fins, while only golden redhorse males had head tubercles. We suggest that these differences in spawning habitat, behavior, and morphology act as reproductive isolating mechanisms between the species and that the dichotomy in habitat and behavior may be due to competitive interactions.

Introduction

Golden redhorse, *Moxostoma erythrurum*, and black redhorse, *M. duquesnei*, frequently occur syntopically (Rivas 1964) over much of their ranges, thereby creating the potential for hybridization. However, virtually no interspecific hybrids have been described within (*Moxostoma*). Spawning behavior and habitat of suckers (Catostomidae), summarized by Breder & Rosen (1966) and Page & Johnston (1990), have been described primarily in qualitative terms limiting both inter- and intraspecific comparisons. Descriptions and notes on spawning of the redhorses (*Moxostoma* spp.), specifically

the black redhorse (Bowman 1970), golden redhorse (Reighard 1920, Smith 1977, Curry & Spacie 1984), silver redhorse, *M. anisurum* (Hackney et al. 1970), shorthead redhorse, *M. macrolepidotum* (Burr & Morris 1977, Curry & Spacie 1984), river redhorse, *M. carinatum* (Hackney et al. 1968), and greater redhorse, *M. valenciennesi* (Jenkins & Jenkins 1980), describe generally similar behavior wherein one or more males spawns with a single female over shallow gravel shoals or riffles.

Careful observations of golden redhorse and black redhorse spawning simultaneously within the same stream reach allow us to present further documentation of spawning behavior, chronology, and

morphology. It is also our objective to characterize and quantify critical spawning habitat for these species. Comparisons between observations made and measurements collected within the same area indicate potential effective isolating mechanisms between these closely related species.

Methods

Study area

Stony Creek is a third order (Horton 1945, Strahler 1957) mainstem tributary of the Salt Fork drainage of the Vermilion River, Vermilion County in east-central Illinois. Stony Creek drains 178 km² of agricultural land at a mean gradient of 1.9 m km⁻¹. The area of Stony Creek where fish were observed spawning was 3.0 km upstream of its confluence with the Salt Fork. The study area was located below a 169 km² drainage area, at a mean slope of 1.94 m km⁻¹ and a mean width of 14.4 m.

Observations, data collection, and analysis

Spawning observations were made during the springs of 1984 through 1987. Species were identified according to descriptions in Jenkins (1970), Pflieger (1975), and Smith (1979). Habitat variables were measured at the precise locations where fish were observed spawning undisturbed. Individual golden redhorse could be recognized by size and distinguishing marks (e.g., torn flesh, scars, missing scales). Male golden redhorse that defended a primary spawning site where spawning occurred at least once were considered dominant, and males that were found on the edge of a spawning area and rarely spawned were deemed subordinate. Night observations of spawning fish were possible by briefly shining a hand-held light source on the fish.

Physical characteristics of microhabitat were measured only once at each spawning location regardless of the number of fish that spawned there or the frequency of use of the location during the spawning season. Depth was measured using a top-

set wading rod. Mean column water velocity ($0.4 \times$ total depth for depths ≤ 0.76 m; 0.2 and $0.8 \times$ total depth for depths > 0.76 m) and velocity at the stream bottom were determined using a Marsh-McBirney Model 201 digital flow meter. Bottom water velocity was measured because both species studied are bottom dwelling; thus, such a measurement would be the best descriptor of the actual conditions a fish was experiencing. In 1984 surface flows were estimated by timing a 2.5 cm float over a measured distance. These surface flows were later converted to mean velocities using a vertical-velocity curve (Buchanan & Somers 1969). Substrate composition was classified by size and texture according to a modified Wentworth particle-size scale (Bovee & Milhous 1978). Habitat availability was determined by proportionally sampling ten transects selected according to the criteria of Bovee & Milhous (1978) within a representative stream reach which included both spawning and non-spawning areas. Stream discharge was measured using the midsection method (Buchanan & Somers 1969) with the wading rod and flow meter described above.

Habitat suitability curves were constructed from physical measurements collected from spawning microhabitat of golden and black redhorses. Depth and velocity measurements were tabulated and grouped into increments of 0.1 m and 0.1 m sec⁻¹, respectively. Substrates were classified into 10 groups ranging in particle size from bedrock to boulder. In observations of mixed substrate, only the most prevalent substrate class was considered for suitability curves. Frequencies of measurements within a parameter range were normalized to unity for comparison; i.e., the modal range of each habitat parameter was assigned a value of 1.0, and frequencies of other intervals were expressed as a proportion of the mode. A curve was then fitted to the data by interpolation. To facilitate a smooth curve, a range of no use between two ranges of a habitat variable used for spawning was not incorporated into the curve. Bovee (1986) suggested that such distributions are likely the result of schooling, inadequate sample size, or measurement error rather than discriminatory behavior on the part of the fish, and he advocated smoothing.

Use of terminology and calculations of habitat utilization, availability, and preference were according to Bovee (1986): utilization is defined as the relative frequency of observations across the range of a measured microhabitat variable; availability is the relative frequency of the variable range available during the observation period; and preference is computed as the ratio between utilization and availability ($P_i = U_i/A_i$).

A Smith-Root Type VII pulsed DC backpack electrofisher was used to collect spawning fish. Fish were measured (mm TL), lateral scales were removed to estimate the age of selected fish, and sex, coloration, distribution of tubercles, and fish location were noted. Age was estimated by scale impression analysis (Smith 1954) and was independently confirmed by two biologists. A No. 0 (500 μ m) mesh drift net with a 0.09 m² opening was set to collect drifting eggs approximately 1 m downstream of the most intensely used area of a golden redhorse spawning shoal for a recorded time period of at least 3 h in each of 1985 and 1987. After the downstream drift net was removed, the substrate of a 0.19 m² area on the spawning shoal was agitated and the suspended material that resulted was allowed to flow immediately downstream into another drift net to collect eggs deposited on the shoal.

Results

Timing and conditions

Golden redhorse were observed spawning in Stony Creek on 19 May 1984 at a water temperature of 21.0°C and on 3 May 1985 at 16.0–16.5°C. Black redhorse were observed spawning on 29 April 1986 at 18.0°C. Both species spawned simultaneously in different habitats within the same stream reach on 1–2 May 1987 with water temperatures of 15.0–17.5°C. Stream discharge during the 1987 spawn was 1.05 m³sec⁻¹. Spawning in both species was usually terminated for the season by a rain event.

Both species spawned throughout daylight hours. In 1987, golden redhorse were observed spawning continuously for over 2 h after sunset

(until 2100 h Central Standard Time; 1847 h sunset), following which the observer left the stream. Upon return 1 h before sunrise (0454 h sunrise), male golden redhorse were exhibiting territorial behavior on spawning shoals, but no spawning took place until 0.5 h after sunrise. Black redhorse spawned until sunset and at sunrise, but observation of this species during dark hours was impossible even with a light source due to extreme water turbulence in riffles. However, much activity and splashing was heard at black redhorse spawning locations after dark and may have indicated spawning.

Habitat

Habitat measurements were collected from 13 golden redhorse spawning sites from three shoals within a 400 m stream reach during 1984, 1985, and 1987. No other golden redhorse spawning habitat was encountered during the examination of 2.5 km stream length in 1987. The shoals may be characterized as shallow extensions into the stream channel with low to moderate nonturbulent flow over substrates of sand and gravel. Shoal areas ranged from 1.1–22.4 m² (mean = 8.6 m²). One particular shoal (Site 1) was used for spawning by golden redhorse all three years. The spawning shoals were shallow, with depths ranging from 0.12–0.24 m (mean = 0.18 m). Moderate mean column water velocities (mean = 0.28 m sec⁻¹; range = 0.19–0.45 m sec⁻¹) and bottom velocities (mean = 0.15 m sec⁻¹; range = 0.04–0.29 m sec⁻¹) were measured on the shoals. Substrates ranged in size from sand (0.06–2.0 mm diam.) to small cobble (64–130 mm diam.); fine gravel (2–8 mm diam.) was encountered most frequently (46% of locations).

All golden redhorse spawning shoals were adjacent to or immediately downstream of a deep pool that served as a holding area for females and subordinate males and as a refuge for all spawning fish. The pools were deeper (mean = 0.48 m; range = 0.29–0.67 m) than the shoals and had more widely ranging mean velocities (mean = 0.27 m sec⁻¹; range = 0.11–0.56 m sec⁻¹) and bottom velocities (mean = 0.15 m sec⁻¹; range =

Fig. 1. Utilization (frequency of use) and preference (ratio of utilization to availability) curves for spawning microhabitat of golden redhorse and black redhorse in Stony Creek, based on measurements collected in 1984, 1985, and 1987 for golden redhorse and in 1986 and 1987 for black redhorse.

0.06–0.36 m sec⁻¹). Pool substrates were finer, ranging from bedrock to coarse gravel (16–64 mm diam.). Periphyton-covered bedrock was the predominant pool substrate.

Black redhorse spawned in riffle habitats, usually at the upstream or downstream margins, and apparently avoided the swiftest areas. Riffles were shallow areas with a relatively steep water surface gradient that caused high velocities and turbulence over coarse bottom materials of gravel and cobble. Microhabitat measurements were gathered from 25 spawning locations in six riffles within a 1 km reach. Spawning locations were shallow, ranging from 0.12–0.37 m (mean = 0.22 m). Both mean and bottom water velocities were varied and ranged from 0.17–1.29 m sec⁻¹ (mean = 0.55 m sec⁻¹) and 0–0.66 m sec⁻¹ (mean = 0.31 m sec⁻¹), respectively. Spawning substrates ranged in size from fine gravel to large cobble (130–250 mm diam.); small cobble was used most frequently (48% of locations). In 1987 black redhorse were observed spawning in a swift water area that had served as a spawning shoal for golden redhorse in 1985 when water depths and velocities were lower.

Utilization and preference curves (Fig. 1) show considerable overlap in depth of spawning habitat selected by golden redhorse and black redhorse. Black redhorse spawned in a wider range of water velocities than did golden redhorse. Narrow ranges of mean velocity and bottom velocity were used by both species, but the ranges used most frequently by each species are clearly distinct. This separation of habitat by velocity is apparent in the utilization curves and is magnified in the preference curves, thereby considering availability. Golden redhorse spawned over finer substrates and a narrower range of substrates than did black redhorse. The distinction between the spawning substrates selected by each species is apparent in the utilization curves, with fine gravel used most frequently by golden redhorse and small cobble by black redhorse. However, the preference curves reveal that fine gravel may also be a suitable spawning substrate for black redhorse. Based on these findings, golden redhorse and black redhorse probably use water velocity and/or substrate as a cue in selecting distinctly different spawning microhabitats. The

primary stimulus in spawning microhabitat selection cannot be determined using field data, because water velocity and substrate are confounded variables in a natural system (higher velocities are associated with coarser substrates).

Behavior

Golden redhorse were extremely active and aggressive during spawning. Male golden redhorse established territories on the spawning shoal, an activity that included much agonistic behavior between dominant males holding positions on the shoal and subordinate males from the holding pool or shoal margins attempting to establish territories. Two areas and behaviors are described in detail for golden redhorse.

The largest golden redhorse spawning area, Site 1 on 19 May 1984, consisted of a shoal approximately 9.1 m long and 2.4 m wide with a deeper pool area immediately adjacent. Three specific spawning sites within the shoal (designated by X; Fig. 2a) were defended by three pairs of dominant males (A1–A6) at all times, and as many as 17 males and 3 females were observed on the shoal at one time. At least one of the dominant males was involved in every observed mating event at Site 1, and 8 of 16 events involved only males A1 and A2. Subordinate males (B1–B10) rarely mated but were constantly sparring among themselves, an activity that involved substantial physical contact and rearrangement of their positions at the downstream shallow edge of the shoal (Area B). Males B1 and B2 appeared to be the most dominant of the subordinate males and maintained relatively stable locations on the shoal. Male B2 mated in only 1 of 16 observed events and was the only subordinate male that we observed spawning.

On 3 May 1985 lower water levels had reduced the shoal size at Site 1 to 1.8 m by 1.5 m, with only a single primary spawning site. Two dominant males were involved in all observed matings. Considerable agonistic behavior by these dominant males and by a single subordinate male excluded all other males from the shoal. Only a single female at any given time was observed on the shoal.

Fig. 2. Arrangement of male golden redhorse on spawning shoals at Site 1 (a) and Site 2 (b) in Stony Creek. Dominant males and subordinate males are numbered with a leading A and B, respectively. Most spawning occurred at primary spawning depressions (designated by X) in Area A at each site; little spawning took place in each Area B, which served as an intermediate holding area. Movement of individuals is indicated by broken arrows.

Approximately 9 m downstream of Site 1 in 1985, a second spawning group was observed. At this location (Site 2; Fig. 2b) all mating occurred near the depression defended by A1 and most involved males A1 and A2 (13 of 14). Male B1 maintained its position in swiftly flowing water near a constricted riffle and mated with a female once with male A2, but male A1 interfered with that event. Male B2 maintained a territory approximately 0.8 m upstream of A2 and often attempted to engage in mating but was never observed to be successful. Females approached laterally, tail first, downstream from the deep pool holding area. Subordinate males and females often paused at a small

shallow area on the edge of the shoal (Area B) before entering the primary spawning area (Area A). When males were active or agonistic, the female would quickly retreat to the pool without mating. No more than one female appeared on the shoal at any one time, but electrofishing efforts recovered two females at this location.

Breeding golden redhorse males had large head tubercles (Fig. 3a). Torn flesh marks, wounds likely received as a result of aggressive encounters using these tubercles, were found on the backs of several males. When subordinate males ventured too close to primary spawning sites (i.e., those used most frequently), dominant males charged the sub-

ordinates and often drove them from the shoal to the adjacent pool.

The primary spawning sites were approximately 5 cm deeper than the surrounding area. We were not able to ascertain if these substrate depressions had been excavated prior to spawning, as has been observed for river redhorse (Hackney et al. 1968), but we saw no preparatory activity. Much sand and gravel was violently stirred up during the mating quiver, which may well have resulted in the excavation.

The most efficient mating sequences, i.e., those that achieved the most mating with the least amount of time and effort, appeared to occur when a female entered from the adjacent pool and immediately aligned herself directly between two dominant males over one of the primary spawning sites. Such a sequence occurred in 26 of 30 matings observed at two sites and is described as follows. Prior to the female's entrance, males had already aligned themselves facing upstream on either side of a primary spawning site, and they remained essentially motionless at that location. Drifting in from upstream tail first, moving in laterally facing upstream, or entering directly from downstream, the female was flanked on both sides by males. With fins flared and caudal areas pressed tightly together, the release of gametes ensued with tetanic vibrations of the group lasting from 3–6 sec (Fig. 3b). Given the shallow water at these locations, the anterior dorsal surface of the fish occasionally broke the water surface during the vibratory period. The mating act terminated abruptly as the trio separated; the males returned to their original posts, while the female either rested at the margin of the shoal or returned to the adjacent pool.

Single male-single female encounters were brief and resulted in mating less often than events with two males. The participation of more than two

Fig. 3. Photographs of spawning golden redhorse and black redhorse in Stony Creek: a – Head tubercles of a breeding male golden redhorse. b – A female golden redhorse flanked by two male conspecifics releasing gametes over a spawning shoal. Note secondary male under the trio. c – A female black redhorse flanked by two male conspecifics releasing gametes in a riffle (photographs by L.M. Page).

males often (but not always) occurred when dominant males were positioned close to adjacent males on the shoal. Timing appeared to be critical for successful involvement of secondary males (i.e., the third or fourth male in a mating). If secondary males appeared too soon or too late in the sequence, a primary male would either give chase or the mating act would abruptly end. Once the mating vibratory period had been initiated, secondary males were allowed at least 1–2 sec of involvement. Numerous mating quivers were terminated with a secondary male 'diving' under the mating trio (Fig. 3b). The intent of this male behavior is unknown, but egg consumption, disruption of mating, or an attempt to fertilize eggs are all possible.

Considering all observed golden redhorse spawning, the number of males on a shoal ranged from 1–17. The mating act involved 1–4 males with a single female, but two participating males was the most common number. No type of 'nuptial dance' (Hackney et al. 1968) or jumping or rolling (Burr & Morris 1977, Bowman 1970) as seen in other *Moxostoma* species was noted for golden redhorse. During daylight hours, a golden redhorse mating event generally occurred every 10–13 min if the fish were left undisturbed. If disturbed, fish on the shoal retreated to the adjacent pool, and reestablishment of the territory grid followed shortly. Golden redhorse spawning behavior at dusk and after dark was similar to that observed during the day; however, near dusk males on the shoal were grouped more closely together (ca. 0.4 vs. 0.6 m distance), agonistic behavior was more frequent and aggressive, and fewer mating acts occurred. After sunset, mating events took place with greater frequency (ca. 1–9 min apart).

Eggs were found both in the substrate of golden redhorse spawning shoals and in drift nets placed downstream of the sites (Table 1). The drift rate of eggs was greatest at Site 1 in 1985 when no eggs were found in the spawning substrate. Given the high water velocities found in black redhorse spawning habitat, a portion of the eggs of that species also probably drifted. Breder & Rosen (1966) state that suckers bury their eggs under gravel. Stony Creek redhorse deposited their eggs in

the substrate, but did not actively cover them. Comment regarding the functional design of *Moxostoma* eggs would be speculative; their fate, however, is that they incubate in the spawning substrate and are also dispersed downstream as drift. No parental care of eggs was shown by either species. On several occasions, we observed longear sunfish, *Lepomis megalotis*, and northern hog suckers, *Hypentelium nigricans*, foraging on, or downstream of, a golden redhorse spawning shoal, but we were unable to determine whether or not these fish consume redhorse eggs.

Black redhorse spawning behavior was much less aggressive and more communal than that of the golden redhorse. Large numbers of both sexes ranging from 7 to about 80 fish gathered at the upstream and downstream edges of riffles and divided into smaller groups as they moved into riffles. Both sexes took up positions in the riffles, with no apparent pattern but often behind large rocks. There was no apparent territoriality, and groups of up to six fish with individuals positioned within a few cm of each other were common. Both males and females shifted positions frequently and joined other small groups in the riffle or moved into a nearby pool, always maintaining a position facing upstream. Stony Creek black redhorse often rolled over the backs of other members of the spawning group in shifting positions, behavior similar to that described for the shorthead redhorse by Burr & Morris (1977). Females were flanked by up to four males. The black redhorse mating event took place with a quiver of the caudal regions by all fish involved (Fig. 3c) similar to that of the golden redhorse (Fig. 3b), but lasted only about 2 sec. The

Table 1. Density and drift rate of eggs sampled from substrate and downstream of golden redhorse spawning shoals in Stony Creek.

	Spawning substrate (no. eggs m ⁻²)	Downstream drift (no. eggs h ⁻¹)
1985		
Site 1	0	4.7
Site 2	335	2.8
1987		
Site 1	173	2.0

mating was often terminated when one or more of the group members fled rapidly to new positions, but in some cases the group gradually diminished vibrating and maintained their positions.

Morphology

In accord with descriptions of golden redhorse and black redhorse by other investigators (Bowman 1970, Jenkins 1970, Smith 1977), we found sexual dimorphism in both species in Stony Creek during the spawning period. Males of both species exhibited nuptial body coloration and had tubercles on their anal and caudal fins, but only the golden redhorse had large stout head tubercles (Fig. 3a). Males of both species had bold longitudinal stripes of black and a color ranging from orange to pink along their sides. Golden redhorse males involved in the most agonistic behavior showed the most brilliant color and darkest stripes. The coloration vanished immediately when a fish was captured by electrofishing. The females of both species showed little or no spawning color and had no tubercles.

Four male and three female spawning golden redhorse collected from two sites in 1985 had mean total lengths of 335 mm (range = 326–352 mm) and 351 mm (range = 338–362 mm), respectively. Four black redhorse captured in the adjacent holding pools, but not observed spawning, were larger with a mean length was 370 mm (range = 338–403 mm). Three dominant golden redhorse males were essentially equal in length (326–334 mm). Ages of all spawning fish collected were estimated at 5 or 6 yr. Although these ages were not validated, the tentative age estimates in combination with equivalent lengths of dominant males indicate that there were no great age differences between golden redhorse dominant spawning males or between dominant and subordinate males.

Discussion

Natural hybridization or survival of hybrids to a collectable size are unknown events in the tribe Moxostomatini, whereas intersubgeneric and in-

tergeneric natural hybrids are known to occur within Catostomini (Hubbs 1955, Smith 1966, Schwartz 1972, 1981). Schwartz (1972, 1981) found no reports of any interspecific hybridization in *Moxostoma* in a compilation of world literature on fish hybrids. In his extensive examination of thousands of specimens, Jenkins (1970) identified only one possible *Moxostoma* interspecific hybrid and speculated that effective isolating mechanisms must be operating. Environmental factors that weaken isolating mechanisms are most frequently invoked as allowing interspecific hybridization to occur within Catostomini (Hubbs et al. 1943, Hubbs 1955, 1961, Nelson 1973), but Nelson (1968) could not attribute the occurrence of hybrids between *Catostomus commersoni* and *C. macrocheilus* to such causes. Many factors can serve as isolating mechanisms that effectively reduce the occurrence of hybridization between closely related fish species. Among these are time, space, morphology, and behavior.

Spawning dates for golden and black redhorse reported by other investigators are variable due to climate and seasonal differences, yet most authors cited black redhorse as spawning before golden redhorse but with a potential for overlap (Cross 1967, Jenkins 1970, Curry & Spacie 1984), whereas Smith (1977) noted the reverse sequence in Clear Creek, Ohio. The environmental cues that regulate initiation of spawning by *Moxostoma* are largely unknown, but temperature, photoperiod, and stream discharge are likely contributing proximate factors. Stony Creek seems to offer a common range of stimulating cues, because we observed golden redhorse and black redhorse spawning synchronously there in 1987, as did Page & Johnston (1990) in 1988 at the same location. These observations negate time as an operating isolating mechanism.

The distributions of golden redhorse and black redhorse overlap significantly, and they are frequently syntopic (Jenkins 1970), as in Stony Creek. The two species do, however, segregate into different microhabitats for spawning, as is clearly described in this study, thereby lowering the likelihood of interspecific fertilizations.

The spawning behavior of Stony Creek golden

redhorse is similar to that described for conspecifics in Ohio (Smith 1977) and Virginia (Jenkins 1970), but it is also similar to that described for black redhorse in Missouri (Bowman 1970). The spawning behavior of golden redhorse and that described for Missouri black redhorse suggest that an optimal location on the shoal is vigorously defended with no apparent value other than for mating. Males determine relative positions of dominance among themselves within a stable assemblage that is marked by a highly skewed operational sex ratio, and females choose mates primarily on the basis of male status. This type of mating system is best described as male dominance polygyny, and such aggregations of males may be referred to as leks (Emlen & Oring 1977). In contrast, Stony Creek black redhorse spawn in riffles and are not territorial. Our observations indicate that black redhorse spawning occurs in unstable, clumped assemblages that include both sexes; mate choice appears to be random within the species. These interspecific behavioral differences in Stony Creek, along with associated morphological variation, create another reproductive barrier between the species. The reason for interpopulational variation in black redhorse behavior is unknown, but it may involve coexistence with congeneric species.

At least three hypotheses could account for the dichotomy in habitat, behavior, and morphology associated with the spawning of golden redhorse and black redhorse in Stony Creek. First, the two species may be genetically programmed, through natural selection, to segregate into distinct spawning habitats. A second and equally plausible hypothesis is that the two species differ in spawning characteristics as a result of phylogenetic constraint (Stearns 1984, Partridge & Harvey 1988), whereby spawning behavior, habitat, and morphology are traits fixed within each lineage and involve no previous competition or ecological relationship between the species. A third explanation that may be tested in future studies, is that Stony Creek black redhorse are excluded by golden redhorse from spawning in the limited optimal habitat, i.e., gravel shoals. The establishment of spawning territories on gravel shoals by black redhorse in the Big Piney River, Missouri (Bowman 1970), followed by

spawning behavior similar to that of golden redhorse in Stony Creek adds some support to this displacement hypothesis, but is not conclusive. Assuming that no significant genetic differences exist between Illinois and Missouri black redhorse populations, gravel shoals are likely optimal spawning habitat for black redhorse, and some degree of plasticity in spawning behavior and habitat occurs within the species.

We suggest that the variations in habitat, behavior, and morphology found in these species may well act as effective isolating mechanisms, but the possibility exists that genetic incompatibility or other postmating isolating mechanisms alone may prevent significant natural hybridization or viability of hybrids. The variation that we perceive as physical isolating mechanisms may indeed be the expression of considerable genetic differences between the species, and a viable hybrid may not be produced under any circumstance. This issue may be resolved only through laboratory breeding studies and phylogenetic analysis.

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