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[Article]

Seasonal and Diel Movements and Habitat Use of Robust Redhorses in the Lower Savannah River, Georgia and South Carolina

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Abstract.—The robust redhorse *Moxostoma robustum* is a large riverine catostomid whose distribution is restricted to three Atlantic Slope drainages. Once presumed extinct, this species was rediscovered in 1991. Despite being the focus of conservation and recovery efforts, the robust redhorse's movements and habitat use are virtually unknown. We surgically implanted pulse-coded radio transmitters into 17 wild adults (460–690 mm total length) below the downstream-most dam on the Savannah River and into 2 fish above this dam. Individuals were located every 2 weeks from June 2002 to September 2003 and monthly thereafter to May 2005. Additionally, we located 5–10 individuals every 2 h over a 48-h period during each season. Study fish moved at least 24.7 ± 8.4 river kilometers (rkm; mean ± SE) per season. This movement was generally downstream except during spring. Some individuals moved downstream by as much as 195 rkm from their release sites. Seasonal migrations were correlated to seasonal changes in water temperature. Robust redhorses initiated spring upstream migrations when water temperature reached approximately 12°C. Our diel tracking suggests that robust redhorses occupy small reaches of river (~1.0 rkm) and are mainly active diurnally. Robust redhorses were consistently found in association with woody debris and gravel streambed sediments along the outer edge of river bends. Fish exhibited a high degree of fidelity to both overwintering and spawning areas. Our observations of long-distance seasonal migrations suggest that successful robust redhorse conservation efforts may require an ecosystem management approach.

The robust redhorse *Moxostoma robustum* is a large-bodied riverine catostomid whose known native distribution is currently restricted to three Atlantic Slope drainages in the southeastern United States. This species was originally described from the Yadkin River within the Pee Dee River basin in North Carolina (Cope 1870) but subsequently was effectively lost to science for over a century (Bryant et al. 1996). Its rediscovery in 1991 prompted conservation efforts to prevent further population decline and prompted listing under the Endangered Species Act (Bryant et al. 1996; Cooke et al. 2005). Populations have been discovered in the lower Piedmont and upper coastal plain regions of the Oconee and Ocmulgee rivers in the Altamaha River system (Georgia); the Savannah River (Georgia and South Carolina); and the Pee Dee River system (North Carolina and South Carolina). Robust redhorses probably occurred in river systems between the Pee Dee and Altamaha rivers, such as the Santee River basin (Bryant et al. 1996); however, populations have yet to be identified from these other rivers and are presumed to be extirpated. The decline of robust redhorses, like that of other catostomid species, has been blamed on numerous factors, including introduced predators (flathead catfish *Pylodictus olivaris*: Bart et al. 1994) and competitors (buffalo *Ictiobus* spp.: Moyle 1976); habitat degradation and fragmentation (Jennings 1998; Weyers et al. 2003); and recruitment failure (Jennings 1998; Weyers et al. 2003). However, the exact causes of decline and the current status of robust redhorse populations are currently uncertain.

Despite being the focus of conservation and restoration efforts, virtually nothing was known about the movement or habitat use of adult robust redhorses before this study. Adult fishes have been observed to form spawning aggregations on shallow main-channel gravel bars in the Oconee and Savannah rivers during May and June, when the water temperature is 18–22°C (Freeman and Freeman 2001). Anecdotal reports suggest that adults are generally collected in association with woody debris and swift current throughout much of the year. To date, there have been few

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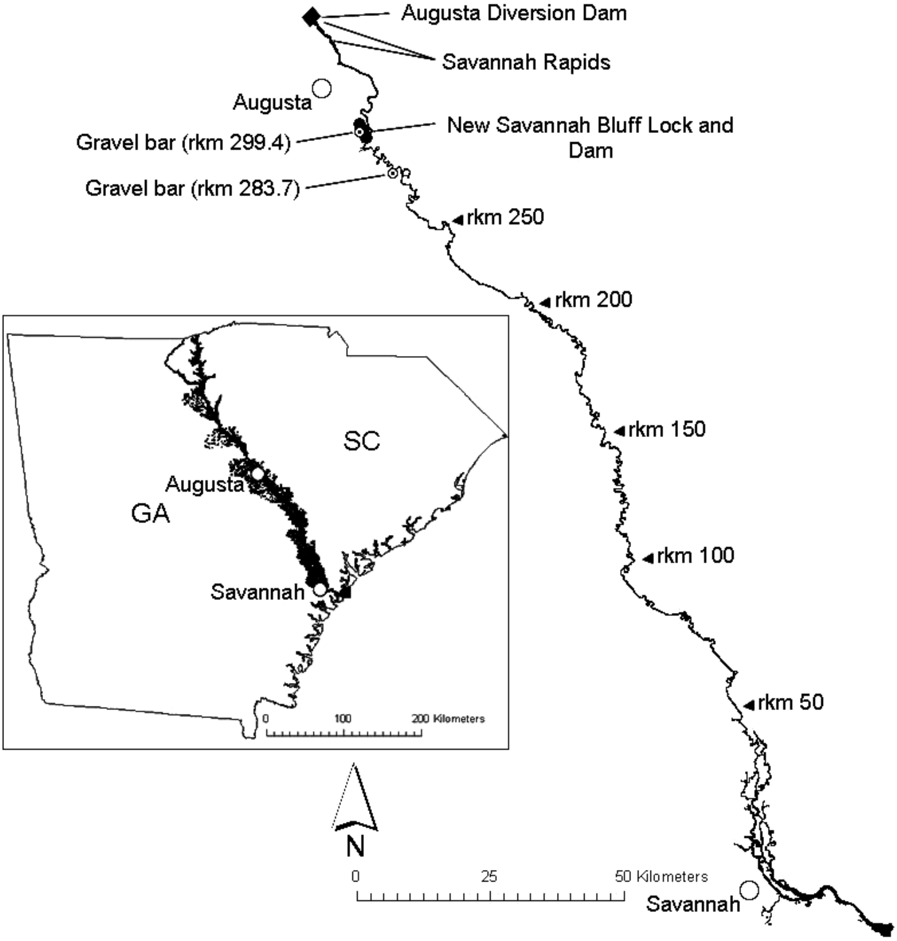

FIGURE 1.—Map of the study area, consisting of the lower Savannah River below the Augusta Diversion Dam, where the movements and habitat use of robust redhorses were monitored. River kilometers (rkm) below New Savannah Bluff Lock and Dam are indicated by solid triangles. The inset shows the Savannah River watershed; the cities of Augusta and Savannah, Georgia, are indicated by open circles.

comprehensive, long-term telemetry studies of the movement or habitat use of catostomids and no such studies of adult robust redhorses.

Our objectives for this study were to characterize seasonal migration, diel movement patterns, and essential habitat of the robust redhorse in the Savannah River. We assessed the effects of temperature and flow as cues for seasonal upstream and downstream migrations. We also determined the degree of site fidelity in relation to spawning, staging, and overwintering habitats.

Methods

Study area.—The Savannah River is one of the largest Atlantic Slope drainages, encompassing a watershed of approximately 25,000 km^2 (Marcy et al. 2005). It is 505 km in length; however, only the lower 300 km below New Savannah Bluff Lock and Dam (NSBL&D) in Augusta, Georgia, is free flowing (Figure 1). The NSBL&D is the terminal dam on the Savannah River and acts as the first barrier to upstream migration. It is passable only during lock operation and high-water events, when river discharge exceeds 566.34 m^3/s. Upstream of NSBL&D is a 26.7-river-kilometer (rkm) segment that encompasses Savannah Rapids (also commonly referred to as the Augusta Shoals) and ends at the impassable Augusta Diversion Dam. Native populations of robust redhorse in the Savannah River currently are known only from these two river segments.

Data collection.—Robust redhorses were captured during June 2002 by use of standard electrofishing techniques. We sampled once immediately below Savannah Rapids and twice near a main-channel gravel bar at rkm 283.7 (measuring from the river's confluence with the Atlantic Ocean). We collected fish in May 2004 from the spawning aggregation at this gravel bar to replace individuals who had died or shed tags. The sex of each individual was determined based upon presence of nuptial tubercles and gamete expression. We also measured total length (TL, mm) and weighed (g) each fish. Fish were anesthetized in a 100-mg/L buffered tricaine methanesulfonate (MS-222) solution, and a passive integrated transponder tag and two T-bar anchor tags were inserted into the musculature near the dorsal fin.

To ensure that the transmitter weight never exceeded 1.5% of the body weight of the fish, we used one of two sizes of pulse-coded radio transmitters with trailing-wire antennae (Lotek Wireless, Inc., Newmarket, Ontario, Canada). A 10.0-g transmitter with a minimum battery life of 560 d was used for fish smaller than 500 mm TL, and a 26.0-g transmitter with a minimum battery life of 912 d was used for larger fish. Both transmitters were detectable at a range of approximately 500 m when submerged. We implanted a radio transmitter into the peritoneal cavity of all captured fish following the surgical procedures of Walsh et al. (2000). Briefly, a small (<30 mm) incision was made off the ventral midline between the pelvic fins and vent after the fish was anesthetized. The transmitter was inserted and the incision was closed with three interrupted 3–0 coated absorbable sutures. The antenna was allowed to exit the body through the original incision. The procedure took approximately 3 min, and fish were allowed to recover for approximately 30 min in an aerated holding tank before release. Water temperatures in the Savannah River were less than 20°C during the surgeries.

We established the locations of radio-tagged robust redhorses by means of a Lotek SRX-400 telemetry receiver (Lotek Wireless) with a four-element yagi antenna. Fish were considered located when maximum signal strength was received for three consecutive pulses. Fish position was recorded (±8.0 m) with a handheld global positioning system receiver. Additionally, we plotted the location of each fish to within 100-m sections on National Oceanic and Atmospheric Administration nautical charts (11514 and 11515) after visual triangulation to river markers, terrestrial landmarks, and river features, such as inlets, tributaries, and cutoffs. Using these charts, we calculated movement to within 0.1 rkm and verified the calculations with ArcView 3.2 (ESRI, Redlands, CA). We recorded the position of the fish relative to the bank or center of the channel. Fish were located approximately every 2 weeks by boat from June 2002 to September 2003; however, tracking frequency was increased to once per week during the 2003 and 2004 spawning seasons. After September 2003, frequency was reduced to once per month until tagged fish began upstream migrations. The fish captured and released near the Savannah Rapids frequently moved into areas inaccessible by boat, necessitating that we track these fish from shore.

Additionally, we used the protocol described above to locate a subset of individuals once every 2 h during a consecutive 48-h period over a fixed transect. Transects typically were 26 rkm in length (range = 16.0–27.7 rkm) and contained 5–10 radio-tagged robust redhorses. Diel tracking was conducted once per calendar season on 18–20 October 2002 (fall), 27 February–1 March 2003 (winter), 11–13 June 2003 (spring), and 12–13 and 20 September 2003 (summer). The summer diel tracking was interrupted because of mechanical problems with the boat.

Data analysis.—We calculated absolute distance moved, range, displacement, and estimates of minimum daily movement for both seasonal and diel data sets. Absolute distance moved is the sum of the distance moved between relocations. Range is the distance between the upstream-most and downstream-most locations within a season or day. Displacement was calculated as the net distance moved (upstream movements were positive, and downstream movements were negative). Estimates of minimum daily movement were calculated only for the seasonal data and are equal to the absolute distance moved between subsequent observations divided by the number of days elapsed. These above values were similarly calculated for diel movement data. We used *t*-tests to evaluate the null hypothesis that these values did not differ from zero (Zar 1996). The hypothesis that these values differed seasonally among sexes (fixed effects) was tested with a mixed-model analysis of variance (ANOVA) while controlling for individuals and year (random effects). The hypothesis that these values differed among seasons (fixed effect) was tested with a mixed-model ANOVA while controlling for individuals, sex, and year (random effects; Zar 1996). Diel data were analyzed in a similar manner wherein photoperiod (daytime, nighttime, twilight) and season were used as fixed effects and individuals and sex were used as random effects. Season was used as a random effect when testing the null hypothesis that diel movement patterns did not differ among photoperiods. We used Dunnett's multiple comparisons of the least-squares means to perform pairwise comparisons of each season or photoperiod (Zar 1996). A significance level (α) of 0.05 was used for all tests.

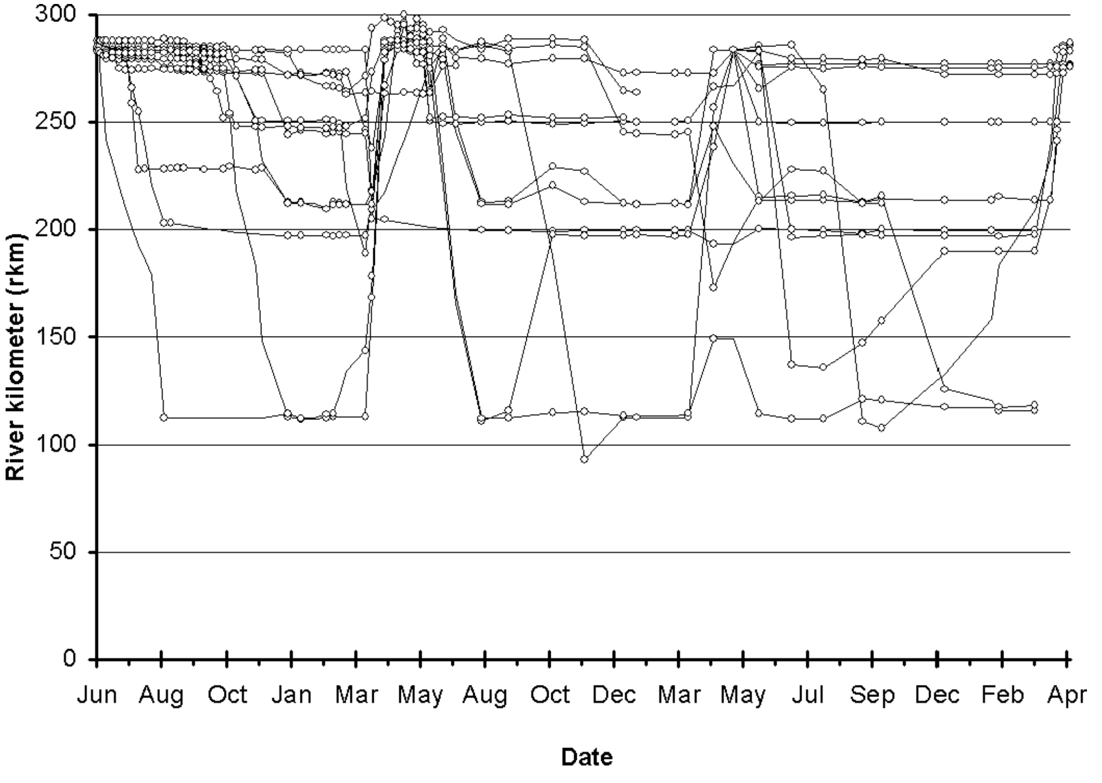

FIGURE 2.—River kilometer (rkm) positions of individual radio-tagged robust redhorses in the lower Savannah River below New Savannah Bluff Lock and Dam from June 2002 to April 2005. The solid lines connecting points indicate the movements of individual fish.

Results

We captured a total of 19 adult robust redhorses that ranged in size from 460 to 690 mm TL during June 2002. Two males were captured immediately below Savannah Rapids at rkm 324.2. Another 17 individuals (12 males, 5 females) were captured below NSBL&D from a main-channel gravel bar at rkm 283.7. The individuals captured from this gravel bar were presumably part of a spawning aggregation. Captured fish exhibited characteristics consistent with those described for breeding *Moxostoma* spp., such as fully formed nuptial tubercles, a loss of mucus, and cornified scales (Jenkins and Burkhead 1993). In addition, most of these individuals expressed gametes with mild abdominal pressure. Four robust redhorses died or shed their transmitters within the first 2 weeks after release, and one female died or shed the transmitter after 21 months. An additional five individuals (4 males, 1 female) were captured at the same gravel bar in May 2004. Two of these fish died or shed transmitters within 2 weeks of release.

Between June 2002 and April 2005, we relocated radio-tagged robust redhorses 1,182 times. Diel tracking accounted for 515 of these observations. Individuals were relocated from 10 to 165 times. Individual females were relocated an average ($\pm$SE) of 71.6 $\pm$ 15.59 times, and males were relocated an average of 73.1 $\pm$ 14.93 times. The two individuals captured above NSBL&D were relocated a combined 60 times. These two fish, along with fish captured in 2004 and fish number 48, were not incorporated in at least one of the diel tracking transects.

Most of the robust redhorses remained near (within 6.5 rkm of) their release sites throughout summer 2002 (Figure 2). However, one individual moved 172.8 rkm downstream within 1 week of release and remained there throughout the fall and winter before moving upstream in spring 2003. The remaining fish below NSBL&D began downstream migrations to overwintering areas in early to mid-fall 2002 (Figure 2). Overwintering fish dispersed along the length of the river down to rkm 90 (Figure 2). The majority of radio-tagged robust redhorses showed a high degree of overwintering-site fidelity (Figure 2), returning to the same 100–200-m lengths of shoreline each year. These

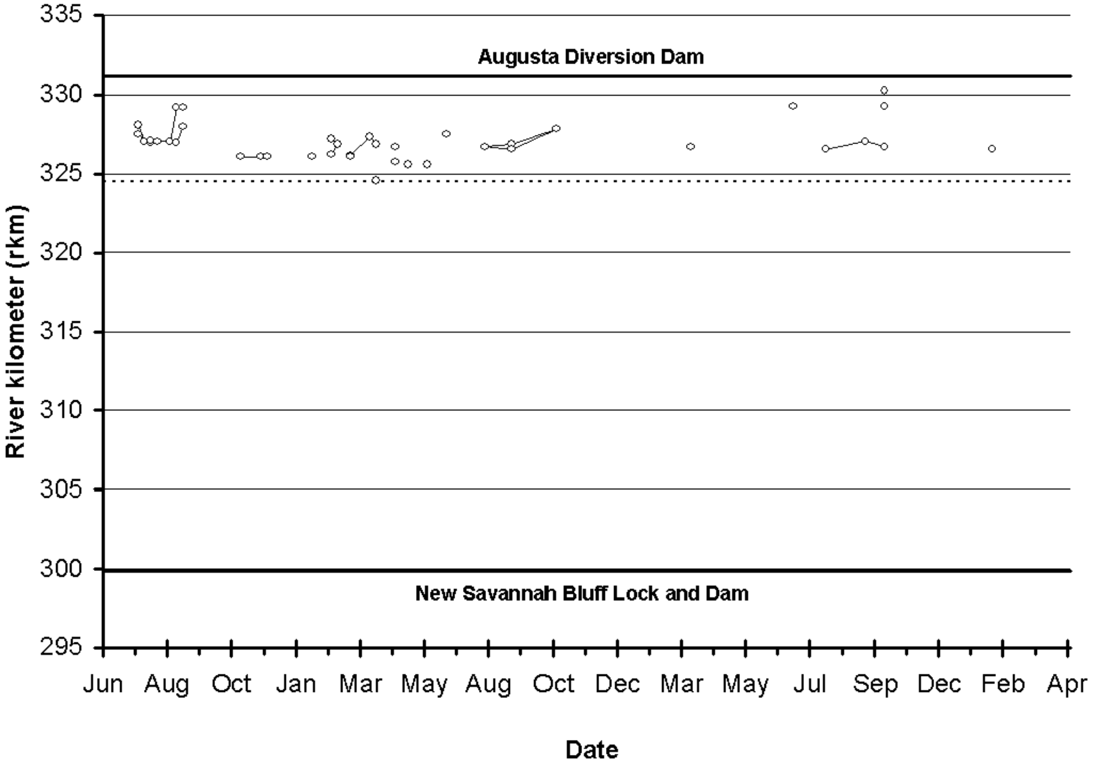

FIGURE 3.—River kilometer (rkm) positions of individual radio-tagged robust redhorses in the Savannah River between the Augusta Diversion Dam and New Savannah Bluff Lock and Dam from June 2002 to April 2005. The dashed line represents the downstream limit of Savannah Rapids. The solid lines connecting points indicate the movements of individual fish.

overwintering areas were distributed along the outside edge of river bends in water 3.0–5.0 m in depth. Observations with an underwater camera system showed coarse-gravel streambed sediment and structurally complex habitats consisting of large woody debris. During 2003–2005, fish began to make upstream migrations in early to mid-March (Figure 2), when water temperatures were approximately 10–12°C. Most individuals made upstream migrations each year. However, one or two individuals in each year did not make a migration (Figure 2). These individuals were not the same from year to year and were observed to make spawning migrations the following year. Radio-tagged robust redhorses also demonstrated a high degree of spawning-site fidelity. Fish returned to either the gravel bar at rkm 283.7 or to staging and holding areas immediately upstream or downstream of it (Figure 2). Fish spent the remainder of spring and early summer in the vicinity of their spawning grounds before dispersing downstream in late June and early July to their overwintering areas (Figure 2).

This general pattern of behavior was somewhat different during the high-water year of 2003. High flows occurred in winter and spring and continued into late summer. In contrast, 2002 and 2004 were drought years, when flows rarely exceeded the median daily streamflow. During high water, radio-tagged robust redhorses accessed the floodplain and occupied flooded forest habitats, particularly in areas at rkm 200–250 and rkm 100–125. Individuals frequently moved far enough onto the floodplain to be just barely detectable with our telemetry receiver. This was the only time during the study when we observed robust redhorses out of the main river channel. Our fish did not use any of the smaller-order streams that flow into the Savannah River, regardless of flow conditions. Spawning-habitat fidelity also appeared to decrease during high water. Radio-tagged robust redhorses spent time at both main-channel gravel bars during spring 2003 (Figure 2). One radio-tagged robust redhorse was able to pass NSBL&D during high-flow periods in 2003. Fish number 51 was last observed below the dam at rkm 276.2 on 28 June 2003 and was not seen again until it was relocated above NSBL&D on 9 August 2004 at rkm 326.6 in the Savannah Rapids.

Radio-tagged robust redhorses above NSBL&D did

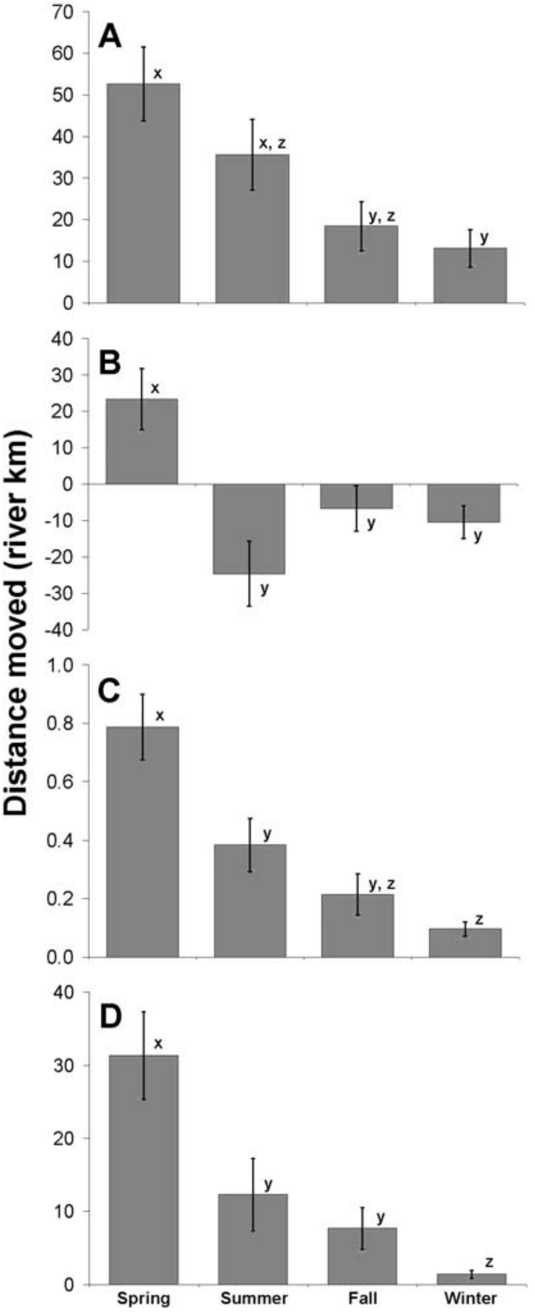

FIGURE 4.—Mean (±SE) seasonal (**A**) absolute movement, (**B**) displacement, (**C**) minimum estimate of daily movement, and (**D**) range of radio-tagged robust redhorses in the lower Savannah River below New Savannah Bluff Lock and Dam from June 2002 to May 2005.

not exhibit any seasonal movement patterns (Figure 3). These individuals remained in the shoal and pool habitats of the Savannah Rapids. Gaps in the data are presumed to occur when fish moved out of range of the receiver within the shoals, as they were never located in the navigable portion of the river below the shoals between rkm 323.0 and NSBL&D.

Season was the most important correlate to robust redhorse activity and movement over the course of a year. No differences between sexes in absolute movement ($F_{1,132} = 3.40$, $P = 0.0676$), displacement ($F_{1,132} = 0.03$, $P = 0.8552$), seasonal range ($F_{1,132} = 0.23$, $P = 0.6354$), or minimum estimates of daily movement rates ($F_{1,132} = 0.02$, $P = 0.8954$) were observed. Spring and summer were the only seasons in which any of these parameters statistically differed from zero ($t_{155} \geq 2.14$, $P \leq 0.0336$). Radio-tagged robust redhorses were most active in spring ($F_{3,155} = 7.27$, $P = 0.0001$), exhibiting mean (±SE) absolute movement of 52.7 ± 8.9 rkm (Figure 4). In terms of directed movement or displacement, movement patterns were different in spring and summer ($F_{3,155} = 7.76$, $P < 0.0001$). Fish migrated a mean (±SE) distance of 23.4 ± 8.4 rkm upstream in spring and returned 24.6 ± 9.0 rkm downstream in summer (Figure 4). Minimum (mean ± SE) estimates of daily movement rate were highest in spring ($F_{3,155} = 14.02$, $P < 0.0001$) and ranged from 0.8 ± 0.1 rkm/d in spring to 0.1 ± 0.02 rkm/d in winter (Figure 4). Radio-tagged robust redhorses also exhibited the greatest seasonal range in spring ($F_{3,155} = 9.23$, $P < 0.0001$) and had a mean (±SE) distance of 31.3 ± 6.0 rkm between the furthest upstream and downstream locations (Figure 4). Interannual differences in absolute movement, seasonal range, and minimum estimates of daily movement rates were assessed between 2003 and 2004 (the only complete calendar years of data). Absolute movement was the only parameter that differed between 2003 and 2004 ($t_{132} \leq 1.70$, $P \geq 0.0912$). Fish were more active in 2003 than in 2004 ($t_{132} = 2.30$, $P = 0.0229$), moving, on average, 22.6 ± 9.5 rkm more in 2003 than in 2004.

On average, radio-tagged robust redhorses moved between 0.5 and 1.0 rkm over a 24-h period (Figure 5). There was minimal evidence of boat motor noise affecting behavior. On two occasions, fish initially located in shallow water appeared to retreat back to woody debris in deeper water on the opposite side of the channel. There were no seasonal differences in the total activity of individuals ($F_{3,17} = 0.59$, $P = 0.6236$). There was no evidence of directed movement (Figure 5), as mean diel displacement did not differ from zero ($t_{141} \leq 0.28$, $P \geq 0.1638$). Daily-use areas were approximately 1.0 rkm in length (Figure 5) and did not

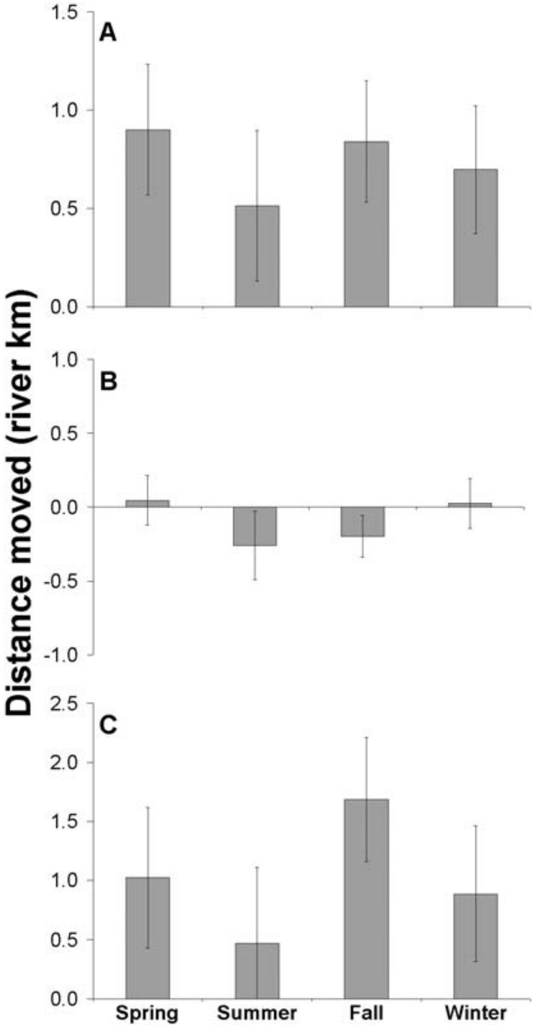

FIGURE 5.—Mean (±SE) diel (**A**) absolute movement, (**B**) displacement, and (**C**) use area of radio-tagged robust redhorses in the lower Savannah River below New Savannah Bluff Lock and Dam from June 2002 to May 2005.

differ among seasons ($F_{3,17}$ = 1.13, P = 0.3464). Absolute time of day did not have any effect on robust redhorse activity ($F_{11,\ 551}$ = 1.46, P = 0.1434). However, activity was influenced by photoperiod ($F_{3,17}$ = 6.96, P = 0.0013); significantly more movement occurred during daylight hours than at night (t_{141} = 2.32, P = 0.0219) or during twilight hours (t_{141} = 3.65, P = 0.0004; Figure 6).

Discussion

Robust redhorses used almost the entire length of the Savannah River below NSBL&D, making extensive upstream migrations to spawning habitat and downstream migrations to overwintering areas. Like other catostomid species, such as the razorback sucker *Xyrauchen texanus* (Tyus 1987; Tyus and Karp 1990; Modde and Irving 1998), white sucker *Catostomus commersonii* (Olson and Scidmore 1963), and southeastern blue sucker *Cycleptus meridionalis* (Mettee et al. 1996), the robust redhorses below NSBL&D appears to be potamodromous. Potamodromy (movements occurring entirely within freshwater) is a migratory strategy employed by numerous riverine fishes, including many species of sturgeons *Acipenser* spp. and *Scaphirhynchus* spp. (Bemis et al. 1997), paddlefish *Polyodon spathula* (Bemis et al. 1997; Stancill et al. 2002; Zigler et al. 2003), large tropical catfishes (Barthem et al. 1991; Barthem and Goulding 1997), large cyprinids (Tyus 1990; Lucas and Batley 1996; Allouche et al. 1999; Winter and Fredrich 2003), and some characoids (Bayley 1973; Duque et al. 1998). Specific information on the migratory behavior of other *Moxostoma* species is very limited, but it appears that Savannah River robust redhorses undertake much longer upstream migrations to spawning habitats than do other redhorse species, such as the greater redhorse *M. valenciennesi* (Bunt and Cooke 2001) and river redhorse *M. carinatum* (Hackney et al. 1968). It also is likely that robust redhorses migrated even further upstream to the extensive gravel bars in Savannah Rapids and beyond before the construction of dams on the Savannah River. Historical records indicate that American shad *Alosa sapidissima* and other anadromous fishes migrated over 614 rkm to the Savannah River headwaters in the Tugaloo and Tallulah rivers before the construction of dams on the system (Mills 1826; Eudaly 1999; Welch and Eversole 2000). Also, the capture locality of the holotype indicates that robust redhorses penetrated well into the Piedmont region of the Pee Dee River basin (Cope 1870). The possibility that dams have limited availability or access to suitable spawning habitats for robust redhorse populations in the Savannah River needs to be assessed. The wide-ranging nature of these fish means that conservation efforts focused only upon key habitats without providing for passage between them are unlikely to be successful and that a whole-system management approach should be encouraged (Cooke et al. 2005).

In addition to making long-distance migrations, robust redhorses display a high degree of site fidelity, returning to the same areas used in previous seasons for staging, spawning, and overwintering. Fidelity to spawning habitat has been demonstrated in many riverine fishes other than salmonids, including white suckers (Olson and Scidmore 1963; Werner 1979), river carpsuckers *Carpiodes carpio* and common carp *Cyprinus carpio* (Bonneau and Scarnecchia 2002),

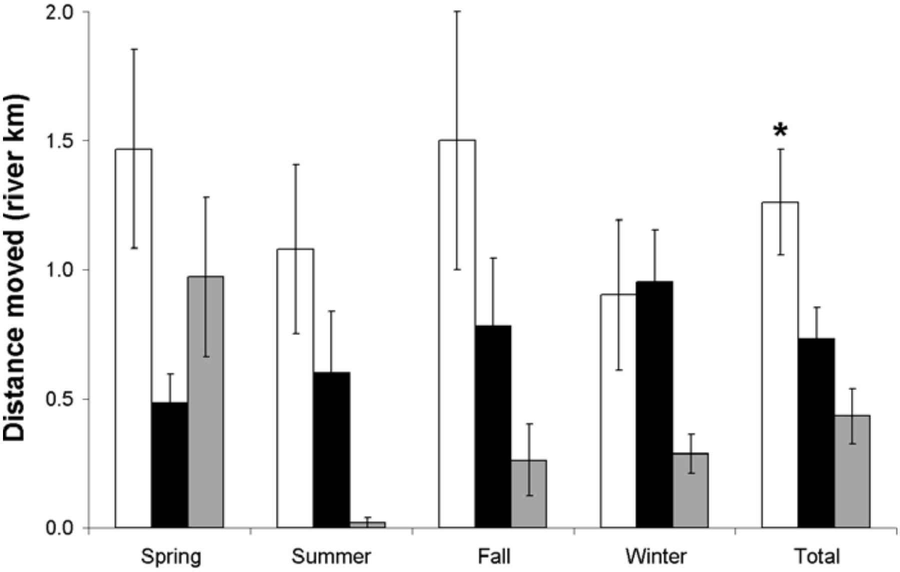

FIGURE 6.—Mean (±SE) absolute movement between 2-h tracking periods for robust redhorses in the lower Savannah River below New Savannah Bluff Lock and Dam from June 2002 to May 2005. The white, black, and gray bars represent daylight, nighttime, and twilight periods, respectively.

Colorado pikeminnow *Ptychocheilus lucius* (Tyus 1990), razorback suckers (Mueller et al. 2000), and paddlefish (Stancill et al. 2002). However, unlike most of the abovementioned species and the majority of catostomid species (Curry and Spacie 1984; Page and Johnston 1990), our radio-tagged robust redhorses did not ascend tributaries to spawn. Instead, they used main-channel gravel bars similar to other large riverine redhorses, such as the river redhorse (Hackney et al. 1968), greater redhorse (Jenkins and Jenkins 1980; Cooke and Bunt 1999), and copper redhorse *Moxostoma hubbsi* (R. Dumas, Société de la Faune et des Parcs du Québec, personal communication). Therefore, fidelity to spawning habitat in the lower Savannah River may be overestimated, as there are only two main-channel gravel bars to choose from. For example, individuals exhibited a high degree of site fidelity when conditions were suitable for spawning in 2004 and 2005. However, individuals visited both gravel bars in May and June 2003, when high water rendered depth and current velocities on both bars unsuitable for robust redhorse spawning (Freeman and Freeman 2001). This pattern of wandering among a few sites within a relatively small area during the spawning season has been observed in razorback sucker (Tyus and Karp 1990; Modde and Irving 1998; Mueller et al. 2000) and paddlefish (Paukert and Fisher 2001; Stancill et al. 2002) and suggests some assessment of habitat quality and suitability occurs before committing to a spawning site, regardless of past use.

The degree of fidelity displayed for staging and overwintering areas by radio-tagged robust redhorses was unexpected. Radio-tagged robust redhorses often migrated more than 100 rkm to spawning habitats and then returned a few weeks later to the same fallen tree where they spent much of the previous winter. In many cases, this site specificity was on the order of 0.1 rkm for overwintering areas. Other telemetry studies of riverine fishes have not noted this level of specificity of individuals to overwintering and staging areas. However, fidelity to overwintering or oversummering areas has been identified on coarser scales in reservoir populations of striped bass *Morone saxatilis* (Jackson and Hightower 2001; Young and Isely 2002), razorback sucker (Mueller et al. 2000), and Gulf sturgeon *Acipenser oxyrinchus desotoi* (Wooley and Crateau 1985; Clugston et al. 1995; Heise et al. 2005). It is not clear why robust redhorse would display such a high degree of fidelity to overwintering and staging habitats. Reports on the behavior of other catostomids offer no clear patterns. Some studies suggest these fishes are generally more active and wide ranging (Dauble 1986; Chart and Bergersen 1992), while others hint at a similar behavior pattern (Matheney and Rabeni 1995; Bunt and Cooke 2001). It is important to note that these studies were conducted on populations in smaller streams, were short-duration telemetry studies, or relied upon mark–recapture, making direct comparisons to this study difficult.

A possible reason for the high degree of site fidelity to overwintering areas exhibited by robust redhorse is that they are able to fulfill all of their requirements except for spawning in a relatively small area. Robust redhorses appear to use their entire home range during the course of a day. In so doing, their behavior and activity are consistent with that detailed in the restricted-movement paradigm. The restricted-movement paradigm holds that resident stream fishes spend the majority of their lives within short reaches (Gerking 1953, 1959; Rodriguez 2002). This theory has come under criticism (see Gowan et al. 1994; Rodriguez 2002) and has recently been revised to account for both potamodromy and infrequent home-range shifts (Crook 2004). Our results suggest that this species is mostly sedentary and occupies relatively small linear home ranges for extended periods of time interspersed with long-distance seasonal migrations. Infrequently, some individuals were observed to abandon previous home ranges and establish new ones in different locations. This usually occurred during downstream migrations. It was rare for individuals to do so at other times of the year. The razorback sucker (Mueller et al. 2000) was the only catostomid species for which we could find a similar pattern reported in the literature; however, this behavior pattern has been described in other large riverine fishes, such as golden perch *Macquaria ambigua* and common carp (Crook 2004).

Robust redhorses moved into previously unused habitats during winter and spring floods on the Savannah River in 2003. High-water events were the only times we observed radio-tagged robust redhorses outside of the main river channel. In some cases, fish entered flooded tributaries, oxbows, and other backwater areas, but most fish were located on the floodplain immediately adjacent to the river channel. Movement of riverine fish into these habitats during flood events has been attributed to (1) avoidance of displacement by high current velocities (Matheney and Rabeni 1995; Allouche et al. 1999; David and Closs 2002), (2) foraging on the floodplain (Ross and Baker 1983; Turner et al. 1994; Snedden et al. 1999), or (3) spawning in floodplain habitats (Welcomme 1979; Snedden et al. 1999). We were not able to ascertain the reason that robust redhorses left the main river channel during high-water events, but we hypothesize that they are using the floodplain habitats for feeding in preparation for spawning. This species spawns from May to mid-June and may improve condition or fecundity by foraging on the floodplain in March and April.

The behavior of the two individuals captured above NSBL&D was markedly different from the behavior of their downstream counterparts. These individuals did not undertake long migrations; instead, they preferred to remain in the Savannah Rapids and did not use the river below the shoals. This section of the river flows through downtown Augusta and is highly channelized. After flowing through the city, the river becomes more lentic in nature as it approaches the dam. These fish also did not appear to have the same affinity for large woody debris even though this habitat was available to them. It is also notable that the one fish that was able to pass NSBL&D during the course of our study adopted a pattern of behavior similar to the two individuals that were originally captured in the Savannah Rapids. We hypothesize that the robust redhorse population above NSBL&D may be confined to a relatively small stretch of river (approximately 8.0 rkm) based on the inability or unwillingness of the radio-tagged fish to move out of the Savannah Rapids. This requires further investigation because of the small sample size and difficulty in locating these fish during our study.

Our observations of the behavior of radio-tagged robust redhorses in the Savannah River help to explain how this species was able to remain "lost to science" for over 100 years after its initial discovery. While historical overfishing (Cope 1870) and general apathy toward suckers (Cooke et al. 2005) probably contributed to its "disappearance," robust redhorses demonstrate behaviors and habitat preferences that render them cryptic. This species spends the majority of its time in habitats that are inaccessible or difficult to sample effectively with common gear types, such as boat electrofishers or gill nets. Individuals are easy to capture in their spawning habitat, but their late spawning season puts them out of reach of the spring monitoring programs of state resource management agencies. Knowledge of the movement patterns and habitat use of this species should help with continuing investigations of the basic biology and ecology of the robust redhorse in the Savannah River and throughout the species' range.

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Natural Resources, and the Wildlife Management Institute. Reference to trade names does not imply endorsement by the U.S. Government.

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