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REGULAR ARTICLE

PICKY PIGS PREFER PIGTOES: EVIDENCE FOR SPECIES-SELECTIVE FERAL PIG PREDATION ON FRESHWATER MUSSELS

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ABSTRACT

We observed evidence of predation on freshwater mussels during a field experiment. Mussels within the stream reach and experimental enclosures were dislodged from the sediment and shells were crushed whole, and the substrate and enclosures were extensively disturbed. Of the 12 mussel species detected in pre-experiment sampling, a Jacob's electivity index suggested that only two species (*Fusconaia cerina* and *Elliptio arca*) were positively selected for by the predator, with *F. cerina* being strongly preferred; other dominant species were avoided. We estimated that 1% of the mussel community and 6% of the *F. cerina* population was predated. We found that 70% of the experimental enclosures were disturbed, but those containing *F. cerina* were disturbed at a higher rate than other treatments. Water depth was a significant factor predicting disturbance of enclosures, and disturbance was not as severe for enclosures in deeper water. Based on characteristics of the event, we suggest that feral pigs (*Sus scrofa*) were responsible for the predation and disturbance. While only a small portion of the mussel community was predated, continued species and spatial selection could shift community structure and distribution. Feral pigs also may pose an indirect threat to mussel populations because substrate disturbance by rooting could decrease sediment stability.

KEY WORDS: feral pigs, freshwater mussels, selective predation, species selection, invasive species, community structure, predator–prey

INTRODUCTION

Selective predation plays a key role in structuring and regulating biological communities and processes (Schmitz et al. 2010). Predators exert top-down influence on multiple aspects of prey ecology, including behavior (Schmitz et al. 1997), metabolism and stoichiometry (Dalton and Flecker 2014), and life history (Reznick and Endler 1982). Predators may select based on prey size, morphology, nutritional value, defense mechanisms, or spatial distribution, resulting in varying magnitudes of predation pressure on different species or populations (Jokela and Mutikainen 1995; Watters 1995; Diggins and Stewart 2000). Over time, selective predation may result in shifts in community dynamics such as spatial distribution, species abundance, and diversity (Watters 1995; Tyrrell and Hornbach 1998; Diggins and Stewart 2000).

Freshwater mussels have many known predators including muskrats, otters, raccoons, turtles, catfish, and flatworms (Haag 2012). Lesser-known mussel predators are domesticated and feral pigs (*Sus scrofa*). Accounts of pig predation on mussels are scarce but have been reported for many years (Rafinesque 1820; Simpson 1899; Tudorancea 1972; Williams and Benson 2004). Feral pigs are an invasive species that have proliferated across the USA in the past few decades and now cause extensive economic and ecological damage (Mayer and Brisbin 2008; Ivey et al. 2019). They forage by rooting, which can result in severe disturbance in terrestrial and aquatic ecosystems (Kotanen 1995; Cushman et al. 2004; Barrios-Garcia and Ballari 2012). The expansion of feral pig populations in the USA poses an additional threat to the imperiled mussel fauna by direct predation and indirect effects of habitat disturbance.

There is little or no quantitative information about the magnitude of pig predation on mussels, species selectivity, or other features of this predator–prey relationship. We observed

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apparent pig predation on mussels during a field experiment in a lowland river in the southeastern USA. We used pre- and postpredation data on the mussel community present in the reach to evaluate species and water depth selectivity exhibited by the predator during foraging. We show evidence supporting pigs as the predator and discuss the consequences of pig predation for mussel conservation.

METHODS

Study Area

Our study was conducted on the Sipsey River, Alabama, a fifth-order alluvial river flowing mostly through the Eastern Gulf Coastal Plain physiographic province and draining into the Tombigbee River. The Sipsey River is unregulated, with extensive, forested floodplain wetlands, and it supports dense mussel aggregations (Haag and Warren 2010; Atkinson et al. 2019). Our observations were made within a 60-m reach of the river in Greene County, Alabama, that had been established previously for a field experiment (see Experimental Setup, below). The study reach consisted of a shallow run (maximum depth = 0.7 m) with gravel and sand substrate.

Experimental Setup

Our observations were made during an experiment designed to investigate the impact of mussel biodiversity on sediment processes, described briefly as follows (see Nickerson 2018 for additional details). The experimental setup consisted of 36 open-topped 0.25-m^2 enclosures designed to contain manipulated mussel assemblages. Enclosures consisted of a 25 × 25 × 15–cm frame of 5 × 5–cm lumber covered with steel mesh and buried so that the top edge was flush with the sediment surface. Enclosures were installed approximately every 4 m along eight cross-sectional transects spaced 6 m apart (Fig. 1). Enclosures were installed July 29, 2017. Prior to installation, each 0.25-m^2 area was excavated to a depth of 20 cm and sieved, and all naturally occurring mussels were identified and counted; 39 0.25-m^2 quadrats were excavated (representing 2.75% of total reach area), but ultimately, only 36 enclosures were installed. After installation, each enclosure was refilled with the sieved sediment and stocked with one of five experimental mussel assemblages: (1) only *Cyclonaias asperata*, (2) only *Fusconaia cerina*, (3) a 50/50 mixture of *C. asperata* and *F. cerina,* (4) sham mussel shells (empty valves glued together), and (5) a control with no mussels or shams. Mussel and sham assemblages were stocked at two densities, 24 and 48 individuals/m^2 (6 and 12 individuals/enclosure, respectively); this resulted in a total of nine treatments with four replicates each and a total of 216 stocked mussels. All experimental mussels and sham mussels were tagged with numbered fly-fishing line (Fig. 2A). Enclosures were stocked with mussels of similar size to standardize biomass within treatments.

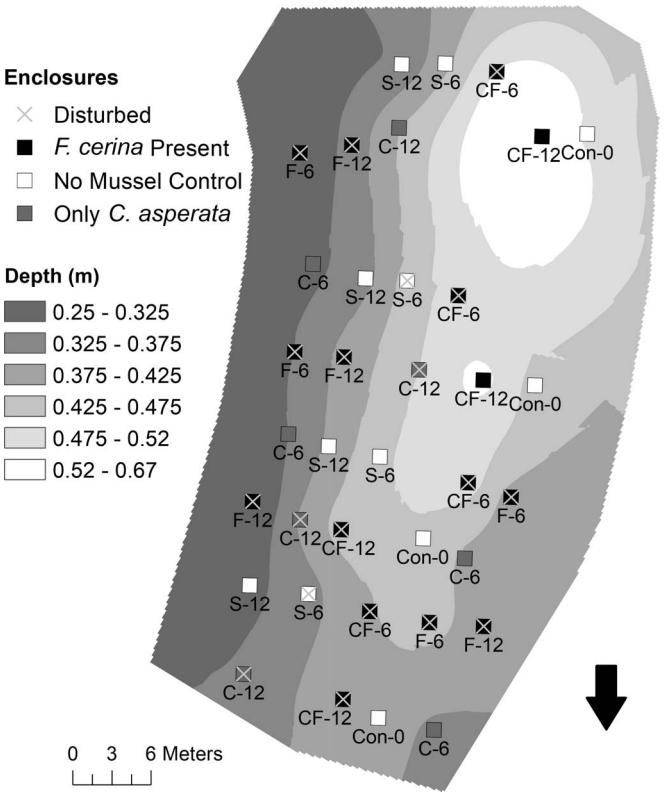

Figure 1. Map of the study reach in the Sipsey River, Alabama, showing placement of 0.25-m^2 experimental enclosures. Depth contours were interpolated from depth measurements at each enclosure. Alphanumeric codes indicates experimental treatment: F = *Fusconaia cerina* only, C = *Cyclonaias asperata* only, CF = 50/50 mixture of *F. cerina* and *C. asperata*, S = sham control, Con = no mussel control, 0 = no individuals, 6 = six individuals (24 individuals/m^2), and 12 = 12 individuals (48 individuals/m^2). Arrow indicates direction of stream flow.

Predation Event

We observed disturbance to a subset of enclosures and evidence of mussel predation during low-flow conditions on September 22, 2017, and again on September 26, 2017. Immediately upon discovering the disturbances, we identified which enclosures showed signs of disturbance, recorded which mussels were missing from enclosures, and returned individuals we found to their enclosures; many individuals could not be found and were recorded as missing. We collected all freshly dead shell material within and 4 m downstream of the study reach, as some fragments had drifted or were consumed outside of our established reach. Because many shells were crushed or disarticulated, we estimated the number of individuals predated based on the number of umbos recovered, with two umbos representing one individual. Fragments were confirmed as experimental individuals based on the presence of numbered ID tags, but the origin of all individuals (experimental or wild) could not be determined. We combined counts of disturbed enclosures and predated individuals from both events, and we did not consider differences in stocking densities among enclosures in our analyses.

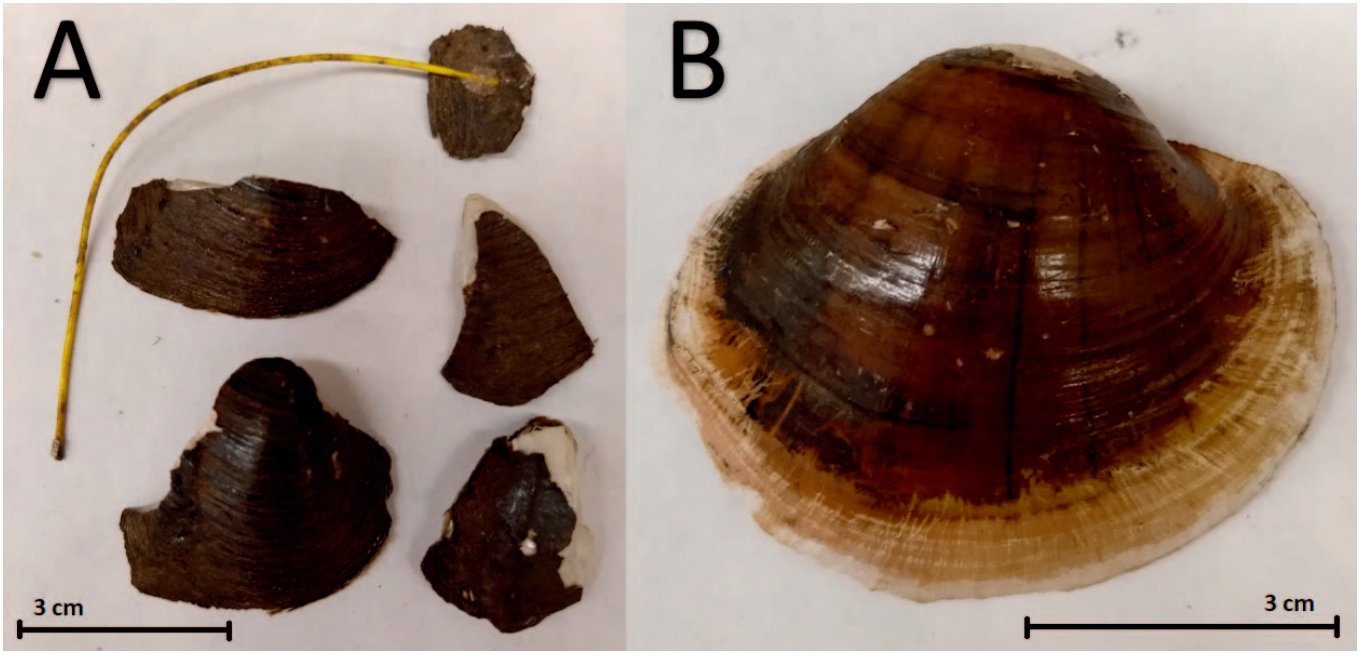

Figure 2. (A) Crushed shells of *Fusconaia cerina* recovered after apparent pig predation; top fragment shows attached fly-fishing–line tag. (B) Abrasion pattern on *Lampsilis ornata*, in which the shell margin was broken to access soft tissue.

Analysis of Selective Predation

We were unable to assess size selectivity in our analysis of selective predation due to standardization of individual size within enclosures. Rather, we focused on two other aspects of selective predation: species selectivity and water-depth limitation. We tested for evidence of species selection during the predation event by calculating Jacob's electivity index (Jacobs 1974) with species-abundance estimates from initial enclosure excavation representing available prey and counts of predated shell umbos representing consumed prey. Some of the mussels stocked into enclosures originated from outside the study reach; these individuals were included in estimates of available prey, but they constituted a small proportion of the mussel assemblage in the reach (Fig. 3). We used the "ivlev" function within the "selectapref" R package (Richardson 2017) to compensate for the difference in abundance between prey species, standardizing all scores between −1 and 1.

We tested for an effect of depth and species treatment on

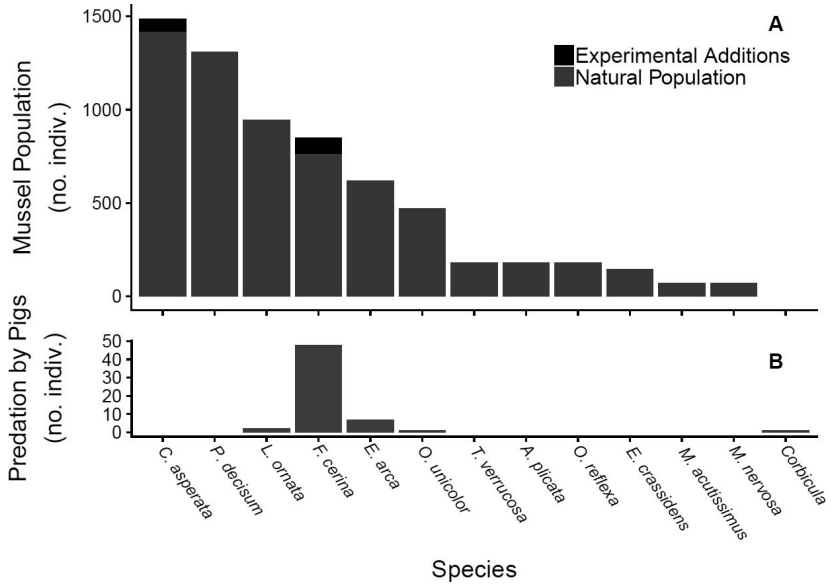

Figure 3. (A) Pre-predation mussel community structure in the experimental reach obtained from substrate excavation and including mussels stocked into experimental enclosures from outside the reach (black portion of histogram bars). (B) Apparent pig predation in the experimental reach.

enclosure disturbance, with disturbance quantified in three different ways: the proportions of dislodged, missing, or killed mussels in an enclosure. We tested for these effects using multiple linear regression with disturbance as the dependent variable and enclosure depth, species treatment, and the interaction term as the independent variables. We conducted separate multiple linear regressions for each measure of disturbance. We tested for differences among treatment combinations using Tukey post hoc tests. These analyses showed that species treatment was the only significant factor, and enclosures containing *F. cerina* were predated at a higher rate (see Results). Consequently, we explored potential depth selection further using linear and piecewise regressions including only those enclosures containing *F. cerina* (both *F. cerina*–only and mixed treatments) to eliminate noise that may have been introduced by the lower predation rate on other species treatments. Piecewise regression allows for the detection of a critical threshold or breakpoint, indicating that the relationship is not linear but changes abruptly at a threshold (Toms and Lesperance 2003). We compared linear and piecewise regressions to determine if a significant threshold depth existed. We used a Davies test to determine if breakpoints were significant and the relationship was better represented as multiple linear relationships (Muggeo 2016). We calculated linear regressions and conducted Tukey post hoc tests with the "aov," "lm," and "TukeyHSD" functions in base R; piecewise regressions and Davies test were calculated with the "segmented" and "davies.test" functions within the "segmented" R package (Muggeo 2008; R Core Team 2017).

RESULTS

Substrate within and outside of enclosures was heavily disturbed, indicating rooting, and mussels were dislodged from the enclosures or missing. Nineteen of 36 enclosures (52.8%) were disturbed, including 70.0% of the 24 enclosures containing mussels and 16.7% of the 12 enclosures containing sham mussels or no mussels.

Evidence of predation on mussels consisted of crushed shells and scratch marks on shells indicating severe abrasion (Fig. 2). In addition, many mussels were dislodged from enclosures but were not eaten. Crushed shells were found only within the stream channel and not on the shore. Initial excavation yielded 12 species and a total mussel population estimate of 6,516 individuals in the reach (Fig. 3A). We found a total of 59 predated individuals, including 48 *F. cerina*, seven *Elliptio arca*, two *Lampsilis ornata*, one *Obovaria unicolor*, and one *Corbicula fluminea* (Fig. 3B). These numbers correspond to 0.9% of all mussels predated, 5.6% of *F. cerina*, 1.1% of *E. arca*, and <0.4% of all other species. Of the 216 stocked mussels, 62.1% remained in the enclosures, 9.7% were dislodged from the sediment but not killed, and 28.2% were missing. Tags recovered from shell fragments confirmed that 27 of the missing *F. cerina* were predated, representing 44.3% of mussels missing from enclosures. All predated, tagged mussels were *F. cerina*, and these represented 25% of stocked individuals of that species. Only two sham mussels were confirmed predated, and both were *F. cerina* shells.

Enclosures were observed for 7 wk prior to the predation event. During that time, only five mussels became dislodged (mussels were replaced in the enclosures after dislodgement) and three mussels were lost. Three of the dislodged and two of the missing mussels were associated with a high-flow event at the beginning of the experiment that scoured a subset of enclosures.

Species Selection

General patterns of predation indicated strong selection for *F. cerina*. All eight enclosures containing only *F. cerina* were disturbed, and 75.0% of mixed-species enclosures were disturbed, but only 37.5% of the eight *C. asperata*–only enclosures were disturbed. Of the 108 stocked *F. cerina*, 40.8% remained in the enclosures, 11.1% were dislodged from the sediment, and 48.1% were predated or missing. Of the 108 stocked *C. asperata,* 83.4% remained in the enclosures, 8.3% were dislodged, and 8.3% were missing; none of the latter were confirmed predated.

Jacob's electivity index supported strong selection for *F. cerina*, which had the highest index score (0.70; Fig. 4). *Elliptio arca* was the only other species with a positive score (0.26), and all other species had negative scores, including species that dominated the wild community (e.g., *C. asperata*, *Pleurobema decisum*, *L. ornata*, and *O. unicolor*). *Corbicula fluminea* was not included in this analysis because it was not detected during the initial survey.

Depth Selection

Species treatment ($P = 0.001$) was the only significant variable for predicting dislodgement (depth, $P = 0.390$; depth × treatment, $P = 0.280$). A Tukey post hoc test showed that *F. cerina*–only ($P = 0.001$) and mixed ($P = 0.019$) treatments were both dislodged significantly more than *C. asperata*–only enclosures; *F. cerina*–only and mixed treatments ($P = 0.366$) were not significantly different from each other. Species treatment ($P < 0.001$) was the only significant variable for predicting the number of missing mussels (depth, $P = 0.283$; depth × treatment, $P = 0.265$). A Tukey post hoc test showed that *F. cerina*–only ($P < 0.001$) and mixed ($P = 0.008$) treatments had more missing mussels than *C. asperata*–only treatments, but they were not significantly ($P = 0.210$) different from each other. Species treatment ($P < 0.001$) was the only significant variable for predicting the number of killed mussels (depth, $P = 0.296$; depth × treatment, $P = 0.104$). A Tukey post hoc test showed that *F. cerina*–only ($P < 0.001$) and mixed ($P = 0.002$) treatments had more killed mussels than *C. asperata*–only treatments, but they were not significantly ($P = 0.136$) different from each other.

The proportion of individuals dislodged from *F. cerina*–containing enclosures was significantly and negatively corre-

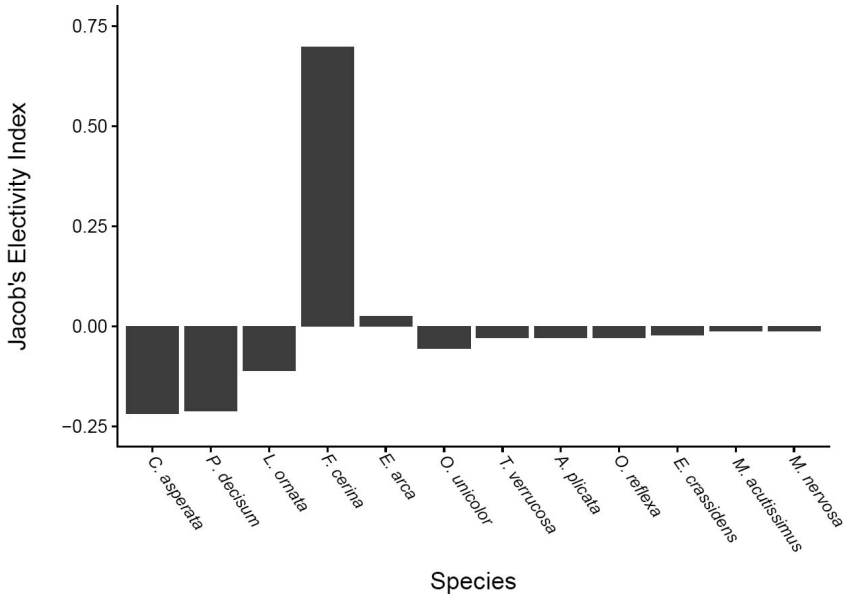

Figure 4. Jacob's electivity index scores for the 12 mussel species detected in the reach prior to predation.

lated with depth ($y = -2.03x + 1.73$, $P = 0.035$, $R^2 = 0.23$), as was the proportion of individuals killed ($y = -1.75x + 1.16$, $P = 0.007$, $R^2 = 0.37$). However, the proportion of individuals missing from *F. cerina*–containing enclosures was not significantly correlated with depth ($y = -1.46x + 1.38$, $P = 0.055$, $R^2 = 0.18$). Piecewise regression found breakpoints in depth in relationships for all three measures of disturbance, but the Davies test determined these breakpoints were not significant (dislodged, breakpoint in depth = 0.41 m, $P = 0.14$; missing, breakpoint = 0.49 m, $P = 0.13$; killed, breakpoint = 0.34 m, $P = 0.065$).

DISCUSSION

We did not directly observe the predation event, but several pieces of evidence support feral pigs as the culprit. First, we observed numerous pig tracks on the bank the day we discovered the event. We had monitored the experiment 3 d per week for the preceding 7 wk and did not observe pig tracks prior to the predation event. Second, the presence of crushed shells only within the stream channel is inconsistent with predation from smaller predators, such as muskrats. Muskrats, and other terrestrial predators, typically open the valves to consume the soft tissue, and deposit intact shells in middens on the shore (Tyrrell and Hornbach 1998; Diggins and Stewart 2000; Owen et al. 2011). Third, the pattern of disturbance and predation we observed indicates a large organism with a well-developed and strong crushing apparatus. Large catfish have bony crushing plates in their throat and are reported to crush heavy-shelled mussel species (Forbes 1888; Tiemann 2011). Apparent catfish predation was observed commonly in the Sipsey River prior to the proliferation of feral pigs in the watershed, and the appearance of these crushed shells is similar to those we observed (Haag 2012). However, crushed shells attributed to catfish predation occurred most frequently in deeper water under submerged logs or undercut banks, and their occurrence was not associated with notable substrate disturbance (Haag 2012; W. Haag, US Forest Service, personal communication). Our observations of crushed shells and substantial disturbance to the substrate is consistent with rooting and predation by feral pigs, and the lower rates of dislodgement and predation in deeper water supports a terrestrial predator. Our observations are similar to those of suspected pig predation during drought conditions, which presumably give pigs increased access to mussels (Williams and Benson 2004).

Predation during this event was highly selective. Of the 12 unionid species detected in the reach, feral pigs positively selected only *E. arca* and *F. cerina,* but *F. cerina* was highly favored and other dominant species in the reach appeared to be avoided (e.g., *C. asperata*, *P. decisum*, *L. ornata*). Furthermore, *C. asperata* and *F. cerina* were present in equal numbers in the mixed-species enclosures, yet *F. cerina* was selectively consumed in these enclosures even though both species were dislodged at similar rates. It is difficult to speculate why pigs so heavily favored *F. cerina* because its shell is similar in size, thickness, cubosity, and volume to *C. asperata* (see Owen et al. 2011).

Regardless of the basis for selectivity, pigs appeared to show a remarkable ability to detect the presence of *F. cerina*. Not only did pigs strongly favor this species, they disturbed enclosures containing *F. cerina* more frequently than other enclosure types. Visual clues are unlikely to be important because most mussels in the Sipsey River bury themselves in the substrate with only a small portion of the shell margin exposed (B. van Ee, personal observation). Pigs have well-developed olfactory and tactile capability in the snout, which helps them locate food in terrestrial environments (Allwin et

al. 2016). The ability of pigs to detect prey underwater is unknown, but other mammals have underwater olfactory capabilities (Catania 2006).

Effects of pig predation on mussel assemblages are largely unknown. Long-term selective predation can shift the composition and distribution of prey communities (Power 1984; Englund and Krupa 2000). Pigs consumed approximately 1% of the entire unionid community and approximately 6% of the *F. cerina* population in the experimental reach. Long-term selection for *F. cerina* could shift the community structure, and selective foraging in shallower areas could shift the community's spatial distribution. Indirect effects of pig predation also could influence mussel communities. Mussels dislodged from enclosures and scattered on the sediment surface could be vulnerable to other predators; they might be transported downstream by high flow; and they would be subject to increased stress and energy expenditures as a result of the need to rebury. Rooting by pigs also severely disturbs the streambed itself, which could decrease sediment stability and increase the erosion of previously stable substrate (Rafinesque 1820; Simpson 1899; Williams and Benson 2004; Butler 2006).

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