

Articles

Size-Specific Advantage in Shelter Competition between the Mountain Madtom and Crayfishes

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Abstract

Shelter is a crucial component to many species' survival, and when shelter becomes limited, resulting competition can have negative effects on growth and survival. In Little Chucky Creek, a tributary to the Nolichucky River in Tennessee, the severe population decline of Chucky Madtoms *Noturus crypticus* has been partially attributed to an increase in the abundance of cavity-dwelling crayfish after the establishment of two nonnative species. Although it has been suggested that the crayfish exclude the cavity-dwelling fish from shelter, we are not aware of studies that have been conducted to demonstrate that crayfish directly outcompete madtoms in this regard. Our objective was to experimentally test the hypothesis that shelter competition between crayfish and Mountain Madtoms *Noturus eleutherus*, a surrogate species for Chucky Madtoms, is a function of relative size. We conducted behavioral trials in which shelter was the limited resource for the two potential competitors. We recorded the madtoms' success at occupying the provided cover object for 5 d as well as health condition at the end of the competition phase. Both madtom occupancy and health condition were positively correlated with increasing relative size. As the size differential increased between madtoms and crayfish, madtoms were more successful at occupying the cover object, and overall condition was greater at the end of the trial. Conversely, when madtoms were smaller than crayfish, individuals were more commonly excluded from the cover object or even killed. Juvenile madtoms experienced 100% mortality. We concluded that crayfish exhibit a size-specific competitive advantage over Mountain Madtoms when shelter is limited, and that crayfishes may catalyze fish population declines at least partially through shelter exclusion and predation on juveniles.

Keywords: Chucky Madtom; interspecific competition; invasive species;; Kentucky River crayfish; Mountain Madtom; virile crayfish

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Introduction

The world is currently undergoing a decline in the populations of freshwater fishes, with the species of the southeastern United States, the hot spot for aquatic biodiversity, being disproportionately affected (Ricciardi and Rasmussen 1999; Duncan and Lockwood 2001). As human development continues to sprawl into previously isolated environments, issues such as nonnative species introductions and agricultural runoff tend to follow (Holdich 1999; Wang et al. 2001; Helms et al. 2005; Bar-Massada et al. 2014). For benthic fishes, these factors can pose a greater threat when sediment settles to the river bottom, filling in interstitial spaces and embedding larger rocks beneath which prey live, eggs are laid, and shelter from predators is found (Kawanishi et al. 2015). Additionally, the introduction of large, aggressive crayfishes has been associated with native fish population declines, extirpations, and extinctions (Twardochleb et al. 2013). Benthic fishes are at a heightened risk to the detrimental effects of crayfish because they share many significant life-history traits (e.g., diet and microhabitat), resulting in increased potential for agonistic interspecific interactions (Bubb et al. 2009). In addition to sharing a diet comprised primarily of macroinvertebrates, crayfishes and many fishes require cavities as shelter from predation and as spawning sites (Rahel and Stein 1988; Momot 1995; Guan and Wiles 1997; Holdich, 1999). When these cavities become limited, crayfishes may exclude small benthic fishes from shelter, decreasing the body condition of the latter and increasing predation risk (Rahel and Stein 1988; Guan and Wiles 1997; Light 2005). As more crayfish introductions occur worldwide, understanding and quantifying the intensity and direction of competitive interactions with native fishes for shelter is necessary for effective freshwater ecosystem management and conservation.

Invasive crayfishes and sedimentation have been cited specifically as putative factors in the decline of Chucky Madtoms *Noturus crypticus* Burr, Eisenhour and Grady, a diminutive benthic catfish with an extremely restricted range (Kuhajda et al. 2016a). This species has been collected only from two small tributaries to the Nolichucky River in Tennessee: a single specimen from Dunn Creek and 13 individuals from Little Chucky Creek (Burr et al. 2005). In the 1990s, the species' last known population underwent an apparent crash, and no individuals have been observed since 2004. Simultaneously, two nonnative crayfish species, Kentucky River crayfish *Faxonius juvenilis* (Hagen) and virile crayfish *Faxonius virilis* (Hagen), were recorded as having invaded Little Chucky Creek where they quickly increased the overall abundance of crayfishes (Kuhajda et al. 2016a). These species inhabit the same type of cavities beneath rocks required by Chucky Madtoms for shelter and spawning (Bovbjerg 1969; Taylor 2000) and have been observed occupying artificial nest structures that were intended to increase Chucky Madtom reproduction (J.R. Shute, Conservation Fisheries, Inc., personal communication). Both species of introduced crayfishes may grow much larger than the madtom (Pflieger 1996; Taylor and

Schuster 2004), and previous studies have found that body size plays a significant role in determining the outcome of interspecific interactions between fishes (Robertson 1998; Balshine et al. 2005) and between native and nonnative crayfishes (Vorburger and Ribic 1999; Nakata and Goshima 2003). In addition, severe sediment runoff from streamside agricultural practices has resulted in reduced availability of cavities that madtoms require for shelter and reproduction (Kuhajda et al. 2016b). Thus, the Chucky Madtom recovery plan (Kuhajda et al. 2016b) calls for eradication of the invasive crayfishes and improved land use practices to reduce nonpoint source sediment loading. However, the hypothesis that crayfish outcompete madtoms for limited shelter has not been empirically tested to our knowledge, and studies would assist in determining if this competition could have precipitated the decline of Chucky Madtoms.

The purpose of this study was to test this competitive interaction hypothesis in a laboratory setting by conducting an inclusion–exclusion experiment with shelter as the limited resource. Because size differential is known to have a significant effect on interspecific competition (Persson 1985), we hypothesized that 1) the occupancy rate of a madtom species under a shelter object is lower in the presence of relatively larger crayfish as a result of asymmetrical competitive interactions, and 2) crayfish competition would decrease the health condition of madtoms along a size differential, with relatively smaller madtoms in poorer condition than relatively larger madtoms.

Methods

Animal conditioning

We selected Mountain Madtoms *Noturus eleutherus* Jordan as the surrogate species for Chucky Madtoms because they are native to the same watershed and have a similar life history (Starnes and Starnes 1985; Burr et al. 2005). We collected Mountain Madtoms ($N = 27$) by backpack electroshocking and seining from the nearby French Broad River (Figure 1) in the summer of 2017. We housed the madtoms in four 75-L aquaria containing dechlorinated municipal water and bubbling sponge filters at the Johnson Animal Research and Teaching Unit facility at the University of Tennessee Institute of Agriculture. An automatic timer on the lights switched on at 0600 hours and off at 1800 hours each day, and the temperature range was 23–26°C. We fed the madtoms live blackworms and frozen bloodworms ad libitum.

We collected crayfishes ($N = 51$) with a backpack electroshocker and D-frame dip net from Bent Creek, a tributary to the Nolichucky River (Figure 1), in the summer of 2017. We only used late instar and adult *Faxonius* spp. in this study as they are known to use the same shelter as Chucky and Mountain Madtoms. Because of the difficulty of identifying form II males, females, and juveniles to species, we did not differentiate the crayfish to the species level. We housed the crayfish in a flow-through aquaculture system using dechlorinated munic-



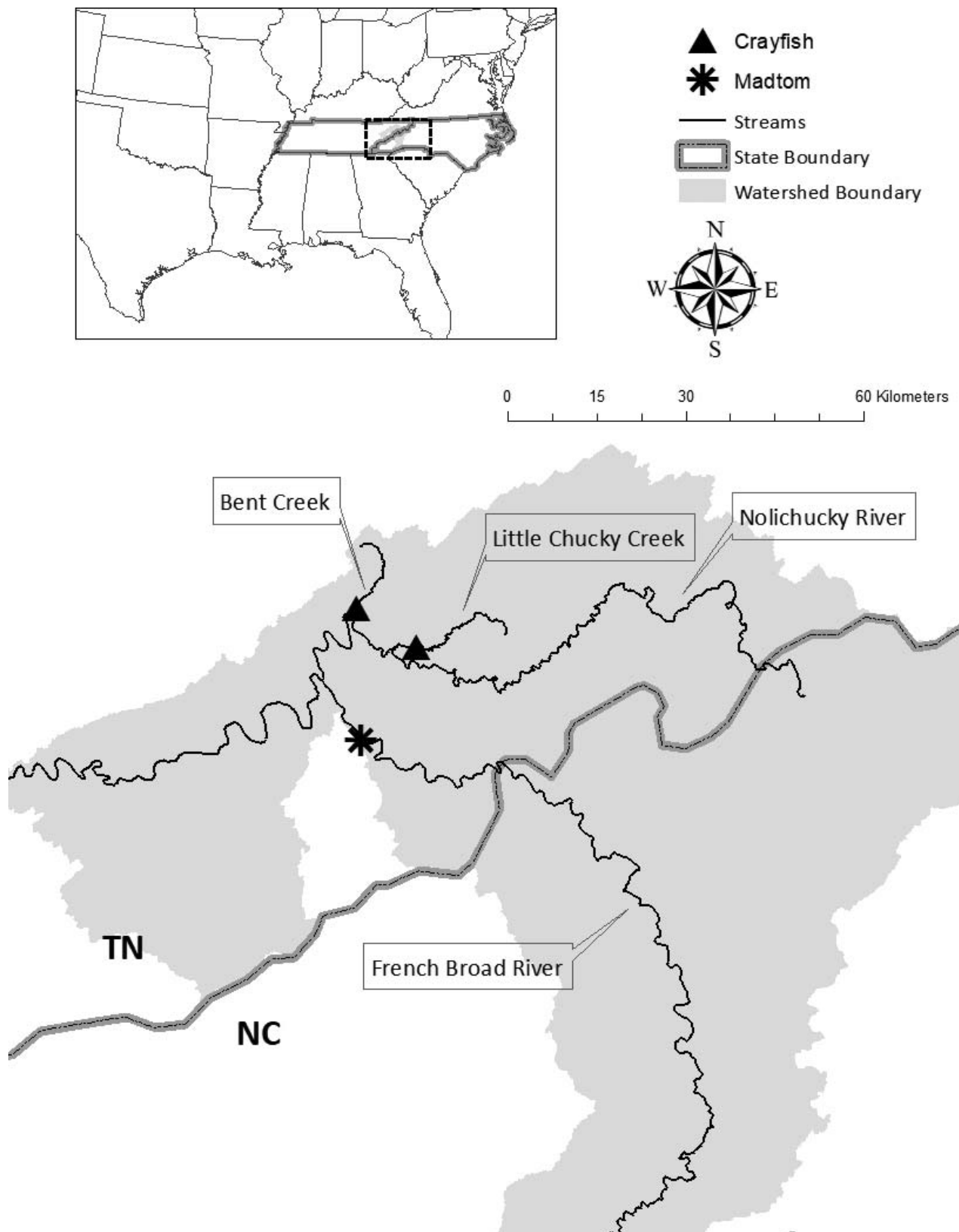


Figure 1. Map of study area and collection sites in northeast Tennessee. We collected Mountain Madtoms *Noturus eleutherus* used in the shelter competition experiment from the French Broad River, indicated by a black asterisk, by backpack electrofishing and seining. We collected crayfishes *Faxonius* spp. used in the experiment from Bent Creek, indicated by a black triangle, by backpack electrofishing and dip netting. We collected all animals in the summer of 2017. A black triangle also marks the site where Chucky Madtoms *Noturus crypticus* were last collected in Little Chucky Creek in 2004 and where crayfish density was sampled on August 21, 2019 (C. Williams, Tennessee Wildlife Resources Agency, unpublished data; Table S1).

ipal water at the Johnson Animal Research and Training Unit facility in a 300-L tank oxygenated with air stones. We fed them frozen bloodworms and commercial fish pellets ad libitum. Light regime and temperature range were as detailed above. All organisms acclimated to captivity for at least 1 wk before being used in experimental trials and were apparently healthy. We did not use any individual for more than one trial to ensure independence of replication.

Experimental design

We designed the competition experiment to test the effect that varying relative sizes of crayfish have on the ability of Mountain Madtoms to take shelter under a cover object. Since shelter competition as a result of invasive establishment or habitat degradation is often a constant, persistent stressor, we set the competition period to 5 d to observe the stronger effects of chronic stress than would occur in a shorter period. We stocked each 0.2-m² 75-L glass aquarium with a control group ($N = 2$) of a single madtom, a treatment group ($N = 10$) of a madtom paired with two smaller crayfish, or a treatment group ($N = 12$) of a madtom paired with two larger crayfish. This amounted to an experimental density of 10 crayfish/m² in each aquarium. Although this is somewhat higher than the reported density of more than 7 crayfish/m² in Little Chucky Creek (C. Williams, Tennessee Wildlife Resources Agency, unpublished data; Table S1, *Supplemental Material*), other field studies have documented densities greater than 10 crayfish/m² in areas where nonnative crayfishes have become established (Kuhlmann and Hazelton 2007; Kuhlmann 2016; Forsythe et al. 2018). Because of the limited number of available aquaria, we ran a series of four trials with six independent replicates each back to back for a total of 24 replicates at the Johnson Animal Research and Training Unit facility with light and temperature regime as detailed above. Each aquarium contained an air stone, a layer of sand-gravel substrate, and screens covering the top to prevent escape.

We fed all animals 24 h before the start of the experiment to minimize effects of foraging but did not feed them during the experimental phase to minimize confounding effects of competition for food. Madtoms are predators with relatively low metabolic rates and are known to go extended periods of time (up to 3 wk) without food in the natural environment when courting and nesting (Starnes and Starnes 1985; Méndez and Wieser 1993; Dinkins and Shute 1996; Fu et al. 2005, 2009). Crayfish have been shown to be highly resistant to starvation, relying on the nutrient reserves in a specialized organ called the hepatopancreas for as long as 7 mo (Jones and Obst 2000; Stumpf et al. 2011; Calvo et al. 2012). Thus, we did not anticipate any negative effects on the animals' health from a 6-d fast.

At the start of each experimental trial, we placed an opaque plastic divider in the middle of the tank to separate the fish from the crayfish for 24 h. This acclimation period followed a similar experimental study

of competitive effects for shelter between a nonindigenous and native fish species held in aquaria (Lorenz et al. 2011). We randomly selected a madtom and placed it on one side of the divider. Then we placed two crayfish that were larger than the madtom in half of the replicates and two crayfish that were smaller in the other half. At the end of this 24-h phase, we removed the divider and placed a single cover object in the middle of the tank. The cover object was a 200-mm square ceramic tile propped up on one side by a 9-mm plastic lifter, which are approximately the dimensions of cover rocks preferred by Chucky Madtoms and Mountain Madtoms (P. Rakes, Conservation Fisheries, Inc., personal communication). Even large individuals of both madtoms and crayfish were able to use the cover object as refugia by excavating the substrate beneath the tile.

The competition phase lasted 5 d, during which time madtoms and crayfish could move freely about their tanks, interact with each other, and compete for the cover object. We recorded the position of the madtom as being either "out" (i.e., not under the tile) or "under" (i.e., under the tile) once every 24 h until the end of the trial. A madtom was considered successful if it occupied the space under the tile. To minimize the effect human activity might have had on the experimental animals, an opaque tarpaulin hung in front of the experimental tanks, and we recorded observations quickly and discreetly. We took all records during the daytime as shelter use is more prevalent during this time for both the nocturnally active crayfishes and Mountain Madtoms.

At the end of each 5-d competition phase, we calculated the success frequency of each madtom by dividing the number of observations in which the madtom was under the tile by the total number of observations (Table S2, *Supplemental Material*). If a madtom was killed before the end of the 5 d, we used only data taken while it was alive to calculate occupancy frequency. We measured the total lengths (TLs) of crayfish and madtoms and calculated the average size difference between crayfish and madtom in each replicate. In addition, we qualitatively assessed the health condition of each fish and scored it on a scale of 1 (dead) to 5 (healthy; Table 1).

We analyzed the effect of average size differential on the frequency of madtom success at cover object occupancy using analysis of variance. To determine whether the data fit the assumption of normality, we performed a Shapiro-Wilk test and created quantile-quantile plots for each variable. We conducted a Spearman's rho correlation analysis on mean ranks to determine if there was a relationship between size differential and condition score. We carried out all analyses in R v. 3.6.3 (R Core Team 2020).

Results

All fish-only control treatments during this particular study ($N = 2$) yielded 100% madtom occupancy of the



Table 1. Criteria for condition scores assigned to each Mountain Madtom *Noturus eleutherus* at the end of each 5-d competition phase whereby it competed against two crayfish *Faxonius* spp. of either larger or smaller relative size for access to a cover object. We assigned the scores qualitatively on the basis of body condition and behavior and they range from 5 (healthy, no gross symptoms of stress, injury, or disease) to 1 (dead). We conducted the experiment in 2017.

Score	Description
1	Dead
2	Injury on all fins; heavily diseased; behavior abnormal (gasping, pacing, etc.)
3	Injury on more than two fins; mild sign of disease; behavior normal
4	Injury on one to two fins; behavior normal
5	Healthy; no signs of stress, injury, or disease

cover object and received a health condition score of 5 (Table S2), indicating that there were no observable negative effects from food deprivation. In addition, a preliminary study in which madtoms were observed for 2 d also yielded 100% shelter occupancy in madtom-only controls ($N = 3$; Table S2). In all fish–crayfish treatments ($N = 22$), madtom occupancy fell to 67% (Table 2), and this decrease in occupancy was related to the size differential between the madtoms and crayfish. Madtom lengths ranged from 50 to 89 mm TL with a mean (\pm SD) TL of 64 ± 11 mm (Table S2). Crayfish TLs ranged from 41 to 87 mm with a mean of 65 ± 11 mm (Table S2). Madtom occupancy was positively correlated ($R^2 = 0.374$) with madtom size relative to crayfish size ($P < 0.003$; $F_{1,20} = 11.950$; Figure 2). Thus, our results displayed a relative size-occupancy gradient, whereby fish paired with comparatively larger crayfish occupied cover objects less frequently than fish paired with smaller crayfish. Similarly, the fish's health condition was significantly positively correlated with an increase in the relative size differential gradient, whereby fish paired with relatively larger crayfish were in poorer condition by the end of the trial ($P < 0.002$; Spearman $\rho = 0.630$; Figure 3). Evidence of poor condition included injuries to fins and body consistent with crayfish aggression as well as white spot

Table 2. Number of observations that Mountain Madtoms *Noturus eleutherus* were successful at occupying the 200-mm ceramic tile cover object (“under”) and unsuccessful (“out”) during each competition phase whereby madtoms competed against two crayfish *Faxonius* spp. of either larger or smaller relative size for access to the cover object. We took observations every 24 h for the 5 d each competition phase lasted. Control treatments (madtom only) had 100% success; madtoms paired with two smaller crayfish were successful 82% of the time; madtoms paired with two larger crayfish were only successful 56% of the time and 9% were killed. We conducted the experiment in June 2017.

Treatment	Under	Out	Killed
Control	16	0	0
Madtom larger	41	9	0
Madtom smaller	24	19	4

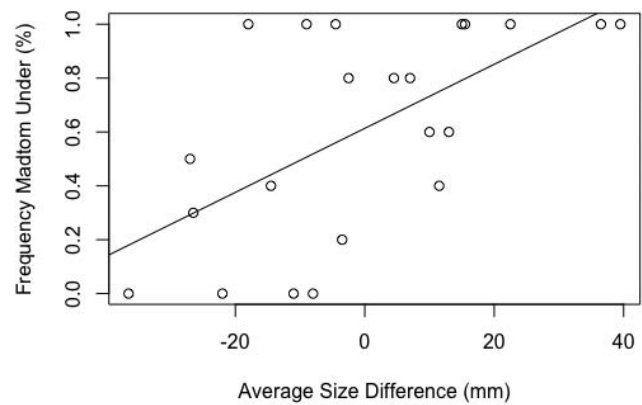


Figure 2. Mountain Madtom *Noturus eleutherus* occupancy of cover object as average relative size difference increases ($R^2 = 0.374$) during each competition phase in a 0.2-m² 75-L glass aquarium whereby a single madtom competed for access to the cover object against two crayfish *Faxonius* spp. of either larger or smaller relative size. The x-axis indicates the average size difference (mm) between the madtom and the two crayfish paired with it. We calculated frequency (y-axis) as the number of observations in which a madtom was occupying the space under the cover object divided by the number of observations for each replicate. As the size differential increased (i.e., as madtoms were increasingly larger than the crayfish), the frequency of success increased as well ($P < 0.003$; $F_{1,20} = 11.950$). We conducted the experiment in June 2017.

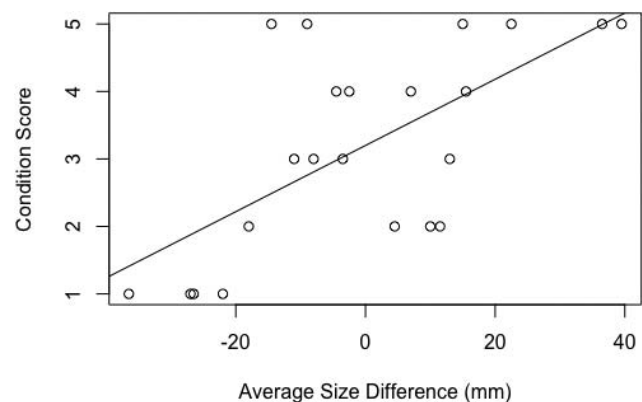


Figure 3. Health condition score of Mountain Madtom *Noturus eleutherus* by size differential ($R^2 = 0.429$) at the end of each 5-d competition phase in a 0.2-m² 75-L glass aquarium whereby a single madtom competed for access to a cover object against two crayfish *Faxonius* spp. of either larger or smaller relative size. We qualitatively assigned scores on the basis of the outward appearance and behavior of each fish and they range from 5 (healthy, no gross symptoms of stress, disease, or injury) to 1 (dead). We significantly positively correlated health condition score with an increase in the size differential between madtom and crayfish ($P < 0.002$; Spearman $\rho = 0.630$). As madtom size decreased relative to the crayfish it competed against, health condition tended to decrease as well, with many smaller madtoms having abnormal behaviors, stress-related disease, injury, or death. We conducted the experiment in June 2017.

disease caused by the protozoan *Ichthyophthirius multifiliis* Fouquet that was not present on fish at the start of the trials. Juvenile madtoms <55 mm TL were especially vulnerable, with 100% mortality in treatments with larger crayfish ($N = 4$). In every instance, mortality occurred within the first 24–48 h.

Discussion

Our results support the first hypothesis that the occupancy rate of a madtom species under a shelter object is lower in the presence of relatively larger crayfish as a result of asymmetrical competitive interactions. This finding is consistent with many ecological studies suggesting that larger species tend to be competitively superior to smaller ones (Schoener 1983) as well as the common theme of size-specific advantage in several crayfish competition studies (Rabeni 1985; Figler et al. 1999; Vorburger and Ribic 1999). This finding provides some evidence for the hypothesis suggested by Kuhajda et al. (2016a, 2016b) that the decline of Chucky Madtoms is in part due to the increase in crayfish abundance subsequent to the introduction of nonnative crayfishes and ensuing shelter competition. Therefore, an asymmetrical interaction between large-bodied crayfishes and Chucky Madtoms could have been one factor in the precipitous decline of Chucky Madtoms in the wild if shelter was limited.

There are several species of crayfishes native to Little Chucky Creek that are known to attain large body sizes relative to madtoms, such as surgeon crayfish *Faxonius forceps* (Faxon), but it is likely that competitive interactions with them were less frequent under environmental conditions before human influences. An increase in agricultural activity in the Little Chucky Creek watershed has resulted in significant nonpoint sediment runoff, and rocks that both cavity-dwelling crayfishes and Chucky Madtoms require became embedded with sediment, making them unsuitable for shelter and reproduction (Kuhajda 2016a). Shelter possibly became a limited resource as a result and increased the potential for competitive interactions between both native and nonnative cavity-dwelling crayfishes and the madtoms. Although we only tested competitive interactions against late instar and adult crayfish, which represented approximately 52% of the crayfish in the field survey (C. Williams, unpublished data; Table S1), this is the age and size that Chucky Madtoms would be most likely competing against because of shared preference for shelter. *Faxonius* spp. typically partition habitat on the basis of size, with smaller, earlier instars using smaller rocks for cover than Chucky Madtoms, Mountain Madtoms, or large crayfish would use (Rabeni 1985; Starnes and Starnes 1985; Burr 2005). It should be noted, though, that the crayfish density of 10 crayfish/m² used in this study was slightly higher than the current reported density in Little Chucky Creek of 7.15 crayfish/m² (Table S1), and thus may have resulted in stronger effects than occurred in that particular stream.

In addition to increased shelter exclusion, our results also support the second hypothesis that crayfish compe-

tion would decrease the health condition of madtoms along a size differential, with relatively smaller madtoms in poorer condition than relatively larger madtoms. Competitive shelter exclusion and ensuing increased risk for predation has profound effects on species, including madtoms. Prior studies have documented a decrease in growth rate and an increased mortality rate of cavity-dwelling benthic fishes (e.g., darters and sculpin) that have been evicted from cover (Rahel and Stein, 1988; Light 2005; Bishop et al. 2008). In this study, many madtoms had injuries consistent with aggression from crayfish. We observed crayfish grabbing and tearing the madtoms' fins throughout the experiment, and this constant agonistic interaction with a predator could induce stress responses in fish. This would explain the presence of *I. multifiliis*, a disease known to affect fish immunocompromised from stress (Fairfield 2000), on several madtoms ($N = 7$).

Diseased and injured fish cannot expend as much energy on feeding or reproducing and are more susceptible to predation (Abrams et al. 1996; Light 2005). We observed this effect in our study: juvenile madtoms ($N = 4$) were being killed and consumed by larger crayfish. Although it has been documented that virile crayfish starved for more than 1 wk exhibit higher levels of aggression (Hazlett et al. 1975), most of the mortality in our study occurred in the first 48 h of competition (Table S2), indicating that starvation may not have been the major driver of crayfish predation. However, the confinement in aquaria and lack of escape for the madtoms may have made them more susceptible to crayfish aggression.

Other detrimental effects of nonnative crayfish introductions not tested in our study are predation on eggs and larvae. Crayfish predation on benthic fish eggs and larvae is well documented (Rahel 1989; Holdich 1999; Dorn and Wojdak 2004; Forsythe et al. 2018). The reduction of egg and larval survival would only exacerbate the decline of madtoms like Chucky Madtoms, as they have relatively low fecundity (Starnes and Starnes 1985). Furthermore, the many indirect effects of invasive crayfish on the ecosystem could have negatively affected the madtoms, including increased stream turbidity, competition for food (i.e., benthic aquatic insects), or shifts in whole trophic organization through macrophyte grazing and increased detrital processing rates (Freeman et al. 2010; Twardochleb et al. 2013). Last, it is important to recognize the potential role of abiotic factors (e.g., declining water quality and agricultural runoff) in the decline of Chucky Madtoms, and that the possible reasons for this decline may be the result of synergistic effects between biotic and abiotic factors.

This study is an important first step in understanding the effect that shelter competition may have had on Chucky Madtoms after the introduction of Kentucky River and virile crayfishes and the habitat degradation from siltation. The broader implication of this study is that management of nonindigenous, cavity-dwelling crayfishes in streams where shelter may be limited is recommended for the recovery of imperiled benthic fishes like Chucky Madtoms. Although complete eradi-



cation is often an impossible task once an invasive species has become established, ongoing targeted reduction of large-bodied nonnative crayfishes could be an achievable and effective goal as relative size appears to be the significant factor in shelter competition between madtoms and crayfish. Ultimately, habitat improvement is likely necessary as well before negative effects from competition with crayfishes—native or invasive—can be alleviated.

Supplemental Material

Table S1. Results of a catch-per-unit-effort survey for crayfish in Little Chucky Creek, Greene County, Tennessee (36°7′27.8544″N, 83°3′12.5892″W) by Tennessee Wildlife Resources Agency Wildlife Technician Carl Williams on August 21, 2019. We counted and categorized individuals of each species in each transect by sex and age as F (adult female), FJ (juvenile female), LIJF (late instar juvenile female), LIJM (late instar juvenile male), MI (first form male), MII (second form male), or MJ (juvenile male). Species present in the survey were longnose crayfish *Cambarus longirostris* (Faxon), reticulate crayfish *Faxonius erichsonianus* (Faxon), surgeon crayfish *F. forceps*, and nonindigenous virile crayfish *F. virilis*. The mean density was 7.15 crayfish/m², with *F. forceps* being the most abundant species and *F. virilis* the second-most abundant. The majority of crayfish was late instars or adults.

Found at DOI: <https://doi.org/10.3996/042019-JFWM-023.S1> (17 KB XLSX).

Table S2. Daily observations for all control and experimental treatments recorded at the Johnson Animal Research and Training Unit in Knoxville, Tennessee in June 2017, with total lengths of madtoms and crayfish, calculated average size differential, and the qualitative condition score assigned to each madtom at the end of the competition phase with notes on physical appearance used to assign a score. We calculated the frequency for each replicate as the number of times we observed a madtom under the tile divided by the total number of observations. We calculated the average size difference by taking the mean of the total lengths of two crayfish in each replicate and subtracting it from the total length of the madtom (a negative number indicates crayfish larger than the madtom).

Found at DOI: <https://doi.org/10.3996/042019-JFWM-023.S2> (17 KB XLSX).

Reference S1. Kuhajda BR, George AL, Chance S. 2016a. Species biological report for Chucky Madtom (*Noturus crypticus*). Washington, D.C.: U.S. Fish and Wildlife Service.

Found at DOI: <https://doi.org/10.3996/042019-JFWM-023.S1> (717 KB PDF); also available at https://www.fws.gov/cookeville/pdfs/10202016_Chucky%20Madtom_Species_Biological_Report.pdf.

Reference S2. Kuhajda BR, George AL, Chance S. 2016b. Recovery implementation strategy: Chucky Mad-

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Found at DOI: <https://doi.org/10.3996/042019-JFWM-023.S2> (160 KB PDF); also available at https://www.fws.gov/cookeville/pdfs/10202016_Chucky%20Madtom_Recovery%20Implementation%20Strategy.pdf.

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