

Influence of Water Flow on Neosho madtom (*Noturus placidus*) Reproductive Behavior

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ABSTRACT.—The Neosho madtom is a small, short-lived catfish species endemic to gravel bars of the Neosho River in Kansas, Oklahoma and Missouri, U.S.A. It spawns during summer in nesting cavities excavated in gravel. Although the species has survived dam construction within the Neosho River basin, its declining numbers resulted in it being added to the federal threatened species list in 1991. To test how water flow affects the reproductive behavior of Neosho madtoms, we compared activities of male-female pairs in static versus flowing-water aquaria. Using a behavioral catalog, we recorded their behavior sequences during randomly selected 5-min nighttime periods. For males and females, Jostle and Embrace were the most performed reproductive behaviors and the Jostle-Embrace-Carousel was the most performed reproductive behavior sequence. Water flow decreased the mean frequency of occurrence, percentage of time spent and mean event duration of male Nest Building. Because Neosho madtom courtship, reproduction and parental care is a complex and extended process, disturbances such as heightened river flows during the species' spawning season may negatively affect nest quality and reproductive success.

INTRODUCTION

Many environmental cues trigger spawning in temperate fish species, including food abundance, photoperiod, temperature, flooding, lunar cycles and social interaction (Bye, 1984; Munro *et al.*, 1990). The nature of these cues and how they are used can differ from family to family, and even between closely-related species, depending upon geographic location and prevailing environmental conditions (Bye, 1984). Within order Siluriformes, the environmental factors that trigger reproduction include temperature, photoperiod and water flow (Brauhn, 1971; Brauhn and McCraren, 1975; Vasal and Sundararaj, 1976; Davis *et al.*, 1986; Kelly and Kohler, 1996; Stoeckel and Burr, 1999). For the ictalurid genus *Noturus*, flowing water has not been examined as a factor affecting reproduction, even though most species occur in flowing water habitats (Taylor, 1969; Burr and Stoeckel, 1999).

Altering a river's natural flow regime can affect fish spawning and reproductive success. For example, discharges that mimic natural flow regimes facilitate reproduction in striped bass (*Morone saxatilis*; Zincone and Rulifson, 1991) and lake sturgeon (*Acipenser fulvescens*;

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Auer, 1996). In contrast, alterations of the natural flow regime negatively affect fish spawning success by impeding upstream migration to the spawning grounds (Votinov and Kas'yanov, 1978) and decreasing survival and growth of eggs and fry (Reiser and White, 1990; Gomes and Agostinho, 1997).

Numerous flood control and low-head dams have been constructed in the Neosho River basin (U.S. Army Corps of Engineers, 1993), which is the only habitat of the Neosho madtom, *Noturus placidus* (Taylor, 1969; Cross and Collins, 1995). The effects of dam and reservoir construction on this river's hydrology are typical. The low-head dams have changed the riverine habitat upstream and downstream, together with the associated fish assemblages (Gillette, 2005), and Neosho madtoms are less abundant in gravel bars directly above and below these dams (Tiemann *et al.*, 2004). Following placement of the John Redmond flood control reservoir and dam on the Neosho River, the river exhibits less variable flow rates, increased winter flows, high flow events of greater and more variable durations, and delayed maximum annual flows of more variable timing (Wildhaber *et al.*, 2000). These changes are problematic because Neosho madtom density is correlated with the magnitude, duration, and timing of flow minima (Wildhaber *et al.*, 2000). Despite its scope, the aforementioned research has examined water flow modification impacts only at the population level. How water flow impacts Neosho madtom individuals during reproduction has not been studied.

Five species of madtoms are included on the U.S. Fish and Wildlife Service's threatened and endangered species list (Burr and Stoeckel, 1999). The Neosho madtom was classified as threatened in 1991 (U. S. Fish and Wildlife, 1991; 55 FR 21148). A typical wild adult Neosho madtom is 35–70 mm in total length (Fuselier and Edds, 1994; Bulger and Edds, 2001). Most wild Neosho madtoms live 1 to 2 y (Bulger and Edds, 2001). Neosho madtoms occur almost exclusively within mainstems of the Neosho River. Like most madtoms, they are typically found in association with gravel bars in areas of flowing water (Deacon, 1961; Taylor, 1969; Moss, 1983; Fuselier and Edds, 1994; Cross and Collins, 1995; Bulger and Edds, 2001). During the breeding season, which spans May to August/September (Bulger and Edds, 2001), laboratory studies have shown that nest cavities are constructed under large objects in the gravel and that spawning occurs at temperatures ranging from 21 to 28 C (Bulger *et al.*, 2002b; Bryan *et al.*, 2005); high turbidity in the Neosho River inhibits direct observations (Pfungsten and Edds, 1994). Male parental care is typical of madtoms (Burr and Stoeckel, 1999), and Neosho madtom males provide 8–9 d of post-spawning parental care (Bulger *et al.*, 2002b). Compared to longer-lived fish species, Neosho madtoms approach semelparity: because they appear to live only one or two years in nature (Bulger and Edds, 2001), their opportunities for reproduction seem to be limited.

To better understand Neosho madtom reproduction and the effects of water flow on it, we conducted a laboratory study comparing Neosho madtom reproductive behavior under flow and non-flow conditions. We chose to study reproductive behaviors over other facets of reproduction because: (1) examining spawning success in the wild is almost impossible due to the high and continuously turbid in situ water conditions (Pfungsten and Edds, 1994), (2) sacrificing individuals to obtain information regarding reproductive/gonadal status was unwise due to the species' conservation status, necessitating work with live individuals, (3) reproduction in this genus and species is both lengthy and complex (Fitzpatrick, 1981; Bowen, 1980; Chan, 1995; Bulger *et al.*, 2002a), providing frequent opportunities for flow-related disruptions of spawning to occur and to be assessed and (4) madtoms in the laboratory rarely complete the entire spawning process, from nesting to fry dispersal (Stoeckel and Burr, 1999; Bulger *et al.*, 2002b; Bryan *et al.*, 2005), necessitating an emphasis on events culminating in spawning.

METHODS

GENERAL FISH MAINTENANCE

The Neosho madtoms used in this study were collected from Kansas sections of the Neosho ($n = 24$) and Cottonwood rivers ($n = 34$) in April–July 1998 (Bulger, 1999). At the time of collection, these fish were assumed to be one-year-olds due to their small size (40 to 67 mm). In 1998 the fish were used in another reproductive behavior study conducted by Bulger (1999). Our study of these fish began in the summer of 1999 and continued through the summer of 2000, when the fish were assumed to be 2+ and 3+ years of age, respectively.

The holding aquarium for the fish was a single Living Stream^R System (Frigid Units, Inc., Toledo, Ohio, 720 L, model LS-900) housed in an isolated photoperiod- and temperature-controlled room. To minimize inter-gender aggression, we kept the genders separate in the Living Stream using perforated partitions (four total compartments). Water temperatures (9–27 C, winter vs. summer) and laboratory photoperiods (8–16 h of light) were manipulated throughout the year (Bryan *et al.*, 2005) to mimic the natural environment of the Neosho River at the latitude and longitude of Emporia, Kansas (38°26'N, 96°12'W). Fish were fed to satiation thrice weekly [frozen brine shrimp (*Artemia salina*), frozen bloodworms (*Chironomus* sp.) or Sinking Carnivore Pellets (Hikari^R, Hayward, California)]; excess food was removed routinely to prevent fouling of the water.

EXPERIMENT

Our work was conducted at the U.S. Geological Survey Columbia Environmental Research Center in Columbia, Missouri, U.S.A. Behavioral monitoring of male/female pairs was conducted at the same time as the wild Neosho madtom spawning season (May through July; Bulger and Edds, 2001). Each year's experiment continued until all signs of spawning activity ceased. Consequently, the laboratory spawning season lasted 63 d in 1999 (starting May 22 at 19 C) and 44 d in 2000 (starting June 3 at 20 C). Photothermal manipulations successfully induced the gonad and secondary sexual characteristic development common to breeding Neosho madtoms (Pfungsten and Edds, 1994; Bulger *et al.*, 2002b; Bryan *et al.*, 2005). Fish that exhibited the most pronounced secondary sexual characteristics were paired and randomly assigned to treatment groups (*see below*).

Aquaria.—In 1999 we used 21.9-L aquaria (12 tanks: six flow and six non-flow). In 2000 we increased the size of the aquaria to 43.7-L (six tanks: three flow and three non-flow) because the fish had grown considerably. While in the aquaria, our maintenance of the fish continued as described above.

We provided each aquarium with a nesting cavity cover made of a length of PVC pipe halved lengthwise. Larger nest cavity covers were used in 2000, again because the fish had grown (1999: 13.3 cm long \times 10.2 cm wide \times 5.0 cm high; 2000: 12.7 cm long \times 14.0 cm wide \times 6.4 cm high). For each aquarium, this nest cover was placed concave side down with one end positioned against the front wall of the aquarium to allow for direct viewing into the nest. The substrate for each aquarium was natural chert-limestone gravel similar in size to that of spawning sites in nature (1.37 ± 0.52 cm; Bulger and Edds, 2001). Aquaria were illuminated during the day by eight overhead fluorescent bulbs (34 W, General Electric Company, Cleveland, Ohio, 120 cm long \times 3.8 cm diameter), and at night by six overhead infrared illuminators (30 W, American Dynamics, Orangeburg, New York, model 1020/3050), which allowed camera viewing of fish during darkness.

Water flows.—Each year, aquaria were randomly assigned to flow and non-flow treatments. All aquaria were plumbed similarly and filled with well water. Current in each flow aquarium was generated using an external recirculating pump plumbed to draw aquarium water from

just below the water surface and to aim flows across the substrate directly into the nest cavity. Velocities of 30 cm/s at the nest cavity opening were established at the start of each experiment, a rate similar to that found at substrate level at adult Neosho madtom collection sites (Bulger and Edds, 2001). Corresponding outflow pipe velocities were measured weekly thereafter to avoid disrupting the fish in their nest cavities. These flow measurements were also taken in the non-flow aquarium to ensure equal disturbance between treatments.

Behavioral data collection.—Fish behavior was recorded using a monochrome video multiplexer (American Dynamics, Orangeburg, New York, model 1480/16), time lapse video recorder (Panasonic, Secaucus, New Jersey, model AG-6760P or Toshiba America C.P. Inc., Buffalo Grove, Illinois, model KV-7168A) and six black and white cameras (Panasonic, Secaucus, New Jersey, model WV-BP310). The VCRs alternately recorded successive 12-h periods and were set to record $1/60^{\text{th}}$ of a second every $1/10^{\text{th}}$ s. Cameras were positioned directly in front of each aquarium and provided a full aquarium width view that included a view underneath the nest cavity cover.

Although we recorded around the clock, the Neosho madtoms proved to be nocturnal and, thus, largely inactive during the daytime (*see also* Bulger *et al.*, 2002a). Consequently, we collected behavior data only from the nighttime. Nights with disturbances (power/camera/recording failure and/or feeding nights) were excluded from data collection, leaving 56 and 57% of the nights for behavior sampling in 1999 and 2000, respectively (35 out of 63 and 25 out of 44 nights). For each aquarium, we randomly selected a sub-sample of 17 of the undisturbed nights for data collection (a 49% sub-sample for 1999 that we matched in 2000). This random selection yielded different subsets of nights for each aquarium.

For each tank-night selected, a random 5-min period was further sub-sampled from each hour, with the night's hour count beginning the moment the lights were turned off. Because night length varied progressively through the experiment, each night's duration was not an even multiple of 60 min. Consequently, we also excluded from consideration any hour within which the morning transition to light occurred.

For every randomly selected 5-min period, each fish's behavior was observed and the beginning and ending time of every behavioral act was recorded by gender. For single individuals, we could not confidently distinguish single acts of long duration from several continuous repetitions of the same act that lacked intervening pauses. Therefore, we considered all such cases as the former, which precluded the reporting of repeats of the same behavior. Although the fish were not marked, we could always distinguish the male from the female by their secondary sexual characteristics. Gender was confirmed later using ultrasound examination (Bryan *et al.*, 2005).

Behaviors.—Twenty-three Neosho madtom behaviors had previously been cataloged by Bulger *et al.* (2002a) which defined behaviors using position in the aquaria and whether one or both fish performed the behavior. We modified this catalog by defining the behaviors without aquaria position or performance by one or both fish (Table 1). Ten behaviors were observed during videotape analyses; five additional behaviors were not seen during our sub-sampled time intervals, but were observed at other times. Four of the 10 observed behaviors are considered Reproductive Behaviors in madtoms (Carousel, Embrace, Jostle, and Nest Building; Fitzpatrick, 1981; Stoeckel, 1993; Chan, 1995; Bulger *et al.*, 2002a, b). Three of the Reproductive Behaviors were further categorized here as Pair-Based, because both genders participated (Carousel, Embrace and Jostle).

For each of the 10 observed behaviors, we calculated an overall mean for each of three parameters using SAS (1999–2001): (1) frequency of occurrence (number of times a behavior was performed during a 5-min period), (2) percentage of time (total time spent

TABLE 1.—Neosho madtom ethogram (modified from Bulger *et al.*, 2002a)

Behavior	Description
Bite	Fish approaches a conspecific head first, then closes its mouth on or against the point of contact, the latter being other than the mouth.
Carouse ^{1,2,3}	While oriented head to tail, both fish swim in a circular pattern, following one another, during which one fish rubs and nudges the caudal peduncle area of the conspecific.
Chase ¹	Fish swims close behind a conspecific, rapidly following it around the tank.
Embrace ^{2,3}	With both fish oriented laterally head to tail, one or both curls caudal fin across and over other fish's snout.
Feeding	Fish is ingesting food accompanied by chewing-like mouth movements.
Jostle ^{2,3}	While in contact with a conspecific, fish bumps and pushes a conspecific with its body during a series of twists and turns.
Mouth Bite ¹	With conspecifics oriented head-on, one approaches the other then clasps its mouth onto the other's, after which the two fish thrash their tails back and forth, while remaining joined.
Nest Building ²	At a developing nest site, fish moves a substrate particle either by seizing the substrate particle with its open mouth then pushing or lifting it, or by levering its head under the particle then pushes it across the bottom.
Nudge	Fish swims toward a conspecific then bumps headfirst into it.
Oral Flare	Fish opens mouth and splays its opercula, directing this display toward a conspecific.
Parallel Swim Display ¹	With two fish positioned side by side, facing in the same direction, one spreads its fins and laterally flexes its body resulting in a sinusoidal wave passing down the length of the body.
Resting	Fish is stationary on the bottom.
Scratching ¹	Fish swims forcefully, causing its body to graze against or/and glance off a stationary object.
Spawning ^{1,2}	Gamete release by both the male and female.
Swimming	Fish propels itself around the tank using its caudal fin.

¹ Indicates behavior that did not occur during data collection, consequently no analysis could be done

² Indicates Reproductive Behavior

³ Indicates Pair-Based Reproductive Behavior

performing a behavior during a 5-min period divided by $5 \text{ min} \times 100$), and (3) mean event duration (total time spent performing a behavior during a 5-min period divided by frequency of occurrence). These parameter means were then used to test for an effect of water flow on Neosho madtom behavior.

DATA ANALYSIS

Individual behaviors.—This analysis was designed to determine for males and females whether each separate Neosho madtom behavior parameter differed between the flow and non-flow treatments. The three parameter values above were extracted from all 5-min samples for each behavior under consideration. Then the three parameter means for each aquarium/gender/behavior combination were generated for each hour, the hourly means were then averaged within each night and these per-aquarium/per-night means were then averaged over the sampled nights of the spawning season. Because some behaviors did not occur during many of the 5-min periods, the data was not normally distributed and the

variance was not constant. Consequently, we tested for treatment effects on each behavior's parameters using a multi-response permutation procedure (BLOSSOM, Version W2001.05a, Cade and Richards, 2000), this being the non-parametric equivalent of a multivariate analysis of variance (Bonferroni-adjusted alpha level = 0.025, *i.e.*, 0.05/2, accounting for the separate male and female tests of each parameter).

Behavior sequences.—This analysis was designed to test for each gender whether the four Reproductive Behaviors were performed in any prevailing order and, if so, to describe such ordering and test whether it differed between flow and non-flow conditions. A Reproductive Behavior Sequence was defined as a series of successive acts performed by individual fish where both the first and last act were any one of the four Reproductive Behaviors. Data analyzed were the sequences of all behaviors that each individual fish performed during the 5-min samples from 1999 and 2000. Data for each fish within the pairings were analyzed separately because male/female interactions were not the focus of this analysis.

Each Reproductive Behavior Sequence was designated using any two of the four Reproductive Behaviors, the first being termed the "given" behavior, the last being termed the "target" behavior. The sequences we evaluated included those where the target behavior occurred immediately after the given behavior (lag 1), two steps after (one intervening behavior, lag 2) or three steps after (two intervening behaviors, lag 3). Intervening behaviors could be any of the behaviors we observed. For example, the sequence Jostle-Swimming-Resting-Carousel would designate Jostle as the given behavior, Swimming and Resting as intervening behaviors, and Carousel as the target behavior (lag 3). Any sequence with Nest Building as a target or given behavior was designated as a Nest Building Reproductive Behavior Sequence and any sequence with a Pair-Based Reproductive Behavior as both the target and given behavior were designated as a Pair-Based Reproductive Sequence. Sixteen different given/target combinations could be derived from the four Reproductive Behaviors; consequently, a total of 44 different combinations of sequences and lags were possible (16 sequences \times 3 lags = 48 combinations minus 4 sequences that would have required distinguishing repeats of the same behavior = 44).

To examine behavior interdependence, we summed the Reproductive Behavior Sequence occurrence for each lag/gender/treatment/year combination and used lag sequential analysis to test the degree to which some Reproductive Behaviors followed others more frequently than expected by random using a Pearson chi-square test (*i.e.*, tended to occur in a sequence; GSEQ for Windows version 4.1.2 software; Sackett, 1979, 1980; Bakeman and Quera, 1995; Bakeman and Gottman, 1997). A Bonferroni-adjusted alpha level was used to assess significance (alpha = 0.000142 = 0.05/352 comparisons; 352 chi-square tests = 44 sequences \times 2 γ \times 2 treatments \times 2 genders). We also tested the effect of flow on the mean frequency of occurrence of each Reproductive Behavior Sequence/lag/gender/treatment combination using the same nonparametric multi-response permutation procedure described above, and a Bonferroni-adjusted alpha level to assess significance (n = 18; alpha = 0.000568 = 0.05/88 comparisons; 88 permutation tests = 44 sequences \times 2 genders).

Finally, we also examined the 12 sequences that only contained the three Pair-Based Reproductive Behaviors, designating, these as Pair-Based Only Reproductive Behavior Sequence Trios (Carousel-Embrace-Jostle, Embrace-Carousel-Jostle, etc.). We tested the effect of flow on the mean frequency of occurrence of each again using the nonparametric multi-response permutation procedure and a Bonferroni-adjusted alpha level to assess significance (alpha = 0.002083 = 0.05/24 comparisons; 24 permutation tests = 12 sequences \times 2 genders).

RESULTS

INDIVIDUAL BEHAVIORS

Overall, our Neosho madtoms spent little time performing Reproductive Behaviors (Table 2) and spent the vast percentage of time Swimming or Resting (unpubl. data). Nest Building was always performed substantially more often by males (Table 2). Because most of the separate Reproductive Behaviors were usually performed by the fish together as a pair, the performance parameter values are similar for both genders (Table 2). For males and females, Jostle was generally the most frequently performed behavior (Table 2). Both Jostle and Embrace were generally performed with the highest percentage of time and mean event duration.

Flow effects on individual behaviors.—Because the BLOSSOM software precluded the simultaneous testing of both year and flow effects, we tested first for the year effect. Females were significantly more active (*i.e.*, exhibited greater frequencies of occurrence and percentages of time spent performing various behaviors) in 1999 than in 2000 (Table 3). We negated the significant year effect using an alignment procedure (Mielke and Iyer, 1982), which used each behavior/parameter/gender/year combination average and subtracted it from each respective behavior/parameter/gender observation within that year. This alignment procedure successfully removed the year influence for both males and females (Table 3), allowing the adjusted behavior/parameter observations to be compared between treatments with both years combined. Post-alignment, male Nest Building was the only behavior significantly affected by water flow (Table 3), its' frequency of occurrence, percentage of time spent and mean event duration all being significantly lower in flow than in non-flow aquaria. Female Neosho madtoms also performed Nest Building behaviors, although the associated parameters showed no differences between the treatments (Tables 2, 3).

Using the same statistical procedure, we also examined only the 5-min periods wherein at least one Reproductive Behavior was performed, thereby eliminating most of the zeros in the original data set. The results (data not shown) were consistent with those above, except that the mean event duration of male Nest Building behavior was not significantly different between the flow and non-flow aquaria, and the frequency of occurrence of female Carousel behavior was significantly lower in the flow treatment.

BEHAVIOR SEQUENCES

Of the 352 possible male and female Reproductive Behavior Sequences, 109 male and 74 female sequences yielded expected occurrence values of 5 or more, necessary criterion for valid chi-square testing (Bakeman and Quera, 1995). Fifty-one male and 39 female Reproductive Behavior Sequences yielded significant chi-squared test results (7 out of the 12 sequences that were different between males and females were Nest Building Reproductive Behavior Sequences due to the lack of Nest Building by females). Because three of the four Reproductive Behaviors were Pair-Based, the results for each gender were very similar where 46 male and 37 female Reproductive Behavior Sequences were performed significantly more than expected. Albers (2001) provides details regarding all the Reproductive Behavior Sequences.

Seven out of the 51 significant male Reproductive Behavior Sequences were Nest Building Reproductive Behavior Sequences. For male Neosho madtoms under both flow conditions, the performance of Nest Building was followed most often by more Nest Building (3 significant sequences; lag 2: 1999 Non-Flow $X^2 = 454.66$, $df = 1$, $P < 0.0001$, 1999 Flow $X^2 = 265.16$, $df = 1$, $P < 0.0001$; lag 3: 1999 Flow $X^2 = 16.75$, $df = 1$, $P = 0.0001$). All four of the

TABLE 2.—Male and female Neosho madtom Reproductive Behavior parameters for 1999 and 2000 under flow and non-flow conditions for an average 5-min period. Entries are mean \pm standard deviation

Year/Treatment	Behavior	Frequency of occurrence (#)		Percentage of time (%)		Event duration (s)	
		Male	Female	Male	Female	Male	Female
1999 Non-Flow (n = 6)	Carousel	0.59 \pm 0.43	0.59 \pm 0.43	2.83 \pm 1.94	2.86 \pm 1.96	3.14 \pm 2.48	3.15 \pm 2.49
	Embrace	0.35 \pm 0.28	0.34 \pm 0.28	3.01 \pm 3.76	3.02 \pm 3.78	4.65 \pm 5.99	4.69 \pm 6.10
	Jostle	0.63 \pm 0.42	0.62 \pm 0.42	2.27 \pm 1.51	2.23 \pm 1.52	2.62 \pm 2.00	2.61 \pm 2.01
	Nest Building	0.73 \pm 0.45	0.08 \pm 0.11	3.91 \pm 2.44	0.49 \pm 0.69	4.96 \pm 2.61	0.96 \pm 1.34
1999 Flow (n = 6)	Carousel	0.44 \pm 0.48	0.44 \pm 0.48	2.54 \pm 2.61	2.53 \pm 2.59	2.85 \pm 2.76	2.84 \pm 2.75
	Embrace	0.28 \pm 0.29	0.28 \pm 0.29	3.37 \pm 3.90	3.36 \pm 3.88	5.41 \pm 6.16	5.38 \pm 6.12
	Jostle	0.48 \pm 0.42	0.47 \pm 0.41	2.46 \pm 1.62	2.46 \pm 1.58	3.09 \pm 1.82	3.11 \pm 1.72
	Nest Building	0.23 \pm 0.20	0.06 \pm 0.03	1.54 \pm 0.94	0.41 \pm 0.26	2.87 \pm 1.27	0.83 \pm 0.45
2000 Non-Flow (n = 3)	Carousel	0.28 \pm 0.33	0.28 \pm 0.33	0.79 \pm 1.04	0.83 \pm 1.12	1.33 \pm 1.86	1.41 \pm 2.00
	Embrace	0.22 \pm 0.28	0.22 \pm 0.28	2.25 \pm 3.19	2.24 \pm 3.17	4.29 \pm 6.07	4.24 \pm 5.99
	Jostle	0.67 \pm 0.78	0.67 \pm 0.77	3.84 \pm 4.32	3.79 \pm 4.24	3.92 \pm 4.28	3.90 \pm 4.24
	Nest Building	0.21 \pm 0.25	0.06 \pm 0.06	1.24 \pm 1.42	0.38 \pm 0.35	1.86 \pm 2.31	0.73 \pm 0.64
2000 Flow (n = 3)	Carousel	<0.01 \pm <0.01	<0.01 \pm <0.01	0.01 \pm 0.01	0.01 \pm 0.01	0.02 \pm 0.03	0.02 \pm 0.03
	Embrace	<0.01 \pm <0.01	<0.01 \pm <0.01	0.01 \pm 0.01	0.01 \pm 0.01	0.02 \pm 0.03	0.02 \pm 0.03
	Jostle	0.05 \pm 0.02	0.05 \pm 0.02	0.20 \pm 0.15	0.20 \pm 0.15	0.38 \pm 0.28	0.38 \pm 0.28
	Nest Building	0.01 \pm 0.01	<0.01 \pm <0.01	0.02 \pm 0.03	<0.01 \pm <0.01	0.05 \pm 0.08	<0.01 \pm <0.01

TABLE 3.—Results of the permutation tests examining the effect of year and flow treatments on male and female Neosho madtom Reproductive Behaviors. Entries are P-values ($n = 18$, α level = 0.025)

Year effect or Treatment effect by Behavior Sequence	Frequency of occurrence (#)		Percentage of time (%)		Mean event duration (s)	
	Male	Female	Male	Female	Male	Female
Year, Pre-Alignment						
all behaviors except Resting	0.09	0.01 ^b	0.09	0.02 ^a	0.08	0.03
Year, Post-Alignment						
all behaviors except Resting	0.99	0.76	0.98	0.83	1	0.85
Treatment, Post-Alignment Reproductive Behaviors						
Nest Building	0.01 ^c	0.30	0.01 ^c	0.51	0.01 ^c	0.39
Pair-Based						
Carousel	0.38	0.39	0.53	0.52	0.47	0.47
Embrace	0.49	0.50	0.96	0.96	0.91	0.91
Jostle	0.21	0.20	0.44	0.45	0.68	0.68

^a Indicates summer 1999 value significantly exceeded summer 2000 value

^b Indicates summer 2000 value significantly exceeded summer 1999 value

^c Indicates non-flow treatment value significantly exceeded flow treatment value

significant Nest Building Reproductive Behavior Sequences that involved Nest Building and one Pair-Based Reproductive Behavior occurred less frequently than expected (all occurred in the 1999 Non-Flow group; lag 1: Nest Building-Carousel $X^2 = 21.44$, $df = 1$, $P < 0.0001$, Nest Building-Embrace $X^2 = 31.26$, $df = 1$, $P < 0.0001$, Embrace-Nest Building $X^2 = 24.60$, $df = 1$, $P < 0.0001$; lag 2: Nest Building-Jostle $X^2 = 16.77$, $df = 1$, $P < 0.0001$). None of the 10 female Nest Building Reproductive Behavior Sequences expected at least 5 times were significantly different than expected (Bonferroni-adjusted alpha level of 0.000142; P-value range 0.0049–0.7102).

Of the male Reproductive Behavior Sequences that were performed significantly more than expected, 93.5% involved only the Pair-Based Reproductive Sequences, indicating the Pair-Based Reproductive Behaviors occurred in conjunction with one another (43 out of 46 sequences; all P-values < 0.0001). Only 5 out of the 43 male Reproductive Behavior Sequences that were performed significantly more than expected were not significant for the female (lag 2: 1999 Non-Flow Embrace-Carousel $X^2 = 12.37$, $df = 1$, $P = 0.0006$; lag 3: 1999 Non-Flow Jostle-Jostle $X^2 = 5.59$, $df = 1$, $P = 0.0172$, Embrace-Jostle $X^2 = 5.38$, $df = 1$, $P = 0.0193$, Embrace-Embrace $X^2 = 9.54$, $df = 1$, $P = 0.0022$, 2000 Non-Flow Embrace-Jostle $X^2 = 12.16$, $df = 1$, $P = 0.0006$). These five sequences are not involved in the two most performed Pair-Based Only Reproductive Behavior Sequence Trio, consequently, our detailing of the males' reproductive behavior patterns below is also applicable to the females.

Irrespective of treatment, the most frequently performed Pair-Based Only Reproductive Behavior Sequence Trio was Jostle-Carousel-Embrace (211 out of 929 total performances). When a male Neosho madtom performed a Jostle-Carousel lag 1 sequence (426 performances), 49.5% (or 211) of the times it was followed by Embrace. Additionally, for the Jostle-Embrace lag 2 sequence (212 performances), 99.5% (or 211) of the times the intervening behavior was Carousel (212 performances of the Jostle-Embrace lag 2 sequence). Irrespective of treatment, the second most frequent Pair-Based Only

TABLE 4.—Results of the permutation tests examining the effect of year and flow on the frequency of male and female Neosho madtom Reproductive Behavior Sequences. Entries are P-values ($n = 18$, alpha level = 0.000568). NP Indicates a sequence of which was that combination was not possible, given how we scored behaviors

Year effect or Treatment effect by Behavior Sequence	Lag 1		Lag 2		Lag 3		
	Male	Female	Male	Female	Male	Female	
Year, Pre-Alignment							
all behavior sequences combined	0.12	0.06	0.05	0.08	0.07	0.08	
Year, Post-Alignment							
all behavior sequences combined	0.14	0.15	0.19	0.20	0.24	0.18	
Treatment, Post-Alignment Reproductive Behavior Sequences							
Nest Building Sequences							
Nest Building	Carousel	0.22	0.05	0.07	0.46	0.21	0.22
Nest Building	Embrace	0.64	0.64	0.28	0.64	0.06	0.36
Nest Building	Jostle	0.01	0.40	0.17	0.32	0.04	0.54
Nest Building	Nest Building	NP	NP	0.04	0.73	0.38	0.64
Carousel	Nest Building	0.09	0.65	0.05	0.83	0.11	0.44
Embrace	Nest Building	0.02	0.64	0.22	0.26	0.64	0.65
Jostle	Nest Building	0.04	0.50	0.03	0.05	0.03	0.09
Pair-Based Sequences							
Carousel	Carousel	NP	NP	0.41	0.39	0.33	0.51
Carousel	Embrace	0.56	0.56	0.95	0.91	0.57	0.45
Carousel	Jostle	0.26	0.26	0.21	0.30	0.10	0.07
Embrace	Carousel	0.67	0.74	0.45	0.51	0.54	0.89
Embrace	Embrace	NP	NP	0.76	0.75	0.37	0.42
Embrace	Jostle	0.30	0.09	0.26	0.44	0.41	0.51
Jostle	Carousel	0.49	0.32	0.36	0.35	0.15	0.19
Jostle	Embrace	0.81	0.80	0.64	0.68	0.81	0.84
Jostle	Jostle	NP	NP	0.17	0.16	0.31	0.38

Reproductive Behavior Sequence Trio was Carousel-Embrace-Jostle (170 out of 929 total performances). When a male Neosho madtom performed a Carousel-Embrace lag 1 sequence (451 performances), 37.7% (or 170) of the times it was followed by Jostle. Additionally, for the Carousel-Jostle lag 2 sequence (209 performances), 81.4% (or 170) of the times the intervening behavior was Embrace.

Flow effects on sequences.—Due to the marginally significant year effects for male and female sequences (Table 4), we used the same alignment procedure described above to test for flow effects on both the Reproductive Behavior Sequences and the Pair-Based Only Reproductive Behavior Sequence Trios. Post-alignment, occurrence of the male and female Reproductive Behavior Sequences did not differ between the non-flow and flow treatments using a Bonferroni-adjusted alpha level (Table 4), as was the case for the male and female Pair-Based Only Reproductive Behavior Sequence Trios (Bonferroni-adjusted alpha level of 0.002083; P-value range 0.27–0.91).

DISCUSSION

Neosho madtom Reproductive Behaviors were generally uncommon in their occurrence. The only other study to quantify madtom behaviors, Bulger (2002a), also observed low levels

of reproductive behaviors. The Pair-Based Reproductive Behaviors were performed most often (Carousel, Embrace, Jostle), followed by Nest Building. Carousel and/or Embrace have been observed in other madtom species (Bowen, 1980; Fitzpatrick, 1981; Stoeckel, 1993; Chan, 1995), although, Jostle has only been observed in Neosho madtoms (Bulger *et al.*, 2002a). Male Neosho madtoms were the primary nest builders with female Neosho madtoms performing Nest Building at a much lower level. This observation parallels previous findings for brown madtoms (Chan, 1995), brindled madtoms (Bowen, 1980), freckled madtoms (Fitzpatrick, 1981) and Neosho madtoms (Bulger *et al.*, 2002a), where both genders have been observed performing nest building behaviors. However this is contrary to the majority of previous madtom studies, where only male madtom nest building was observed (Burr and Stoeckel, 1999).

In the flow treatment, all of the male Nest Building behavior parameters were significantly reduced (frequency of occurrence, percentage of time spent and mean event duration). Because Nest Building involves energetically costly movements like nudging or carrying large stones in the mouth, relative to their body size, heightened water flows that further elevate energy expenditures during Nest Building are of concern from multiple perspectives. First, the nest site is occupied for an extended period: male madtoms spend at least 3 wk at a nest, from site selection to spawning to departure of young (Chan, 1995; Bulger *et al.*, 2002b). Second, nests provide shelter from predators for the spawning pair and eggs/young (Mayden *et al.*, 1980; Mayden and Burr, 1981) and, when disturbed, the eggs or fry are immediately consumed by predators or displaced by the current (Burr and Dimmick, 1981; Mayden and Burr, 1981; Walsh and Burr, 1985). In either case, the lower quality of a nest fashioned with less Nest Building may result in reduced reproductive success.

No previous work has addressed the sequencing of madtom Reproductive Behaviors (Burr and Stoeckel, 1999). Our finding that the Jostle-Carousel-Embrace and Carousel-Embrace-Jostle Reproductive Behavior sequences were so prevalent in their occurrence broadens our appreciation of madtom reproduction. Even though Carousel and Embrace have previously been shown to be prominent components of reproduction in other madtom species (Bowen, 1980; Fitzpatrick, 1981; Stoeckel, 1993), our study demonstrated the linkage between these behaviors and the Jostle behavior. Biologically, these behaviors appear to be important for madtom mate assessment (Jostle) and positioning the pair for the spawning act (Carousel and Embrace).

The flow-related reduction in frequency of occurrence of Nest Building discussed above suggested that effects might be seen in our behavior sequence analyses. However, the majority of Nest Building Reproductive Behavior Sequences that involved one Pair-Based Reproductive Behavior occurred at frequencies below what were expected. This lack of a detectable flow effect on Nest Building Reproductive Behavior Sequences is likely a consequence of the temporal organization of spawning behavior in Neosho madtoms. To explain, nest building typically occurs before egg deposition (Fitzpatrick, 1981; Chan, 1995), and our analyses confirmed that it was unlikely to immediately precede or follow any of the Pair-Based Reproductive Behaviors. Consequently, detecting a reduction in the occurrence of Nest Building Reproductive Behavior Sequences that involved Pair-Based Reproductive Behaviors was improbable, given that we only considered sequences that were a maximum of four acts long (*i.e.*, lag 3).

Whereas dams typically hamper fish reproduction by impeding migration (Li *et al.*, 1987), this is less relevant to madtoms since they are largely sedentary (Burr and Stoeckel, 1999). Instead, madtom reproductive success is more apt to be negatively impacted by dam- or flood-related hydrologic changes that occur during the spawning season, similar to other stream-nesting fish species like salmonids, centrarchids, cyprinids and catostomids (Seegrist

and Gard, 1972; Noltie and Keenleyside, 1986; Pearsons *et al.*, 1992; Lukas and Orth, 1993; Jennings and Philipp, 1994). Since construction of the John Redmond Dam the chance of flooding during the Neosho spawning season has increased due to the delayed maximum annual discharge of the Neosho River (Wildhaber *et al.*, 2000). Such high discharges during the spawning season are apt to have deleterious effects on Neosho madtoms constructing and maintaining their nests. One solution to this problem might be to manipulate reservoir discharges to duplicate the historic timing of peak flows (*i.e.*, earlier in the year), in addition to maintaining the yearly minimal flows and annual variability suggested by Wildhaber *et al.* (2000).

In conclusion, we found evidence that elevated water flows negatively affect Neosho madtom reproductive behavior. However, our study addressed only the relative impacts of moderate versus absent water flows on Neosho madtom reproductive behavior. We recognize that Neosho madtoms in spawning condition have been found at substantially higher velocities than we employed [*i.e.*, up to 71 cm/s at the substrate (Bulger and Edds, 2001)]. Consequently, we suggest that future research extend the range of water flows examined and involve in situ studies at the population level. This would broaden our understanding of how differing hydrologic regimes affect Neosho madtoms.

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