Functional constraints on nest characteristics of pebble mounds of breeding male hornyhead chub *Nocomis biguttatus*

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Breeding male hornyhead chub *Nocomis biguttatus* constructed nests in areas with relatively high but less than maximum flow rate and greater than average water depth. Nests comprised c. 3000 pebbles for a total mass of 11 kg. Males selected pebbles of smaller diameter but higher density than pebbles in the immediate vicinity. Thus, nests balanced the risk of mound erosion and energetic cost of nest construction with the benefits of protection from egg predators and a stable internal flow rate for oxygenation. These data help establish environmental management goals for the conservation of *N. biguttatus* and the lotic ecosystems dependent upon them.

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Key words: flow; functional constraints; nest construction; *Nocomis*; pebble size.

INTRODUCTION

The degree to which abiotic factors shape the evolution of behaviour and life history is often governed by trade-offs. In species that construct nests, the location and quality of nests determine reproductive success because of the often narrow sub-set of available environmental variables necessary for optimal offspring development. For example, in a study on marsh-nesting birds (Storey *et al.*, 1988), willets *Tringa semipalmata* selected a narrow band of habitat bound by risk of flooding and grass height. High ground has low flood risk and low ground has tall grass that affords nest crypticity. In another study, piping plovers *Charadrius melodus* preferentially select white pebbles over dark pebbles to form their nest (Mayer *et al.*, 2009). White pebbles reflect heat and reduce heat stress on eggs when eggs are not being actively incubated. This reduction in heat stress is traded-off against increased visual conspicuousness of the nest. In this study, ecological trade-offs in nest-building behaviour by male hornyhead chub *Nocomis biguttatus* (Kirtland) was studied.

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Nocomis biguttatus are medium-sized stream-dwelling cyprinids found throughout the prairie region of North America (Lachner, 1952). Males build a doughnut-shaped nest, court and spawn with females, then pile gravel on top of the eggs (Fig. 1), creating dome-shaped mounds of pebbles that serve as egg incubators (Lachner, 1952; Vives, 1990; Maurakis et al., 1991). Fertilized eggs occupy the interstitial voids between pebbles where they are safe from egg predators. Males build the nests in areas of fast current so that water percolates through the pebble mound and oxygenates the developing eggs.

Nest structure and construction behaviour are described in detail by Vives (1990) and Maurakis et al. (1991). Energy investment in nest construction is significant. For example, males in the closely related congener Nocomis micropogon (Cope) construct mounds comprising thousands of individually placed pebbles, averaging $2.5 \text{ cm} \times 2.5 \text{ cm} \times 3.2 \text{ cm}$ with an aggregate underwater mass of 40 kg (Reighard, 1943; Lachner, 1952). Pebbles are transported for an average of 4 m, culminating in a total pebble-carrying distance of $>25$ km to complete one nest (Reighard, 1943). This is a remarkable feat, achieved in few days by a fish only 12–17 cm in standard length ($L_s$). Nocomis biguttatus are slightly smaller in size and as a result their nests are smaller and use smaller gravel (Maurakis et al., 1991).

Nest construction in N. biguttatus presents males with the challenge of finding optimal solutions to several pairs of opposing requirements simultaneously. The first trade-off males must make is to select a location with optimal current conditions. Current speed must be fast enough to afford percolation through the nest for oxygenation of the eggs and to preclude silt build-up in interstitial spaces that would asphyxiate the eggs, but not so fast that percolating currents flush eggs from the mound or erode pebbles from the mound and expose eggs to predators. The second trade-off a male must make is to select pebbles that are of the right diameter. Pebble diameter determines the porosity of the pebble mound and therefore the percolation rate. Pebble diameter also determines pebble mass and resistance of the mound to
erosion. Pebbles must be small enough to fit within the gape of the male’s mouth, and not larger than necessary to minimize energetic costs to the male. The final trade-off males must make is the constituent material of each pebble. Pebbles available for construction vary in density. Pebbles of dense material will be relatively more resistant to erosion than pebbles of less dense material.

The nests of *N. biguttatus* are used facultatively as a spawning substratum by other fish species, known collectively as nest associates, and *N. biguttatus* may accordingly be considered as a keystone species (Mills *et al.*, 1993) that shape structure and species stability in lotic ecosystems (Wallin, 1989; Vives, 1990; Johnston & Page, 1992). Anthropogenic modifications of stream habitats endanger populations of *N. biguttatus* and the communities that depend on them (Mammoliti, 2002; W. J. Miller, D. E. Rees, R. J. Carr & D. S. Berube, unpubl. data). In this study, the current speed, water depth and pebble quality used in *N. biguttatus* nests are described to gain a better understanding of the environmental needs of *N. biguttatus* and future conservation of the habitat required for this species to thrive.

**MATERIALS AND METHODS**

**STUDY SITE**

Data were collected on 19 June 2007 from 13 nests in the headwaters of the Mississippi River in Itasca State Park in central Minnesota (47° 14’ 40” N; 95° 12’ 42” W). Nests were surveyed along a 200 m stretch of the river downstream from the culvert on Wilderness Drive, located c. 500 m downstream of the river’s origin at the outlet from Lake Itasca. Within the protected environs of a state park, the Mississippi River is a relatively pristine creek characterized by shallow, clear, steady flowing water over a sandy, gravelly substratum ranging from 4 to 10 m wide, and <0.5 m in depth during the time of the sampling. Riparian vegetation varied from overhanging mixed deciduous and coniferous forest to more open regions characterized by riparian patches of reeds and bulrushes.

**PROTOCOL**

River cross-sectional transects were conducted coincident with each nest, along which water current speed and water depth were recorded at 500 mm intervals across the width of the river. Current (m s\(^{-1}\)) was measured using a standard current metre positioned 100 mm above the substratum at each sample point. Current speeds at nests were measured in front of the nest. In addition, position of the nest, local depth and current data were noted. Nest dimensions were measured to the nearest mm. Twenty-five pebbles were collected arbitrarily from each nest and another 25 pebbles were sampled from the area immediately adjacent (<300 mm) to the nest at the same depth and current conditions. Measurements of minimum and maximum diameters were taken for each pebble using callipers. These measurements were averaged to produce an estimate of mean radius, from which pebble volume was calculated using \( V = \frac{1}{3} \pi r^3 \) using a method adapted from Dürr (1994). The aggregate mass of the 25 pebbles from each nest was weighed on a portable battery-operated electronic balance.

Water percolation rates through the nest were determined by injecting 1 ml of dye (composed of water and green food colouring) into the front, upstream edge of the nest, centred between the near and far edges of the nest, halfway between the substratum and the top of the nest. The time from injection to appearance of the dye at the downstream edge of the nest was recorded using a stopwatch. The distance the dye travelled was measured from the injection site to the downstream reappearance site. This procedure was repeated three times for each nest and averaged.
Table I. Mean ± s.e. values for nest dimensions, current speed, rate of percolation through the nest, nest depth and pebble quality for 25 pebbles from each nest and 25 pebbles for the area surrounding each nest. Thirteen nests were measured. Statistics are for paired t-tests.

<table>
<thead>
<tr>
<th>Nest dimensions (mm)</th>
<th>Width</th>
<th>Length</th>
<th>Height</th>
</tr>
</thead>
<tbody>
<tr>
<td>Nest descriptors</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>In front of nest</td>
<td>Transect average</td>
<td></td>
</tr>
<tr>
<td>Current (m s$^{-1}$)</td>
<td>0.380 ± 0.020</td>
<td>0.290 ± 0.014</td>
<td>3.40</td>
</tr>
<tr>
<td>Water depth (m)</td>
<td>0.354 ± 0.014</td>
<td>0.273 ± 0.006</td>
<td>5.45</td>
</tr>
<tr>
<td>Percolation rate (m s$^{-1}$)</td>
<td>0.022 ± 0.003</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Pebble descriptors</td>
<td>Nest pebbles</td>
<td>Area pebbles</td>
<td></td>
</tr>
<tr>
<td></td>
<td>t</td>
<td>d.f.</td>
<td>P</td>
</tr>
<tr>
<td>Diameter (mm)</td>
<td>13.6 ± 0.6</td>
<td>38.7 ± 1.6</td>
<td>13.54</td>
</tr>
<tr>
<td>Mass (g)</td>
<td>3.59 ± 0.31</td>
<td>73.33 ± 8.23</td>
<td>9.28</td>
</tr>
<tr>
<td>Density (g cm$^{-3}$)</td>
<td>72.52 ± 4.24</td>
<td>59.13 ± 6.73</td>
<td>3.34</td>
</tr>
</tbody>
</table>

*One outlier was removed because it exceeded 7 s.d. of the mean ratio of area pebble density and nest pebble density.

RESULTS

Mean ± s.e. transect width was 6.07 ± 0.75 m, mean transect depth was 349 ± 37 mm and mean current speed was 0.291 ± 0.018 m s$^{-1}$ (Table I). The estimated discharge from the Mississippi River on the day these data were collected was 0.70 ± 0.023 m$^3$ s$^{-1}$ ($n$ = 7 transects). Water temperature at 1100 hours on 19 June was 21°C. Nests were located along each transect in areas with above-average flow rate and deeper than average depth (Table I and Fig. 2). Minimum current speed for nest building to occur was 0.270 m s$^{-1}$ and the maximum current speed in which a

Fig. 2. Current and depth readings at 0.5 m intervals across seven transects of the Mississippi River where *Nocomis biguttatus* nests occurred: O, all transect data; ▲, current and depth in front of 13 nests.

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nest was observed was 0.470 m s\(^{-1}\). Locations of maximum flow rates were avoided. Nest site selection seemed to be constrained more by current speed than by the water depth because the range of current speeds where nests occurred was narrower than the range of water depths where nests occurred (Fig. 2).

On average, nests of *N. biguttatus* measured 350 mm × 260 mm × 50 mm (raised above streambed surface) for an estimated volume of 4.2 l, comprising c. 3000 pebbles and a total (above water) mass of about 11 kg. Males selected pebbles that were significantly smaller in diameter than the average pebbles in the immediate surrounding area (Table I and Fig. 3). Pebble diameter was not correlated with current speed in front of the nest \( (F_{1,11}, \ P > 0.05) \). Density of pebbles selected for nest construction was typically 23% greater than density of random pebbles in the immediate surrounding area (Table I). The rate of water percolation through the pebble mound, as revealed by dye tests, was 22 mm s\(^{-1}\) and was not correlated with current speed in front of the nest \( (F_{1,10} = 1.13, \ P > 0.05) \).

**DISCUSSION**

*Nocomis biguttatus* nests balance three conflicting demands: transportation (pebble diameter and density), nest location (nest erosion or percolation) and percolation (risk of siltation or benefit of oxygenation). Pebble diameter in nests was significantly smaller than those in the surrounding area, allowing each male to carry them in his mouth and to create a nest with small interstitial voids to preclude access by egg predators. Small pebble size limited the maximum water velocity in which nests could be located. To partially diminish the risk of nest erosion, males selected pebbles that were of greater than average density. Consequently, the range of pebble sizes used in
nest construction was narrowly confined between the minimal size to withstand current erosion and the maximum size that could be carried. This narrow range of values may explain why there was no significant relationship between current speed at the nest and pebble size. These results concur with those of Vives (1990) on *N. biguttatus* in Allequash Creek, Wisconsin. In that study, nest dimensions were larger (500 mm × 400 mm × 64 mm), and nests were found in areas with greater than average current (0.18 m s⁻¹, low compared with the present 0.38 m s⁻¹) and greater than average depth (0.43 m, deeper than 0.35 m observed in the current study). Thus, current speed and water depth at *N. biguttatus* nests vary among populations and may reflect differences in stream morphology. Comparing more broadly, current speed in front of the nest in the current study ranged from 0.250 to 0.500 m s⁻¹, remarkably similar to current speeds preferred by salmonids for redd construction. Most redds are built in currents ranging from 0.300 to 1.000 m s⁻¹ using gravel of 20–30 mm in diameter (Crisp & Carling, 1989).

Notably, there was no significant correlation between current speed in front of the nest and percolation rate through the nest. This may reflect that current velocity next to the substratum is always low and independent of the current speed in the water column. Alternatively, percolation rates may be dictated primarily by pebble diameter and the porosity of the interstitial voids they create.

Gravel grain size was not recorded by Vives (1990) but Maurakis et al. (1991) reported that nests made by *N. biguttatus* contained more small pebbles (6.0 mm), equal number of medium-sized pebbles (11.3 mm) and fewer large pebbles (23.0 mm) than its congeners, *Nocomis leptcephalus* (Girard) and *Nocomis micropegon* (Cope), probably reflecting the smaller body size and mouth structure of *N. biguttatus*.

Egg survival was not recorded in this study. The presence of egg predators may exert an influence on pebble size in that small interstitial spaces would make access to eggs more difficult and lower the risk of egg wash out. In sand gobies *Pomatoschistus minutus* (Pallas), the presence of egg predators (Lissåker & Kvarnemo, 2006) and potential cuckoldors (Svensson & Kvarnemo, 2003) causes nest-building males to reduce the size of nest openings. Unlike *P. minutus*, male *Nocomis biguttatus* (Cope) do not fan their eggs to oxygenate them. Instead, they use ambient water currents to create water flow over the eggs. Whereas *P. minutus* trade-off predation and cuckoldry risks with higher parental investment in fanning behaviour (Jones & Reynolds, 1999a; Svensson & Kvarnemo, 2003; Lissåker & Kvarnemo, 2006), *N. biguttatus* may choose small pebble sizes to exclude predators at the risk of egg asphyxiation by siltation.

In some nest-building species, females use nest architecture as an indicator of male mate quality (Jones & Reynolds, 1999b; Barber et al., 2001; Östlund-Nilsson, 2001; Östlund-Nilsson & Holmlund, 2003). Jones & Reynolds (1999b) hypothesized that female common gobies *Pomatoschistus microps* (Krøyer) favour nests with ornamentation because ornamentation confers camouflage benefits to the nest. In three-spined stickleback *Gasterosteus aculeatus* L. nest neatness is correlated with male immuno-competence and thereby serves as an honest indicator of male quality (Barber et al., 2001). In another study, proteinaceous kidney secretions (tangspiggin) used by male 15-spined stickleback *Spinachia spinachia* (L.) to glue the nest together are also an honest measure of a male energy stores (Östlund-Nilsson, 2001). An added benefit to nests with copious tangspiggin is that the adhesive quality of tangspiggin causes
particles to adhere to the nest surface, thereby camouflaging it from visual predators (Östlund-Nilsson, 2001). The degree, if any, to which female N. biguttatus base their spawning decisions on nest location and quality is not known. In Baya weaver birds Ploceus philippinus, nest location is determined through male–male competition, whereas nest quality is an indicator of male skill at nest making (Quader, 2006). Both may be important mate choice criteria for female N. biguttatus. For example, in an analogous system, stone carrying behaviour for nest construction by male black wheatears Oenanthe leucura is correlated with early laying date and high nest success (Soler et al., 1996).

Studies on salmonids show that egg burial depth and redd size are affected by body size (Van den Berghe & Gross, 1984), water velocity (Fraser, 1975) and gravel composition (Burner, 1951). No data on male size nor reproductive success associated with nest location and quality documented are available in the current study.

The data presented here help define the baseline description of the natural breeding ecology of this keystone species. Nocomis biguttatus are obligate lotic fish that require flowing water with low silt load and bare gravel substratum. Habitat loss due to abstraction for irrigation or water storage is a threat to N. biguttatus (W. J. Miller, D. E. Rees, R. J. Carr & D. S. Berube, unpubl. data). Impoundments alter the natural hydrograph of flow and temperature that cue N. biguttatus reproduction. Habitat fragmentation by impounding flowing water restricts fish access to refuge in lower reaches during times of low flow and access to spawning habitat during times of high flow (Mammoliti, 2002; W. J. Miller, D. E. Rees, R. J. Carr & D. S. Berube, unpubl. data). Moreover, habitat fragmentation restricts gene flow among components of a metapopulation and significantly increases the risk of local extirpation. A third threat to N. biguttatus is habitat modification through stream channelization, scouring or sedimentation (Crisp et al., 1984; W. J. Miller, D. E. Rees, R. J. Carr & D. S. Berube, unpubl. data). As a consequence of anthropogenic alteration of lotic habitat, the range of N. biguttatus has declined in the south-western part of its range, leading to its designation as a sensitive species by the U. S. Department of Agriculture Forest Service Rocky Mountain Region (W. J. Miller, D. E. Rees, R. J. Carr & D. S. Berube, unpubl. data). The conservation status of N. biguttatus population in Minnesota is under pressure from habitat degradation, climate change and loosely regulated harvest by the bait industry (Johnson et al., 2005; K. P. Schmidt, unpubl. data). Population data in Minnesota are often anecdotal (K. P. Schmidt, unpubl. data). Basic population data are needed to determine whether this species should be designated as a species of greatest conservation need. Resource managers can use N. biguttatus as a tool for the conservation of natural waterways (Heithaus & Grame, 1997) because a thriving population of N. biguttatus could predict ecosystem stability and biodiversity.

Nocomis biguttatus nests are of great interest on scientific merit because they are used as a spawning substratum by a range of nest associating fish species (Lachner, 1952; Wallin, 1989; Vives, 1990; Johnston & Page, 1992). Nocomis biguttatus are considered to be a candidate keystone species because of their role in shaping community structure (Vives, 1990). Co-evolutionary and ecological questions relating to ecosystem structure and the evolution of the mating ecology of many non-game lotic fish species await further investigation.

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References


