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Mutualism or parasitism: Partner abundance affects host fitness in a fish reproductive interaction

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Abstract

1. Mutualisms are ubiquitous in nature but are understudied in freshwater ecosystems. Mutualisms can be unstable, shifting to commensal or even negative outcomes with context. Quantifying context dependency in mutualisms is critical for understanding how biotic interactions will shift along disturbance gradients in freshwater systems.
2. A common reproductive interaction among stream fishes, *nest association* occurs when individuals of one species spawn in nests constructed by a host fish. Hosts benefit from a dilution effect: high proportions of associate eggs decrease the odds of host brood predation. Thus, partner abundance can be an important source of biotic context influencing the outcome of an association.
3. We conducted a large in situ experiment manipulating abundance of partner yellowfin shiner (Leuciscidae: *Notropis lutipinnis*) (absent, low, high) at constant abundance of host bluehead chub (Leuciscidae: *Nocomis leptocephalus*), and quantified chub reproductive success using genetic tools.
4. Evidence suggests that the nest association switched from mutualistic to parasitic outcomes as shiner abundance decreased. Chub reproductive success was highest at high shiner abundances. However, chub reproductive success was actually higher in the complete absence of shiners than at low shiner densities.
5. This study shows that outcomes of biotic interactions in freshwater systems are context-dependent, and that partner abundance can be a key source of context-dependency in nest associations. We encourage future studies on freshwater mutualisms, which are thus far largely overlooked, relative to competition and predation.

KEYWORDS
context dependency, freshwater, nest association, *Nocomis*

1 | INTRODUCTION

Positive biotic interactions such as mutualism and commensalism are important drivers of population abundance and community structure (Boucher, James, & Keeler, 1982; Bruno, Stachowicz, & Bertness, 2003), but are understudied relative to negative interactions (competition, predation, and parasitism; Bronstein, 1994a, 1994b, 2009). An important feature of positive interactions is that their outcomes are rarely static: they can switch from being positive to negative with changing context (Bronstein, 1994b; Noë & Hammerstein, 1995).

Context-dependency may arise from reduced interaction strength, relative to antagonism (Moore, 2006; Sachs & Simms, 2006; but see Frederickson, 2017 for an alternative perspective), or complexity of resource transfers among participants (Chamberlain, Bronstein, & Rudgers, 2014). Context dependency may also arise from changing abiotic (i.e., the environment in which the interaction occurs; Lee, Kim, & Choe, 2009; Thomas, Creed, & Brown, 2013) or biotic (i.e., identity, traits or abundance of participants; Brown, Creed, Skelton, Rollins, & Farrell, 2012) factors. Understanding how context dependency alters the costs and benefits of biotic interactions will improve general ecological models and provide better tools for predicting biological responses to environmental change.

Mutualisms and context dependency are understudied in freshwater systems; most of our knowledge on the subject comes from studies of terrestrial plants (He & Bertness, 2014). In fact, a review of biotic interactions in freshwater systems (Holomuzki, Feminella, & Power, 2010) included little information on mutualisms—not because of oversight by the authors, but because so few case studies exist outside of interactions with habitat modifying species (see Moore, 2006). Moreover, the review made no mention of the effect of context dependency on mutualisms. More mechanistic studies are required to quantify the roles of context-dependent mutualisms in shaping population- (Horn et al., 2011; Johnston, 1994a), community- (Brown, Creed, & Dobson, 2002; Johnston, 1994b; Nakano, Yamamoto, & Okino, 2005; Peoples, Blanc, & Frimpong, 2015; Skelton, Doak, Leonard, Creed, & Brown, 2016) and ecosystem-level (Moore, 2006; Skelton et al., 2016) processes in freshwater systems.

One common positive interaction among North American freshwater fishes is nest association, in which "associate" species (partners) spawn in nests constructed by a host. Nest association can be considered a disjunctive symbiosis, as the species have an intimate short-term relationship, but lack the physical attachment or longevity typically associated with the more emblematic conjunctive symbioses. In North America, chubs (Leuciscidae: *Nocomis* spp.; Tan and Armbruster 2018) are widespread hosts; their nests are used by at least 35 associate species throughout their range (Johnston & Page, 1992). Adult male chubs build spawning nests in the spring and early summer by collecting gravel in their mouths and depositing the individual stones into a mound. Associates benefit from nest association with chubs via two mechanisms. First, the concentrated gravel of the nest provides suitable spawning substrate and keeps eggs from smothering in silt (Maurakis, Woolcott, & Sabaj, 1992; Peoples & Frimpong, 2013; Vives, 1990). Second, male chubs provide an element of parental care by moving and adding stones even after their own spawning has ceased (Wallin, 1992), further protecting eggs from most predators (Johnston, 1994a). In return, hosts benefit from a dilution effect (*sensu* McKaye & McKaye, 1977) when predators are present; high proportions of associate eggs on nests decrease the likelihood of predation on chub eggs (Johnston, 1994b; Wallin, 1992). It is common for large chub nests to attract hundreds of individual associates, even when only one associate species is present (McAuliffe & Bennett, 1981; Meffe, Certain, & Sheldon, 1988). Brood dilution rates of up to 97% have been documented as a result of high adult associate abundance (Cashner & Bart, 2010; Wallin, 1992). However, associate abundance is naturally variable across ecological gradients such as stream size and land use (Peoples et al., 2015), resulting in some nests attracting low abundances of associates or even none (Y. Kanno, unpublished data). Because brood dilution is a key mechanism making the relationship beneficial for hosts, heterogeneity in associate abundance is a form of biotic context that may determine interaction outcomes.

In this study, we conducted an in situ experiment to examine associate abundance as biotic context in determining outcomes of a reproductive interaction between host bluehead chub *Nocomis leptocephalus* (hereafter, *chub*) and partner yellowfin shiner *Notropis lutipinnis* (hereafter, *shiner*), a common nest associate in the southeastern USA. In this system, shiners always benefit from the interaction (versus spawning in the absence of chubs); thus, context dependency would be evident in differences in host reproductive success. Under a uniform treatment of predation, we hypothesised a commensalistic interaction at low associate abundances because the dilution effect on chub reproductive success should be negligible. We hypothesised the interaction would shift to being mutualistic at higher associate abundances due to the positive effects of brood dilution on chub reproductive success.

2 | METHODS

We conducted an in situ experiment with a randomised complete block design to test for effects of shiner abundance on the reproductive success of host chubs. We constructed 12 instream enclosures, removed non-focal species, and manipulated shiner abundance to three levels (absent, low and high) while holding constant abundance of chubs and piscine egg predators, which are necessary to provide a mechanism for brood dilution (i.e., brood dilution is not meaningful in the absence of predation). Three days after spawning, eggs were removed from nests and later identified to species using microsatellite genetic markers. Once all spawning had ceased, we reran the experiment with a new batch of individuals, resulting in four replicates of three treatment levels in each of two temporal blocks (n = 24). Using chub egg count as a proxy for host fitness, we compared treatment means to quantify effects of partner abundance on host reproductive success.

2.1 | Study site and experimental methods

This study was conducted from April to June of 2017 in Six Mile Creek, a second-order tributary to the Savannah River of northwestern South Carolina, USA (34.822, −82.828). This stream is typical of the Piedmont ecoregion (Omernik, 1987), with moderate gradient, regular pool/riffle sequences, and a narrow but intact buffer of riparian vegetation. The watershed is a mix of low-intensity agriculture (mainly livestock grazing) and deciduous forest, resulting in substrate dominated by sand in pools, and gravel and cobbles in riffles. Site selection was based on experimental feasibility—

perennial flow, stream size, contiguous access from landowners (*c.* 500 m), and abundance of focal species.

We constructed 12 experimental units (EUs), consisting of in-stream enclosures constructed of 4.75 mm fabric block nets, supported by a frame of steel posts and backed by two-panel strips of 5 × 10 cm welded fencing (*sensu* Peoples & Frimpong, 2016; Wallin, 1992). Block net height was 122 cm, with >30 cm above the ordinary high-water mark (OHWM). Net width extended laterally beyond the OHWM as well, ranging from 20 to 50 cm per side. To prevent fish movement between EUs, a block net apron of ≥30 cm was anchored to levelled substrate using 23 kg form-fitting sandbags. Enclosures were constructed to provide each EU with the necessary spawning (Bolton, Peoples, & Frimpong, 2015; Wisenden et al., 2009) and feeding (Rohde, Arndt, Foltz, & Quattro, 2009) microhabitats for each species (typically one riffle-pool sequence).

We removed all fishes from EUs using double-backpack electrofishing. We electrofished until no fishes >40 mm were captured, then followed with a final pass using increased voltage; a minimum of seven electrofishing passes were conducted in each EU. Adult individuals of all focal species were retained in flow-through holding tanks and monitored for signs of handling stress; all non-focal species and focal species exhibiting stress (e.g., lethargy, laboured breathing, erratic swimming) were released outside of the experimental area. Focal species were then restocked at predetermined abundances (Table 1). Each EU received two mature male chubs (with total length ≥115 mm total length and prominent nuptial tubercles; *sensu* Jenkins & Burkhead, 1994) and 15 female chubs (≥70 mm total length with visibly engorged abdomens; Jenkins & Burkhead, 1994) of approximately equal total length. Potential females not exhibiting obviously engorged abdomens were excluded to reduce the potential for mistakenly stocking immature males. Adult shiners (≥60 mm) were stocked at either high (80), low (15), or control (0) abundances, with each treatment randomly assigned to four EUs. Ambiguous secondary sexual characteristics prevented us from knowing exact sex ratios of shiners. However, we are confident that shiner stockings represented natural sex ratios because (a) all individuals came from within a close proximity of the experiment, and (b) individuals were randomly stocked. The control treatment lacking associates was necessary to determine a baseline level of reproductive success for chubs in the absence of a dilution effect. Shiner abundances in EUs were chosen to reflect abundances observed in nearby streams of similar characteristics, based on ongoing community sampling (Y. Kanno and B. Peoples, unpublished data), and are consistent with previous experimental studies of nest association (Peoples & Frimpong, 2016; Wallin, 1992). While as many as 500 shiners can be located on a nest at a given time in some streams (Meffe et al., 1988), our *high* treatment (80 individuals) is more realistic when considering the small stream size and limited number of host individuals per EU.

TABLE 1 Stocking abundances for each of the three experimental treatments

Treatment	BHC ♂	BHC ♀	YFS	NHS	STJ
Control	2	15	0	1	1
Low	2	15	15	1	1
High	2	15	80	1	1

Note. All fish were removed from each experimental unit via backpack electrofishing prior to stocking. Species codes are as follows: BHC (bluehead chub *Nocomis leptocephalus*), YFS (yellowfin shiner *Notropis lutipinnis*), NHS (northern hogsucker *Hypentelium nigricans*), STJ (striped jumprock *Moxostoma rupiscartes*).

To standardise egg predation among EUs, we included one individual of each species of the egg predators striped jumprock (Catostomidae: *Moxostoma rupiscartes*) and northern hogsucker (Catostomidae: *Hypentelium nigricans*). These are large-bodied fishes that have been documented to prey on fish eggs (Frimpong & Angermeier, 2009), and this density reflects abundances observed in nearby streams of similar characteristics (Y. Kanno and B. Peoples, unpublished). Because a previous study of similar design (Peoples, Floyd, & Frimpong, 2016) found no effect of predator density (low versus high) on chub reproductive success, we did not vary predator density and instead focused only on the effects of partner density. Other co-occurring cyprinids may function as egg predators on chub nests, but also as nest associates, and were accordingly not used as egg predators in this experiment. Other potential egg predators include crayfishes (Cambaridae: *Cambarus* and *Procambarus* spp.; Dorn & Wojdak, 2004; Eversole, 2014), juvenile salamanders (Plethodontidae: *Desmognathus* and *Eurycea* spp.; Blaustein, Sadeh, & Blaustein, 2014; Parker, 1994), and various other predacious invertebrates that have been observed burrowing in chub nests in previous studies (Light, Fiumera, & Porter, 2005; Swartwout, Keating, & Frimpong, 2016) as well as the present one. Manipulating abundance of these egg predators was not feasible, and we assumed equal effects of these taxa across EUs.

Beginning the day after stocking, spawning observations were recorded at least twice daily using methods modified from Peoples et al. (2015) for the duration of the experiment. Initial stocking of block 1 occurred on 07 May and observations continued until 20 May; block 2 was stocked on 27 May with observations continuing until 8 June. Wearing polarised sunglasses, one worker walked the length of the experimental area and located fish and nests to record whether they were spawning. All nests were measured daily for size (i.e., length, width and height) to indicate whether unobserved activity had occurred. Chub spawning was evidenced by the presence of a conspicuous gravel mound in the experimental unit. Several EUs had deep undercuts and/or pools, and in these areas underwater video observations were made periodically to ensure no nests went undetected. Due to the conspicuous spawning of both target species which can last for several days, and since the study stream was small (no more than 4 m wide and 1 m deep), we are confident that no nest construction went undetected. Spawning began in the EUs on 08 May 2017, and nest-building and spawning activity continued within the EUs until 26 June. Video and/or binocular observations were made when active spawning was identified. We harvested eggs from nests 3 days after initial nest observation to maximise the time available for spawning to occur without the risk of eggs hatching

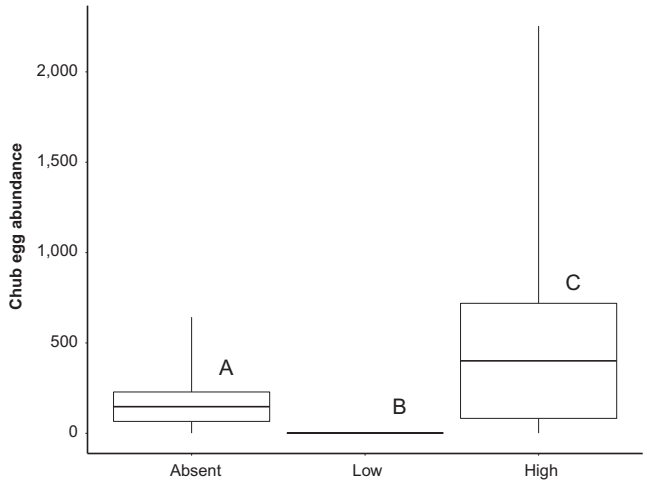

FIGURE 1 Bluehead chub (host) egg abundance for each treatment of yellowfin shiner (associate) abundance. The solid black midline represents the treatment mean, and the surrounding box depicts standard error. Significant differences among treatment means were determined using a post hoc Tukey's test and are signified by unique letter labels. Our results indicate significant differences between each of our three treatments. Number of nests sampled for each treatment was: absent = 8, low = 5, high = 7

into larvae; in warm months, mobile larvae have been observed in as few as 3 days after initial spawning (Peoples & Frimpong, 2016). Consistent with Maurakis and Woolcott (1996), all nests were initiated at night, and thus all new nest observations were made in the early morning hours. To harvest eggs, we placed a 1 m^2, 500-μm drift net immediately downstream of the nest and anchored it to the substrate to prevent sample loss. Stones were removed from the nest by hand and agitated in the water column, allowing eggs, invertebrates and detritus to drift into the net. Once the nest had been completely deconstructed, the contents of the drift net were transferred into 100% non-denatured ethanol.

2.1.1 | Egg identification and statistical analysis

Eggs of confamilial species are very difficult to distinguish based on external characteristics. However, molecular tools are becoming increasingly useful for identifying eggs and larvae of lotic leuciscids (Cashner & Bart, 2010, 2018; Peoples, Cooper, Frimpong, & Hallerman, 2017). Eggs were identified to species using microsatellite genetic markers developed at the South Carolina Department of Natural Resources Populations Genetics Lab housed within the Hollings Marine Laboratory in Charleston, SC (details provided in Supplemental Materials). In brief, genomic DNA was isolated from eggs using a modified spin-column procedure. Isolated DNA was then amplified via polymerase chain reaction using a multiplexed group of three primer pairs, each with a unique allelic size range and dye colour, corresponding to one of three microsatellite loci (Ca5, Nme25C8.208 and RSD53) diagnostic for the two focal species. Fragment analysis was then conducted on the amplified DNA using capillary gel electrophoresis on a CEQ™ 8000 (Beckman Coulter, Inc; Fullerton, CA) automated sequencer. Finally, each chromatogram was scored for species identification using Beckman Coulter CEQ™ 8000 Fragment Analysis Software. Detailed methodology for selection of microsatellite loci and genetic analyses can be found in Supporting Information Appendix S1.

Due to variable egg abundances and the costs and logistics of genetic analysis, some EUs necessitated subsampling, while egg samples from other EUs could be analysed in total. When 35 or fewer eggs were collected from an EU, all eggs were identified using molecular markers and direct abundance of chub eggs was determined. For EUs with >35 intact eggs, two separate subsamples were analysed, and the percentages of chub eggs were compared to ensure subsampling was representative of true proportions. In all cases, the proportion of chub eggs in the two subsamples were within 5% of one another, so the weighted average was calculated and that value was used for extrapolation. All activities were ethically reviewed and improved, and were conducted under the Clemson University Institutional Animal Care and Use Committee protocol number 2017-015.

We used a generalised linear model of a Poisson distribution (appropriate for count data), with trial number as a block, to quantify the effect of shiner abundance on chub egg abundance as a proxy for host fitness. The data were analysed with a blocked analysis of variance (ANOVA) fit to a Poisson distribution through the log-link function, to account for the count data of chub egg abundance. We then used a conservative post hoc Tukey's test to compare treatment means. All analyses were conducted in R version 3.4.3 (R Core Team, 2017).

3 | RESULTS

Chubs constructed nests in 20 of the 24 EUs, and chubs spawned in several EUs of each treatment. A total of 8,692 eggs were collected between the two blocks; genetic analysis identified 3,974 chub eggs and 4,718 shiner eggs. Although we never observed piscine egg predators disrupting nests, most nests we sampled contained high densities of juvenile salamanders and a diversity of predacious invertebrates.

Chub egg abundance differed among the three treatments ($F_{2,23}$ = 30.1, p < 0.0001), indicating that associate abundance affected host reproductive success (Figure 1). Nest association was mutualistic at high shiner abundance; in this treatment, chub egg abundance ($\bar{x}$ = 400.0, standard error [*SE*] = 297.7) was significantly greater than control ($Z_{1,24}$ = 32.0, p < 0.0001) and low abundance treatments ($Z_{1,24}$ = −10.5, p < 0.0001). The Tukey's test also revealed that host egg abundance was significantly reduced at low associate abundance ($\bar{x}$ = 0.6, *SE* = 0.5) when compared with the control ($\bar{x}$ = 146.4, *SE* = 81.4), suggesting a parasitic interaction ($Z_{1,24}$ = −8.5, p < 0.0001). Of more than 7,000 eggs deposited in high abundance treatments, more than 60% were identified as shiner ($\bar{x}$ = 671.9, *SE* = 400.5). In contrast, only a total of 15 shiner eggs were identified in all low abundance treatments ($\bar{x}$ = 3.0, *SE* = 2.3). See Supporting Information Figure S1 in Appendix S2 for a plot of all chub egg abundance data for each nest per treatment.

4 | DISCUSSION

This work represents one of the first studies to document interaction outcome shifts from mutualism to parasitism that result solely from changes in partner abundance. Shiners should always benefit from spawning with a host (Johnston, 1994a) based on the simple fact that they must have a host to spawn (Wallin, 1992); they will not spawn in the absence of a nest-building host. Even though the outcome remained positive, the per-capita benefit for shiner varied drastically; we observed a 200-fold increase in per-capita egg abundance from low to high density experimental units. Reproductive success of host chub, however, varied with shiner abundance and caused a shift in the interaction outcome from mutualism at high partner abundance to parasitism at low partner abundance. These findings support our hypothesis of mutualism at high shiner abundance, but do not support our hypothesis of commensalism at low shiner abundance. Thus, our results provide several key insights into context dependency in our study system. First, the outcomes of nest association depend on biotic context. Second, nest association appears to be mutualistic only when associate abundance is high enough for the benefits of brood dilution to outweigh the costs of egg predation. Finally, our results suggest chubs will benefit from higher reproductive success when disengaging entirely from associative spawning than spawning together with a low number of shiners.

In this system, brood dilution is the most likely mechanism that makes partner abundance function as a source of biotic context. Mutualisms incur both costs and benefits, and an interaction is only mutualistic if all participants receive a net benefit. As large piles of concentrated gravel, chub nests are conspicuous features on the streambed, advertising food availability for egg predators and representing a baseline cost for chub reproduction. However, chub spawning bouts are generally brief and inconspicuous (Sabaj, Maurakis, & Woolcott, 2000), drawing little attention to the nest. Conversely, spawning groups of shiners are highly conspicuous and can last for days on a nest. Congregated shiners on chub nests represent an additional fitness cost to host chubs because they make the nest even more conspicuous to egg predators. With high associate abundances typical of productive streams, associate eggs comprise the majority of eggs on an active nest (Cashner & Bart, 2010; Wallin, 1992). While predation was not directly observed in the experiment, the presence of predatory invertebrate taxa in the nests suggests that egg predation did occur. Alternatively, the presence of egg predators may have altered the behaviour of chubs through perceived rather than actual predation. Thus, it is possible that female chubs did not reciprocate the male's invitation to spawn. Regardless, brood dilution by associates still affords a mechanism for host benefits. As the strength and mode of predatory behaviour may provide additional sources of biotic context, examining these conditions represents a logical next step. Future work should include control treatments without piscine or other egg predators to untangle host responses to perceived versus realised egg predation.

Because it is so important to host fitness, many hosts have evolved unique strategies to manipulate symbiont or partner abundance to their own advantage (Cunning et al., 2015; Parkinson, Gobin, & Hughes, 2016; Parkinson et al., 2017). For example, crayfish hosts (Cambaridae: *Cambarus chasmodactylus* and *Orconectes cristavarius*) actively reduce density of branchiobdellidan worms to prevent a mutualistic cleaning symbiosis from switching to parasitism (Farrell, Creed, & Brown, 2014). Host chubs may also engage in a form of partner control by withholding spawning activity until associate abundance is high enough to benefit the host. Indeed, results of daily surveys concomitant with our experiment (Y. Kanno, unpublished data) in nearby streams suggest that nearly a third of chub nests are immediately abandoned upon being constructed. While not all nests constructed are utilised for spawning by associates, no abandoned nests were observed to attract any associates. Further research on the factors determining nest abandonment will yield important insight into the role of partner control in nest associative interactions.

Like many other studies, we simplified our system to quantify pairwise interaction outcomes between two participants. However, it is widely recognised that mutualism must be understood in a whole-community context (Palmer, Pringle, Stier, & Holt, 2015; Thrall, Hochberg, Burdon, & Bever, 2007). To the best of our knowledge, *Nocomis* occurs nowhere without at least one associate species (Pendleton, Pritt, Peoples, & Frimpong, 2012), and spawns with up to six associates simultaneously in parts of its range (Peoples et al., 2015). Moreover, associates usually have the opportunity to spawn among several nest-building host species, each with slightly different nesting habits (Peoples et al., 2016). Quantifying interactions between partner diversity and abundance is necessary for understanding context dependency in this system.

Partner abundance is a key source of context dependency in symbioses (Chomicki & Renner, 2017; Cunning & Baker, 2014; Kiers, Palmer, Ives, Bruno, & Bronstein, 2010). Maximum host fitness occurs at intermediate partner density in many symbioses (Brown et al., 2012; Izzo & Vasconcelos, 2002; Morales, 2000; Palmer & Brody, 2013). For example, a common finding is that interaction outcomes switch from commensalistic or mutualistic at lower to intermediate partner abundances, to parasitic at high abundances (e.g., Brown et al., 2012; Thomas et al., 2013). However, the fitness outcomes we observed along our continuum of partner abundance differed from these other studies. We found the opposite pattern, with parasitism at low partner abundances and mutualism at high abundances; this is probably due to the novelty of the resources being traded, spawning substrate/parental care and brood dilution, between hosts and associates. Unlike cleaning symbioses where high symbiont densities can be detrimental to hosts (i.e., switching from mutualism to parasitism with increasing symbiont density), we can think of no mechanism that would cause increased brood dilution by associates to decrease host fitness. Our findings illustrate that, although partner abundance is a key source of biotic context, predictions on abundance-related fitness outcomes will require detailed system-specific information.

Although ecologists broadly recognise that mutualism is ubiquitous in nature (Bronstein, 1994a; Herre, Knowlton, Mueller, & Rehner, 1999; Sachs, Mueller, Wilcox, & Bull, 2004; Sachs & Simms, 2006; Stachowicz, 2001), it has until recently been largely overlooked in freshwater systems (Holomuzki et al., 2010). In addition to a few other interaction types (worm/crayfish cleaning symbiosis; Brown et al., 2002, 2012; Lee et al., 2009; Skelton et al., 2013; Thomas, Creed, Skelton, & Brown, 2016; frugivorous fish seed dispersal—Correa et al., 2015; Horn et al., 2011), nest associative spawning fishes provide an excellent model system for understanding mutualisms and context dependency in freshwater ecosystems. Mutually beneficial nest associations have been documented previously in systems of other nest building taxa (Goff, 1984; Johnston, 1994b; Wisenden & Keenleyside, 1992), and more recently with *Nocomis* hosts (Peoples & Frimpong, 2013). Moreover, studies have found variable outcomes of nest association with varying biotic context; for example body size of host sunfishes (Shao, 1997a, 1997b), or host brood parasitism by spawning partners (Baba, Nagata, & Yamagishi, 1990; Fletcher, 1993; Yamane, Watanabe, & Nagata, 2013). Continued research into nest associative spawning will help shed light on the role of mutualisms in freshwater ecosystems.

Mutualisms form the foundation for many fundamental ecological processes (Bronstein, 2009) and conserving mutualism will be a key component of conserving biodiversity under global change (Bronstein, Dieckmann, & Ferrière, 2004; Correa et al., 2015). Understanding context dependency is critical to predicting how interaction outcomes, and their consequent effects on population and community processes, will shift under changing scenarios. In freshwater systems, which are home to some of the richest, and yet most imperilled faunas on earth (Jelks et al., 2008), this is particularly evident. Identifying mutualisms and their context dependency will be important for understanding dynamics of freshwater ecosystems.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

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