ORIGINAL ARTICLE

Behavior outweighs body size in mediating male reproductive success in a nest-building fish, bluehead chub

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Abstract

In polygamy, individuals interact in a non-random manner to shape reproductive networks. However, relative importance of behavior versus individual physical traits (e.g., body size) in determining access to partners and reproductive success varies by species and is poorly understood in small-bodied aquatic species for which direct observations are challenging in the wild. Here, we coupled automated individual tracking and genetic parentage techniques to characterize reproductive networks and their consequences on reproductive success in bluehead chub (*Nocomis leptocephalus*), a nest-building stream fish native to the southeastern USA. Fish were marked with 12-mm passive integrated transponder (PIT) tags, and loop-shaped PIT antennas were deployed around 18 nests to monitor behavioral encounters of 311 individuals (34 males and 277 females and immature males) during the spawning season in 2017. After spawning, genetic samples of 326 young-of-the-year fish (i.e., offspring) were collected. The mating system was polygynandrous, and factors affecting access to partners and reproductive success differed between males and females. Male body size did not affect number of encounters with females and reproductive success, instead behavior indexing reproductive effort (number and size of nests occupied) explained variation in reproductive success. On the contrary, body size was a key determinant of female reproductive success. Fecundity (i.e., number of eggs) increased with body size, and higher encounters rates with males did not result in higher reproductive success. In males and females, mating with more partners led to higher reproductive success, which may have contributed to the evolution and maintenance of polygynandry in this species.

Significance statement

Is bigger better? This question has been investigated with respect to animal mating behavior and reproductive success, and the answer appears to vary by species. Using an intensive individual-based approach with PIT antenna and molecular markers, we show that behavior outweighed body size in mediating reproductive success of males but not females of a nest-building stream fish. Males increased access to females and ultimately number of offspring by occupying larger and more nests, which are proxies of reproductive effort. In females, body size was more important than behavior in determining reproductive success, and behavior explained much less of variation in reproductive success. Diverse and complex reproductive patterns of males may explain why behavior outweighed body size in mediating reproductive success, a hypothesis that warrants further research across species with a gradient of mating systems and behavioral complexities.

Seoghyun Kim and Yoichiro Kanno contributed equally to this work.

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Introduction

In polygamy, individuals mate with multiple partners, but mating patterns are typically non-random (Andersson 1994; Reynolds 1996; McDonald and Pizzari 2016; Ziv et al. 2016). Some individuals mate with more partners than others, forming a complex web of reproductive interactions (Serbezov et al. 2010; McDonald and Pizzari 2016; Sabol et al. 2020). Characterizing reproductive interactions is critical to understanding behavioral ecology and evolution (Wey et al. 2008; Leu et al. 2010), because the number of mates is a key determinant of reproductive success, defined here as the number of offspring assigned to individuals (Bateman 1948; Emlen and Oring 1977; Andersson 1994; Jones et al. 2002). However, much of our understanding of the relative importance of behavior versus individual physical traits (e.g., body size) in determining access to partners and ultimately reproductive success comes from terrestrial taxa for which reproductive behavior may be readily observed in the wild or characterization of reproductive networks can be facilitated due, for example, to prolonged parental care (e.g., birds and mammals) (Friedl and Klump 2000; Wolff and Macdonald 2004; Asher et al. 2008; Ziv et al. 2016; Sabol et al. 2020).

Males increase reproductive success by mating with more partners in a variety of species (Bateman 1948; Reynolds 1996; Jones et al. 2002). Because sperm production is energetically less costly than egg production (Ginsberg and Huck 1989; Wedell et al. 2002), male reproductive success is limited by access to females (Bateman 1948; Jennions and Petrie 1997). Males compete with each other for access to females (Emlen and Oring 1977; Andersson 1994), and outcomes of this competition often depend on body size (Oliveira et al. 2000; Asher et al. 2008), which may also correlate with secondary sexual characteristics such as body coloration in birds (McDonald and Potts 1994), antlers in mammals (Andersson 1994), and kypes (protruded hooks on the lower jaw) in fishes (Järvi 1990). In nest-building species, body size is important because larger males construct nests of larger size or higher quality (Soler et al. 1998; Lehtonen et al. 2007; Barber 2013; Bose et al. 2018) and outcompete smaller males for the most suitable nesting sites (Oliveira et al. 2000; Forstmeier 2002). However, smaller males may still reproduce by employing alternative reproductive behaviors, such as constructing more nests and segregating spawning temporally (Gross 1996; Friedl and Klump 2000; Forstmeier 2002). Therefore, in addition to individual characteristics such as body size, male reproductive success of nest-building species can be affected by behavioral variation among individuals (Lehtonen and Lindström 2009; Barber 2013).

In females, body size and behavior similarly determine their reproductive success, but via mechanisms that differ from males (Emlen and Oring 1977; Reynolds 1996). Fecundity (number of eggs) increases with female body size in oviparous species (Trippel et al. 1997; Soler et al. 1998; Nafus et al. 2015), and larger females produce larger and higher-quality eggs (Barneche et al. 2018). The Bateman's principle posits that female reproductive success does not typically depend on number of mates, contrary to male reproductive success (Jennions and Petrie 1997; Serbezov et al. 2010; but see Jones et al. 2002). However, mate choice by females affects reproductive success of their own and males via selection of certain male characteristics such as body size, courtship display, coloration, and auditory signals (Andersson 1994; McDonald and Potts 1994; Trainer and McDonald 1995; Jennions and Petrie 1997). Mate choice by females is particularly important in nest-building species in which males construct and defend their nests but females are mobile (Brooks and Couldridge 1999; Leiser et al. 2015). However, questions remain whether females choose mates based on characteristics of males versus nests. Specifically, male body size is more important than nest characteristics in some studies (Oliveira et al. 2000; Lehtonen et al. 2007; Bose et al. 2018) but not in others (Soler et al. 1998; Friedl and Klump 2000; Lehtonen and Lindström 2009). The mixed findings indicate that mate choice by female varies by species and environmental and social context (Emlen and Oring 1977; Wey et al. 2008; Lehtonen et al. 2010).

Direct observations of reproductive behavior are difficult for many species in the wild, but particularly for aquatic species that do not provide prolonged parental care for hatchlings. Molecular markers have facilitated characterization of animal mating systems, and they frequently discover cryptic and complex reproductive networks among individuals (Marshall et al. 1998; Wolff and Macdonald 2004; Serbezov et al. 2010). More recently, automated tracking systems (e.g., radio frequency identification or RFID) have been added to the toolbox of behavioral ecologists to quantify individual behavior and interactions (Rehmeier et al. 2006; Newey et al. 2009; Sabol et al. 2018). Molecular markers and automated tracking complement each other and together provide richer information because animal tracking data reveal behavioral mechanisms that can explain variation in reproductive success inferred from molecular techniques. However, applications of both tools in combination have been limited in aquatic species.

Bluehead chub (*Nocomis leptochepalus*) provides a unique opportunity to study reproductive networks and their consequences on reproductive success. They are a small-bodied minnow (Leuciscidae), and adult body size ranges between 70 and 200 mm (Lanchner 1952; Jenkins and Burkhead 1994). Breeding males develop the blue head with tubercles, and males are larger than females at maturity (Jenkins and Burkhead 1994). Bluehead chub are distributed throughout the Atlantic slope of North America and are common in small streams in Blue Ridge and Piedmont regions (Lanchner 1952;

Marcy Jr et al. 2005). Males prefer pool tails and slow runs covered by gravel and pebble to construct dome-shaped pebble mounds as nests for spawning (Wallin 1989; Sabaj et al. 2000). Their nests are used by other species (i.e., nest associates: up to 20 species), which spawn at the same time with bluehead chub (Marcy Jr et al. 2005; Peoples and Frimpong 2016; Kim et al. 2020). Males move thousands of pebbles after spawning as a form of parental care (Wallin 1989, 1992; Kim et al. 2020). Females spawn on nests by approaching from the rear of a male, who curves his body toward females to induce them to deposit eggs; thus, females primarily choose their mates (Sabaj et al. 2000). Bluehead chub spawn periodically at intervals of 4–6 days between April and June (Kim and Kanno 2020), and males may construct multiples nests in a single spawning season (Wallin 1989). In addition, multiple males often construct and use the same nest (Kim et al. 2020), which is not common among nest-building species (Taborsky 2009; Díaz-Muñoz et al. 2014). These observations on reproduction of bluehead chub suggests complex behavioral interactions among males and females, but we have limited knowledge on how behavioral and individual physical traits affect reproductive success in such a complex system due partly to the technical challenges in tracking individuals.

Here, we investigated the relative importance of behavior versus body size in determining access to partners and reproductive success in male and female bluehead chub. The study goal was to characterize the mating system of bluehead chub and use this information to address three specific objectives (Fig. 1). Based on direct behavioral observations, males attract and mate with multiple females on their nests (Wallin 1989; Sabaj et al. 2000; Kim et al. 2020), but mating patterns of females are cryptic and less well understood. Thus, we sought to characterize whether their mating system is polygynandrous (i.e., both males and females mate with multiple partners). Our first specific objective was to assess the relative importance of factors affecting number of potential mates each male and female encountered across nests in a single spawning season (hereafter "number of encounters") using an automated tracking system. In males and females,

we tested whether number of encounters is explained by size of their body, and size and number of nests that males occupied or females visited (i.e., behavior) (Q1 in Fig. 1). Secondly, we examined the relationship between number of encounters based on tracking and number of mates inferred genetically to ascertain whether higher encounter rates increased access to mates (Q2). We deemed this would not always be the case if only a subset of individuals detected at nests reproduce successively. Lastly, we evaluated whether reproductive success (i.e., number of offspring) was influenced by body size or behavior (number of encounters and mates) (Q3).

Methods

Study area

This study was conducted in an 880-m-long segment of Shoal Creek (34° 48′ 12″ N, 82° 47′ 02″ W), a second-order perennial stream (mean wetted width = 3.1 m) in the Savannah River Basin in the upper Piedmont region of South Carolina, USA (Appendix S1). Shoal Creek harbored riffle-pool habitat sequences with pebble and cobble substrates in riffles, and silt and sand in pools. The riparian area was covered by mixed hardwood canopy. We chose our study segment because it was a semi-isolated riverine habitat for bluehead chub, suitable for tracking individuals throughout the spawning season. Their abundance declined farther upstream due to small stream size and land use (i.e., grazing and residential development), and farther downstream due to a series of beaver (*Castor canadensis*) dams that converted riverine habitats into slow-moving pond-like habitats. Other common species in the study area were bluegill (*Lepomis macrochirus*), creek chub (*Semotilus atromaculatus*), mottled sculpin (*Cottus bairdii*), rosyface chub (*Hybopsis rubrifrons*), striped jumprock (*Moxostoma rupiscartes*), and yellowfin shiner (*Notropis lutipinnis*). Rosyface chub and yellowfish shiner spawn on nests constructed by bluehead chub (Marcy Jr et al. 2005).

Fig. 1 Schematic diagram of study objectives
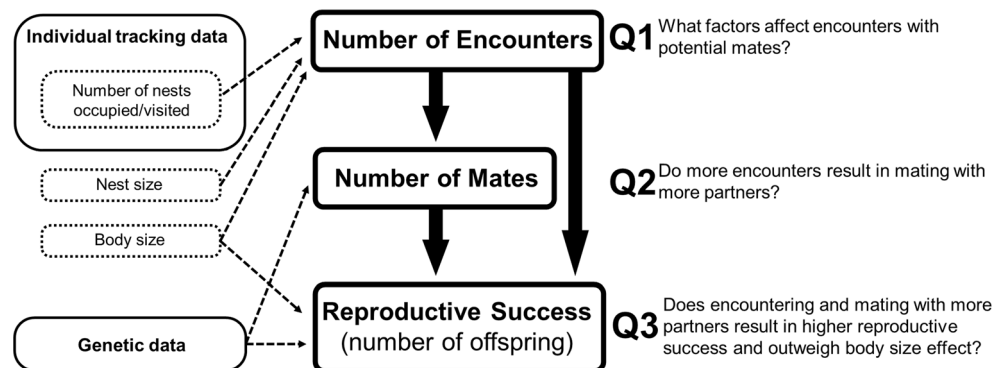
Yellowfin shiner was more abundant than rosyface chub in Shoal Creek.

Fieldwork

To address study objectives (Fig. 1), we used PIT antenna technology to identify males and females that visited each nest and characterize number of potential mates each male and female encountered across nests. We also collected tissue samples of potential parents and their offspring (young-of-the-year (YOY) individuals) to genetically assign parentage and quantify reproductive success. To minimize observer bias, blinded methods were used when fish were collected and marked, and nests were monitored using an automated tracking system (PIT antenna).

Adult bluehead chub were collected twice before the spawning season (January and April), and three times during the spawning season between May and June in 2017. Backpack electrofishing units were used to stun fish temporarily for capture with dip nets. Fish were then measured for total length (TL in mm) and weight (g), and genetic samples were taken non-lethally from anal fins. Individuals ≥ 60 mm in total length were tagged with 12-mm half duplex PIT tags (Oregon RFID, Portland, OR) by making a small ventral incision between pectoral and pelvic fins to insert a tag into the body cavity; the procedure resulted in high tag retention and survival rates in our previous study (Cary et al. 2017). During the study period, mature males could be identified based on conspicuous secondary sexual characteristics such as tubercles on their head and body colors (Marcy Jr et al. 2005). However, females and immature males could not be distinguished from one another; thus, individuals without male characteristics were defined as potential females. A total of 686 unique individuals (64 males and 622 potential females) were captured and tagged across sampling events (Table 1). Electrofishing does not capture all individuals present in the sampling area. For individuals detected on nests by PIT antennas but not recaptured physically during the spawning period (April–June 2017), linear regression models were developed to predict TL of individuals in April, May, and June

based on their TL in January, April, and May, respectively, based on TL measurements of a total of 147–306 individuals collected as part of a seasonal mark recapture survey in the study stream (Appendix S2).

Spawning was monitored daily from April 1 to July 12 in 2017. This period included pre- and post-spawning windows to ascertain that nests were monitored during the entire spawning season. Observers walked on the bank to locate bluehead chub nests. Nests were readily identified because male bluehead chub construct conspicuous pebble mounds (Wallin 1989; Sabaj et al. 2000). In addition, yellowfin shiner use bluehead chub nests for spawning in the Savannah River Basin (Marcy Jr et al. 2005) and the two species spawn at the same time (Wallin 1992; Kim and Kanno 2020). Missing nests was highly unlikely because yellowfin shiner spawn in large groups and display brilliant breeding colors (i.e., red body color with yellow fins; Fig. 2). When a nest was located, a marker with a unique identification number was placed on the nearby bank. To identify individuals on each nest and timing of visits, loop-shaped PIT tag antennas made of copper wire (5.26 mm^2 in diameter) were deployed around it (Fig. 2). Antennas were anchored to the stream bed with pebbles. We monitored up to 6 nests simultaneously using 3 multi-antenna HDX readers (Oregon RFID, Portland, OR), and we could not deploy PIT antennas on 3 nests due to technical issues related to the equipment. A total of 18 nests were monitored during the spawning season. Using individual identity and the time of detections in PIT antenna data, we considered an encounter between a male and a female to have potentially occurred when both were detected in the same hour on a particular nest; the number of encounters based on the hourly scale was significantly correlated with that based on the minute scale in males and females (Spearman $\rho \geq 0.95$, $P < 0.001$). In addition, nest dimensions (length, width, and height) were measured daily until spawning ceased on the nest. Size of each nest was estimated using the volume of elliptical cone (cm^3) averaged across days on which spawning was recorded. We also monitored water temperature (°C) and water level (m) hourly during the spawning season using a logger (U20L-004, HOBO Onset Computer Corp.).

To infer reproductive success, YOY were collected between August 25 and September 10 in 2017, approximately 2 months after the spawning season. YOY were collected using backpack electrofishing units, and a small (10-cm diameter) anode ring was used to increase sampling efficiency of small-bodied fish (Copp 1989). All captured YOY were measured for total length, and fin clips were taken for genetic analysis. YOY were sampled at the 880-m study site, plus additional 100-m immediately downstream to account for potential larval drift. We deemed

Table 1 Sample size of individuals marked with PIT tags, detected on nests by PIT antennas, and to which at least one offspring (young-of-the-year) was assigned genetically (i.e., reproductive success)

Sex	Number of individuals		
	Marked	Detected on nests	Reproductive success
Males	64	49	15
Potential females[1]	622	277	45

[1] Includes females and immature males because they could not be distinguished visually in the field
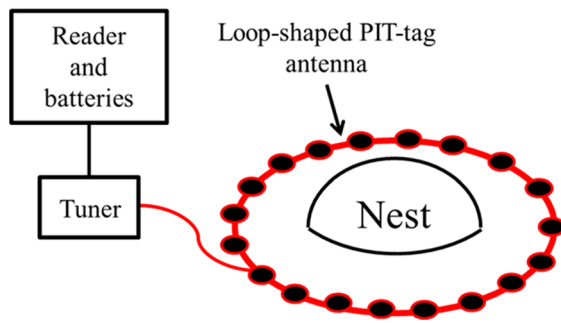
Fig. 2 Design of the loop-shaped PIT antenna that was placed around a nest to detect individuals. Photo showing the PIT antenna (black wires) anchored with rocks while bluehead chub (a male with a blue head and tubercles in the center) and yellowfin shiner (red individuals) spawn on the nest

downstream drift of larval fish (i.e., emigration from the study area) minimal because we did not capture a single YOY individual at the lowermost 80 m of the study area or 100 m farther downstream despite collecting similar-sized individuals of other species (e.g., bluegill), indicating that electrofishing was effective at capturing individuals of these sizes. A total of 326 YOY (total length: mean = 31 mm, range = 16–49 mm) were collected.

In addition, we characterized the relationship between body size and fecundity. Females were dissected for counting the number of eggs. To avoid mortality of fish at Shoal Creek, mature females (n = 49) were collected in April 2017 at Sixmile Creek, a third-order stream (mean width = 7.4 m) located in the same watershed, approximately 9 km from Shoal Creek (Appendix S1).

Genetic analyses

A set of 8 polymorphic microsatellite loci (Cushman et al. 2020) was used for the genetic parentage assignment. Laboratory protocols are detailed in Cushman et al. (2020). We genotyped 64 males, 277 potential females detected on nests by PIT antennas, and 326 YOY for parentage analysis (Table 1). Mean number of alleles was 22 (range 7–42), and mean expected heterozygosity was 0.74 (range 0.33–0.93) across loci (Appendix S3).

Genetic parentage analysis was conducted using program COLONY2 version 2.0.6.5 (Jones and Wang 2010). COLONY2 identifies both sampled and inferred (unsampled) parents, which is suitable for characterizing mating systems, particularly number of mates (Jones and Wang 2010). We used the following parameter settings: polygamy, a marker error rate of 0.01, a full likelihood method, and medium-length run with 3 simulations. Paternity and maternity were assigned when their probability was ≥ 95%. In addition, a sensitivity analysis was conducted to assess the consistency of parentage assignments across different probabilities that sampled males and females were included in parent samples (Appendix S4). We developed 9 scenarios of parentage analyses with different inclusion probabilities (0.5, 0.6, and

0.7 in males; 0.4, 0.5, and 0.6 in females). Relative rankings of reproductive success (i.e., number of YOY assigned to males and females) were consistent among individuals across scenarios (mean Spearman ρ = 0.88 in males and 0.80 in females; Appendix S4). We report assignment test results using the inclusion probability of 0.7 for males and 0.6 for females because a mark-recapture survey conducted at the peak spawning time (May 3 and 15) indicated that our electrofishing capture probability was 0.72 for males and 0.64 for females based on the two-sample Lincoln-Petersen method (Appendix S5).

Data visualization

We visualized encounters of males and females at nests based on PIT antenna data and mating system based on genetic parentage analysis. Prior to visualization, we evaluated PIT antenna data for evidence of behavioral signs of reproduction. Female bluehead chub may visit nests only temporarily and leave nests immediately after spawning (Sabaj et al. 2000). We retained all 45 females confirmed with reproductive success regardless of the number of detections by PIT antenna on each nest. However, male bluehead chub invest much more time than females in building and guarding their nests (Wallin 1989; Sabaj et al. 2000; Kim et al. 2020), and an alternative behavior (e.g., sneaking other males' nests for spawning) is not known in bluehead chub. We considered that males detected repeatedly over time occupied a particular nest for spawning. Typically, males continue to move pebbles for nest construction and maintenance, and multiple males may occupy the same nest (Wallin 1989; Kim et al. 2020). For each nest, the number of PIT antenna detections for a single male was divided by the total detections across all males that visited the nest (Appendix S6); the proportion of detections was used to index relative duration of time spent on the nest by each male. Males with genetically confirmed reproductive success had proportion of detections ≥ 0.07 on at least one

nest. Thus, we used this threshold value to filter out males that visited nests but did not reproduce. As a result, 34 out of 49 males were retained for visualizing encounters with the 45 females at 18 nests (Table 1). These 34 males spent much more time (number of hours detected on each nest: mean = 28; range = 3–89) on nests than the other 15 males removed (mean = 4; range = 1–43) (t test: $t = -8.37$, df = 74.64, $P < 0.001$). In addition, mating system was visualized based on parentage assignment. We included 15 males and 45 females with reproductive success as sampled parents, and additional 11 males and 54 females inferred by genetic parentage assignment but not collected physically (Table 1). Encounters and mating system were drawn using the *igraph* package (Csardi and Nepusz 2006) in R version 3.5.1 (R Development Core Team 2018).

Statistical analyses

We conducted a sequence of regression analyses to address our study objectives by determining factors structuring number of encounters (i.e., behavior) based on PIT antenna data (Q1), linking number of encounters with genetically inferred number of mates (Q2), and integrating PIT and genetic data to assess the relative importance of factors affecting reproductive success (Q3) (Fig. 1). In all regression analyses, predictors were standardized by mean (mean = 0 and SD = 1). The variance inflation factor (VIF) was used to assess multicollinearity between predictors in each analysis (O'Brien 2007), and all pairwise VIF values were < 1.5 (i.e., lack of multicollinearity). Statistical significance was set at $\alpha < 0.05$, and all analyses were conducted in R version 3.5.1 (R Development Core Team 2018).

Number of encounters (Q1)

To examine factors structuring number of encounters, a Poisson generalized linear model (GLM) was used for females ($n = 45$), and a quasi-Poisson GLM was used for males ($n = 34$) to account for overdispersion. The response variable was the number of encounters with potential mates across nests based on PIT antenna data. Predictors were body size and number and size of nests occupied (males) or visited (females). We chose the largest nest on which an individual was detected as a predictor because encounter occurred disproportionately on the larger nests (see "Results" section).

A set of models was constructed using all possible combinations of three predictors. Akaike's information criterion corrected for small sample size (AIC_c) was used to compare the Poisson GLM for females, and quasi-likelihood Akaike's information criterion corrected for small sample size ($QAIC_c$) was used to compare the quasi-Poisson GLM for males.

Competing models were identified using Akaike weights (i.e., Akaike weight ≥ 0.1: Burnham and Anderson 2002). Effect size of predictors was averaged across competing models using the package *AICcmodavg* (Mazerolle 2016), and statistical significance was declared if 95% confidence interval (CI) did not overlap zero.

Number of mates (Q2)

Detections at nests by PIT antennas do not necessarily confirm reproduction by those individuals. The relationship between number of encounters with potential mates across nests (PIT antenna) and number of mates (genetic assignment) was assessed in males ($n = 34$) and females ($n = 45$) using the Spearman's rank correlation test. The number of mates included sampled and unsampled individuals inferred genetically.

Reproductive success (Q3)

We evaluated whether reproductive success was affected by number of encounters, relative to body size. The response variable was the number of offspring genetically assigned and the predictors were number of encounters and body size (TL). Because males were confidently identified in the field and not all males reproduced based on genetic data, we identified males with behavioral signs of reproduction based on PIT antenna detections but to which YOY were not assigned (i.e., no confirmed reproductive success). This was not the case for females, for which reproductive success was used to distinguish them from immature males. Thus, we used a zero-inflated Poisson (ZIP) model for males ($n = 34$) and Poison GLM for females ($n = 45$). The ZIP model is a mixture model that estimates effects of predictors on the probability of zero (no reproduction) by a logistic model and variation in count (number of offspring, given reproduction) by a Poisson log model. The ZIP model was fit using the *pscl* package (Jackman 2020). Competing models were identified using Akaike weights (i.e., Akaike weight ≥ 0.1), and effect size of predictors was averaged across competing models. Lastly, we used a linear regression model to assess the relationship between number of mates and reproductive success in each sex (i.e., Bateman's gradient).

Results

We located and monitored 18 nests by deploying PIT antennas around them. The first nest was recorded on April 29, and the last nest was recorded on June 23, 2017. A total of 49 males and 277 potential females were detected by antennas (Table 1). Thirty-four males were deemed to occupy nests for reproduction based on their frequency of detections by PIT antennas (Appendix S6, Table 1). Based on parentage

analysis, 169 of the 326 YOY (51.8%) were assigned to males in the sample and 100 YOY (30.7%) were assigned to sampled females. A total of 15 males had reproductive success and were detected on at least one nest (range = 1–5), demonstrating the exhaustive sampling and monitoring. In potential females, 45 of 277 individuals had reproductive success; thus, we confirmed them as females (Table 1).

Body size of the 15 males with reproductive success ranged between 115 and 172 mm (mean = 141) in TL, and did not differ significantly from the 19 males without reproductive success despite behavioral signs of reproduction (proportions of PIT antenna detections ≥ 0.07) (mean TL = 135; range = 103–180) or the 15 males excluded from analyses due to lack of behavioral signs of reproduction (mean TL = 129; range = 102–178) (one-way ANOVA: $F_{2,46} = 1.30$, $P = 0.28$). The 45 females confirmed with reproduction (mean TL = 93 mm; range = 72–116) were significantly larger than the 232 potential females without reproduction (mean TL = 85; range = 65–112) (t test: $t = -4.32$, df = 61.13, $P < 0.001$), suggesting that the latter group likely included immature individuals that could not be sexed in the field.

Fecundity (number of eggs) increased exponentially with body size (Appendix S7). Fecundity of females (TL 76–151 mm, $n = 49$) was explained as $\ln(Fecundity) = -10.23 + 3.45 \times \ln(TL)$

Spawning activities at nests inferred from PIT antennas

Male and female bluehead chub occupied or visited multiple nests during the spawning period (male, mean = 2, range = 1–5, $n = 34$; female, mean = 5, range = 1–8, $n = 45$; Fig. 3a). Nests ranged in size between 8759 and 28,904 cm³ (mean = 17,922, $n = 18$). Nest size was positively correlated with number of males (Spearman, $\rho = 0.68$, $P = 0.002$) and females (Spearman, $\rho = 0.60$, $P = 0.009$) detected on the nest, and encounters between males and females occurred more commonly on larger nests (Fig. 3a). Multiple males typically shared the same nest, and the number of males detected by PIT antennas varied by nest (mean = 3, range = 1–6; Fig. 3a). An average of 11 females (range = 2–32) were detected per nest (Fig. 3a).

Mating system

Parentage analysis demonstrated a polygyandrous mating system in bluehead chub. A total of 139 male-female pairs was reconstructed from the parentage analysis, and 43 pairs were between sampled males and females. The remaining 96 pairs were between sampled and inferred (unsampled) individuals and 88 pairs between inferred individuals (unsampled males and females). Both sexes typically mated with multiple

Fig. 3 Diagrams showing **a** encounters of males and females on nests using PIT antennas and **b** mating system based on genetic parentage analysis
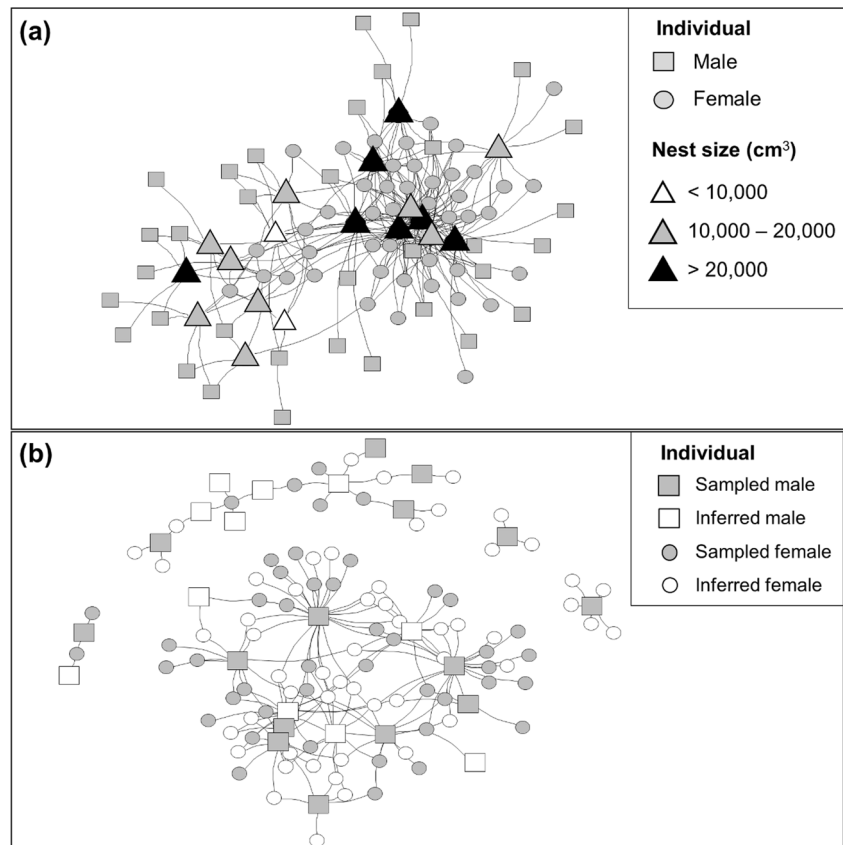
Table 2 A list of models to explain number of encounters at nests, ordered by ascending values of quasi-likelihood Akaike's information criterion corrected for small sample size (QAIC$_c$) for males and Akaike's information criterion corrected for small sample size (AIC$_c$) for females. Models differed in the combination of predictors, number of parameters (K), difference in AICc and QAICc between the given model and the top-ranked model (ΔAICc and ΔQAICc), and Akaike and quasi-likelihood Akaike weight (Weight)

Sex	Model	K	logLik	AIC$_c$/ QAIC$_c$	ΔAIC$_c$/ ΔQAIC$_c$	Weight
Male	Number of nests occupied + largest nest size occupied	3	− 156.31	66.99	0.00	0.53
	Number of nests occupied + largest nest size occupied + body size	4	− 151.07	67.82	0.83	0.35
	Largest nest size occupied + body size	3	− 169.68	71.92	4.92	0.05
	Number of nests occupied	2	− 178.73	72.68	5.68	0.03
	Largest nest size occupied	2	− 179.15	72.82	5.84	0.03
	Number of nests occupied + body size	3	− 176.29	74.36	7.36	0.01
	Null	1	− 245.68	94.94	27.95	0.00
	Body size	2	− 239.34	95.01	28.02	0.00
Female	Number of nests visited + largest nest size visited	3	− 99.73	203.75	0.00	0.38
	Number of nests visited	2	− 98.60	203.78	0.03	0.37
	Number of nests visited + largest nest size visited + body size	4	− 99.69	205.97	2.22	0.13
	Number of nests visited + body size	3	− 98.52	206.03	2.28	0.12
	Largest nest size visited	2	− 118.63	241.54	37.79	0.00
	Largest nest size visited + body size	3	− 118.50	243.58	39.83	0.00
	Null	1	− 126.66	255.41	51.65	0.00
	Body size	2	− 126.51	257.31	53.56	0.00

sampled and inferred mates (male, mean = 7, range = 1–26; female, mean = 2, range = 1–4; Fig. 3b). When using only sampled individuals, males mated with an average of 5 females (range = 1–12) and females mated with an average of 1 male (range = 1–2).

Number of encounters (Q1)

Males encountered, on average, 14 females (range = 1–42), and females encountered an average of 11 males (range = 2–22) across 18 nests. Behavior was more important than body size in increasing number of encounters with individuals of the opposite sex in males and females. Two competing GLMs were identified in both males and females (Table 2), and we report model-averaged effects of predictors. Males encountered with females more frequently by occupying multiple nests (coefficient = 0.28, SE = 0.11, 95% CI = 0.06–0.44; Fig. 4) and larger nests (coefficient = 0.41, SE = 0.15, 95% CI = 0.15–0.69). In females, visiting multiple nests increased encounters with males (coefficient = 0.37, SE = 0.06, 95% CI = 0.25–0.47; Fig. 4), but visiting larger nests did not significantly affect their encounters with males (coefficient = 0.14, SE = 0.09, 95% CI = − 0.02–0.33). Body size did not affect number of encounters in males (coefficient = − 0.17, SE = 0.12, 95% CI = − 0.40–0.06) or females (coefficient = − 0.02, SE = 0.05, 95% CI = − 0.12–0.08) (Fig. 4).

## Number of mates (Q2)

Number of mates, inferred genetically, was positively correlated with number of encounters based on PIT antenna data in males (Spearman $\rho = 0.64$, $P < 0.001$) (Fig. 5), suggesting that males who encountered with more females mated with more females. However, number of encounters did not affect number of mates in females (Spearman $\rho = 0.23$, $P = 0.13$) (Fig. 5).

Reproductive success (Q3)

Reproductive success (number of assigned offspring) was highly variable in males (mean = 10, range = 1–33) but not in females (mean = 2, range = 1–5). Competing models were identified in both sexes (Appendix S8); thus, we report model-averaged effects of predictors. The number of encounters outweighed body size in increasing male reproductive success, but female reproductive success depended on body size. Based on the ZIP model for males, encounters with more females not only minimized reproductive failures (logistic binary portion: coefficient = − 1.39, SE = 0.57, 95% CI = − 2.75–− 0.37) but also led to higher number of YOY assigned to them (Poisson count portion: coefficient = 0.78, SE = 0.10, 95% CI = 0.63–1.01) (Fig. 6). Male reproductive success did not depend on body size (logistic binary portion: coefficient = − 0.76, SE = 0.45, 95% CI = − 1.66–0.12; Poisson count portion: coefficient = 0.13, SE = 0.12, 95% CI = − 0.10–
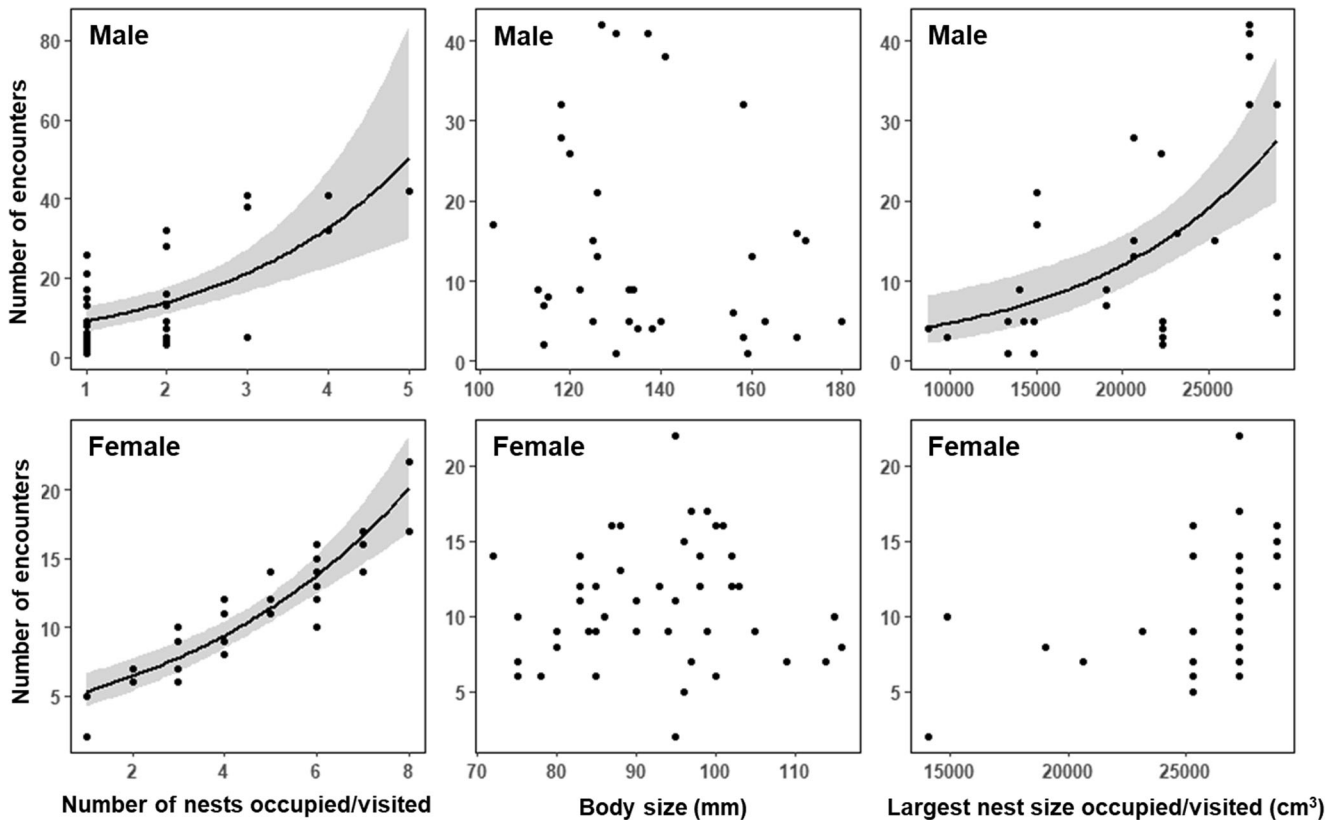
Fig. 4 Model-averaged effects of the number of nests occupied (males) or visited (females), largest nest size occupied or visited, and body size on number of encounters in male (top, 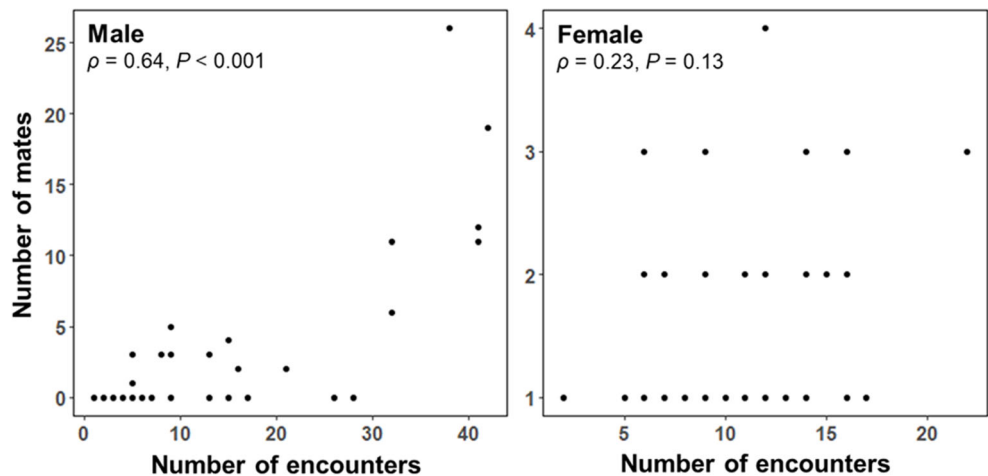$n = 34$) and female (bottom, $n = 45$) bluehead chub. Black lines indicate mean response, and gray shading shows 95% confidence interval

0.38) (Fig. 6). On the contrary, larger females had higher reproductive success (coefficient = 0.25, SE = 0.10, 95% CI = 0.06–0.46), but increasing number of encounters did not result in higher reproductive success in females (coefficient = 0.06, SE = 0.11, 95% CI = − 0.16–0.26) (Fig. 6). Finally, reproductive success increased with number of mates in males (coefficient = 1.37, SE = 0.08, $P < 0.001$) and females (coefficient = 0.90, SE = 0.13, $P < 0.001$) (Fig. 7).

Discussion

By tracking individuals aided by a combination of automated tracking systems and molecular markers, we characterized behavioral encounters and reproductive success of a small-bodied, nest-building aquatic species. We provided evidence that bluehead chub are polygynandrous, which could not be identified if based solely on direct observations of unmarked

Fig. 5 Relationships between the number of mates and number of encounters in male ($n = 34$) and female ($n = 45$) bluehead chub using the Spearman's rank correlation test

Fig. 6 Model-averaged effects of number of encounters and body size on reproductive success (number of offspring) of male (top, $n = 34$) and female (bottom, $n = 45$) bluehead chub. Black lines indicate mean response, and gray shading shows 95% confidence interval
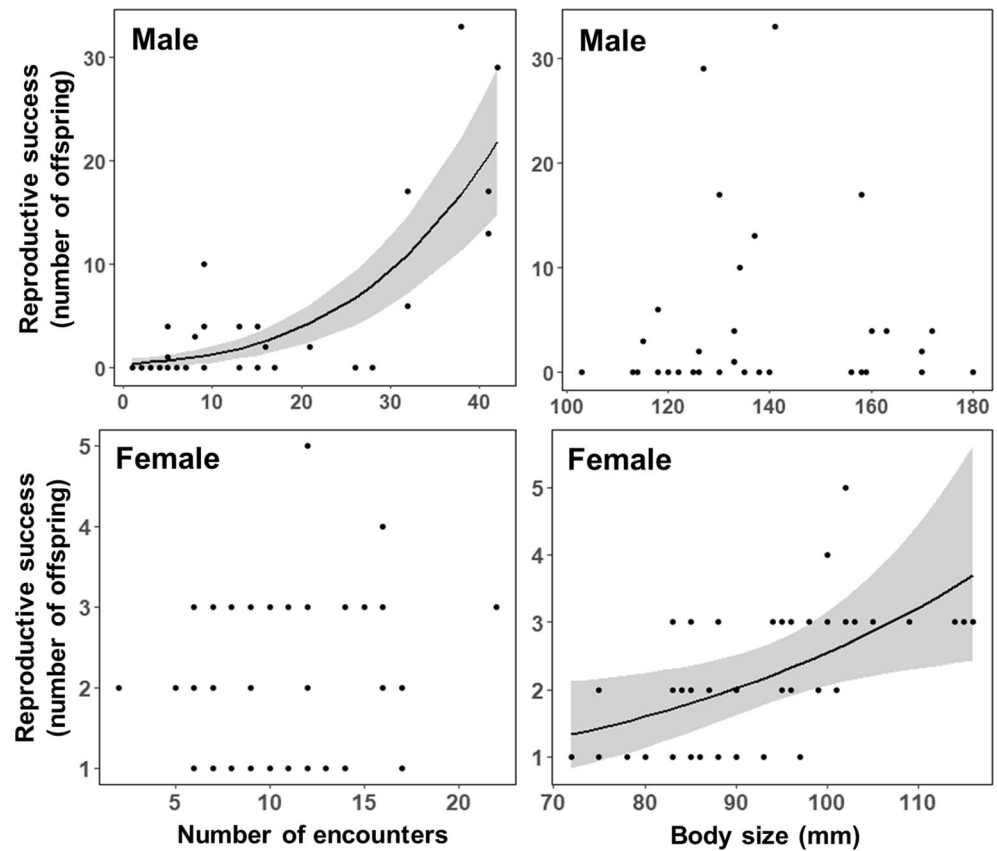
individuals during reproduction. Additionally, we discovered that animal behavior was more important than body size in explaining number of encounters with individuals of the opposite sex across nests (Q1), higher encounters resulted in mating with more partners in males but not in females (Q2), and ultimately reproductive success depended on number of encounters in males but body size in females (Q3).

The consistent lack of male body size effect on behavioral encounters and reproductive success was intriguing, given that body size differed greatly among males with reproductive success (range 115–172 mm in TL) and males were larger

than females (72–116 mm) (i.e., sexual dimorphism) in the study population and others (Lanchner 1952; Jenkins and Burkhead 1994). Males typically compete with each other for gaining access to females, involving physical interactions in which larger males outcompete smaller ones (Lehtonen et al. 2007; Bose et al. 2018). Agonistic behavior among males to secure space on nests was observed in this study (SK, pers. obs.) and other studies of bluehead chub (Wallin 1989; Sabaj et al. 2000; Kim et al. 2020). The finding that just 15 out of 49 males detected on nests by PIT antennas had reproductive success similarly indicates that competition

Fig. 7 Relationships between the number of mates and reproductive success (number of offspring) of male ($n = 15$) and female ($n = 45$) bluehead chub using linear models. Black lines indicate mean response, and gray shading shows 95% confidence interval. Points were jittered for visual clarity
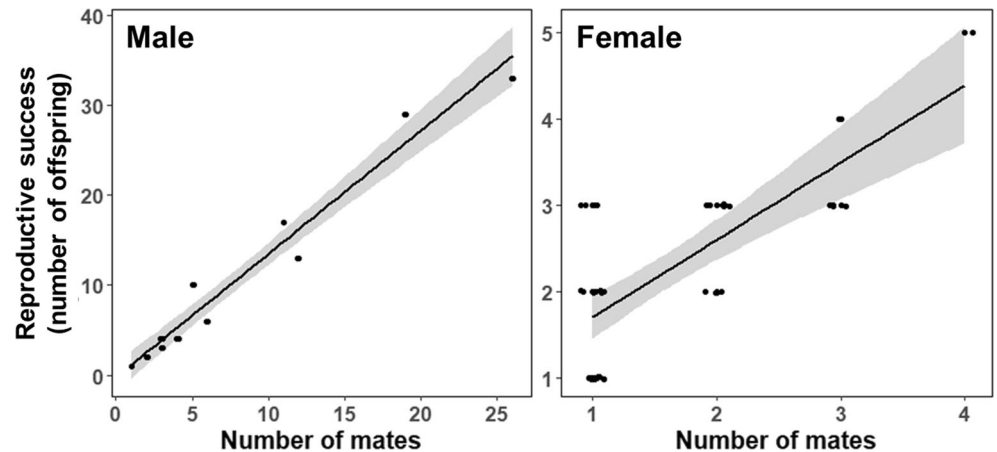
among males occurred during nest establishment and subsequent reproduction. Body size is a key factor of male reproductive success in some species, in which males compete with each other to gain access to females (Brooks and Couldridge 1999; Friedl and Klump 2000; Leiser et al. 2015). When males construct nests (e.g., bluehead chub), males must attract females to their nests for mating. Several tactics to attract females have evolved in males, including auditory signals (Trainer and McDonald 1995; Bose et al. 2018), behavioral display (McDonald and Potts 1994), and nest size and quality (Soler et al. 1998; Lehtonen and Lindström 2009). In nest-building species, male body size may not always be the most influential trait in determining reproductive success (Gross 1996). We acknowledge that this study was conducted in a single stream for one spawning season due to the exhaustive field sampling. Additional research is needed to ascertain whether male body size is not a key factor affecting behavioral encounters and reproductive success over space and time in bluehead chub (Lehtonen et al. 2010).

Behavior of males explained their variation in number of encounters with females and reproductive success, which differed widely among males (range = 1–33 offspring) in comparison with females (range = 1–5). The relationship between increased males' encounter with females and subsequent reproductive success is likely the result of two reasons. First, occupying more nests increased number of encounters with females that led to higher reproductive success. Male bluehead chub move thousands of pebbles by mouth to construct their nests and provide care for the nests for 5–15 days after spawning (Wallin 1992). Although males seemingly expend much energy in nest construction, potential for increased reproductive success may offset such a cost, particularly when females are abundant. In this study, we recorded 45 females with reproductive success in an 880-m study area and inferred genetically 54 additional females that had evaded capture by electrofishing (Appendix S4). These data indicate that potential mates were commonly available for males. Second, males who built larger nests were more reproductively successful. More encounters with females occurred at larger nests (Fig. 3a). In addition, Kim et al. (2020) reported that larger nests attracted more individuals of yellowfin shiner, which also spawn on nests of bluehead chub in the study area. Yellowfin shiner greatly outnumber bluehead chub when these species spawn together (Fig. 2), and these additional yellowfin shiner eggs reduce predation risk on chub eggs (i.e., dilution effect) while eggs incubate in nests (Cashner and Bart 2010; Silknetter et al. 2019). In males, behavior indicative of reproductive effort (i.e., occupying more or larger nests) increased encounter with females, which then resulted in higher number of mates and ultimately higher reproductive success in this nest-building species.

In contrast, body size was more important than number of encounters in female reproductive success. Similar to males, females increased their encounter with potential mates by visiting more nests. However, higher encounter neither led to an increased number of mates nor reproductive success in females. This result indicates that females visit nests constructed by males, but they may not always mate with those males. Females play the primary role in mate choice in many species, especially when males build nests (Barber 2013; Leiser et al. 2015). In fact, females likely have choices among nests or males during spawning because bluehead chub spawn periodically at intervals within local streams, in which spawning occurs on multiple nests on the same days followed by a lack of spawning activities for up to 1 week (Kim and Kanno 2020). Egg production is more energetically costly than sperm production, and female reproductive success is typically influenced by fecundity (Trippel et al. 1997; Barneche et al. 2018). In our study, females with reproductive success ranged in body size between 72 and 116 mm in TL, and this translates into approximately a fivefold increase in estimated number of eggs from the smallest (92 eggs) to the largest female (478 eggs) in Shoal Creek. We postulate that body size–dependent variation in female reproductive success could be even greater in larger streams (e.g., Sixmile Creek) than Shoal Creek, which contained a narrower range of female body size due to its small stream size. Body size range of females was 76–151 mm in TL in Sixmile Creek, and given the exponential increase in fecundity with body size (Appendix S7), estimated number of eggs ranged from 111 to 1188 among females in Sixmile Creek.

In addition, female reproductive success increased with number of mates, a behavioral mechanism independent of body size. It is plausible that mating with multiple males is a bet-hedging strategy by females when some nests fail to produce offspring. While we monitored 18 nests during the study period, four additional nests were not completed because increased stream flows due to precipitation events dislodged pebbles that formed nests (SK, pers. obs.). Nest failures occur at only modest increases in stream flows (i.e., without floods), and male bluehead chub cease nest construction and parental care when stream flows increase over a short period of time (Kim and Kanno 2020). Given uncertainties related to flow conditions when eggs incubate in nests (4–12 days: Wallin 1992), females could avert complete reproductive failures in a given season by mating with multiple males on different nests. Because male and female reproductive success increased by mating with more partners, this result should partly be responsible for the evolution of a polygynandrous mating system in bluehead chub. This study adds novel knowledge to this species' mating system by not only providing the first quantitative evidence for polygynandry but also the behavioral mechanism that explains why such a mating system may have been maintained.

Our intensive approach using individual identification indicates that only a portion of individuals that visit nests have reproductive success. Of 49 mature males detected at nests, 15 did not show behavioral signs of constructing nests and providing parental care based on their infrequent and short-term detections by PIT antennas. Our data cannot discern whether these 15 males attempted to reproduce but could not (e.g., outcompeted by other males), or they visited nests for non-reproductive reasons. Peoples and Floyd (2017) documented that individuals of other minnow species frequented nests of bluehead chub to feed on eggs. Our data indicate that some individuals of bluehead chub also visit nests for feeding or other non-reproductive purposes because body size of females with reproductive success was significantly larger than that of "potential females," a group of fish which likely included immature males and females that could not be identified in the field. If immature individuals indeed visit nests for feeding, eggs are likely important seasonal pulses of energy for them. We speculate that some immature individuals at the onset of the spawning season may take advantage of these resources to mature later in the spawning season because body size of spawning males decreases through the spawning season in bluehead chub (Kim et al. 2020). Given that other species use nests of bluehead chub and other *Nocomis*, reproductive interactions of conspecific and heterospecific mature and immature individuals are complex, but understanding the functional importance of nest association likely leads to novel insights on community assembly.

In conclusion, behavior outweighed body size in mediating reproductive success of males, but not females, in this nest-building species. The relative importance of behavior and body size on reproductive success varies among species and is context dependent (Gross 1996; Díaz-Muñoz et al. 2014). However, it remains largely unknown under which circumstances behavior outweighs body size and vice versa in affecting reproductive success. Bluehead chub provides an insightful case because their mating system is polygynandrous, and their reproductive behavior includes unique traits represented by shared use of the same nest by multiple males who may also construct multiple nests in a single reproductive season. It is plausible that increased complexities in male reproductive behavior in this species provide them with flexibilities to offset effects that body size may have on reproductive success. This hypothesis warrants additional research towards synthetic understanding of context dependency of behavior versus body size on reproductive success across species with a gradient of mating systems and behavioral complexities.

Compliance with ethical standards

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