ORIGINAL ARTICLE

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Male size and mating tactic influence proximity to females during sperm competition in bluegill sunfish

Abstract Many fishes are characterized by intense sperm competition between males that use alternative mating tactics. In externally fertilizing fishes, males' proximity to females during spawning can be an important determinant of fertilization success. Here, we assess how mating tactic, body length, speed during streak spawns, and periphery cover affect males' proximity to females during sperm competition in the externally fertilizing bluegill (*Lepomis macrochirus*). Bluegill are characterized by three mating tactics referred to as parental, sneaker, and satellite. Parentals are territorial and construct nests, while sneakers use a streaking behavior, and satellites use female mimicry to steal fertilizations from parentals. We show that a small body length is important for sneakers but not for satellites to obtain a close position to the female during spawning. Specifically, smaller sneakers obtain a closer position to females than larger sneakers in part by positioning themselves closer on the periphery of a parental's nest before streaking but show no difference in the speed at which they streak. The amount of peripheral vegetation around a parental's nest did not appear to affect proximity of sneakers to females, and there was no relationship between the amount of peripheral vegetation and the frequency of intrusions by either sneakers or satellites. Finally, parentals were farther from the female when a sneaker or satellite intruded than when they spawned alone with the female.

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Introduction

Sperm competition, defined as the competition between the sperm from two or more males to fertilize the eggs of a female, is a powerful yet often cryptic form of sexual selection (Hildemann and Wagner 1954; Parker 1970). To enhance the success of a male's sperm relative to those of a rival male's, sperm competition can lead to a wide range of behavioral, morphological, and physiological adaptations (Parker 1970; Smith 1984; Snook 2005). It is now well understood that males can differ in their competitiveness during fertilization (e.g., Gage et al. 1995; Arnqvist and Danielsson 1999), but the mechanisms underlying these differences are only beginning to be understood.

Fish exhibit a wide diversity of sperm competition ranging from mate monopolization to large breeding assemblages (Stockley et al. 1997; Taborsky 1998). Among fishes, species that have external fertilization are likely to experience higher levels of sperm competition than fishes with internal fertilization (Petersen and Warner 1998; Taborsky 1998). In such species, proximity of males to females during spawning can play an important role on the competitiveness of males' ejaculate. For example, closer proximity of a male to a female during egg release has been demonstrated to increase the male's probability of fertilization in brook trout, *Salvelinus fontinalis* (Blanchfield et al. 2003), Atlantic cod, *Gadus morhua* (Hutchings et al. 1999), and coho salmon, *Oncorhynchus kisutch* (Schröder 1973). Generally, all else being equal, the male that obtains a closer position to the female has a competitive advantage because his sperm is more likely to reach the egg first. Furthermore, eggs and sperm may quickly diffuse in the aqueous environment, particularly when the eggs and sperm are released in flowing or turbulent water (Petersen and Warner 1998; Petersen et al. 2001).

Research on sperm competition in externally fertilizing fishes has focused on males that use alternative mating tactics (Taborsky 1998). These tactics typically involve a "bourgeois" behavior in which the male obtains access to female gametes by monopolization and a "parasitic" behavior in which the male attempts to parasitize bourgeois

males (Taborsky 1998). The use of such tactics is widespread in fishes. For example, Taborsky (1998) found evidence for bourgeois and parasitic males in 140 externally fertilizing fish species from 28 different families. Parasitic males typically use a streaking tactic, whereby they obtain refuge on the periphery of a bourgeois male's territory and dart in to release sperm during egg release. Thus, remaining cryptic is paramount to ensure these males can circumvent female monopolization by bourgeois males and obtain a close proximity to females during egg release. Alternatively, parasitic males of some species use female mimicry, in which case, remaining cryptic is less important. Female mimics presumably deceive bourgeois males into perceiving them as females and allowing them to remain in their territory during spawning (e.g., Gross 1982; also see Hanlon et al. 2005).

In bluegill (*Lepomis macrochirus*), males are characterized by three mating tactics (Gross 1982; Neff et al. 2003). The bourgeois-type males are referred to as "parentals," which, in the population we study, become sexually mature at around the age of 7 years. Parentals construct nests in colonies, which number up to several hundred nests (Cargnelli and Gross 1996). "Sneakers" are young parasitic males (age 2–3 years) which mature precociously and steal fertilizations from parentals by hiding in the vegetation at the edge of a parental's nest and streaking in during a female dip (when she releases a small batch of eggs), stopping momentarily and releasing sperm (Gross 1982). If detected, sneakers are aggressively chased out by parentals. Sneakers grow into "satellites," which are older parasitic males (age 4–6 years) that mimic female morphology and behavior and can mislead parentals into identifying them as a second female in their nest (Gross 1982; Neff and Gross 2001). Parentals will allow satellites to access their nest and may even court them, suggesting that the parental often cannot distinguish them from true females (Gross 1982).

Here, we determine the proximity of bluegill males to females during spawning and assess sources of variation in proximity within each of the three mating tactics. For example, smaller sneakers may be more cryptic and be able to position themselves closer to the nest before streaking than larger sneakers and thereby obtain a superior spawning position than larger sneakers when the eggs are released. Conversely, larger satellites may better mimic females than smaller satellites because satellites as a group overlap with the lower end of the size distribution of mature females (Gross 1982). Better mimicry may allow larger satellites to obtain a superior spawning position than smaller satellites. We also determine the effect of speed during streaks (for sneakers) and peripheral vegetation on the proximity of males to females during sperm competition.

Methods

Study site

Filming of spawning bluegill was done in Lake Opinicon (Ontario, Canada: 44°16′N and 76°30′W) during the breeding season (May–July) of 2003. Lake Opinicon is an 890-ha mesotrophic lake which has a large native population of bluegill (Keast 1978). The breeding habitat and study population are described in Gross (1982) and Gross and MacMillan (1981). Our study involved breeding colonies ranging in water depth from 1 to 4 m along the north shore of the lake (see map in Gross and Nowell 1980).

In Lake Opinicon, parentals compete to construct nests in colonies, which number up to several hundred nests (Cargnelli and Gross 1996). The colonies vary in vegetative cover around the nests (Gross 1991). Spawning involves up to eight discrete bouts throughout the reproductive season, and at any one colony, spawning typically lasts for a single day. During spawning, a female enters a parental's nest, and, through a distinctive motion referred to as a "dip," releases a small batch of eggs (ca. 30–100) at her utmost horizontal position (Gross 1982). Egg release is accompanied by a distinctive quiver behavior performed by the female. A female may dip hundreds or even thousands of times within a parental's nest.

Proximity and body length measurements

Upon discovery of a spawning colony, nests were opportunistically selected for filming based on spawning activity between the hours of 11:00 and 17:00 Eastern Standard Time (EST). Using a self-contained underwater breathing apparatus (SCUBA), two SONY digital video cameras (Digital 8 DCR-TRV 140; Digital 8 DCR-TRV 250) housed in underwater Ikelite casings were introduced at a right angle to one another (based on directions of the optical axes) near the perimeter of a parental's nest and about 45 cm from the center of the nest. The cameras record 30 frames per second. The cameras did not appear to affect spawning behavior. A reference shot was taken at the beginning of each recording by placing an object of known size (length=8 cm) in the center of the nest, and this was later used to standardize the distance measurements. The object was chosen to approximate the height of a parental, and we displayed the object in the center of the nest because this is where most spawning occurs. A total of 794 min of spawning were filmed from nine nests (average=44 min per nest; range=9–79 min per nest).

We projected the films using an Epson PowerLite 600p projector on a white background (with a grid of 2.5×2.5-cm squares). The image was projected horizontally from a table, and its overall size was 64×48 cm (W×H), and the reference object was approximately 15 cm in length. We used the grid to ensure a consistent projection size of the image and that the image was not distorted. First, for spawning situations in which parentals and females were spawning alone, we obtained a distance measurement between the urogenital pores of the two individuals. From each camera, we took the frame involving the egg release (when the female obtained her utmost horizontal position and began to quiver) and measured the distance between the urogenital pore of the parental and the urogenital pore of the female as well as the horizontal and vertical distances

between the urogenital pores (such that the three vectors formed a right angle triangle). These distances were used to calculate the actual proximity of the urogenital pores based on the Pythagorean formula; i.e., the actual distance is the square root of $x^2+y^2+z^2$, where x and y represent the standardized horizontal distances between the urogenital pores from camera 1 and camera 2, respectively, and z represents the standardized vertical distance between the urogenital pores.

Next, proximity measurements were made when sneakers intruded on a spawning parental and female. The parental's proximity to the female was calculated as described above. For the sneaker, we obtained two proximity measurements and a time measurement because at egg release, sneakers were invariably at the nest edge and not ejaculating. Instead, these males would dart in a short time afterwards, stop momentarily near the female (and ejaculate), and then depart the nest. We calculated the proximity of the sneaker's and female's urogenital pores when female dipped (and the sneaker was at the nest edge) and when the sneaker reached his closest position to the female. We also measured the time difference between egg release and the moment when the sneaker reached his closest position to the female. We could not always get both distance measurements for individual sneakers, so our sample sizes differ for the two measurements.

Finally, proximity measurements were made when a satellite was spawning with a parental and female. We calculated the proximity of each male's urogenital pore to the female's urogenital pore at egg release. We assumed that parentals and satellites ejaculated at the same time (i.e., at egg release). This is a plausible assumption because both parentals and satellites spawn alongside the female, and the quiver likely cues the males to release their sperm. Furthermore, satellites dip synchronously with females.

To avoid pseudoreplication, proximity measurements taken on the same individual were averaged into a single data point for subsequent analyses. Although some sneakers and satellites repeatedly parasitized a given nest, they remained near the nest and within the field of view of the cameras. We therefore assumed that when a sneaker or satellite left the field of view of both cameras, he did not return to the nest.

Using the film footage, we also made body length measurements from the tip of the snout to the end of the hypural bones (standard length) for each spawning individual. As for the proximity measurements, the length measurements were made using corresponding frames from each camera and triangulation.

Although bluegill typically spawn close to the center of their nest, they do occasionally spawn closer to the perimeter of the nest, and when this occurs, there will be error in our standardization calculation because the reference object was placed in the center of the nest. To determine the potential error, we estimated the size of our reference object at distances of 35 and 55 cm from the camera lens using the standardization calculation based on the reference object at 45 cm from the lens (each camera was about 45 cm from

the center of the nest where the reference object was initially placed). We determined that objects 35 cm from the lens would be overestimated by 23%, while objects 55 cm from the lens would be underestimated by 17%. If all of spawning actually occurred at these distances (i.e., half at 35 cm and the other half at 55 cm), then our mean distance measurements would be overestimated by only about 3% [(23−17)/2]. The actual error is likely considerably lower because bluegill typically spawn near the center of the nest. Furthermore, any error should not lead to a systematic bias between parentals, sneakers, and satellites.

To examine the relationship between parental body length and their mean proximity to the female's urogenital pore, we used a simple linear regression. Next, for the sneaker body length data, we initially used three analyses of covariance (ANCOVAs), with nest ID entered as a random factor and body length entered as a covariate. The three dependent variables were (1) sneaker's closest proximity to the female's urogenital pore, (2) sneaker's proximity to the female's urogenital pore at the moment of the dip (i.e., egg release), and (3) the difference in time between the dip and the moment when sneakers obtained their closest position to the female's urogenital pore. Nest ID was entered as a random factor in the ANCOVAs to determine if there was an effect of individual nests or parental males on the proximity of sneakers to females. An analogous ANCOVA was used to compare satellite body length and their proximity to the female's urogenital pore. Each ANCOVA utilized a restricted maximum likelihood (REML) method, which is superior to a traditional method when the design is unbalanced (Lynch and Walsh 1998, p. 779). To display the various body length and proximity data, we then used a scatter plot and lines from simple linear regressions. These analyses examined the relationship between males' body length and their ability to get close to females' eggs.

To compare the proximity of parentals' urogenital pore to that of females' when parentals were spawning in the absence of a sneaker or satellite, in the presence of a sneaker, and in the presence of a satellite (sneakers and satellites are rarely present simultaneously during a female dip and were never both present in our sample), we used an ANOVA on mean proximity estimates for each parental and a Tukey's post hoc test.

Peripheral vegetation and cuckoldry

The grid drawn on the white background that the film was projected on was used to determine the amount of vegetation around the periphery of each parental's nest. The periphery of a parental's nest was defined as the area in which the parental was circling (Colgan et al. 1979). For each cell touching the periphery of the nest, the presence or absence of vegetation was recorded. Vegetation was defined as any plant that was present in a grid square. The amount of peripheral vegetation was calculated as the average proportion of cells from each camera angle that

contained vegetation. Next, to calculate cuckoldry frequency and female spawning frequency in each nest, we determined the number of intrusions per minute by either sneakers or satellites and the number of dips per minute by females. To establish the relationship between cuckoldry frequency and peripheral vegetation, we used a partial correlation between periphery vegetation and either sneaker intrusion frequency or satellite intrusion frequency, with female dip frequency controlled. We controlled for female dip frequency so any effect of peripheral vegetation on cuckoldry frequency would not be biased by female spawning frequency. We used simple linear regressions to establish the relationships between peripheral vegetation and the mean proximity of sneakers to the urogenital pores of females at the dip, the closest proximity of sneakers to the urogenital pores of females, and the difference in the time between egg release and the moment when sneakers obtained their closest position to females.

Speed of sneakers

In addition to peripheral vegetation, it is conceivable that a sneaker's speed while streaking into the nest could play a role in how close he gets to the female. To determine the speed of sneakers during streaking, we calculated the total distance traveled by subtracting a sneaker's closest proximity to the female's urogenital pore from the proximity to the female's urogenital pore while on the nest periphery. The time to travel this distance was determined by the number of frames that elapsed and multiplying this number by 30^{-1} s (the frame rate of the cameras). Finally, we divided the total distance traveled by the time to determine speed and expressed this in centimeters per second. We performed three ANCOVAs, the first two with sneaker body length entered as a covariate, nest ID as a random factor, and either speed or distance traveled as the dependent variable, and the third with distance traveled entered as a covariate, nest ID as a random factor, and speed as the dependent variable.

Statistical calculations were performed with SPSS (v. 13.0) and JMP (v. 4.0.4). All mean values are expressed with ±1 standard error. Statistical tests were performed with a two-tailed level of significance and $\alpha=0.05$. Where indicated, data were logarithm (base 10)-transformed to achieve a distribution that did not statistically deviate from normality.

Results

Proximity and body length measurements

The proximity measurements are summarized by nest in Table 1. There was no relationship between parental body length and proximity to the female's urogenital pore when spawning alone (Fig. 1), but there was a positive relationship when a sneaker intruded ($R^2=0.80$, $P=0.007$, $n=7$). There also may have been a positive relationship between parental body length and proximity to the female's urogenital pore when a satellite intruded ($R^2=0.96$, $P=0.12$, $n=3$), but we had insufficient data to effectively test this relationship. For sneakers, there was a positive relationship between their body length and the closest proximity obtained to the female's urogenital pore (ANCOVA with log-transformed data, $F_{1,28}=17.3$ and $P<0.001$; nest ID, $F_{6,28}=0.19$ and $P=0.98$; Fig. 1) and between their body length and proximity to the female's urogenital pore when the female dipped and sneakers were at the nest periphery (ANCOVA, $F_{1,36}=5.9$ and $P=0.020$; nest ID, $F_{6,36}=0.06$ and $P=0.99$; Fig. 2). There was no relationship between sneaker body length and the difference in the time between egg release and the moment when sneakers obtained their closest position to the female's urogenital pore (ANCOVA, $F_{1,29}=0.28$ and $P=0.60$; nest ID, $F_{6,29}=1.15$ and $P=0.36$).

Table 1 Summary of proximity measurements during spawning for nine nests in the bluegill sunfish (*Lepomis macrochirus*)

Nest	Parental proximity			Sneaker proximity			Satellite proximity (mm)
	Alone (mm)	Sneaker (mm)	Satellite (mm)	Closest (mm)	At dip (mm)	Time (s)	
1	13±0.1 (39)	36±0.6 (12)	–	48±8 (9)	184±15 (12)	0.31±0.09 (10)	–
2	13±0.1 (49)	30±1.0 (6)	–	41±6 (5)	195±60 (6)	0.44±0.11 (5)	–
3	17±0.4 (9)	8±0.1 (5)	–	35±8 (4)	100±10 (5)	0.35±0.13 (4)	–
4	10±0.1 (45)	19±0.5 (13)	–	24±5 (6)	179±25 (8)	0.97±0.31 (6)	–
5	8±0.0 (42)	–	–	–	–	–	–
6	9±0.1 (20)	22±0.5 (7)	84±2.2 (5)	45±14 (7)	184±11 (7)	0.33±0.07 (7)	11±1 (5)
7	10±0.1 (21)	–	42±0.2 (43)	–	–	–	14±2 (11)
8	8±0.1 (36)	18±0.6 (2)	–	42±24 (2)	83±20 (2)	0.45±0.22 (2)	–
9	11±0.1 (24)	27±0.3 (13)	67±1.3 (4)	29±4 (3)	160±40 (4)	0.35±0.11 (3)	26±5 (4)
Average	**11±1**	**23±3**	**64±12**	**38±3**	**155±17**	**0.46±0.09**	**17±5**

Means are displayed ±1 standard error, with the sample size in parentheses. The average of nest means is displayed in bold at the bottom of the table

The data comprise mean proximity of male and female urogenital pores for parentals, sneakers, and satellites. Parental data consist of three spawning situations (alone, during a sneaker intrusion, and during a satellite intrusion), and sneaker data consist of three measurements (closest proximity to the female, proximity at the moment of the female dip when eggs are released, and the time elapsed between the dip and when sneakers obtained their closest proximity)

Fig. 1 The relationships between male body length and proximity to females during spawning in bluegill sunfish (*Lepomis macrochirus*) for three male mating tactics: sneakers (*filled circles*; $R^2=0.25$, $P=0.002$, $n=36$), satellites (*open circles*; $R^2=0.01$, $P=0.68$, $n=20$), and parentals (when spawning alone with female; *filled triangles*; $R^2=0.01$, $P=0.76$, $n=9$)
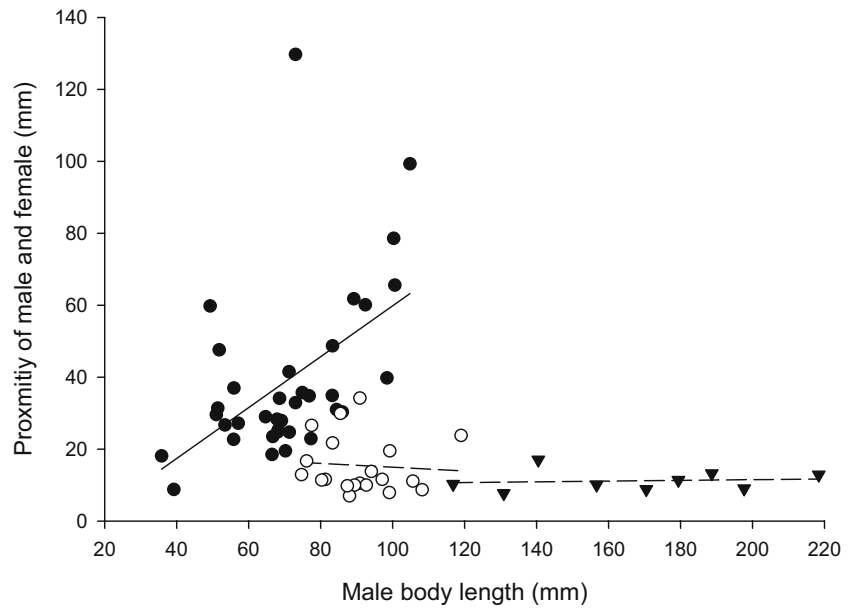
There also was no relationship between satellite body length and proximity to the female's urogenital pore (ANCOVA, $F_{1,16}=0.61$ and $P=0.45$; nest ID, $F_{2,16}=6.7$ and $P=0.008$).

There was significant variation in the distances of a parental's urogenital pore to a female's urogenital pore when spawning alone (i.e., without intrusion, 11.1±1.0 mm), during a sneaker intrusion (23.0±3.4 mm), and during a satellite intrusion (64.3±12.4 mm; ANOVA with log transformed data, $F_{2,16}=26.0$ and $P<0.001$; Fig. 3). A Tukey's post hoc analysis revealed that all three distances were significantly different from one another ($P<0.01$ for each comparison).

Peripheral vegetation and cuckoldry

The average proportion of peripheral vegetation around a parental's nest was 0.38 (range=0.18–0.76). There was no relationship between peripheral vegetation and mean sneaker intrusion frequency ($r=0.19$; $P=0.66$, $n=9$), or satellite intrusion frequency ($r=-0.54$, $P=0.17$, $n=9$) when controlling for female dip frequency. There also was no relationship between peripheral vegetation and the mean proximity of sneakers to the urogenital pore of females at dip ($R^2=0.01$, $P=0.87$, $n=7$), the mean closest proximity of sneakers to the urogenital pores of females ($R^2=0.09$, $P=0.51$, $n=7$), or the

Fig. 2 The relationship between sneaker body length and proximity to females at egg release in bluegill sunfish (*Lepomis macrochirus*). *Different symbols* represent nests from which data were collected, and the *line* is from a linear regression ($R^2=0.12$, $P=0.019$, $n=44$)
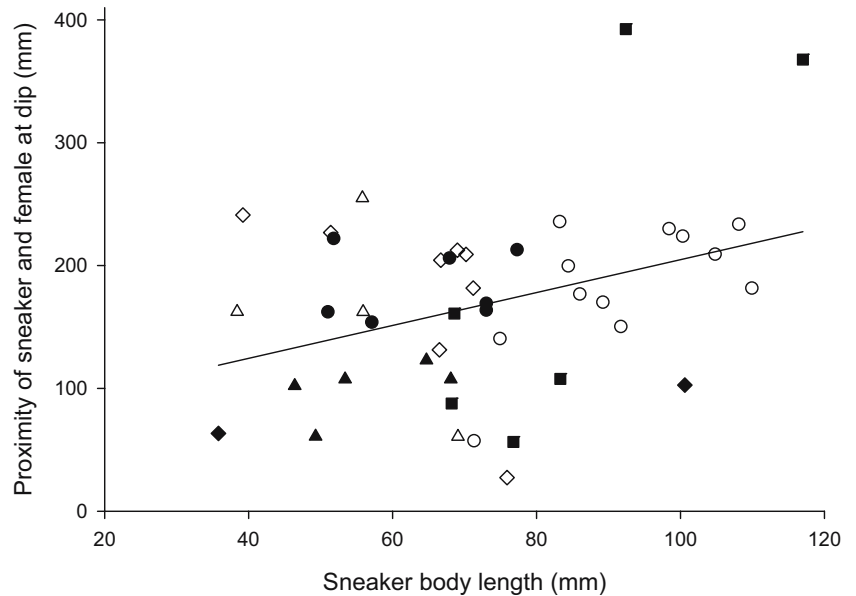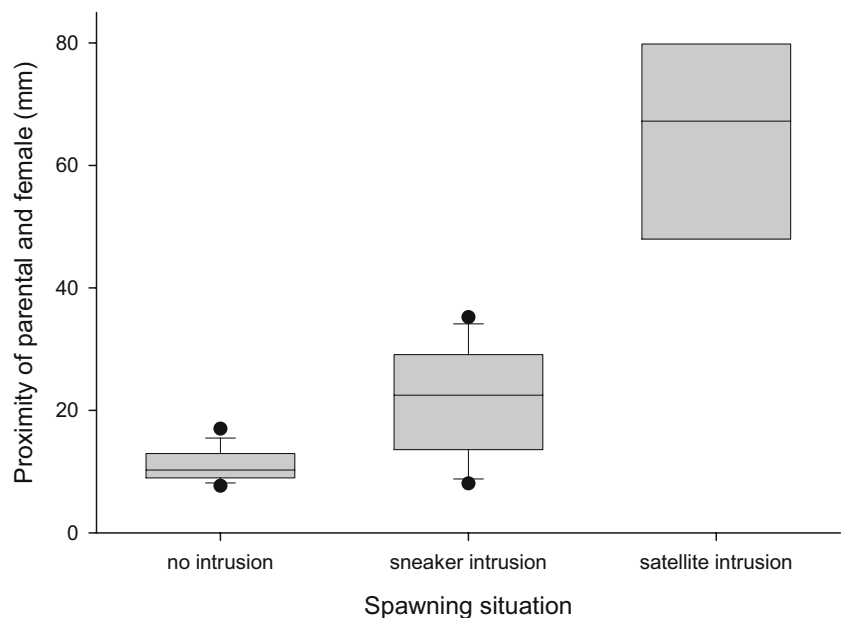
difference in the time between egg release and the moment when sneakers obtained their closest position to the females (R^2=0.02, *P*=0.79, *n*=7).

Speed of sneakers

Average sneaker speed was 44.9 cm/s (range=3–190 cm/s, *n*=36). There was no relationship between sneaker body length and speed (ANCOVA on log-transformed data, $F_{1,28}$=1.69 and *P*=0.20; nest ID, $F_{6,28}$=0.36 and *P*=0.90) or distance traveled (ANCOVA, $F_{1,28}$=0.21 and *P*=0.65; nest ID, $F_{6,28}$=0.53 and *P*=0.78). There was a positive relationship between the distance traveled and speed (ANCOVA on log-transformed data, $F_{1,28}$=12.4 and *P*=0.002; nest ID, $F_{6,28}$=0.63 and *P*=0.71).

Discussion

Alternative male mating tactics have been described in a variety of fishes (reviewed by Taborsky 1994; Henson and Warner 1997). Generally, these mating tactics can be viewed as variations on a basic theme with large bourgeois males parasitized by smaller rivals during spawning (Taborsky 1997, 1999, 2001). Bourgeois males typically compete for access to females' gametes by monopolization, and parasitic males typically attempt to parasitize bourgeois males during spawning. Parasitic males show a diversity of behaviors used to compete for the fertilization of eggs, including streaking (Gonçalves et al. 2003) and female mimicry (Taborsky 1994; for other parasitic behaviors, see Taborsky et al. 1987; Le Comber et al. 2003). Most parasitic males use streaking, and these males rely on inconspicuous approaches or acting swiftly to fertilize eggs during spawning (Gross 1982; Taborsky et al. 1987). Thus, a small body size can increase success because smaller males are less conspicuous and may be more mobile and harder for bourgeois males to pursue (Taborsky 2001). Therefore, for parasitic males, and particularly those that streak, a small body size should enable them to obtain closer proximity to females during egg release.

In bluegill, we found that smaller sneakers do in fact obtain closer proximity to females than larger sneakers. Similarly, Gross (1985) showed in coho salmon that smaller parasitic males (called "jacks") were able to get closer to spawning females than did larger parasitic males. Jacks typically remain hidden, seeking refuge near nests, and streak in on females at oviposition. Conversely, in Atlantic salmon (*Salmo salar*), larger parasitic males (called "parr") achieve higher reproductive success than smaller parasitic males (Thomaz et al. 1997; Jones and Hutchings 2001; also see Garant et al. 2003), presumably because a larger body size leads to an advantage during male–male competition between parasitic males (Huntingford et al. 1990). Similar results to the Atlantic salmon studies were found in masu salmon (*Oncorhynchus masou*) (Koseki and Maekawa 2000). Thus, although a small body size may decrease the conspicuousness of parasitic males that streak, strong male–male competition between parasitic males may instead favor a larger body size. Furthermore, a small body size may have little importance for parasitic males that instead use female mimicry, as we found no relationship between body size and proximity to females among bluegill satellites.

In bluegill, how do smaller sneakers obtain a closer position to females than larger sneakers during spawning? Three factors that may explain this difference are the position on the periphery of the nest just before streaking, speed during the streak, and agility (e.g., turn rate and tortuosity). We found that smaller sneakers were able to position themselves closer to the female on the periphery of the nest just before streaking as compared to larger sneakers. Obtaining a closer position on the periphery of the nest

minimizes the distance sneakers need to travel to reach the female and may minimize the chance of detection by the parental. We could rule out speed because there was no relationship between sneaker size and speed. We did not have a measure of agility and therefore could not address the importance of this variable (but see Crompton et al. 2003 for an example in midges). Nevertheless, in bluegill, small sneakers appear to obtain closer proximity to the female in part by obtaining a closer position on the periphery of the nest just before streaking.

Intrusions by sneakers and satellites had a negative effect on the position that parentals obtain when eggs were released. Parentals were farthest from the female during a satellite intrusion, intermediate during a sneaker intrusion, and closest when spawning alone with the female. Satellites typically position themselves between the parental and female during spawning and displace the parental (Fu et al. 2001). Parental body size did not appear to affect proximity when parentals were spawning alone. However, larger parentals were actually farther from females when a sneaker intruded. During a sneaker intrusion, parentals may have to trade-off proximity to the female with nest defense against the intrusion, and it is possible that larger parentals are more vigilant.

We failed to detect any effect of peripheral vegetation on either the intrusion frequency of sneakers or their proximity to females. The effect of peripheral vegetation may require an understanding of the distribution and density of sneakers in colonies. Gross (1991) manipulated sneaker density and demonstrated that sneaker intrusion success was negatively density dependent—the more sneakers around a parental's nest, the lower the average success of sneakers. Gross (1991) argued that sneakers should distribute themselves among colonies and among nests within colonies to maximize individual success. As such, sneaker success among nests should be similar. If sneakers do indeed distribute themselves based on peripheral vegetation to maximize intrusion success and proximity to females (and therefore equate success across nests), then our analysis may not have been able to detect the relationships between peripheral vegetation and intrusion success or proximity. Detecting such a relationship may have required a manipulation of sneaker density as was performed by Gross (1991).

Finally, it is known that satellites fertilize an average of 67% of the eggs when in direct competition with parentals (Fu et al. 2001). Here, we have shown that this increased competitiveness is in part due to their closer proximity to eggs during spawning. However, sneakers fertilize an average of 89% of the eggs when in direct competition with parentals (Fu et al. 2001), but as we have shown here, sneakers are actually farther than parentals from the eggs and release sperm about half a second after parentals. Thus, proximity alone cannot explain the differences in fertilization success among mating tactics in bluegill. Other colleagues have shown that sperm from sneakers swim faster than sperm from parentals shortly after activation (Burness et al. 2004; but see Burness et al. 2005). Swim speed is an important determinate of fertilization success

(Gage et al. 2004), and thus, faster swim speed may help to explain the increase competitiveness of sneaker ejaculates. Finally, nothing is yet known about the numbers of sperm released by each male during competitive spawning; sneakers may be able to outcompete parentals by releasing more sperm. Elsewhere (Stoltz and Neff, unpublished data), we investigate the interaction of proximity of males to eggs during ejaculation, the timing of sperm release, and the number and quality of sperm released on fertilization success among male mating tactics in bluegill.

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