# Morphological and swim performance variation among reproductive tactics of bluegill sunfish (*Lepomis macrochirus*)

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**Abstract:** Ecomorphology examines the relationship between morphology and ecological characteristics often in relation to foraging, predation, and habitat use. However, ecomorphology may also be linked to reproductive behaviour ("tactic"), but few studies have examined this relationship. We examined bluegill sunfish (*Lepomis macrochirus* Rafinesque, 1819), a species in which some males become "parentals" while others adopt a parasitic "cuckolder" tactic. Parentals build nests, court females, and care for the young. Cuckolders instead act as "sneakers", darting into nests while females are releasing eggs, and then transition to "satellites", mimicking female appearance. We predicted that reproductive tactic would be associated with morphological variation and swimming performance. We collected bluegill parentals, sneakers, satellites, females, and juveniles to compare morphology, burst swim, and swim endurance. We found significant morphological variation among the groups, with only satellites and females having similar body shapes. Interestingly, satellites did not overlap in shape with sneakers, despite representing a single ontogenetic life history, providing evidence for a relationship between reproductive tactic and morphology. We also found that swim performance varied among the groups, with sneakers having the fastest burst swim and longest swim endurance. Our results indicate that reproductive tactic is an important factor in the ecomorphology of fish.

**Résumé :** L'écomorphologie examine la relation entre la morphologie et les caractéristiques écologiques, souvent en fonction de la recherche de nourriture, de la prédation et de l'utilisation de l'habitat. Cependant, l'écomorphologie peut aussi être reliée au comportement reproducteur (« tactiques reproductives »), bien que peu d'études aient examiné cette relation. Nous étudions le crapet arlequin (*Lepomis macrochirus* Rafinesque, 1819), une espèce dans laquelle certains mâles deviennent « parentaux », alors que d'autres adoptent une tactique de « cocufiage » parasite. Les mâles parentaux construisent un nid, courtisent les femelles et s'occupent des petits. Les mâles qui cocufient agissent en « intrus », se précipitant dans un nid alors que la femelle pond ses œufs et se transformant ensuite en « satellites », mimant l'apparence de femelles. Nous avons prédit que ces tactiques de reproduction seraient associées à la variation morphologique et à la performance de nage. Nous avons prélevé des crapets arlequins mâles parentaux, intrus et satellites, des femelles et des jeunes pour comparer leur morphologie, leur nage de pointe et leur endurance durant la nage. Il existe une variation morphologique significative entre les groupes et seuls les satellites et les femelles possèdent des formes corporelles semblables. Il est intéressant de noter qu'il n'y a pas de chevauchement de forme entre les satellites et les intrus, malgré le fait qu'il s'agit d'un même cycle de vie ontogénique, ce qui apporte des preuves d'un lien entre les tactiques de reproduction et la morphologie. La performance de nage varie aussi parmi les groupes et les intrus possèdent la vitesse de pointe la plus rapide et l'endurance la plus grande pendant la nage. Nos résultats indiquent que les tactiques de reproduction sont un facteur important dans l'écomorphologie des poissons.

[Traduit par la Rédaction]

## Introduction

Ecomorphology is a field concerned with describing the covariation of morphological features and ecological factors within and among species (e.g., Winkler 1988; Motta et al. 1995; Aerts et al. 2000). Ecomorphology has been examined in a wide range of taxa, including birds, fish, reptiles, and mammals. These studies have been able to relate form and function while gathering insights into the ecological pressures that drive morphological variation within ecosystems. Most studies to date have focused on the relationship between morphological characteristics and foraging patterns (e.g., Wainwright 1996; Bertrand et al. 2008; Figueirido et al. 2009), predator interactions (e.g., Hambright 1991), hormones (e.g., Moore et al. 1998; Knapp et al. 2003), or habitat use (e.g., Schluter and Rambaut 1996; de Medeiros and da Costa Ramos 2007; Velasco and Herrel 2007).

In fish, one area of ecomorphology that is often examined

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is the covariation between body shape and swimming performance in relation to different ecological niches. Swimming has been the focus of many studies of fishes because swimming is arguably the most important aspect of their fitness (Collar and Wainwright 2009), being essential for evading predators through to foraging efficiently. Additionally, the viscosity of their environment (i.e., water) results in unique demands for locomotion compared with terrestrial organisms. Swimming performance is tightly linked to morphology based on two general principles. The first principle is the ability to generate thrust, which in many fishes is related to the depth of the caudal peduncle (Webb 1984; Jastrebski and Robinson 2004). Deep caudal peduncles have been correlated with increased burst speed (initial swim speed; Webb 1984; Blake 2004; Fisher and Hogan 2007), whereas narrow caudal peduncles are associated with increased swimming endurance (sustained swimming period; Webb 1984; Webb and Weihs 1986). The second principle is drag, with increased body depth associated with increased drag as a fish moves through water (Ojanguren and Braña 2003). Deeper bodied fish tend to have slower burst speeds and reduced swimming endurance. Previous studies have found that deeper body forms benefit fish that consume cryptic prey by increasing their manoeuvrability to capture prey quickly once it has been spotted (Svanbäck and Eklöv 2002, 2003). Conversely, streamlined fish with increased burst speed are more likely to escape a predator (Webb 1984).

Although most studies have focused on relating variation in body shape and swimming performance to foraging and predation, reproductive behaviour should also play a role in the relationship between body shape and swimming performance. Fish have some of the most diverse reproductive tactics of all organisms, with many species exhibiting two or more tactics within a sex. The so-called alternative reproductive tactics commonly involve one type of male that courts females and defends them from other males and a second type of male that steals mating opportunities by streaking between a spawning pair or by mimicking female appearance (Taborsky 1998). Streak-type males must stealthily gain close proximity to the female at the time of oviposition to fertilize eggs (Blanchfield et al. 2003; Stoltz and Neff 2006). On the other hand, female mimics usually gain access to spawning females by deceiving territorial males (Dominey 1980). Because of these striking differences in behaviour, fish species with alternative reproductive tactics provide an exceptional opportunity to examine the influence of reproductive behaviour on morphology and swimming performance.

One common species that exhibits alternative reproductive tactics is the bluegill sunfish (*Lepomis macrochirus* Rafinesque, 1819). Male bluegill exhibit alternative tactics termed "parental" and "cuckolder" (e.g., Gross and Charnov 1980; Gross 1982). In a well studied population of bluegill in Lake Opinicon (Ontario, Canada, 44°34′N, 76°19′W), parentals sexually mature at approximately 7 years of age and then form breeding colonies, court females, and provide sole parental care for the young (Gross and Charnov 1980). The parental care period lasts up to 10 days, during which the parental does not leave the nest. Cuckolders mature at a much younger age and mate by stealing fertilizations from parentals (Gross 1982). Cuckolders first adopt a "sneaker" tactic (2–3 years old) and dart into nests while the female is releasing her eggs. As the cuckolders grow, they switch to a "satellite" tactic (4+ years old) and mimic the appearance and behaviour of females (Gross and Charnov 1980; Gross 1982). Though there have been some early studies examining body shape among the male tactics (e.g., Gross 1982; Ehlinger 1991; Ehlinger et al. 1997), no study in bluegill, or any other fish, has performed an analysis of covariation in body shape among all reproductive tactics within a species or contrasted their swimming performances.

In this study, we set out to compare both the morphology and swimming performance (burst swim and swimming endurance) of bluegill parentals, sneakers, satellites, females, and juveniles. Webb (1984) previously showed that a deeper body shape provides greater manoeuvrability than a streamlined form. Ehlinger (1991) subsequently expected that parental bluegill would benefit from increased manoeuvrability while hovering over their nest and protecting the young from brood predators; therefore, we predicted that parentals would have the greatest body depth. We expected that sneakers would instead be streamlined in body size but with a relatively large caudal peduncle to maximize their burst speed when darting into a nest to steal fertilizations. Additionally, satellite males were expected to be more similar to females in shape as part of their deception during spawning compared with males using other tactics.

## Materials and methods

### Fish collection

We collected 103 bluegill from Lake Opinicon during the period of 8–26 June 2009. Daily snorkel surveys of the littoral habitat were used to identify breeding colonies, and fish were collected using dip-nets starting on the first day that parentals formed nests until the day after spawning occurred. Initial classification of each fish was based on observation of their behaviour immediately prior to collection (see Knapp and Neff 2007). Subsequently, juveniles and cuckolders (sneakers or satellites) were distinguished based on total body length (mm) and gonadosomatic index (GSI; the ratio of gonad mass to body mass). Based on the findings of Gross (1982), we classified juvenile bluegill as those with minimal investment in their gonads, or a GSI of less than 1%; individuals with GSI of approximately 4% and total length < 100 mm were classified as sneakers; and satellites were those with about 3% GSI and total length ≥ 100 mm.

### Experimental procedures

All collected fish were taken to the Queen's University Biological Station and held in aquariums with flow-through water drawn directly from Lake Opinicon prior to experimentation. Experiments were completed within 6 h from the time of capture. We first assessed morphological variation in body shape among the five bluegill groups ($n$ = 26 juveniles, 20 females, 19 parentals, 19 sneakers, and 19 satellites). Photographs of the left side of each fish were taken with a Canon PowerShot A95 (5.0 megapixels) digital camera, and 20 homologous landmarks were placed on each image using tpsDig software (Rohlf 2008; Fig. 1). To describe and compare body shape across bluegill groups, we used partial warp analysis to compare variation across individuals and contrast differences among tactics (Sheets 2002; Zelditch et al. 2004).

**Fig. 1.** Illustration of a bluegill (*Lepomis macrochirus*) with the 20 homologous landmarks used in the morphological analysis comparing body shape among five bluegill groups (juveniles, females, parentals, sneakers, and satellites).
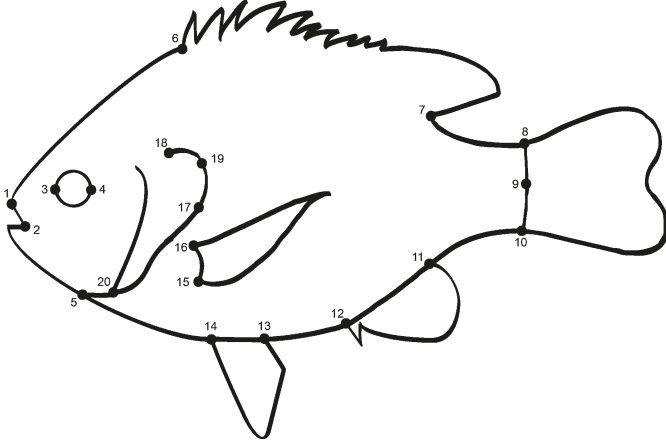


We also obtained measurements of total body length (to the nearest millimetre) from the mouth to the end of the caudal fin, maximum body depth (mm), and caudal peduncle depth (mm) from the digital images of each fish using tpsDig. Measurements of body depth (BD) and caudal peduncle depth (CP) were used to determine the caudal peduncle depth factor (CPDF) using the formula CPDF = CP/BD (Webb and Weihs 1986).

We assessed swim performance on a subset of the fish by obtaining a single burst speed and swimming endurance measurement for each fish ($n$ = 13 juveniles, 10 females, 10 parentals, 9 sneakers, and 11 satellites). Burst speed was estimated because of its predicted importance in the reproductive success of sneakers. We examined swim endurance to provide an estimate of the total swimming capacity of each group. Swimming capacity is important for parental males because they spend several days providing nest care behaviours, including fanning and circling the nest, without rest, and for cuckolders because they must search the littoral habitat for colonies in which to spawn (Gross 1991). Burst speed was tested first by placing the fish at one end of a Plexiglas aquarium (100 cm × 30 cm × 30 cm) oriented towards the far end. An adjustable wall was used to limit the ability of the fish to move in any direction other than forwards but with enough space to allow for their typical burst swimming behaviours (i.e., body coiled into the shape of an S). A high-speed camera (InLine 500, Fastec Imaging, San Diego, California) set to film at 250 frames·s$^{-1}$ was used to film the first 3 s of the burst response following a mild electrical stimulus (5V) used to induce swimming. The high-speed video was used to estimate the burst speed (cm·s$^{-1}$) of each individual during the initial 0.5 s after stimulation. After each trial, we did a complete water change in the aquarium.

Immediately after the burst speed test, the fish was placed in a 32 L swim flume (Swim-30, Loligo Systems, Tjele, Denmark) and left to acclimate for 5 min. The water flow was then set to 0.16 m·s$^{-1}$ and increased by 0.04 m·s$^{-1}$ every minute until the fish stopped swimming against the current. As in similar experiments (e.g., Boily and Magnan 2002), a mild electrical stimulus was applied to motivate the fish to swim when it stopped swimming and rested against a metal-

lic grid. When fish became unresponsive to the stimulus for more than 5 s, the test was ended and the total time (to the nearest second) was recorded as a measure of swimming endurance (e.g., Winger et al. 1999; Hanna et al. 2008). The tank was equipped with a pump that circulated water and assured oxygen levels close to saturation. The temperature of the water was monitored to maintain a range of 21–24 °C, and half of the water was changed every third trial to ensure a consistent environment across trials.

## Statistical analysis

To compare morphological differences across tactics, we compared the partial warp scores of each group using discriminant function analysis (DFA). Multivariate analysis of variance (MANOVA) was used to test for multivariate differences across the five groups. When significant differences were found among groups, post-hoc tests were completed using the Student's *t* test with Bonferroni correction for multiple comparisons to determine which groups differed (based on five groups being compared, significance level became 0.01 for post-hoc comparisons based on a family type I error of 0.05). The main patterns of shape differentiation across tactics were visualized using thin-plate splines produced by regressing each partial warp score onto each of the first discriminant functions using the software tpsRegr (Rohlf 2009). Next, the morphological scores of DFA 1 and DFA 2 for each bluegill were correlated to their total body length using Pearson's correlation coefficient. For each correlation, we visually inspected the residuals of the relationship on a normal probability plot. If the residuals did not conform to a nearly linear pattern, we used a permutation model based on residuals, as they are not prone to increased type I error, and increase the power of the parametric *t* test for Pearson's correlation when residuals are not normal (Anderson and Legendre 1999). To differentiate results based on these two types of approaches, i.e., parametric versus nonparametric (permutation-based test), we reported their associated probabilities as $P_p$ and $P_{np}$, respectively. Additionally, the sneakers and satellites were grouped together as cuckolders, as these individuals represent a single ontogenetic life history (Gross and Charnov 1980), and analyzed for a relationship between size and morphological scores. Next, DFA 1 and DFA 2 scores of sneakers and satellites were compared with the mean female morphological scores for both DFA axes to create a "female likeness" factor using the following equation:

$$(1) \quad \text{FL}_i = \sqrt{(\text{DFA1}_i - \overline{\text{DFA1}_f})^2 + (\text{DFA2}_i - \overline{\text{DFA2}_f})^2}$$

where $\text{FL}_i$ is the female likeness of the *i*th cuckolder, $\text{DFA1}_i$ and $\text{DFA2}_i$ are the scores for the *i*th cuckolder on a given axis, and $\overline{\text{DFA1}_f}$ and $\overline{\text{DFA2}_f}$ are the mean female scores for the two DFA axes. The female likeness scores were used in a logistic regression to test if there was a shift in cuckolder body shape associated with the transition from the sneaker to satellite tactic.

To remove size effects on swim performance, we used the Aitchinson (1986) log-ratio transformation as follows (see also Peres-Neto and Magnan 2004):

$$(2) \quad \text{rsp}_i = \log \text{sp}_i - \frac{(\log \text{sp}_i + \log \text{size}_i)}{2} + K$$

where $rsp_i$ is the relative swimming performance (endurance and burst were transformed separately) of the $i$th individual, $sp_i$ is the untransformed (original) swim performance measurement of the $i$th individual, size was determined based on the sum of all distances between each landmark and the body centroid (Zelditch et al. 2004), and $K$, representing the smallest rsp across all individuals, is included so that all $rsp_i$ values are positive. The transformed values for burst speed and swimming endurance across the five tactics were compared using analysis of variance (ANOVA). When groups were found to differ, pairwise comparisons were made using Student's $t$ test under the Bonferroni adjustment. The relationship between the two measures of swim performance was examined using Pearson's correlation.

To determine the relationships between swimming and morphological differences across tactics, we first looked for differences in scaling between length and maximum body depth among our groups using an analysis of covariance (ANCOVA) and examining the interaction term. After pooling the morphological scores, we correlated the first discriminant axis with burst speed and swimming endurance. To determine if the CPDF was related to burst speed and swimming endurance, we used Pearson's correlation; the probabilities were based on the same permutation procedure used earlier whenever residuals did not follow a normal distribution.

All analyses were performed in the statistical software package JMP v. 8.0 (SAS Institute Inc., Cary, North Carolina), and the level of significance for all tests ($\alpha$) was 0.05 for all tests without multiple comparisons. All means are reported plus or minus 1 standard error (SE).

## Results

### Morphological variation

The mean length, mass, and gonadsomatic index (GSI) scores for the five bluegill groups are presented in Table 1. DFA of body shape revealed significant differences among the groups (MANOVA, Wilks' $\lambda = 0.004$, $P < 0.01$), with 87% of the variation in body shape being explained by the first two discriminant axes: DFA 1 (63%) and DFA 2 (24%). Further examination of the DFA 1 scores found significant differences among the groups (ANOVA, $F_{[4,98]} = 245.0$, $P < 0.01$). Pairwise comparisons indicated that juveniles, parentals, and sneakers differed from each other and between all other groups (Student's $t$, $P < 0.01$ for each pairwise comparison). Females were found to be similar in body shape to satellites (Student's $t$, $P = 0.91$). Thin-plate spline analysis of DFA 1 showed that parentals had a deeper body form, particularly in the cranial region, in contrast to the streamlined body form of sneakers (Fig. 2). We also found differences among the bluegill groups based on the DFA 2 scores (ANOVA, $F_{[4,98]} = 93.0$, $P < 0.01$). Post-hoc comparisons found that the DFA 2 scores differed among all bluegill groups (Student's $t$, all $P < 0.001$). Thin-plate splines of DFA 2 showed that most of the variation in body form was related to the ventral portion of the head, pectoral fin insertion, and caudal peduncle shape (Fig. 2).

There was no relationship between body length and DFA 1 scores for females (Pearson's $r = -0.35$, $n = 20$, $P_{np} = 0.15$), parentals (Pearson's $r = -0.20$, $n = 19$, $P_{np} = 0.39$), or

sneakers (Pearson's $r = -0.01$, $n = 19$, $P_{np} = 0.94$). However, there was a relationship between these variables for juveniles (Pearson's $r = -0.83$, $n = 26$, $P_{np} < 0.01$) and satellites (Pearson's $r = -0.61$, $n = 19$, $P_p < 0.01$). Similarly, no relationship was found between body length and DFA 2 scores for females (Pearson's $r = 0.06$, $n = 20$, $P_{np} = 0.79$), parentals (Pearson's $r = -0.63$, $n = 19$, $P_p = 0.80$), or sneakers (Pearson's $r = 0.13$, $n = 19$, $P_{np} = 0.62$). However, in this case, there also were no relationships found for juveniles (Pearson's $r = -0.01$, $n = 26$, $P_p = 0.65$) or satellites (Pearson's $r = 0.28$, $n = 19$, $P_{np} = 0.27$). When we combined sneakers and satellites into a single cuckolder category, we found a significant relationship between body length and scores for DFA 1 (Pearson's $r = -0.86$, $n = 38$, $P_p < 0.01$) and DFA 2 (Pearson's $r = 0.75$, $n = 38$, $P_p < 0.01$). Finally, we found a strong logistic relationship between the female likeness scores and cuckolder body length, with the inflection point occurring at the transition between tactics (logistic regression, $R^2 = 0.82$, $n = 38$, $F_{[3,33]} = 52.27$, $P < 0.01$; Fig. 3).

The CPDF was significantly different among tactics (ANOVA, $F_{[4,96]} = 16.9$, $P < 0.01$; Table 1). Post-hoc comparisons revealed that sneakers, juveniles, and satellites had similar CPDFs (Student's $t$, all $P > 0.50$). Also, satellite and sneaker CPDFs were similar to that of females (Student's $t$, both $P > 0.02$; corrected $\alpha = 0.01$), but juveniles differed from females (Student's $t$, $P < 0.01$). Parental CPDFs were similar to CPDFs of females and satellites (Student's $t$, both $P > 0.03$), but differed from those of sneakers and juveniles (Student's $t$, both $P < 0.01$).

### Swim performance

The absolute and size-corrected (i.e., Aitchinson-transformed) values for swimming performance of each bluegill group showed limited differences in the rankings of burst speed, with only satellites and sneakers changing positions (Table 1). However, there were changes in the swimming endurance ranks, with sneakers and juveniles increasing in rank and parentals and females decreasing when the transformation was applied (Table 1). Comparison of Aitchinson-transformed burst speed showed significant differences among the five groups (ANOVA, $F_{[4,48]} = 4.86$, $P < 0.01$; Table 1), with sneakers having the fastest burst swim, satellites and juveniles having intermediate values, and parentals and females being the slowest. Similarly, the Aitchinson-transformed swimming endurance scores differed significantly among groups, with satellites having the relatively longest swim duration, followed by sneakers and parentals, with juveniles and females having the shortest swimming endurance (ANOVA, $F_{[4,48]} = 3.34$, $P = 0.02$; Table 1). Finally, across all groups combined, there was no relationship between burst speed and swimming endurance of individuals (Pearson's $r = 0.09$, $n = 53$, $P_p = 0.51$).

### Morphology and swim performance

We pooled the morphological scores of all groups to test for a relationship between DFA scores and swim performance after an ANCOVA indicated that the scaling between body length and depth was similar in all groups (ANCOVA: interaction term, $F_{[3,95]} = 0.68$, $P = 0.57$). Burst speed was positively correlated with DFA 1 (Pearson's $r = 0.33$, $n = 53$,

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**Table 1.** Summary of the mean (± standard error) values of fish measurements taken on bluegill (*Lepomis macrochirus*) classified into one of five groups.

| Group | n | Length (mm) | Wet mass (g) | GSI (%) | CPDF | Burst speed | | Swimming endurance | |
|---|---|---|---|---|---|---|---|---|---|
| | | | | | | Observed (cm s$^{-1}$) | Aitchinson transformed | Observed (s) | Aitchinson transformed |
| Juveniles | 26 | 123±6 | 39±6 | 0.3±0.1 | 0.300±0.002 | 43±7 | 1.5±0.1 | 240±41 | 0.56±0.09 |
| Females | 20 | 162±7 | 85±11 | 6.0±2 | 0.280±0.003 | 31±5 | 1.3±0.1 | 273±78 | 0.55±0.10 |
| Parentals | 19 | 196±2 | 148±8 | 1.3±0.2 | 0.280±0.003 | 40±6 | 1.3±0.1 | 445±75 | 0.69±0.09 |
| Sneakers | 19 | 78±3 | 9.7±1 | 4.0±0.4 | 0.300±0.003 | 43±5 | 1.8±0.1 | 266±43 | 0.92±0.09 |
| Satellites | 19 | 122±6 | 38±5 | 3.1±0.3 | 0.300±0.003 | 46±6 | 1.7±0.1 | 464±113 | 0.89±0.10 |

**Note:** Length measurement represents the total length from the mouth to the extended caudal fin (mm). The wet mass of each individual was used to calculate the gonadosomatic index (GSI), a measure of how much of the body is made up of the gonad tissues. Caudal peduncle depth factor (CPDF) was calculated as the ratio of caudal peduncle depth (mm) to maximum body depth (mm) and as a result is unitless. Also included are the measurements of burst swim and swimming endurance of each bluegill group before and after applying the Aitchinson (1986) log-ratio transformation to remove size as a factor. Aitchinson-transformed values are unitless.

**Fig. 2.** Discriminant function analysis (DFA) of body shape among five groups of bluegill (*Lepomis macrochirus*): juveniles, females, parentals, sneakers, and satellites. The scatterplot depicts the first two discriminant function axes: DFA 1 and DFA 2. Thin-plate splines were used to visualize the body shape associated with the extreme values for both DFA 1 and DFA 2.
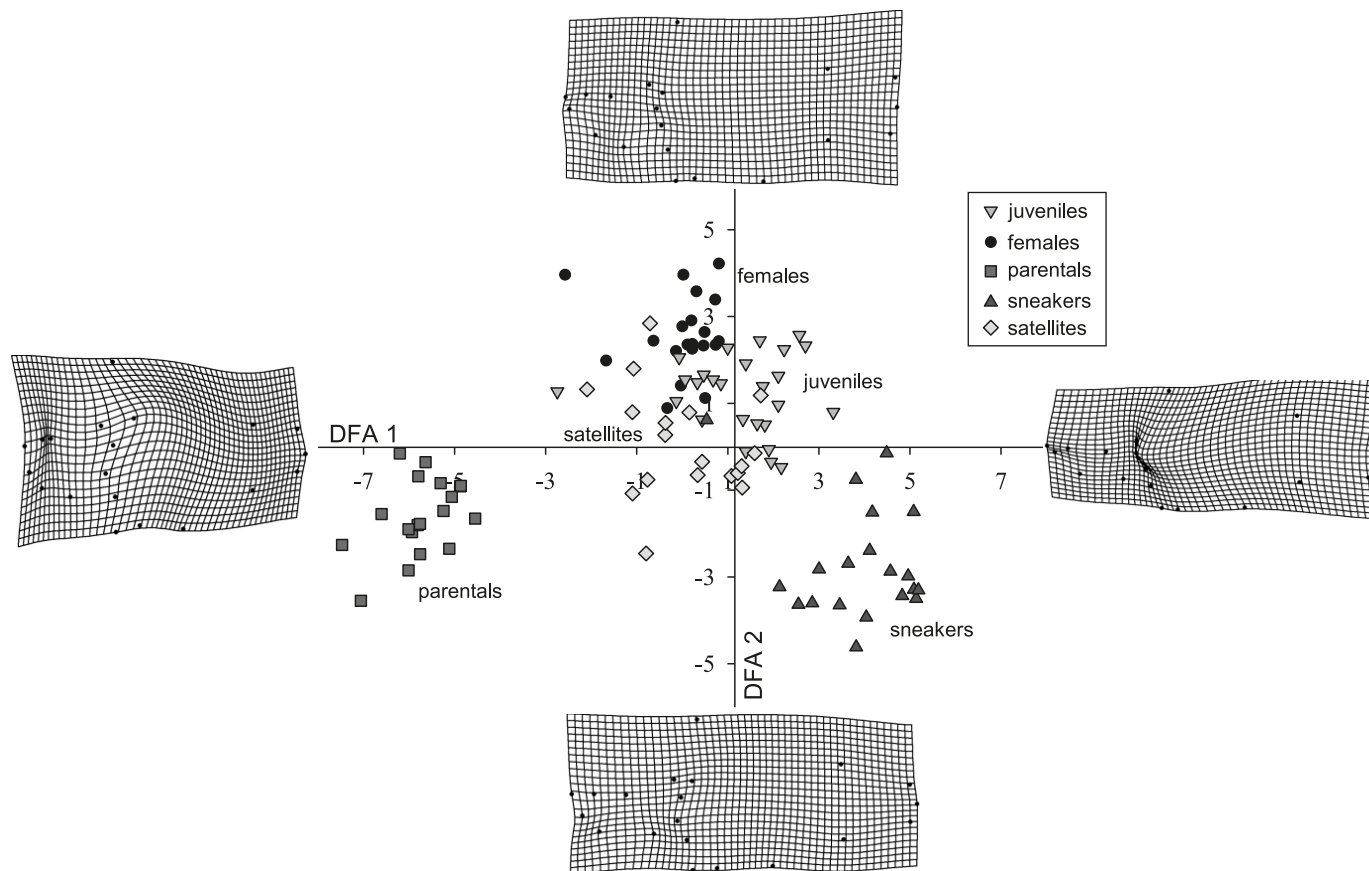


$P_{np}$ = 0.02; Fig. 4*a*), but no relationship was found between swimming endurance and DFA 1 (Pearson's *r* = 0.05, *n* = 53, $P_{np}$ = 0.74; Fig. 4*b*). Burst speed was negatively correlated with DFA 2 (Pearson's *r* = 0.34, *n* = 53, $P_{np}$ = 0.02; Fig. 4*c*), but no relationship was found between DFA 2 and swimming endurance (Pearson's *r* = –0.21, *n* = 53, $P_{np}$ = 0.13; Fig. 4*d*). Examination of the caudal peduncle depth found no relationship with either burst speed (Pearson's *r* = 0.16, *n* = 52, $P_{np}$ = 0.20) or swimming endurance (Pearson's *r* = 0.02, *n* = 52, $P_p$ = 0.89).

## Discussion

We examined morphological and swim performance variation within bluegill by classifying individuals into five groups based on sex, life history stage, and reproductive tactic. Each of these groups is likely under different selection pressures to optimize both survival and reproductive success, which we predicted should result in morphological differences. We found that sneakers had the most streamlined body shape of all bluegill, likely contributing to them having the fastest burst speed and longest swimming endurance. The increased

**Fig. 3.** Logistic regression of total body length and female likeness scores of sneaker (○) and satellite (●) bluegill (*Lepomis macrochirus*). Female likeness scores were determined based on the first discriminant function analysis axes 1 and 2, with higher numbers reflecting decreasing similarity in body shape between cuckolders and females.
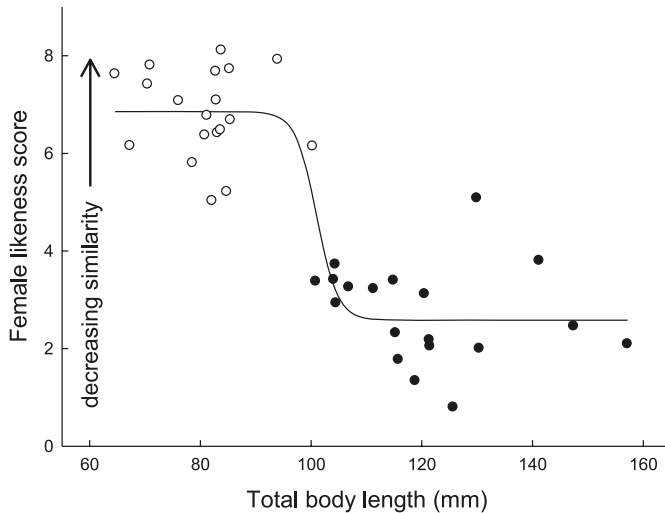


speed no doubt reflects their need to evade predators (Werner and Hall 1977) due to their smaller size, but likely also optimizes reproductive fitness as sneakers must quickly dart into the nest of parentals (Gross and Charnov 1980; Stoltz and Neff 2006). Indeed, sneakers differed in shape from juveniles of a similar size. Similarly, satellite body shape effectively mimicked female morphology, which presumably results in parentals misidentifying them as a second female and permitting them to enter their nest (Dominey 1980; Gross 1982; Neff and Gross 2001). Variation in body shape was not limited to cuckolders, as parentals had a deeper overall body shape than all other groups. The deeper bodies are predicted to facilitate parental care and defensive behaviours such as hovering over and circling the nest, fanning eggs, and rapid movements to chase away brood predators (Ehlinger 1991). Overall, the morphological variation among bluegill may be the result of a variety of selection pressures that vary with age, sex, environmental conditions, and reproductive tactic.

The observed differences in body shape between sneakers and satellites are particularly interesting because the tactics represent a single ontogenetic life history. Sneaking has been described as the most common form of alternative reproductive tactic (Taborsky et al. 1987), but satellites, mimicking female appearance, have been well documented in several species (e.g., Gonçalves et al. 1996; Hanlon et al. 2005; Whiting et al. 2009). However, unlike bluegill, in these other species, sneaking and satellite tactics typically represent independent life histories. We found that bluegill satellite morphology was similar to that of females, the group that they would need to mimic to deceive parental males that defend nests, but sneakers were different in shape from all other groups, including satellites. Importantly, the shift to female-like morphology coincided with the transition in mating tactic, providing compelling data for the influence of reproductive behaviour on morphology. Indeed, our results indicate that there may be strong selection related to reproductive suc-

cess in cuckolders, resulting in a change in morphology that leaves no detectable trace of sneaker morphology in satellite males. These data provide some of the first evidence establishing a strong relationship between reproductive tactic and morphological variation.

Morphological adaptations related to reproductive tactic are not necessarily the result of a single selection pressure, but may be the product of multiple selection pressures. Selection pressures influencing morphology may be antagonistic, resulting in trade-offs to optimize fitness, or reinforce each other and increase the fitness of certain morphological traits. Foraging ecology has been linked to morphology (e.g., Zweers et al. 1995; Figueirido et al. 2009) and therefore is a likely candidate for interacting with selection pressures related to reproductive tactic. In sunfish, morphological variation within some populations has been related to resource polymorphisms and population divergence between the littoral and pelagic habitats (e.g., Robinson et al. 1993; Jastrebski and Robinson 2004). For population divergence based on resource polymorphisms to be maintained, it is likely that reproductive behaviour is also involved, though, to date, no studies have shown this relationship. Reproductive tactics may interact with resource polymorphisms to support the separation of populations through the evolution of reproductive isolation mechanisms, eventually leading to speciation, or may maintain gene flow among groups limiting the potential for speciation (Coyne and Orr 2004). The relationship between different selection pressures is an avenue of research that should be pursued to further our understanding of how various factors such as reproductive tactic and foraging strategy interact and contribute to morphological variation.

Morphology is also an important factor in the swimming dynamics of fish, influencing both the generation of thrust and the drag created when moving through a viscous medium (Ojanguren and Braña 2003). A previous study of the closely related pumpkinseed sunfish (*Lepomis gibbosus*) associated a deep body form with a quick burst speed (Jastrebski and Robinson 2004), despite the increased drag associated with a deeper body form (e.g., Webb 1984). However, we found that burst speed was greatest in sneakers, the most streamlined bluegill group, and not the deeper bodied parentals. Jastrebski and Robinson (2004) only looked at pumpkinseed that would have been classified as females and parentals in our study, limiting the range of body depths that were examined and perhaps contributing to the apparent discrepancy across studies. Our findings are consistent with studies of other fishes, including that of the Eurasian perch (*Perca fluviatilis*; Svanbäck and Eklöv 2002, 2003), which found a strong relationship between streamlining and swim performance. Additionally, some studies have reported that swimming performance is less related to body shape, but is related instead to caudal peduncle depth, the region of the body responsible for the generation of thrust (e.g., Domenici and Blake 1997; Fisher and Hogan 2007). As such, it has been argued that the depth of the caudal peduncle relative to the total body depth, the CPDF, may be a strong predictor of swim performance because it captures both thrust potential and drag. However, we found no relationship between this factor and either burst swim or swimming endurance. Nevertheless, our results indicate that bluegill swimming perform-

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**Fig. 4.** Relationship between morphology and (*a*, *c*) burst swim or (*b*, *d*) swimming endurance of five groups of bluegill (*Lepomis macrochirus*): juveniles, females, parentals, sneakers, and satellites. Swim performance of each fish was assessed by measuring the burst swim response during the first 0.5 s following a mild electrical stimulus and the swimming endurance time (s) of fish placed against a current. All swim performance measurements were transformed using the Aitchinson (1986) log-ratio transformation to account for variability in the size of each fish and are therefore unitless. The DFA axis scores represent scores of morphological variation based on the discriminant function analysis of the five bluegill groups (see text for description).
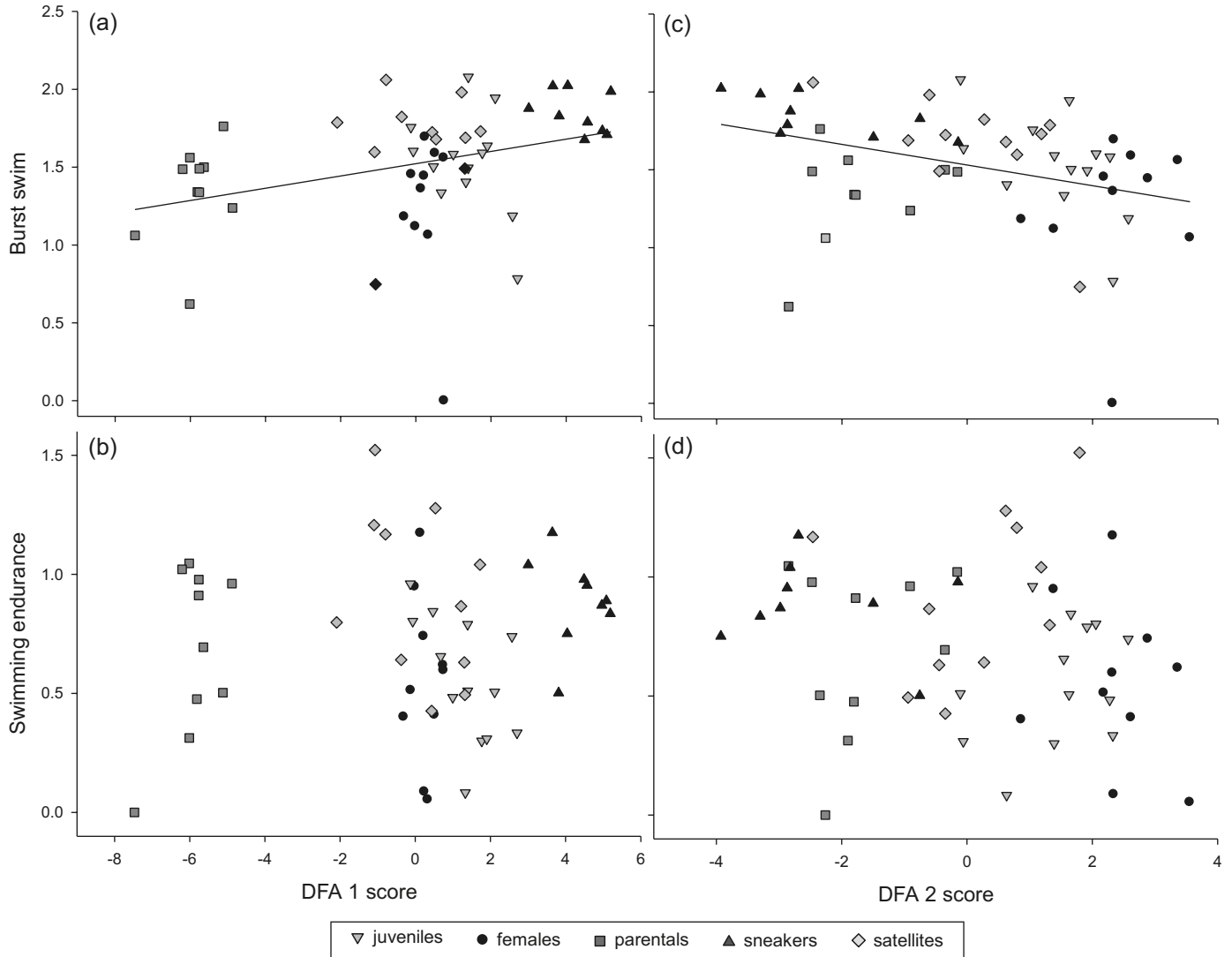


ance is negatively related to body depth and thereby implicates drag as a key factor governing swim performance.

Although these data support the prediction that reproductive tactic is related to morphology through swimming performance, it may not be the sole factor involved. We found no differences in the body shape of females and satellites on DFA 1, accounting for 63% of the variation in body shape, but satellites were significantly better at both burst swim and swimming endurance. This may reflect the different internal conditions of the fish based on reproductive investment. The females collected had a mean GSI of 6% compared with 3% for satellite males. This increased investment in gamete production may influence female swim performance in multiple ways. First, a greater amount of space in the body cavity of females is being filled by the ovaries compared with the testes of the satellites. The reduced space inside the body cavity may restrict the S-shaped movements required during burst swimming in bluegill (Jayne and Lauder 1993). Secondly, females may be in a lower energetic state after investing much of their energy into egg production. Koch and Weiser (1983) found that in roach (*Rutilus rutilus*), the cost of producing gametes in females was recouped by decreasing swimming activity. If a similar relationship between reproductive investment and swimming exists in female bluegill, it is possible that they had less energy available to allocate to swim performance.

In conclusion, we found variation among bluegill groups consistent with adaptations in morphology that may relate not just to survival and foraging, but also to reproductive tactic. Our data suggest that considering the relationship between reproductive tactic and morphological variation can enhance our understanding of the various selection pressures

involved in behaviour and morphology and can contribute to the field of ecomorphology and more broadly functional ecology.

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