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SHORT COMMUNICATION

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Does exaggerated morphology preclude plasticity to cuckoldry in the midshipman fish (*Porichthys notatus*)?

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Abstract In species with more than one male reproductive morph, there typically exists a larger morph with exaggerated secondary sexual characters, and a smaller morph with reduced secondary sexual characters. These "exaggerated" and "reduced" morphologies are commonly thought to represent specializations to alternative behavioral reproductive tactics—large body size and exaggerated secondary sexual characters should both facilitate territoriality, courtship, and pair-spawning; while small body size and reduced secondary sexual characters should facilitate "sneaky" cuckoldry. Given this postulated relationship between morphology and behavior, we examined the relationship between the morphology of exaggerated males and cuckoldry. In a field and aquarium study of the midshipman fish, a fish with both exaggerated and reduced morphs, we demonstrated cuckoldry in some males of the exaggerated morph. Since the "reduced" morphology is thought to be an adaptation towards sneaky cuckoldry, we predicted that, of males with the exaggerated morph, less-exaggerated (smaller) males would be better able to gain proximity to the spawning pair during cuckoldry. In contrast to that prediction, access to the spawning pair during cuckoldry increased with the body size of the cuckolding exaggerated-morph males. This may be related to our observation that exaggerated males often cuckolded aggressively. Thus the "exaggerated" morphology need not preclude adaptive plasticity to cuckoldry, and may even aid it.

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Introduction

In species with reproduction-based male dimorphisms, some males possess a morphology that is large in body size and decorated with exaggerated secondary sexual characters ("exaggerated morphology"), while other males possess a morphology that is by comparison small in size with reduced secondary sexual characters ("reduced morphology") (Gross 1996). Males of the exaggerated morphology may be specialized to fight for territories and court females, while those with the reduced morphology may be specialized to cuckold (Gross 1985; Moczek and Emlen 2000). Cuckoldry is a behavioral tactic that allows males to steal fertilizations from territorial, courting males without investing behaviorally in territory defense or courtship (Taborsky 1994).

Reports on dimorphic vertebrates tend to focus on behavioral differences between morphs, rather than behavioral plasticity within morphs (Taborsky 1994; Gross 1996). Here, we report on a study in midshipman fish (*Porichthys notatus*), in which we determined whether males with the exaggerated morphology exhibit behavioral plasticity that includes both territoriality and cuckoldry.

Early in development, male midshipman fish adopt alternative growth trajectories leading to one of two reproductive morphs known as type I and type II (Bass 1996). Type I males are up to seven times the body mass of type II males (Brantley and Bass 1994). This growth apparently enables larger males to better obtain territories and sire more offspring (DeMartini 1988). Type I males also invest in sonic muscle and associated neural circuitry for acoustic communication during courtship and aggressive interactions (Bass 1996). By comparison, type II males are smaller in body size, invest in larger testes (relative to their body size) that aid in sperm competition, and have reduced sonic muscles and associated neural circuitry. Thus type I males appear specialized for territoriality and courtship, and type II males for cuckoldry.

A relationship in which morphology precludes adaptive behavioral plasticity may be illustrated in the type II

male midshipman. Type II males will not hold territories or court even when offered empty nest sites and females (Brantley and Bass 1994), indicating that type II males are behaviorally fixed as cuckolders. Behavioral rigidity could reflect limitations of their small bodies, which should make it difficult to win in agonistic encounters, and limitations of their drastically reduced sonic muscles and associated neural circuitry, which are insufficient for the production of effective courtship and aggressive vocalizations (Brantley and Bass 1994). Thus, the type II morphology may prevent behavioral plasticity from cuckoldry to courtship.

Here we report a study that tested whether type I males are behaviorally plastic between territoriality and cuckoldry.

Materials and methods

Midshipman fish are distributed along the west coast of North America, where males nest under rocks in the intertidal zone from April to July (DeMartini 1988). From 2000 to 2002, we combined field observations with aquarium manipulations in Washington State, USA.

Aquarium observations

Type I males were collected from Seal Rock Beach (Hood Canal), Washington, in May 2000 and 2001, transported to the Big Beef Creek Field Station in Seabeck, Washington, and fitted with plastic identification tags. To create a situation in which cuckoldry would be adaptive, eight type I males were placed in a large aquarium (1.8×1.8×0.5 m) with four shelters; thus there were twice as many type I males as potential nests. Each shelter consisted of a square ceramic tile, either 30.5×30.5 cm or 40.5×40.5 cm, propped up on a rim of bricks, with one opening that served as the nest entrance. Neither males nor females showed any preference over the two nest sizes in terms of male competition over nests and female choice of a spawning site, so data from the two sizes were combined in our analyses. The male size distribution in each tank reflected the size distribution observed at Seal Rock Beach (see legend to Fig. 1). We replicated this four times in 2000 (experiment ran 24 days) and seven times in 2001 (experiment ran 18 days), totaling 88 type I males. Two type II males were also added to each tank in 2000, but not in 2001 because of difficulties in obtaining them. Nests with multiple type I males, spawning females, but no type II males are common at the field site (personal observation). Type I and type II males were distinguished by a suite of morphological characters (Bass 1996). One female was added to each tank between 2200 hours and 2400 hours; we observed the spawning the following morning. This female-to-nest ratio of one-to-four approximated the ratio observed in the field; the field ratio is one female to 3.5 nests; n=182 nests (A. Bass and A. Lee, unpublished data). For each spawning, we watched for two 15-min periods. Each tank was observed for an average of nine periods (4.5 spawnings). Males quickly inhabited shelters and acoustically advertised for females, and females readily spawned.

Nest residence

We predicted that larger type I males would be more able than smaller type I males to monopolize nests, so we fitted a regression to the proportion of nights spent inside nests as a function of body size rank. The tank in which each fish resided was set as a random effect.

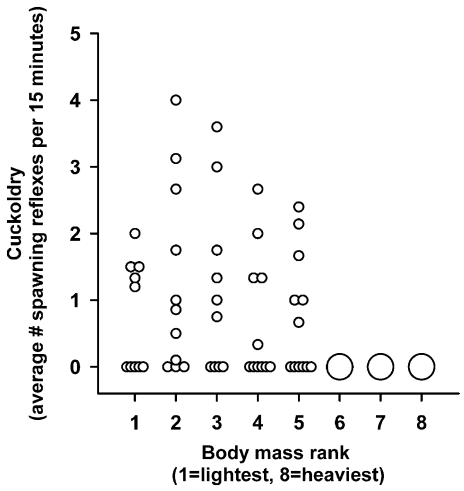

Fig. 1 Cuckoldry rates varied greatly among type I males of the smallest five size ranks, while type I males of the heaviest three ranks never cuckolded (aquarium data). The male size range in each tank reflected the size range observed at Seal Rock Beach (body masses were ranked from lowest to highest in each tank; average for body mass ranks 1 through 8, respectively: 71, 85, 108, 126, 151, 170, 204, 237 g). Each of the three *large circles* represents 11 overlapping data points

Cuckoldry rate

For the spawnings in which a given male was seen outside of a nest, we calculated the average number of cuckoldry events performed by that male per observation period. Cuckoldry events were quantified as the number of spawning reflexes conducted by a male other than the territory-holding male. Spawning reflexes are stereotyped motions that accompany sperm release (body rotates slightly about the long axis, followed by rapid anal fin quivering; see Brantley and Bass (1994) for midshipman fish; Neat and Locatello (2002) for a blenny). Males never observed to cuckold had cuckoldry values of zero.

Cuckoldry proximity

Sperm competition theory and previous studies predict that cuckoldry success increases as the cuckolder achieves closer proximity to the eggs, particularly in species that spawn on territories in nests, as do midshipman fish (Taborsky 1994). We calculated the percentage of time each male spent cuckolding with his tail inserted into the entrance of the nest, or with its entire body inside the nest, since cuckolding from those locations affords greater proximity to the eggs than cuckolding from outside the nest. For those males that cuckolded consistently (cuckoldry rate >1), we compared the cuckoldry proximity of the smallest and largest cuckolder in each tank using a Wilcoxon signed-rank test (calculated for 2001 only because cuckoldry locations were not recorded in 2000). Procedures followed National Institutes of Health guidelines for the care and use of animals and were approved by the Cornell University Institutional Animal Care and Use Committee.

Field low-tide surveys

We inspected 50 randomly selected rocks at low tide at a private beach on the Hood Canal (Brinnon, Washington) in 2001 and 2002. A male was designated as a territory holder if he was the only type I male under a rock, and if a female was spawning with him (see Brantley and Bass 1994). A female was designated as spawning if she was found upside-down under the rock (females invert them-

selves in order to deposit eggs on the rock undersides), and if fresh eggs were present. We measured male body length and mass so that we could compare those parameters to those of cuckolders (see below).

Field high-tide snorkeling

During daylight hours in 2001 and 2002, we snorkeled at the same beach where low-tide surveys were done. Water depth ranged from 1.5 to 4 m, depending on the tide. We snorkeled about the site until we came across a male. If he cuckolded (see below), we captured him by hand, measured his body length and mass, and identified him as a type I or type II male. Type I and type II males were distinguished by a suite of morphological characters (see above). Together with the data from the low-tide surveys, these data allowed us to compare the sizes of cuckolders and territory holders in the field to those in our aquarium experiment.

Results

Aquarium experiment

Nest residence: The heavier-ranked the fish, the more nights it spent in a nest (r=0.764, P<0.0001, df=84).

Spawning observations

Type I males cuckolded; there was an average of two type I cuckolders per spawning. Males of the highest three ranks (ranks 6–8) were never observed to cuckold in these experiments (Fig. 1), but instead pair-spawned with females. Occasionally nests would become unoccupied and were temporarily taken by males of the lower five ranks. When not holding nests, some males of the lower five ranks cuckolded at the periphery, outside the entrance, and inside the entrance of the nest. Often a cuckolder would swim to the entrance of the nest, insert his head into the nest, quickly turn around, insert his tail, and perform a spawning reflex. Cuckolding males, especially those that entered the nest or had their tails inserted into the nest entrance, were often bitten and chased away by the resident male. Displacement from positions around the nest or inside the entrance of the nest among type I cuckolders often coincided with aggressive "grunting" (Brantley and Bass 1994), which could be easily heard from outside the tank. The frequency with which a cuckolding type I male positioned itself at the nest entrance with its tail inserted into the nest or its entire body inside the nest increased with body-size rank (P<0.016; n=6; T^{+}=21; T^{-}=0; Fig. 2). We also obtained the same results when we analyzed the two components (time with either tail inserted or with entire body inside) separately.

Field observations

In nature, type I territory holders ranged in size from 47 to over 300 g, while cuckolding type I males ranged from 42 to 120 g (Fig. 3). We came across cuckolders that already had their tails inserted under rocks and observed them performing spawning reflexes, or we found and followed males that were swimming around. These males would typically perform the "head-in" behavior and move on to the next rock to repeat the behavior. If a male remained at a rock after performing the head-in behavior, he would often quickly turn around, insert his tail under the rock, and perform a spawning reflex. Thus, behaviors were identical to those observed in aquaria. Type II males (10.3 to 12.0 g; mean: 11.1 g) cuckolded in a similar manner. Of 14 observed cuckolders, 11 were type I males and three were type II males.

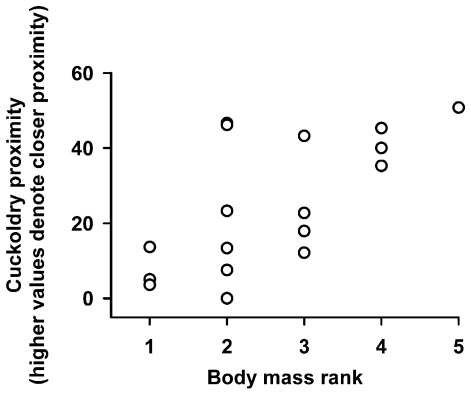

Fig. 2 Of the type I males that cuckolded, heavier males did so closer to the spawning pair (aquarium data). *Cuckoldry proximity* = percentage of time cuckolding with tail inserted into entrance of nest plus time cuckolding with entire body inside nest, divided by total time spent cuckolding (see Methods section)

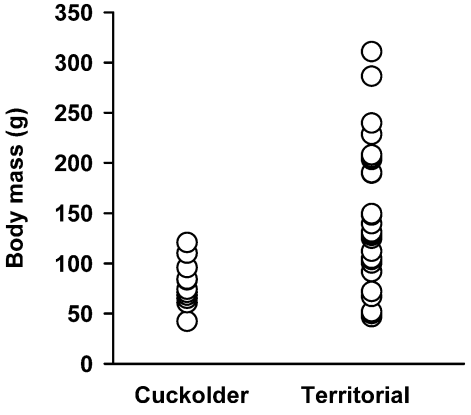

Fig. 3 The size range of territorial type I males exceeds that of type I cuckolders (field data). Two data points for type I cuckolders overlap at approximately 84 g

Discussion

Our observations demonstrate that the type I morphology does not preclude cuckoldry in this species. Given that territories are limiting in the field (DeMartini 1988, 1991), it follows that ecological pressures should select for behavioral plasticity (see Neat and Locatello 2002).

Our data show that the type I morphology does not constrain type I males from behavioral plasticity to cuckoldry.

If the type II (reduced) morphology is indeed an adaptation towards cuckoldry, how does the type I (exaggerated) morphology affect the ability to cuckold? We were drawn to two hypotheses concerning the relationship between body size and the ability to gain proximity to the nest during cuckoldry. The first hypothesis reasons that, compared with smaller type I males, larger type I males could do poorly at gaining access to the spawning pair if larger size makes it more difficult for them to mimic females, sneak into nests unnoticed, or to insinuate themselves into crevices at the borders of the nest (e.g., Gross 1985; Moczek and Emlen 2000). All three tactics have been hypothesized for type II males (Brantley and Bass 1994).

Alternatively, larger type I males could do better than smaller type I males if cuckolders fight for access to the spawning pair. Such aggressive cuckoldry has been observed in other species (e.g., Barlow 1961; Kodric-Brown 1986; Koseki and Maekawa 2000).

Larger type I cuckolders spent more time close to the spawning pair than did smaller type I cuckolders. This correlation may be related to our observation that cuckolding type I males frequently engage in aggressive interactions with resident and other cuckolding type I males. Larger cuckolders should be able to better withstand those interactions and remain at preferred positions at the nest. Indeed, body mass is the strongest predictor of the outcome of aggressive interactions in fishes (e.g., Rowland 1989; Huntingford et al. 1990). We hypothesize that while larger body size may be disadvantageous to "sneaky" cuckoldry, which depends on the ability to avoid detection by the resident, it is advantageous to "aggressive cuckoldry," which depends on the ability to resist ejection by the resident after detection and to resist ejection by competing cuckolders (see Kodric-Brown 1986; Koseki and Maekawa 2000).

We have shown both in aquaria and in the field that type I male midshipman fish will cuckold, and have presented data that show that larger body size does not necessarily preclude, but rather may promote, access to the nest during cuckoldry. The adaptive value of behavioral plasticity to cuckoldry may be related to the observation that a trait that contributes to success at territoriality and courtship (large body mass, DeMartini 1988) also appears to facilitate aggressive cuckoldry. Even if the exaggerated morphology departs significantly from that of females (precluding female mimicry), or makes males large and conspicuous (precluding insinuation into small crevices and sneaking), behavioral plasticity to cuckoldry may still be adaptive in exaggerated morphs of species with male dimorphisms if alternative mechanisms (e.g., aggressive interactions) can be used to attain proximity to the spawning pair.

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