

Competition for territories does not explain allopaternal care in the tessellated darter

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Received: 26 September 2007 / Accepted: 4 April 2008 / Published online: 13 May 2008
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Abstract Extensive research has focused on understanding the evolution of parental care, with fishes providing important model systems for understanding patterns of variation within and between species. Classic theory predicts that individuals will care for offspring when the fitness benefits through increased offspring survival and growth outweigh the cost to the parents through decreased future reproductive opportunities. Yet, a puzzling observation not explained by this basic theory is the fact that in some species individuals defend and provision unrelated offspring and thus exhibit alloparental care. The tessellated darter, *Etheostoma olmstedi*, represents one of the first known examples of allopaternal care in fishes. In this species, males often clean and guard eggs fertilized but deserted by other males. Allopaternal care has been argued to occur in the tessellated darter because of competition for a limited number of mating sites where less dominant males accept territories with eggs when other breeding sites are not available. Here, we test this hypothesis using male territory choice experiments. When allowed to choose between two otherwise identical territories either

containing eggs fertilized by another male or with no eggs, males spent significantly more time at territories with eggs. This demonstrates that competition for mating territories is not the primary factor explaining the existence of allopaternal care in the tessellated darter. Instead, males of this species may exhibit allopaternal care to dilute predator pressure on their own eggs or because females prefer to mate with males whose territories contain eggs.

Keywords Parental care · *Etheostoma olmstedi* · Reproductive strategies · Male competition · Animal behavior · Sexual selection · Alloparental care

Introduction

Parental investment is defined as any parental behavior that increases the survival of offspring at a cost to the parent (Trivers 1972). Most theoretical and empirical research on parental care has focused on understanding the tradeoff between the fitness benefit of increased survival of offspring and the fitness cost to the parent through decreased future reproductive opportunities (Gross and Sargent 1985). Extensive research has also focused on explaining the existence of related and unrelated parental helpers (Taborsky 1994). Allopaternal care, when individuals care for unrelated young alone, has received much less attention (Constanz 1985). Two basic explanations

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for alloparental care have been proposed: First, the behavior may be a mistake or byproduct of not having other alternatives. Second, the behavior may have a direct benefit to the alloparent such as increasing the survival of their own offspring or serving to attract mates (e.g. Jamieson and Colgon 1992). Understanding the existence of alloparental care will not only help explain the presence of this puzzling behavior in some species, but may also illuminate additional benefits of parental care more generally.

In the tessellated darter, *Etheostoma olmstedi*, males exhibit alloparental care (Constanz 1979, 1985). Tessellated darters lay their eggs on the underside of flat-bottomed rocks. Males defend and clean these mating sites, rearing the eggs until hatching. Paternity analyses in the tessellated darter have shown that males care for eggs to which they are unrelated (DeWoody et al. 2000). It has been suggested that males defend territories that already contain eggs because the number of mating sites is limited and intermediate-sized males (that tend to be allopaterents) are not able to find and defend territories without eggs while larger males often move among multiple territories based on mating opportunities (Constanz 1979, 1985). High densities and limited mating sites are observed in numerous species of darters, including the tessellated darter (Page and Schemske 1978). In addition, Constanz (1985) found that when given an artificial cluster of eggs, males concentrated their cleaning efforts on the areas of the territory without eggs. This pattern of cleaning behavior could be interpreted as showing that the male's primary intentions are to clean the available spawning surface and that alloparental care arises accidentally or possibly to prevent the spread of disease to his own eggs (e.g. Knouft et al. 2003).

Alternatively, males may deliberately choose to be allopaterents. This choice could be based on a number of potential benefits of alloparental care. For example, rearing the eggs of other males could dilute predator pressure on a male's own eggs (McKaye and McKaye 1977). Additionally, the presence of more eggs could attract females (e.g. Ridley and Rechten 1981; Unger and Sargent 1988). It has been shown that female tessellated darters are more likely to lay eggs at sites with eggs (Constanz 1979, 1985). This preference could exist for a number of reasons including reduced predator pressure, the proven quality of a territory, the demonstrated parental care ability of the male, sensory

bias, the desire to cannibalize eggs, or due to female mate choice copying (Jamieson 1995).

We conducted a territory choice experiment to determine whether alloparental care in the tessellated darter is driven by competition for limited territories without eggs. To do this, we presented males with two otherwise identical artificial territories with and without another male's eggs. If alloparental care occurs in the darter either purely incidentally or only because territories are limiting and all males cannot find and defend territories without eggs, then males should either prefer territories that do not contain eggs or exhibit no preference among territories. However, if males prefer territories with eggs and perform alloparental care, then the unavailability of territories without eggs alone does not explain the existence of alloparental care in this species.

Materials and methods

Study species

Tessellated darters live in sand or mud-bottomed pools of rivers and in lakes (Page 1983). The tessellated darter ranges along the East coast of North America, from Quebec to Florida (Page 1983). The reproductive season lasts from April to July (Page 1983). The female deposits her eggs onto the undersides of stones in the substrate (Page 1983). In preparation for mating, male tessellated darters invert and wiggle vigorously in order to clean the spawning surface and aerate the eggs (Winn 1958; Constanz 1979). Mating takes place when both fish are inverted under the spawning surface (Constanz 1979). The eggs are subsequently cleaned and guarded by a male until hatching, and eggs that are not cleaned become fungused and die before hatching (Constanz 1979, 1985). Fungus prevention as a result of parental care is most likely due to anti-microbial compounds in the epidermal mucus of the male as is observed in other darter species (Knouft et al. 2003). Evidence from the fringed darter indicates that nest guarding in darters serves to reduce egg predation (Knouft and Page 2004). In the tessellated darter, large males often leave their mating territory and take over a new territory one day after new eggs have been deposited (Constanz 1979) and alloparental males are observed cleaning and guarding eggs which they did not fertilize (Constanz 1979, 1985). Eggs of this species

harden within 24 h and have been argued to be invulnerable to cannibalism after hardening (Constanz 1985). Eggs are frequently found in the stomach of parental males although these eggs were just as likely to be related as unrelated to the defending male (DeWoody et al. 2001).

Experimental methods

The tessellated darters used in the study were collected from three locations in Southern Connecticut: Mill River, Wharton Brook and Laurel Grove Brook. All collections were made during May and June of 2006. All individuals were reproductively mature and may have spawned prior to collection. The fish were kept in 75- and 150-L holding tanks at approximately 21°C. Lights in the facility were timed to turn on at sunrise and turn off at sunset. The fish were fed bloodworms (chironomid larvae) daily and all observations were conducted at least one hour after feeding. Mating territories were constructed by attaching two small pieces of PVC pipe (2.9 cm tall) to 15×15 cm tiles of slate. Territories with eggs were obtained from tanks in which darters were allowed to breed freely or by placing artificial territories in Mill River. All egg territories were initially covered by at least 5 cm² of eggs, but no territories were more than half covered, leaving plenty of available space for new eggs. In addition, all eggs were allowed 24 h to harden before being used in an experiment, as in the wild males do not usually leave their territories until a day after they have spawned. No territory-choice experiments were conducted using eggs that had been sired by the male participating in the observation. At the end of the day following all observations, the mating territories were carefully removed by hand from each aquarium and photographed in order to monitor egg survival as well as discover any new eggs. Males used in experiments were chosen to be large and dark as this indicates sexual maturity in males (range of standard lengths: 44–65 mm). Reproductively mature, gravid females were used in the experiments and as much as possible we used females with eggs clearly visible in their abdomen (range of standard lengths: 32–57 mm).

All territory-choice experiments were conducted in one of four 150-L experimental tanks. One territory with eggs and one territory without eggs were placed at opposite ends of each tank. The position of the

territories was randomized for every trial. After being released into the tank, the male was given a brief 15-min adjustment period. The male was then observed for 30 min. A female was then introduced into the tank and after 10 min the pair was observed for a 30-min interval. We observed male behavior with and without the female in order to determine if male behavior changed in the presence of a gravid female.

Observations were carried out using JWatcher v.1.0 software. During each observation, the position of each fish was recorded at all times. Fish were described as “at egg territory” if they were within 2.5 cm of the territory containing eggs, “at no egg territory” if they were within 2.5 cm of the territory without eggs and “at neither territory” if they weren’t at either territory. The total duration of time spent at each position for each fish in each observation was summed, and average time spent at each territory per observation was calculated. The total occurrence and duration of inversions (which play a role both in paternal care and mate attraction) in each territory were also recorded (Constanz 1979).

Results

A total of 22 territory choice experiments were carried out in May and June 2006. In two experiments, females laid eggs. In both cases, mating occurred in the territory that already contained eggs. Unattended eggs quickly develop fungus and decay even in the lab (personal observations). However fungus did not appear on any of the eggs used in the experiment, and we can thus infer that all of the males exhibited some allopaternal care. Moreover, all males were observed under the egg territory at some point during the observations. Our daily photographs of egg clutches found partial egg cannibalism in over half of the trials despite the fact that the fish were well-fed and the eggs had hardened prior to the experiment. This is unlikely an effect of the experiment or laboratory conditions because all of the remaining eggs were in good condition and hatched normally. Egg clutches were, however, never fully cannibalized.

When females were not present, males did not spend significantly more time under either type of territory (e.g. with or without eggs, paired two-tailed *t* test: *df*=20, *t*=1.62, *p*=0.120). However, in the

second observation in the presence of a gravid female, males spent significantly more time under or near the territories with eggs (Fig. 1, paired two-tailed t test: $t=2.25$, $df=20$, $p=0.035$). No significant preferences between territories were found for females (Fig. 2). Males did not invert significantly more in either territory (paired 2-tailed t test: $t=1.56$, $N=10$, $p=.152$, $1-\beta=0.38$ for $\alpha=0.05$).

Discussion

The observed preference of males for territories containing eggs is not consistent with the hypothesis that males exhibit alloparental care incidentally or solely because of limited territories. Instead, males actively chose to become alloparents. Our study did not explicitly investigate which benefits the behavior confers, but two advantages of alloparental care seem particularly likely for this species: alleviated predator pressure and female preference for males with eggs.

Our observation of frequent egg cannibalism is contrary to previous arguments that the eggs of the tessellated darter become invulnerable to cannibalism after hardening (Constanz 1985), making predation dilution a more likely benefit of alloparental care than previously thought when a male cares for both related and unrelated offspring. However, cannibalism by alloparental males will also be a cost of deserting

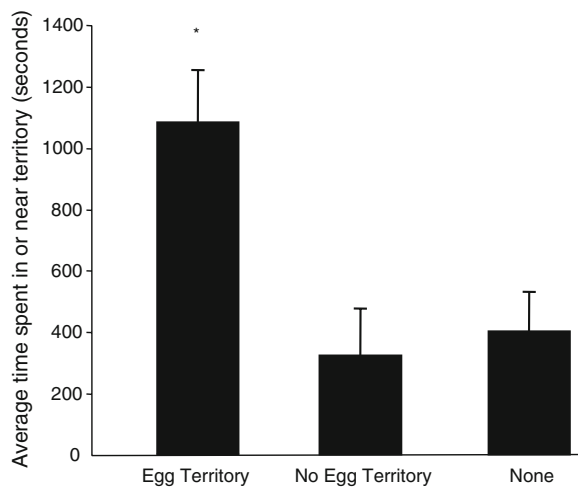


Fig. 1 In the absence of competition for territories, males spent significantly more time in the territory with another male's eggs than in the territory without eggs when in the presence of a reproductive female. Error bars indicate standard error

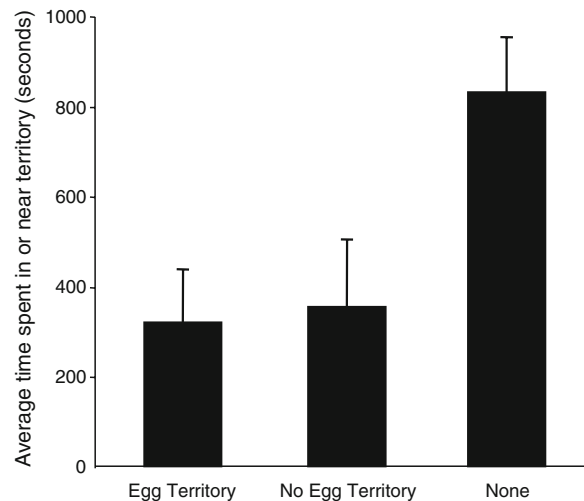


Fig. 2 Females spent most of their time away from both territories. No significant difference was found between time spent in the egg territory and time spent in the no egg territory. Error bars indicate standard error

territories with related offspring in the first place although DeWoody et al. (2001) did not find any evidence that tessellated darter males preferentially cannibalize unrelated young.

Female preference for males with egg territories is another likely benefit of alloparental care in the tessellated darter. Early in the breeding season when mating territories are abundant, female tessellated darters prefer to oviposit on territories with small clusters of eggs rather than on territories containing no eggs (Constanz 1985). In addition, both times mating occurred in our study, it happened in the territory that already contained eggs. A female preference for males with healthy eggs makes sense given the pivotal role that the quality male care plays in this species as well as the potential for the presence of other eggs to dilute predation risk on their own eggs.

Although alloparental care has these potential benefits, choosing territories that contain another male's eggs has a number of potential costs. First, caring for extra eggs could be more time consuming and require more energy and resources. Second, mating in territories that already contain eggs carries the risk that fungal infection will spread from the pre-existing eggs to future eggs. Third, mating in a territory that already contains eggs means that there is less space to lay new eggs. In addition, for males that have already spawned, choosing a new territory that

contains another male's eggs carries the additional cost risk of cannibalism of previously fertilized eggs that have been abandoned. If allopaternal care is adaptive in the tessellated darter, then the benefits of the behavior must outweigh the costs of time, energy, higher disease risk, and reduced spawning area. These costs and benefits of allopaternal care are by no means constant for the tessellated darter, and males exhibit varying degrees of allopaternal care. The largest males in this species do not typically exhibit allopaternal care, instead cruising among and spawning at multiple territories while deserting their own eggs (Constanz 1979, 1985). Thus, while the presence of eggs may attract females in some circumstances, it is also clear that not all males adopt allopaternal care in order to attract mates. Further research is needed to understand the coexistence and expression of both cruising and allopaternal care behavior patterns and the effect of female choice among males on these behaviors.

In conclusion, the results of this study indicate that allopaternal care in the tessellated darter is not explained by competition among males for limited mating territories. Instead males prefer territories with eggs and perform allopaternal care even when territories without eggs are available. Thus, we predict that allopaternal care behavior should occur in the tessellated darter even in populations where mating sites are abundant. Further research is needed on the costs and benefits of territory desertion, allopaternal and paternal care behavior in this and other species. However, our results show that tessellated darter males choose to care for eggs that are not their own, implicating a net benefit of male parental care behavior in this species even when tending unrelated young.

Acknowledgements We thank Joanne Klein for help collecting and maintaining the fish in captivity. We thank Mark Fisher, Erem Kazancioglu, Natasha Kelly, Holly Kindsvater and Stephen Stearns for advice and comments. We also thank two anonymous reviewers and Editor Noakes for helpful comments that improved the manuscript. Funding was provided by Yale University, a Howard Hughes Medical Institute Undergraduate Research Fellowship to MBF and NSF Grant IOB-0450807 to SHA.

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