

Filial Cannibalism and Egg Recognition by Males of the Primitively Custodial Teleost *Cyprinodon macularius californiensis* Girard (Atherinomorpha: Cyprinodontidae)

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Territorial male Salton Sea pupfish, *Cyprinodon macularius californiensis*, engage in limited filial cannibalism but can distinguish between their own eggs and those fertilized by other males using olfactory cues. Females lack this ability. This asymmetry is explained as a function of the polyandrous behavior of females and the persistent occupancy of food-poor spawning territories by males. Egg discrimination appears to have evolved as a defense against the activities of nonterritorial peripheral males, who will spawn in a resident's territory whenever the opportunity arises, and may be considered analogous to the defensive behavior shown by avian victims of brood parasites.

Key Words: Filial cannibalism; Egg recognition; Parental care; Chemical communication; *Cyprinodon*; Sneaker males; Brood parasitism.

INTRODUCTION

Parental care in fishes, in contrast to most vertebrates, is primarily the task of the male (Blumer, 1979; Loiselle, 1978; Ridley, 1978). Because external fertilization provides a more direct assurance of paternity, it has been proposed as a major factor in the evolution of this phenomenon (Barlow, 1976; Blumer, 1979; Per-

rone and Zaret, 1979; Trivers, 1972). Such a view is misleading. Behavioral tactics that allow an outside male either to join a consorting couple in the spawning act or preempt the resident male's fertilization of eggs already deposited are well documented among paternally custodial teleosts (Barlow, 1961, 1967; Dominey, 1980; Fiedler, 1964; Fishelson, 1970; Jones and King, 1952; Keenleyside, 1972; Morris, 1952; Petravic, 1938; Raney et al., 1953; Reeves, 1907). So is the surreptitious spawning with other females by nonterritorial males in another male's territory, behavior analogous to avian nest parasitism (Barlow, 1961; Kodric-Brown, 1977; Langlois, 1929; Ross, 1977; Ross and Reed, 1978; Warner et al., 1975). Under such circumstances, it would seem selectively advantageous for a custodial male to be able to distinguish between his own and alien eggs. Yet experiments testing such ability have yielded negative or equivocal results (van dem Assem, 1967; Baerends and Baerends-van Roon, 1950; van Iersel, 1953; Myrberg, 1964, 1966; Noble and Curtis, 1939). The picture is further complicated by the occurrence of filial cannibalism by custodial males of several teleosts (DeMartini, 1976; Qasim, 1956; Rohwer, 1971).

Pupfishes of the genus *Cyprinodon* (Atherinomorpha: Cyprinodontidae) are small, sexually dimorphic, physiologically plastic herbivores found in a wide variety of aquatic biotopes along the Atlantic and Gulf Coasts, throughout the Caribbean and in the southwestern United

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States and northern Mexico (Turner and Liu, 1977). The male defends a spawning territory, within which the clear, demersal eggs are deposited, and mates with numerous females in the course of an extended breeding season (Barlow, 1961; Raney et al., 1953; Kodric-Brown, 1977; Echelle, 1973; Itzkowitz, 1974). Males too small to sequester a spawning site gather at the edge of a resident male's territory and attempt to spawn therein while he is engaged with another female (Barlow, 1961; Kodric-Brown, 1977). Residents are highly aggressive toward conspecifics of both sexes as well as heterospecific fish. Protection of eggs within a male's territory has been suggested as a fortuitous effect of such behavior in several species (Echelle, 1973; Itzkowitz, 1974), while a true male custodial role has been demonstrated in *C. m. californiensis* (Loiselle, 1982). There is no posthatching spawn defense, but observations in captivity suggest adults ignore mobile fry unless very hungry (Loiselle, 1979). This study provides evidence that while males of the Salton Sea pupfish, *Cyprinodon macularius californiensis* Girard, engage in filial cannibalism, they can distinguish between eggs fertilized by themselves and by other males; the consequences of this behavior are functionally analogous to the rejection of alien eggs by the avian victims of nest parasitism (Rothstein, 1971; Smith, 1968; Welty, 1963).

METHODS

The pupfish used in this study were either wild caught animals taken at Cleveland Street Slough on the eastern shore of the Salton Sea, Imperial County, California, or captive bred fish derived from this population. No differences were observed between wild caught and captive reared individuals of *C. m. californiensis* with regard to the behavior reported herein.

To produce eggs of guaranteed paternity, four 11.0-mm mesh aluminum wire cages, each containing a nylon yarn spawning mop were placed in a 250-liter aquarium containing 10‰ seawater at 28°C on a long day (16 hours light) photoperiod. The mesh size allowed females to pass freely in and out while retaining males in close proximity to the spawning substrata, thus guaranteeing the paternity of the eggs deposited therein. Eggs of known maternity were obtained by allowing females to spawn singly with a male.

The response of subjects to spawn of different provenance was determined by allowing them to interact freely with a substratum containing a known number of eggs for 24 hours. During this interval, the subjects were not fed. The number of eggs remaining at the end of this period was then recorded. The number of surviving eggs was plotted against the number initially present in each substratum. Analysis of covariance was used to test for differences in egg survival between control and treatment in each experiment.

RESULTS

Can Either Sex of the Salton Sea Pupfish Distinguish Between Its Own and Alien Eggs?

To determine his response to his own eggs and to those fertilized by other males, a male was placed within each cage in the arena, following which 12 females were introduced to the aquarium. At the end of 24 hours, the spawning substrata employed by each male were removed and the number of eggs present in each counted. The females were removed from the arena and the egg-laden substrata returned. Two males had their own eggs returned to them, while the substrata used by the other two males were exchanged. After egg survival within each substratum had been determined, the subjects were fed and allowed a day's rest. The procedure was repeated using a different set of females, with control and treatment males reversed. Six replicates were carried out, giving a total of 24 experimental subjects. No male was tested more than once. A separate dummy control, in which egg-laden substrata from other experiments were isolated for 24 hours within the arena, was run to determine egg survival in the absence of any fish.

In order to determine their response to their own and to other females' eggs, eight females were allowed to spawn singly with a male. The egg-laden substrata were treated as previously described. Males were subsequently removed and the unfed females were then allowed to interact with the substrata. Each female was exposed once to a substratum containing her own eggs and one containing those of another female.

The slopes of the lines describing egg survival in the presence of the male are significantly different for control and treatment ($F_{1,44} = 42.38$).

$p < 0.01$), as well as from the zero predation expectation generated from the dummy control (Fig. 1a). While clearly indulging in filial cannibalism, resident male *C. m. californiensis* consumed significantly more alien eggs than they did their own. Females, to the contrary, did not distinguish between their own and alien eggs, consuming both with equal relish ($F_{1,12} = 0.05$, $p > 0.05$).

How Do Male Salton Sea Pupfish Recognize Their Own Eggs?

The design of the initial experiment did not address the question of how a male *C. m. californiensis* recognizes his own eggs. Several such mechanisms can be envisaged. Because eggs were presented to the subjects in the substrata within which they were spawned, the males might have been responding to the nylon substrata rather than to the eggs they contained. To test the hypothesis that the mop in which the eggs occur determines their response to them, four males were set up as initially described. Once the number of eggs present in each mop was recorded, their placement within the substrata was altered according to a Latin square

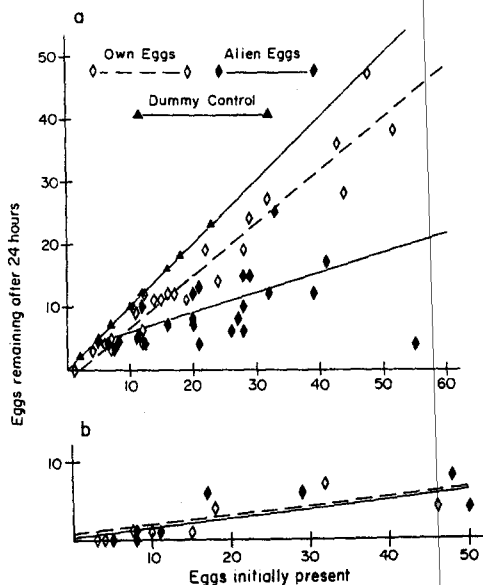


Figure 1. Response of male (A) and female (B) *Cyprinodon m. californiensis* to spawning substrata containing their own and alien eggs.

design. Over the course of the experiment, each male was presented with all possible combinations of his own and alien mops and eggs. Egg survival at the end of 24 hours was determined as previously described. A total of eight males was tested in this manner.

This hypothesis predicts that a resident male should behave towards another male's eggs as he would towards his own if they were presented to him in a substratum previously used by him. This proves not to be the case. The slopes of the lines describing egg survival for control (own mop, own eggs) and treatment (own mop, alien eggs) are significantly different ($F_{1,12} = 58.85$, $p < 0.01$). A male eats more of another male's eggs than he does of his own even if they are presented to him in a substratum within which he has previously spawned (Fig. 2).

The hypothesis additionally predicts that a resident male ought to respond to his own eggs as he would to alien eggs if they were presented in the substratum used by another male. These data also fail to bear out this prediction. The intercepts of the lines describing egg survival for control (alien eggs, alien mop) and treatment (own eggs, alien mop) are significantly different ($F_{1,12} = 10.08$, $p < 0.01$). A male eats fewer of his own eggs even when they are presented to him in a spawning substratum previously em-

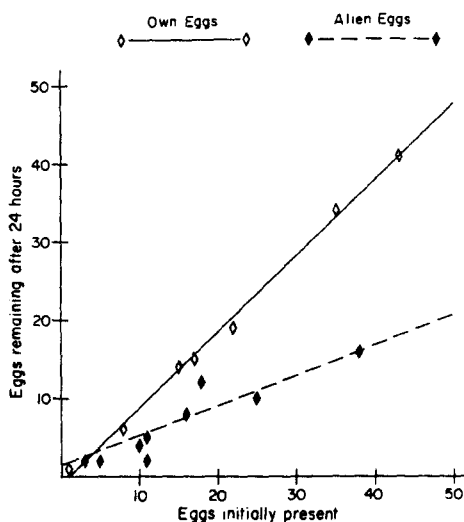


Figure 2. Response of resident male *Cyprinodon m. californiensis* to their own and to alien eggs presented to them in spawning substrata they have previously used.

ployed by another male (Fig. 3). The hypothesis that a male's response to eggs is determined by the substratum in which they occur is not supported.

If the hypothesis of substratum recognition is inadequate to explain the differential response of a male pupfish to his own eggs, it follows that his behavior must be determined by some property of the eggs themselves. Two such mechanisms can be hypothesized. A male might remember the position of each spawning bout within his territory and selectively eliminate eggs encountered outside of their expected locations. Alternatively, he might recognize his own eggs by means of some chemical cue.

To test the first hypothesis, four males were set up as in the initial experiment. After the number of eggs in each male's mop was recorded, the eggs in two were removed and replaced, effectively altering their position within the spawning substratum. Eggs in the remaining mops were not disturbed. Each male's mop was then returned to him. The number of eggs remaining in each after 24 hours was recorded. The fish were fed and rested for 24 hours, then the procedure repeated, with control and treatment males reversed. Eight males were tested. There were no significant differences between control

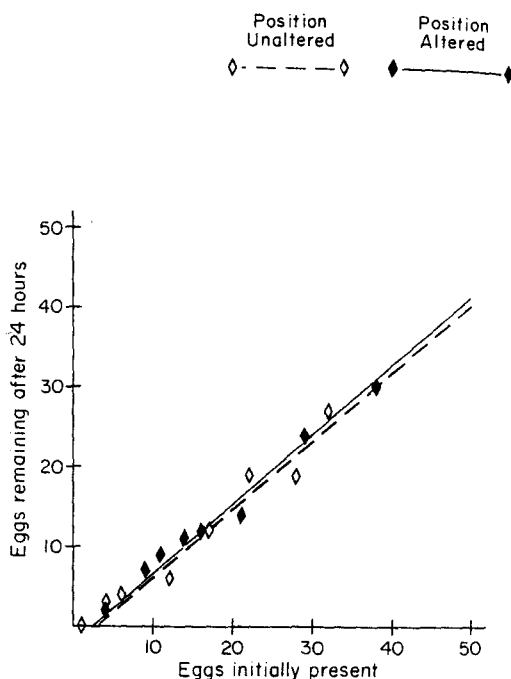


Figure 4. Response of resident male *Cyprinodon m. californiensis* to their own eggs whose position within the spawning substrata was undisturbed compared with that towards eggs whose placement was altered.

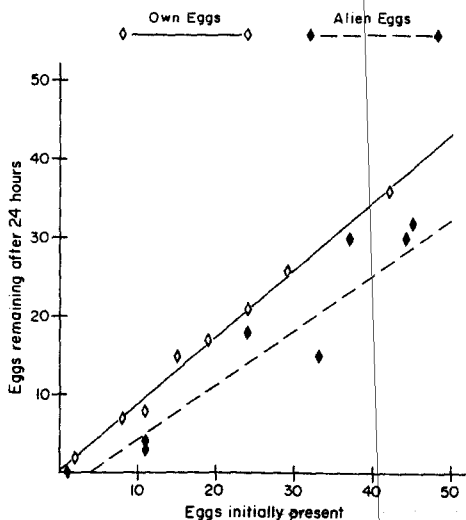


Figure 3. Response of resident male *Cyprinodon m. californiensis* to their own and to alien eggs presented to them in spawning substrata previously used by other males.

(egg position unaltered) and treatment (egg position altered) conditions ($F_{1,12} = 0.05$, $p > 0.05$). Because the position-effect hypothesis predicts that residents should eat more eggs from disturbed than from undisturbed mops, it cannot be supported by these data (Fig. 4).

The remaining possibility is that resident males use chemical cues to recognize their own eggs. If the modality of recognition is primarily olfactory, it would follow that anosmia could suppress egg discrimination. To test this hypothesis, four males were set up as initially described. Before the egg-laden mops were returned to the arena two of the males were rendered anosmic by having their nostrils plugged with Orabase (Partridge et al., 1976). Pilot experiments determined that the nasal plugs persisted for 20 to 24 hours and were completely cleared from the nares within 36 hours treatment. Following a Latin square rotation, each male was presented a mop containing his own and alien eggs before and after being rendered anosmic. The number of eggs remaining

in each mop after 24 hours was recorded. Eight males were tested.

The olfaction hypothesis predicts that untreated and treated males should respond differently to their own eggs. The slopes of the lines describing the response of males to their own eggs before and after being rendered anosmic are significantly different ($F_{1,12} = 14.63, p < 0.01$). It also predicts that anosmic males should fail to discriminate between their own and alien eggs. The data bear out this prediction. The slopes of the lines describing the response of anosmic males to their own and to alien eggs are not significantly different ($F_{1,12} = 0.04, p > 0.05$). Induced anosmia evidently destroys the ability of resident males to recognize their own eggs, with the result that both their own and alien eggs are eaten impartially (Fig. 5). Egg recognition in this pupfish is thus apparently based upon olfactory perception of chemical cues provided by the eggs themselves.

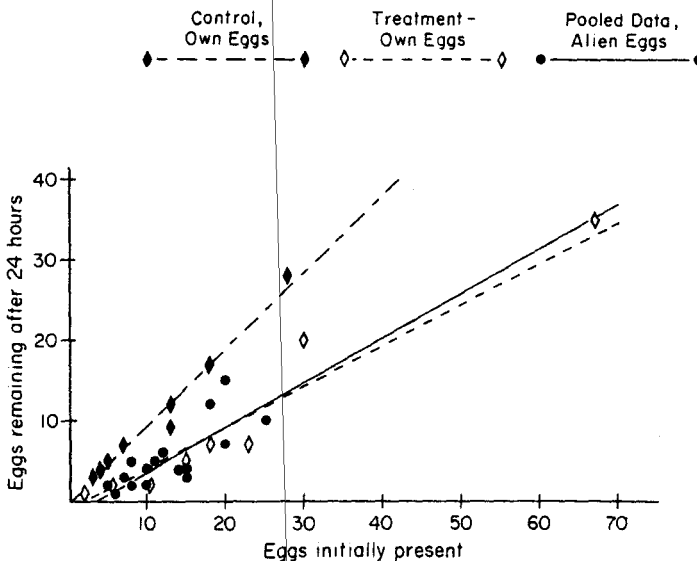
The Probable Selective Advantage of Male Egg Discrimination by the Salton Sea Pupfish

The activities of nonterritorial peripheral males assure that a resident male is likely to encounter alien eggs within the boundaries of his territory. The custodial character of territorial defense reduces the risk of predation upon any eggs present within its limits, yet such behavior is energetically costly. Given these facts, it may be

hypothesized that the differential response of resident males to their own and alien eggs has evolved as a defensive response to the activities of such peripheral males. The necessary precondition for such a hypothesis is the ability of resident males to selectively eliminate alien eggs from a substratum containing both his own and those of other males. The hypothesis further predicts that resident males should respond by eating significantly more alien eggs when these are presented in a substratum previously used by him than when presented in that used by another male.

In order to ascertain if males can selectively remove alien eggs from their territories, six males were allowed to spawn in the manner previously described in nylon substrata divided into numbered quadrants. Egg-laden mops and females were removed from the arena after 12 hours. The number of eggs in each mop was recorded and all the eggs in two quadrants removed and replaced with eggs collected from spawning substrata previously placed in a stock tank. Each male's substratum was then returned to him. The number of eggs remaining in each quadrant after 24 hours was recorded.

Figure 5. Response of untreated and anosmic male *Cyprinodon m. californiensis* to their own and to alien eggs. The response of untreated and anosmic males to alien eggs was identical. Hence these data are pooled to simplify presentation of the experimental results.



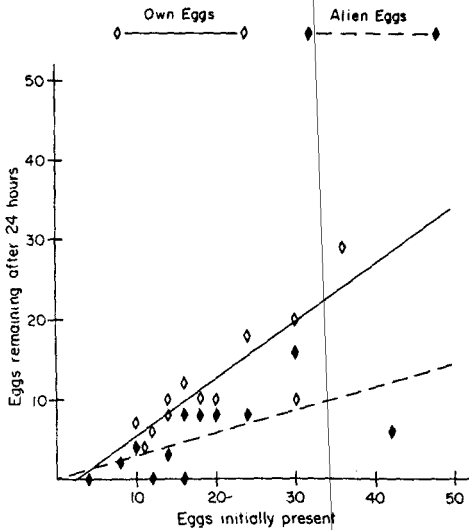


Figure 6. Response of resident male *Cyprinodon m. californiensis* to their own and to alien eggs when both are presented in the same spawning substratum.

The slopes of the lines describing egg survival for the two classes of eggs are significantly different ($F_{1,12} = 5.95, p < 0.05$). A resident male can selectively remove alien eggs from a spawning substratum containing both his own eggs and those of other males (Fig. 6).

To test the prediction that resident males of this pupfish should respond more strongly when alien eggs presented to them in their own substrata, the slopes describing alien egg survival under both conditions were compared. The necessary data for such a comparison were generated by the experiment that tested the substratum effect hypothesis. The two slopes are significantly different ($F_{1,12} = 4.94, p < 0.05$). A resident male will eat more alien eggs when they are presented to him in his own spawning substratum than when they are presented to him in one previously used by another male (Fig. 7). The available evidence thus supports the defensive response hypothesis.

DISCUSSION

The data on egg survival clearly demonstrate the occurrence of filial cannibalism by both sexes. They also show that the two sexes differ in their ability to discriminate between their own and

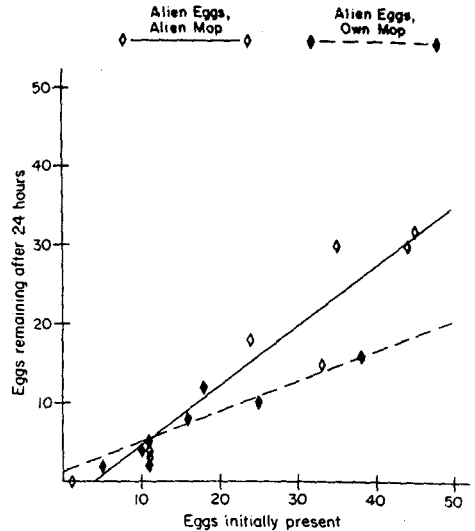


Figure 7. Response of resident male *Cyprinodon m. californiensis* to alien eggs presented in substrata they have previously used and in substrata employed by another male.

alien eggs. The explanation for this asymmetry lies in the territorially-based arena mating system of *C. m. californiensis*. Females move freely throughout the arena and spawn in a polyandrous fashion. Thus only a few of the eggs present in a given male's territory will have been spawned by a particular female. Her access to eggs is further limited by the aggressive response of territorial males to all fish save sexually responsive females (Itzkowitz, 1974; Kodric-Brown, 1977; Loisel, 1982). The likelihood that a female could cannibalize her own progeny under such conditions would thus appear to be too small for selection to have favored the ability to discriminate. However, this explanation cannot account for the apparent paradox of filial cannibalism by resident males.

Both laboratory experiments (Loisel, 1982 in prep.) and field observations (Barlow, 1961; Kodric-Brown, 1977) indicate that the possession of a spawning territory significantly enhances male reproductive success in pupfish. Preferred spawning territories are bare patches of rock or gravel (Barlow, 1961; Kodric-Brown, 1977, 1978), where the risk of egg mortality due to anoxic conditions caused by sedimentation is greatly reduced. However, they are largely devoid of the algal growth and detrital deposits that are the major food source of *Cyprinodon* (Ko-

dric-Brown, 1978; Martin, 1970; Naiman, 1976). Persistent occupation of a spawning territory thus seriously interferes with a male's ability to forage (Echelle, 1973). For a male to leave his territory to feed is to risk its loss to another male, however, and contesting for occupancy with an usurper is energetically costly, entailing a risk of injury or of attracting the attention of predators. Given the advantage of actual occupancy in such contests (Braddock, 1949; Coe, 1966; Figler et al., 1976; Tinbergen, 1953), there is also no guarantee that a male could regain control of an abandoned territory. Adaptations that facilitate persistent territorial occupancy are therefore likely to be strongly favored by selection.

Female pupfish are not territorial and can forage freely. A substantial portion of their foraging effort must be allocated to the maturation of eggs, which represent a concentrated food source. Limited filial cannibalism thus allows a resident male to extend his interval of territorial occupancy by exploiting the superior resource garnering ability of his spawning partners. Such behavior sacrifices a portion of his immediate reproductive output, but as long as the number of eggs he subsequently fertilizes is superior to that consumed, limited cannibalism will be selectively advantageous.

Parental care in *C. m. californiensis* is strictly custodial in nature and ceases as soon as the eggs hatch. A sophisticated defense against the activities of nonterritorial, peripheral males based upon egg discrimination seems anomalous in such a primitive system, given the apparent absence of this ability in both cichlids (Myrberg, 1964) and sticklebacks (van dem Assem, 1967; van Iersel, 1953), whose highly evolved parental care comprises both hygienic and custodial elements while extending to defense of the mobile young. Egg recognition appears absent in cichlids and sticklebacks because there is no selective advantage to such discrimination, while toleration of alien offspring (Burchard, 1967; Collins and Braddock, 1962; Ward and Wyman, 1975) can actually enhance the parent or parents' fitness (McKaye and McKaye, 1977; Rohwer, 1978).

In the case of the Salton Sea pupfish, no selective advantage can be invoked for tolerating alien eggs that will hatch competitors to a resident male's own progeny, while selective predation on alien eggs allows him simultaneously to prolong occupancy of his territory without en-

gaging in extensive filial cannibalism. The ability of a resident male to discriminate between his own and alien eggs should thus prove a common feature of the reproductive biology of persistently territorial, primitively parental fishes whenever the potential for parasitism of the spawning territory by other males is present.

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