Breeding, paternal behavior, and their interruption in *Betta splendens*

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Seven experiments examined the reproductive activities of Siamese fighting fish (*Betta splendens*). Spawning occurred after heterosexual pairs were together for about 24 h, and males cared for eggs, nest, and fry thereafter. The visual cues provided by an intruder male, but not a female, stimulated aggression in the male breeder, and these agonistic behaviors competed with breeding to cause a decrement in reproductive efficiency. Males were found to protect eggs and fry by preventing the growth of a fungus lethal to their offspring.

Several lines of evidence suggest that Siamese fighting fish (*Betta splendens*) breed when isolated from adult conspecifics. First, at temperatures conducive to breeding, males construct nests in relatively isolated areas where detection by other fish could be relatively unlikely (Bronstein, 1981a, Experiment 4). Nest sites are spawning sites also. Second, following the construction of a nest, males become "attached" to their nest sites after they observe a male conspecific (Bronstein, 1981a, Experiment 3). Third, the frontal, gill-cover display of males, elicited by the approach of a conspecific to within 12 cm (Bronstein, 1981b), causes the escape of the fish at the start of a male-male encounter (Bronstein, 1981a, 1981b). Fourth, the extension of the male's operculum is an effective "keep-out" display (Bronstein, 1981a, Experiment 2); fish that most persist in this gill-cover display are able to provoke escape among males that display less tenaciously. Thus, the fish with the more persistent display almost always gains control of boundary areas when two males see each other. Fifth, when housed in groups, a pair of bettas will sometimes remove themselves to a relatively isolated part of their tank and breed (Goldstein, 1975). Sixth, and finally, the presence of a male in breeding condition appears to excite fighting activity among adult females; however, the evidence on this last point is relatively weak (Bronstein, 1980).

The evidence just presented suggests that in domesticated bettas physical isolation among conspecifics is associated with breeding. Furthermore, the males have a set of behaviors (display, escape, nest-site te-

nacity) capable of producing such isolation. The current set of studies was designed to test the converse case. Namely, since isolation regularly accompanies breeding, I sought to determine whether the absence of social isolation would be sufficient to reduce reproductive efficiency in bettas.

EXPERIMENT 1

Method

Subjects and Apparatus. Adult *Betta splendens*, purchased locally or bred in the laboratory, were used in all studies. The animals were at least 8 months old and none showed any fin damage, making it unlikely that the fish had been fighting recently. For at least 2 weeks prior to the start of each experiment, males were maintained in at least 900 ml of water, visually isolated from other fish. Females were housed in an identical manner, but not in visual isolation. Lights went on at 0800 h and off at 2200 h. Temperature was maintained at 28°C by a space heater, and the fish were fed either dry food (Wardley's) or recently thawed brine shrimp (*Artemia salina*) twice daily.

Test environments for all studies were glass aquaria, 40.4 cm long, 25.0 cm high, and 20.3 cm wide. Undyed gravel (2 cm deep) covered the bottoms of the tanks. Tap water (pH = 7.0), left standing for at least 24 h and in which no fish had swum, was used, and there were 15-20 liters of water per tank. Six modifications of each tank were made: (1) Thermostatically controlled heaters were added to eliminate minor fluctuations in water temperature. (2) A clear glass plate covered the tanks to ensure relatively high levels of humidity immediately above the water surface, a condition which my own unpublished observations had suggested facilitates the maintenance of bubble nests. (3) Four strands of *Elodea densa* were planted in a vertically oriented bunch near the center of each tank. (4) A triangular intruder compartment, extending the full height of each tank, was created by placing a piece of glass (15.2 cm wide, and serving as the hypotenuse of the triangle) in a corner of each aquarium. The legs of the triangular cross section (the walls of the tanks) were 8.4 and 12.7 cm long. (5) Tanks were wrapped in brown paper on all but the one short side where the intruder compartment was located. (6) The aged tap water used in the breeding tanks was softened by filtration through an ion-exchange resin (Aquarium Pharmaceuticals, Inc., Perkasie, Pennsylvania). Aquarists recommend this procedure when breeding bettas (cf. Maurus, 1976).

Procedure. A different male was placed in each of 32 tanks, and, after he had had 72 h of adaptation, a female was added to

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each tank and the independent groups were established. For controls ($n=12$ pairs), the intruder compartment remained empty; these fish were isolated from other conspecifics during spawning. For Group M (males; $n=11$), an adult male was placed in the intruder compartment. For Group F (females) ($n=9$), an adult female was placed in the intruder chamber. The intruders were added within 2 min after the female breeder was.

Feeding continued on a twice-a-day schedule, and the intruders were removed after 2 days' residency. After the males were isolated, the tanks were observed for 7 days for nests, spawning behavior, and recently hatched fry. Nests were defined as any collection of surface bubbles. Spawning was judged to have occurred either if eggs were clearly visible in the bubble nest or if the male had been observed to clasp the female. The existence of fry was established by visual inspection. In addition, tanks judged not to contain hatchlings were disassembled immediately following the study. All water was then removed and again inspected, this time in volumes of about 1.5 liter and against a white background. Fry, which are black, were easy to detect in this environment; however, none of my initial judgments was revised as a result of these additional, post hoc observations.

Results and Discussion

Fisher's exact probability test was used for data analyses. All males had bubble nests within 24 h of their introduction into the breeding tanks. Nests were located against at least one wall of these aquaria. With one exception, in which the results were ambiguous, these original nest sites were used for breeding; new locations were not chosen.

As shown in Table 1, between 73% and 100% of each group spawned, and spawning always began within 24 h of the females' being presented to the males. There were no differences between groups on this measure. Relative to controls, the addition of a male intruder significantly reduced the probability of fry being found ($p=.027$). Female intruders did not have this disruptive effect ($p=.45$), while Groups M and F differed reliably ($p=.024$). With one exception, a 4th-day hatch, all hatchings occurred on the 3rd day after females were placed with the males.

It is not clear whether the male intruders disrupted reproduction by acting on the male and/or the female breeders. Neither is it clear by what sensory pathways this effect might be achieved. The experiment was designed to maximize the visual presence of intruders, but chemical communication was also possible. Pheromonal control over social behavior in bettas is known to occur (e.g., Ingersoll, Bronstein, & Bonventre, 1976; Lee & Ingersoll, 1979). Although

the mechanisms are unknown, breeding pairs of bettas, as hypothesized, curtail reproduction when denied social isolation from males. Barash (1976) has documented similar strategies in other species.

EXPERIMENT 2

This study was designed to determine whether a male intruder would interrupt reproduction through nonchemical means, with the intruders being presented in sealed bottles. Second, the study also addressed the question of whether breeding pairs require privacy throughout the entire breeding sequence in order for uninterrupted reproduction to occur. Third, more detailed behavioral records were maintained than in the first study.

Method

In this and all subsequent studies, the clear glass partition used to isolate the intruders of Experiment 1 was not used. All other details of the subjects and apparatus were unaltered.

Male fish were netted and placed in individual aquaria for 72 h. One female was then added to each tank, and the independent groups were established. For the controls ($n=23$ pairs), square, clear-glass jars (8 cm on a side and containing 800-900 ml of water) were placed approximately 15 cm from each male's nest within 2 min after the female's transfer. Group M ($n=24$ pairs) was exposed to the same type of containers, except that each held an adult male conspecific. These jars were left undisturbed for 60 min, after which they were removed for 5 sec and then returned to their original position. Finally, Group 1-H ($n=20$ pairs) had a male added for only the first 60 min the breeders were together. These intruders and their jars were replaced by empty vessels after 1 h with a heterosexual pair. Thus, the Groups M and 1-H experienced the same pattern of physical disruptions—jars added and replaced at the same times. However, the M group encountered far more social stimulation than did the 1-H subjects.

Twice-a-day feedings continued throughout the breeding cycle in this and all subsequent studies, and tanks were observed at least three times a day for the 3 days following the start of cohabitation. Aquaria were observed for 10 sec, and the positions and behaviors of the fish, along with the presence/absence and condition of nests, eggs, and fry, were recorded.

The number of fry in each tank was recorded 72 h after pairs were formed. Hatchlings were collected by rapidly sliding a beaker under each bubble nest, thereby draining fry and nest into that vessel. This procedure was usually adequate for gathering all the young in any tank. Visual reinspection by three observers, along with the occasional emptying of aquaria (as in Experiment 1) confirmed the reliability and completeness of this harvesting procedure. Multiple collections of fry and the removal of adult fish and plants were occasionally required to complete the gathering of hatchlings.

When younger than 48 h posthatch, most fry react to local vibrations by sinking slowly to the bottom of the tank, and, after remaining stationary for approximately 10 min, swimming back to the surface of the water. These characteristics, along with their dark coloration, were exploited in the collection and counting of the hatchlings. Fry that were disturbed, but that evaded initial collection attempts, soon returned to the water surface, where they could be trapped. Following harvest, the fry were poured into white containers, where they remained motionless and easily visible on the substrate for several minutes. Two trained observers, uninformed about the group from which any clutch was taken, were able to count hatchlings to within 5% accuracy.

Table 1
Results of Experiment 1

Group	Total Number of Pairs	Number of Pairs Spawning	Number of Pairs With Hatchlings
Control	12	10	10
Female	9	9	8
Male	11	8	4

Results

Incidental observations suggested that an encounter with an opposite-sex conspecific rapidly produced nest attachment among the males and a pattern of vertical stripes among the females. These effects appeared to occur within minutes, or even seconds, of the animals' initial contact. During the 1st day of cohabitation, control males stayed with their nests and occasionally bit and chased the females. The females escaped during their 1st day with a male, but then tended to follow males to their nests and spawn. Most egg laying occurred at the start of the animals' 2nd day together, and the rate of spawning did not vary as a function of treatment conditions (see Table 2).

The presence of a male intruder stimulated agonistic behavior among the male residents, and between 63% and 79% of the male breeders were seen emitting frontal displays (i.e., gill-cover erections) at each observation. While the intruder did not affect the speed with which copulation was initiated, the additional male did reduce the attention paid to nest sites by males during every observation [$\chi^2(2) \geq 9.19$, $ps < .02$]. As noted in the central portion of Table 2, the 1-H and control groups were not statistically different, while the intruder did interfere with nest-site attachment in the male condition.

Finally, the M group produced reliably fewer fry per clutch than either of the other two groups [$F(2,64) = 9.76$, $p < .005$]. Post hoc *t* tests showed that the control and 1-H groups were not statistically different while comparisons between the M group and the other two conditions were highly significant ($ps < .001$). Also, more of the M pairs had no hatchlings at all than did either of the other two groups [$\chi^2(1) \geq 8.18$, $ps < .01$]. Half of the breeders in the M group produced five or fewer offspring.

Discussion

Taken together, these data replicate the findings of Experiment 1—a male intruder can reduce the breeding efficiency of a pair of bettas without altering their rate of spawning. Furthermore, three new conclusions emerge: (1) The intruder effect is manifest when clutch size as well as the number of clutches

is determined. (2) The intruder is disruptive even in the absence of chemical communication between himself and the breeding pair. (3) In order for a male intruder to interrupt breeding, he must be present for some period other than just the first 60 min of courtship; the 1-H group behaved identically to the controls. Male intruders attract male breeders, and the aggression that emerges appears to affect the post-spawning caretaking. There were 10 pairs in the M group whose nests either disappeared or became scattered after spawning. Such deterioration of nests was never observed in any other group. There was an obvious loss of eggs from the nests of 12 pairs in the M condition. Observations also revealed some effect of the intruder on the quality of spawning. Males were occasionally seen to copulate, but then to display to the intruder while the eggs just expressed from the female fell to the substrate, unattended.

EXPERIMENT 3

This study was undertaken to determine whether, as suggested by Experiment 2, the presence of a male conspecific was sufficient to produce a pattern of high-contrast vertical stripes among females.

Method

The subjects were 24 female bettas. They were housed in individual intruder jars (as used in Experiment 2) and these containers were placed adjacent to each other. Fish could see and be seen by females in adjacent jars.

Each animal's pattern of coloration was judged on four occasions, and each assessment was made independently by two observers who agreed fully. First, a judgment was made while each animal was left undisturbed in its home vessel. Second, the jars housing the females were placed, one per tank, in the standard aquaria used for breeding, and female coloration was assessed 60 sec after transfer. (The tanks lacked vegetation and had an illumination of 344 lx at the water surface.) Third, an adult male, also in an intruder jar, was added to each aquarium, and the females were observed after the pairs had been together for 5 min. Fourth, a final judgment was made after both jars had been in the same tank for 30 min.

Three groups of eight females were used. In one condition, males were placed 23 cm away from the subjects. In another condition, the adjacent jars containing a male and a female, respectively, were touching. An intermediate condition was created by putting the male containers 12.7 cm from the female jars.

Table 2
Results of Experiment 2

Group	n	Cumulative Percentage of Pairs With Eggs							n	Percentage of Males at Their Nests							Fry Available at 72h After Pairing			
		Hours Since Pair Formation								Hours Since Pair Formation							Fry/Clutch			
		3	19	22	26	45	50	68		3	19	22	26	45	50	68	n	Mean	SEM	P*
Male	24	0	4	54	75	88	92	92	24	46	33	54	63	29	42	46	24	154	41	58
Control	23	0	17	69	78	78	87	87	23	96	61	96	100	100	91	100	23	374	40	92
1 h	20	0	5	65	90	95	100	100	20	95	75	85	100	100	100	90	20	373	44	95

*Percentage of pairs with fry.

Results

In the absence of males, no female exhibited the high-contrast, vertical lines. During the first two assessments, some fish had longitudinal stripes, some had pale vertical lines, and others showed uniform coloration, often with a pale ventral crest near their genital papillae. After 5 min of exposure to a nearby male, a pattern of thick dark-and-light vertical bars appeared. All females that were closest to a male showed this change, while only two females in the 23-cm group had this striping. The difference between these two extreme groups was reliable (Fisher's exact probability test, $p < .01$). At a distance of 12.7 cm between animals, 75% of the females showed thick vertical stripes, and no other intergroup differences were significant. The fourth set of judgments produced the same results as the third.

Females show vertical bars when exposed to a proximate male. Chemical communication between animals is not required to produce this pattern. This high-contrast pattern, in conjunction with a slack-finned posture typical of spawning females, reduces the intensity of a male betta's attacks (Robertson & Sale, 1975). This form of disruptive coloration is also thought to serve as effective camouflage in many species (e.g., Cott, 1940).

EXPERIMENT 4

This study was run to determine whether stimulation from conspecifics produces nest-site attachment among resident males and also to find out whether a male intruder alters the number of eggs released by females and placed into bubble nests by the males.

Method

Males were placed in 15-20-liter tanks of water, and 72 h later a female was added to each tank. Within 2 min of each heterosexual pairing, an intruder bottle was placed approximately 15 cm from each male's nest. For the M group ($n = 18$ pairs), the jar contained a male conspecific; for the control group ($n = 15$ pairs), it contained only water. The intruder vessels were not moved once they were inserted in the tanks.

The aquaria were observed 5 min prior to male-female pairings, 30 min after the bottles were added, and at 2-h intervals thereafter, until lights were shut off. Eggs were gathered by draining nests into a submerged beaker 30 h after the breeders were brought together. After collection, the eggs, which are white and opaque at this stage, were trapped in fine mesh, rinsed into a Petri dish, and placed on a black background for counting. This procedure

permitted two independent observers to agree on clutch sizes to within 5%.

Results and Discussion

The findings of Experiments 1 and 2 were reconfirmed. As seen in the left section of Table 3, spawning rate did not vary significantly as a function of whether an intruder was present. Also, between 61% and 94% of male residents were displaying to intruders at each observation. In confirmation both of Experiment 2 and pilot work reported previously (Bronstein, 1981a), the appearance of a female was followed by nest-site attachment among resident males. Only one resident from each group was seen at its nest just prior to the formation of heterosexual pairs, while 93% of control residents and 22% of the male group were at their nests 30 min after pairing. The presentation of a male intruder resulted in reliably fewer males appearing at their nests on all but one observation [$\chi^2(1) \geq 8.26$, $p < .01$]. Males in both groups were equally likely to be seen at their nests 26 h after pairing [$\chi^2(1) = 1.39$, $p > .05$]. (See the central portion of Table 3.)

Intruders attracted male breeders away from their nests; however, this change in behavior did not affect the mean number of eggs per clutch. Controls had numerically more eggs than did M pairs, but the difference did not approach significance [$t(31) = 1.61$, $p < .20$]. These findings suggest that a male intruder reduces the production of hatchlings either by altering the process of fertilization or by disrupting caretaking activities so as to reduce the survivorship of the fertilized eggs. The production and collection of eggs appears to be little affected by an extra male's remaining visible near a resident's nest. Furthermore, the deterioration of nests during the postspawning stage in Experiment 2 shows that intruders do affect caretaking. Only one pair in the M group of Experiment 4 showed any signs of nest deterioration.

EXPERIMENT 5

The specific question posed by this study was whether the inferior caretaking produced by the extra male somehow involved the presence of the female breeder. It is possible, for instance, that the female devours some fertilized eggs while the male resident leaves the nest and displays to the intruder.

Table 3
Results of Experiment 4

Cumulative Percentage of Pairs With Eggs											Percentage of Males at Their Nests											Eggs/Clutch 30 h After Pairing		
Hours Since Pair Formation											Hours Since Pair Formation													
Group	n	.5	1.5	3.5	5.5	7.5	9.5	24	26	28	n	.5	1.5	3.5	5.5	7.5	9.5	24	26	28	n	Mean	SEM	
Male	18	0	0	0	0	0	0	0	56	72	18	22	22	39	45	39	28	40	36	11	18	542	91	
Control	15	0	0	0	0	0	0	13	60	73	15	93	100	93	100	93	93	100	60	100	15	759	99	

Method

An M group and a control group were created, and each was bifurcated to create a total of four independent groups. First, male breeders were isolated in standard aquaria. After 48 h, a female was placed in each resident's tank. Two minutes later, a jar containing a male conspecific was added to each Group M tank and a jar containing only water was added to each control-group tank. Pairs were observed periodically, fed twice daily, but otherwise left undisturbed for the next 30 h. After 39 h of pairing, the females were removed from 17 of the M-group tanks and 17 of the control tanks. When a female was not taken from a particular tank, a net was dipped into that aquarium and withdrawn empty a few seconds later. The tanks were observed periodically for an additional 48 h, after which fry were collected and counted.

Results

On any observation, between 68% and 85% of the Group M residents were displaying to the intruder. Furthermore, the probability of detecting a male at its nest was reliably higher in the control group than in the M group on every observation [$\chi^2(1) \geq 22.83$, $p < .001$]. However, the unexpected finding, noted on the left side of Table 4, was that the M pairs were reliably less likely to spawn and produce eggs than were the control breeders.

As a consequence of this reduction in spawning rate, it was not possible to explore the possible interaction between the female and the intruding male in reducing the quality of egg care and, perhaps, the number of fry produced. The number of M pairs with eggs was so few that the appropriate comparisons could not be made. However, the role of the female during caretaking among the control pairs was assessed. As seen in Table 5, nest attachment among males was not affected by the presence of a female. The female also failed to have any reliable effect on mean clutch size [$t(34) = 1.65$, $p < .20$], although the tendency was for more fry when the females had been removed.

EXPERIMENT 6

Experiment 5 is the first report of a reduction in the speed or probability of egg laying following the appearance of a conspecific male. This reduction may have been due to the reduced amount of time males were alone in their tanks prior to the addition of a mate and the intruder. The males of Experiment 5 were isolated for only 2 days; the fish in Experiments 1, 2, and 4 were alone for 3 days. The current study examined the possible influence of this variable—time of pre-mating residency—on the production of young.

Method

Two groups of breeding pairs were formed. Both had male intruders. The procedures used to create an M group in Experiment 4 were again employed. For a 2-Day group ($n = 17$ pairs), the males were isolated for 48 h prior to being joined by females. For a 3-Day group ($n = 18$ pairs), the resident males were kept alone in their breeding tanks for 72 h prior to the addition of females.

Results

As noted in Table 6, both groups behaved as had the fish exposed to intruders in Experiments 1, 2, and 4. Egg laying occurred among at least 83% of the pairs in each group after 27 h of cohabitation, and the average clutch sizes, which did not vary between groups [$t(33) = .66$] also resembled the values found in Experiments 2 and 4. Between 47% and 94% of each group was displaying on any observation, but there were no reliable intergroup differences on either this measure or on nest attachment (see Table 6) [$\chi^2(1) \leq 3.63$, $p < .10$]. The lack of spawning in Experiment 5 appears not to have resulted from the brief (48-h) residency of the males in that study. The 2-Day and 3-Day groups were not differentiable in Experiment 5.

Table 4
Comparisons of Male and Control Groups in Experiment 5

Group	Cumulative Percentage of Pairs With Eggs						Percentage of Males at Their Nests					
	n	3	20	23*	27*	39*	n	3	20	23*	27*	39*
Male	34	0	6	21	53	53	34	21	32	35	41	26
Control	36	0	17	75	92	94	36	81	100	100	100	92

* $\chi^2(1) \geq 11.37$, $p < .001$.

Table 5
Effects of Female Removal in Experiment 5

Control Group	n	Percentage of Males at Their Nests					Fry Available at 70 h After Pairing			
		Hours Since Pair Formation					Fry/Clutch			P*
		42	45	62	65	69	n	Mean	SEM	
With Females	19	79	84	99	89	95	19	321	65	79
Females Removed	17	94	88	82	94	88	17	465	58	94

*Percentage of pairs with fry.

Table 6
Results of Experiment 6

		Cumulative Percentage of Pairs With Eggs										Percentage of Males at Their Nests										Fry Available at 72 h After Pairing				
Group	n	Hours Since Pair Formation										n	Hours Since Pair Formation										Fry/Clutch			
		3	20	23	27	44	47	51	68	71	3		20	23	27	44	47	51	68	71	n	Mean	SEM	P*		
3 Day	18	0	17	50	83	83	83	83	83	83	18	44	11	6	28	6	23	33	28	28	18	164	48	50		
2 Day	17	0	18	59	88	88	88	88	88	88	17	24	12	12	29	0	29	36	59	53	17	205	57	65		

*Percentage of pairs with fry.

EXPERIMENT 7

The final study, done in two replications, explored the function of the male caring for nests, eggs, and fry. Pilot work from my lab has shown that eggs can develop in the absence of adult caretakers. Furthermore, eggs floating at the water surface appeared more likely to develop than those submerged 10 cm below at the bottom of a glass jar. It is possible that fertilized eggs are more buoyant than unfertilized ova. On the other hand, submerged eggs might develop normally if maintained at the water surface, in contact with moist air.

The behavior of male breeders could serve this physical function since males frequently express bubbles to the water surface, mouth the eggs, and place the eggs into the bubble mass. This sequence of nest-maintenance actions could increase the buoyancy and, indirectly, the survival of fertilized eggs. This hypothesis was tested by removing both male and female breeders following spawning. The number of fry from tanks with a male caretaker were later compared with the count from tanks where neither male nor female remained present after egg laying.

Method

Individual males were placed in separate breeding tanks, and a female was added to each vessel after 72 h. Following egg laying, 30 h after the start of cohabitation, an experimental group was created by netting and removing both adults from some tanks. A control group was also created by removing females only. Hatchlings were then removed and counted. In the initial replication, this procedure was accomplished 30 h after the removal of the adults; the delay between the removal of adults and egg counting was 54 h in the second study.

Results

As seen in Table 7, the presence of a male caretaker improved reproductive efficiency. In each repli-

Table 7
Results of Experiment 7

Group	Hatchling Count					
	Replication 1			Replication 2		
	n	Mean	SEM	n	Mean	SEM
Experimental	11	234	69	12	146	36
Control	10	352	58	9	338	113

cation, a greater number of fry were found in control tanks (with males) than in the experimental aquaria (without caretakers). The difference between groups was not reliable in the first replication [$t(19) = 1.31$] but was significant for the second replication [$t(19) = 2.28$, $p < .05$].

Contrary to the initial hypothesis, males protected their genetic investment not just by keeping their offspring afloat. Rather, the presence of a male prevented the appearance of a saprolegniid fungus among the eggs and fry at the water surface. None of the control tanks contained visible signs of fungus; and no fungus had ever been detected in approximately 300 prior breedings in which a male had been with its eggs and nest after copulation. In contrast, fungus appeared in all but one of the experimental tanks in Replication 1, while nine tanks were visibly contaminated in Replication 2. The fungus appeared as a cotton-like white mass; samples were subsequently identified microscopically. Finally, while my procedure for counting fry was too crude to distinguish reliably between living and dead hatchlings, many fry counted as the reproductive products of experimental pairings were either dead or appeared to be succumbing to the fungal attack at the time of their inclusion in the hatchling count. The effect reported here, although statistically reliable, is an underestimation of the importance of paternal caretaking in permitting the survival of offspring. It is possible that males do keep their eggs afloat and in a physical position where they might develop most rapidly. Males also have a fungicidal or fungistatic benefit for those eggs and fry that are adequately buoyant to float at the water surface.

GENERAL DISCUSSION

Results are consistent with the hypothesis that bettas are territorial, and that reproduction is reduced when males are exposed to the visual presence of other males. When added to the tanks of males, females rapidly develop high-contrast vertical bars and flee from the males, often resting among plants. Both behaviors protect females from males. Equally quickly, the males begin displaying to the females and also become increasingly "attached" to their nests. These changes in behavior and coloration oc-

cur within minutes of initial sightings. Males spend the next day alternating between nest building and displaying near the females. The females generally flee from the approaches of males, but, after about 24 h, the females begin to follow the males to their nests, where spawning, lasting several hours, occurs. The spawning sequence includes the female's lying nearly horizontally near the water surface and being encircled by the male. Release and fertilization of the eggs then occurs. One of the immediate antecedents of the female's assuming this spawning posture is often the male's mouthing of its mate's genital papillae. This tactile stimulation appears to be an important, perhaps reflexive, cause for the female's assuming a receptive orientation. Males find both eggs and genital papillae attractive targets for oral manipulation, and both appear to be approximately the same size, shape, and color. These facts are minimal evidence suggesting a model/mimic relationship between ova and papillae. Wickler (1968) provides further evidence for the existence of ovomimicry among teleosts.

For at least 3 days following egg laying, males typically maintain their nests and place eggs and fry into those nests. They might also attack and spawn with females during this stage. These parental activities can guard the offspring from lethal attacks from fungi (Experiment 7); however, it is not known whether this protection occurs by chemical or physical means. Also, the paternal presence at the nest site probably protects the fry from disturbance by other adult bettas. The sight of a nesting male can provoke escape and nesting in other males (Bronstein, 1981a), as well as the escape of females. The current results show an increase in reproductive efficiency when males or females (Experiment 5) are eliminated from the area near the nest of a paternal male. It should be noted, however, that breeding seemed to be unaffected by the addition of a female (behind glass) in Experiment 1. It may be that the continuation of tactile interactions between males and females is required during the parental phase of reproduction in order for a reduction in reproductive efficiency to occur. In Experiment 1, neither were such tactile interaction between males and female intruders permitted nor were the number of eggs recorded.

As noted in Experiments 1, 2, 5, and 6, the continued presence of a male intruder always led to a deterioration of reproductive efficiency. Chemical communication between breeders and the intruder is not required for this effect, and the disruption can occur during courtship and copulation (Experiment 5, above). The effect is most typically seen during the parental phase (Experiments 1, 2, and 6). Persistent visual stimulation by intruders produces

aggressive display among male breeders (Bronstein, Note 1), and the agonistic sequence typically leads to escape by an intruder, especially at the start of a male/male encounter (Bronstein, 1981a, 1981b). When escape is prevented, aggression becomes intense (Bronstein, 1981a, Note 1) and fighting behavior appears to compete with reproductive activities. The rate at which fighting escalates is largely dependent upon individual differences in visual display among males (Bronstein, 1981a; Robertson & Sale, 1975) and could determine the timing and extent to which breeding is disrupted by an intruder. Given the enormous variability in fighting among males (e.g., Bronstein, 1981a), it is not surprising to find variations in the extent to which fighting interferes with reproduction. The early onset of this interference seen in Experiment 5 is likely to be a consequence of subject selection. Through random events, the males of Experiment 5 could have been animals with a high potential for fighting.

REFERENCE NOTE

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