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Reproductive Behavior and Color Pattern in a Freshwater Serranid Fish, *Coreoperca kawamebari*

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ABSTRACT The behavior and color pattern of the freshwater serranid fish, *Coreoperca kawamebari*, were observed during the breeding season in aquaria simulating natural habitat. The male was very aggressive and territorial during this season, permitting only spawning-ready females to enter his territory so he could court them. The male courtship consisted of aggressive and other certain activities appearing exclusively during the breeding season. The male displayed an intermediate color over his entire body with conspicuous eye-like spots, and as this pattern is the same as the aggressive pattern, the internal breeding system seems to control the male color pattern indirectly through activating the aggressive system. Female courtship, on the other hand, contained both fear and courtship-characteristic components. The female showed a dark color over her entire body with a white vertex band only during courtship encounters, and the white vertex band is the same component appearing in the fear-motivated pattern. Thus the female color pattern is subject to both internal fear and breeding systems. (*Zool. Mag. 92: 207-215, 1983*)

Tinbergen pioneered the study of the internal systems controlling courtship behavior in fish. He stated that a male three-spined stickleback's zigzag dance represents an alternation between a tendency to attack a female and that to lead her to the nest (Tinbergen, 1952). Since then courtship behavior is thought to be controlled not only by a system directly relating to the courtship behavior, but also other systems. Hinde (1953) insisted that the courtship actions of a male chaffinch are expressions of three drives: sex, attacking and fleeing. Morris (1958) also found agonistic elements in the courtship behavior of the ten-spined stickleback, suggesting that the three drives (mating, attacking and fleeing) function in courtship.

However, Boer (1980) who studied the behavior and color patterns of *Chromis cyanea* insisted that courtship behavior is controlled by two systems, I and III (as he called them), rejecting the assumption of an internal 'courtship system'. He stated that a male swimming away from a female in the zigzag dance of the three-spined stickleback can be interpreted by the male's tendency to flee from the female, without assuming a 'sexual' tendency.

Many fishes display body coloration corresponding to their behaviors, accordingly, to their internal states controlling those behaviors (Baerends and Baerends-van Roon, 1950; Baerends, Brouwer and Waterbolk, 1955; Barlow, 1963; Neil, 1964; Baldaccini, 1973; Baylis, 1974; Lanzing and Bower, 1974; Rowland and Lowlands, 1978). Such fishes are suitable for examination of the relationship between the internal systems, because they allow us to analyze the systems by observing body color patterns as well as the behavior. Even more advantageous is the freshwater serranid, *Coreoperca kawamebari*, in which changes in color pattern according to the degree of aggressive and fear motivations have been analyzed in detail in our previous work (Kohda and Watanabe, 1982a and b).

The purpose of the present study is to examine the internal systems controlling courtship behavior of *C. kawamebari* from the aspect of color pattern in addition to behavior.

Materials and Methods

Specimens were adults of the freshwater serranid *Coreoperca kawamebari*, ranging 6.6 to 13.0 cm in total length, collected from streams in Okayama Prefecture, Japan. They were kept in the laboratory from several days to months before observation during the reproductive period, and were fed fish meal pellets, live medaka and guppies, earthworms or tubifex worms every other day.

The breeding season of the fish is from late in April till early in June in the vicinity of Okayama. The specimens were reared under conditions of natural light from the windows of the laboratory or artificial light imitating natural conditions.

For observation, two aquaria were used; 200 × 150 × 25 cm and 180 × 60 × 40 cm deep. To simulate the natural habitat of the fish, many rocks and aquatic plants, and some freswater fishes were put in the aquaria.

Because of the difficulty in sexually discriminating by external morphology, the sex was identified by observing behavior after the fish were placed in the aquaria. When no sexual pair was formed among them, some individuals were replaced by other ones which had been singly reared. After the pairs were formed, their behavior and color patterns were recorded.

The specimens were individually identified according to body size and the pattern of stripes on their body sides.

Observation

Behaviors were clearly identified as follows: *Approaching* (Ap), *Frontal display* (FD), *Tail-beating* (TB), *Biting* (Bi), *Dorsal-rolling* (DR), *Flight* (Fl), *Head-up posture* (HU), *Leading* (Ld), *Following* (Fw), *Prodding* (Pd), *Prodding around genital pore* (PG), *Quivering* (Qv), *Trembling* (Tr), *Resting* (Rs), *Spawning* (Sp), *Insemination* (Is) and *Fanning* (Fn). The first six behaviors were described in our previous paper (Kohda and Watanabe, 1982a) and the latter eleven will be defined in the text.

Pre-breeding period

The fish were inactive below 10°C and became more vigorous with rising water temperature in spring. At low population densities, the fish often showed a coarse coloration with an obscure vertex band and obscure stripes, a coloration seen under solitary conditions (Kohda and Watanabe, 1982a, b) (Fig. $4a_2$). When the population densities were high, a dominance order was recognized among the fish, and each fish displayed a color pattern corresponding to its rank. A dominant fish drove away other fish from its field of view. It rarely attacked heterospecific fish. It changed its own position by degree from day to day. The lower-ranked fish hid themselves behind rocks and plants.

Before spawning in breeding season

Dominant fish had their own distinct territories containing aquatic plants and rocks for refuges in the center. The radius of th territory of a dominant fish was about a half or one meter, although it varied correspondingly to the arrangement of the plants and rocks. Other fish also had territories of an area proportional to their vigor. Weaker fish concealed themselves behind objects located between territories of other fish. In almost all cases, dominant fish having a distinct territory were males, but rarely large females. The dominant male was so territorial that he often attacked heterospecifics intruding into his territory.

The territorial male displayed a yellow-brown color —— intermediate between the darkest and palest colors —— with conspicuous eye-like spots on the edge of its gill covers. When he was defeated by stronger fish newly introduced, this color pattern disappeared temporarily. Both males and females became more red during the breeding season; red patches which existed anteriorly and posteriorly to their real eyes, as well as those that existed anteriorly to their eye-like spots were conspicuous and their bodies turned slightly reddish, too.

The territorial male often came back to vertical stems of plants or strong leaves located at about the center of his territory. In case there were no available plants, he came back to the side of rocks or the wall of the tank. He took a head-up posture attaching his abdomen to the stem, and quivered his body for some seconds (*Quivering*: Qv). This action served as a cleaning of the spawning site. When he found an agnail of the husk of the stem, he held it in his mouth and tore it off. If withered leaves obstructed him, he carried them away with his mouth.

The territorial male drove away other males intruding into his territory. He also attacked females, if they did not display behaviors characteristic of a sexually aroused female. The owner male displayed fast *approaching* (Ap) and/or *frontal display* (FD) toward the intruder. The intruder fled immediately from the attacker. The latter tried to dash toward the fleeing intruder to *bite* it (Bi). As the intruder fled so fast, the Bi often failed. After a short chase the owner came back to his territory. When the intruder did not flee at once, the owner showed *frontal display* (FD) and the intruder fled.

When a female ready for spawning came into the male's territory, the owner male approached her and displayed FD. She did not flee from the approaching male, displayed *dorsal-rolling* (DR), took a *head-up*

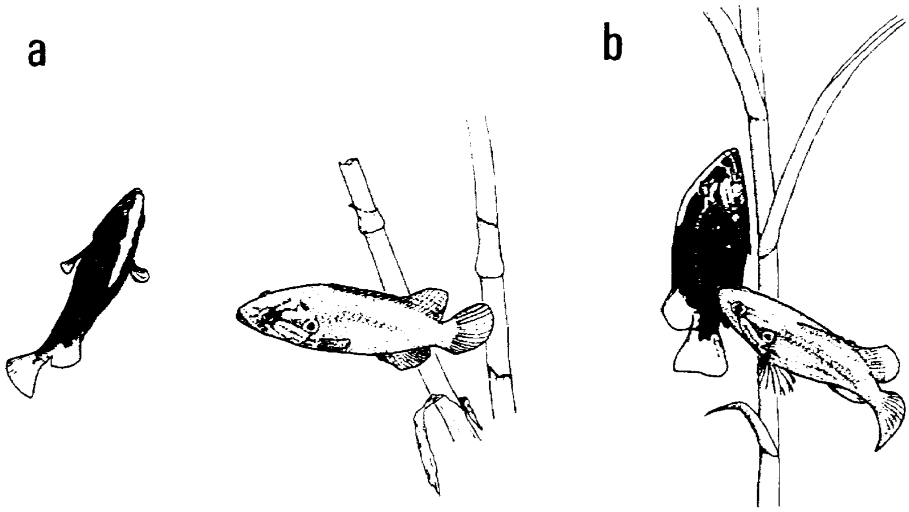

Fig. 1. Reproductive behavior of *Coreoperca kawamebari*. a: A male (right) having intermediate color over the entire body with conspicuous eye-like spots, approaches (Ap) a female (left). The female takes *head-up posture* (HU), changing her coloration to a dark body color with a white vertex band and white upper-peduncle band. b: The female performs *quivering* (Qv) on a stem of a plant, and the male gently prods around her genital pore (PG).

posture (HU), and changed her color pattern from a coarse coloration with an obscure vertex band and stripes, to a black coloration over her entire body with a white vertex and a white upper region of her peduncle (Fig. 1a). In some cases he showed *tail-beating* (TB), but she still held HU. He turned toward the center of his territory and swam about a quarter meter (*Leading*: LD) (Fig. 2). She followed him slowly (*Following*: Fw). He returned to her and displayed FD. When he approached her, she took a HU again. He often prodded her gently with his mouth (*Prodding*: Pd). He swam toward the territory center again. After repeating these behaviors, he led her toward the stem of the plant or the rock where he had performed Qv. He did Qv on the stem, and did FD, TB and/or Pd toward her, and displayed Qv again. She then displayed Qv in place of him (Fig. 1b). He stayed close by her, and when she stopped Qv (*Resting*: Rs), he displayed FD, TB and/or Pd, and Qv. She performed Qv again. During her Qv or HU, he gently prodded her gill covers or face repeatedly (Pd). When he did nothing toward her for a while, she prodded him gently, then he did FD, TB, Pd and/or Qv to stimulate her Qv. As time passed, the interval between her *quiverings* became shorter. The male began to *prod around her genital pore* (PG) instead of the gill covers. She began to show *trembling* (Tr), a finer Qv, after Qv. When she rested, she remained still in HU. Her Qv and Tr were accompanied by a slow upward movement. She climbed the stem up to the surface of water, came down and climbed again. She often came down with a quivering movement. Corresponding to the stimulation by him, she performed Qv and Tr over and over. The frequency of her Tr became greater and at last she spawned.

Until her spawning, other conspecific and heterospecific fish often intruded into the territory. As soon as the owner male

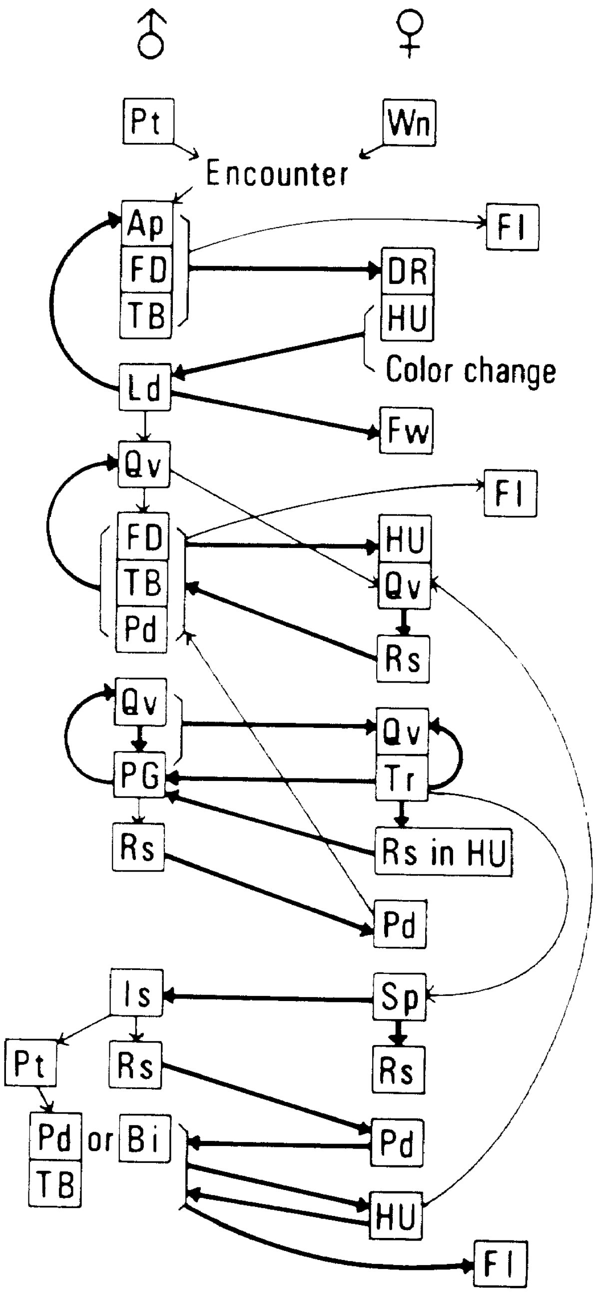

Fig. 2. Behavior sequences in the reproductive behavior of *Coreoperca kawamebari*. Thick arrows mean great frequency of occurrence. Pt: *Patrolling*, Wn: *Wandering*, Ap: *Approaching*, FD: *Frontal display*, TB: *Tail-beating*, Fl: *Flight*, DR: *Dorsal-rolling*, HU: *Head-up posture*, Ld: *Leading*, Fw: *Following*, Qv: *Quivering*, Pd: *Prodding*, Rs: *Resting*, PG: *Prodding around the genital pore*. Tr: *Trembling*, Sp: *Spawning*, Is: *Insemination*, Bi: *Biting*,

found the intruder, he drove it out. During this driving behavior she continued to perform Qv for a while and stood still by the stem. When he did not come back soon, she often left his territory. After driving out the other fish, he came back to her, and tried to stimulate her Qv by his FD, TB, Pd and/or Qv. When she did not respond to him with her Qv, his Pd got violent and she fled from him. If his Pd became too intense, she fled at any time during the courtship sequence. While fleeing from his territory, she lost the color pattern proper to courting females.

In many cases, the female that was driven away by the male or went away during his absence came back to his territory and repeated a series of courtship behaviors. In the other cases, the female went to another territorial male.

After spawning

A female spawned following repeated Qv and Tr for several of minutes to hours. She laid eggs on the underside of the oblique stem, climbing slowly with trembling (*Spawning*: Sp). Immediately a male followed her with his trembling and inseminated the eggs (*Insemination*: Is). The female usually spawned less than one hundred eggs in a double columns.

After Is, he began *patrolling* (Pt). In other cases the male was relaxed. The female stayed by the stem after Sp, and often courted him again with Pd. In many cases he did not respond with Qv but prodded her aggressively, and she fled. The female's proper color pattern faded away and vertical stripes appeared on her body. In some cases, the pair mated over again and spawned.

Thereafter, the male patrolled his territory and drove out intruders. He attacked more violently than before spawning, even heterospecifics more tenaciously. Between intervals of patrolling, he frequently came back to his eggs and performed Qv which was often followed by *fanning* (Fn), an alternate movement of pectoral fins in the same posture as Qv.

For several days after the first spawning, the male courted females coming to his territory and helped them spawn. In the natural habitat we often observed hundreds of eggs guarded by one male. Females spawned several times. According to autopsy, females had about 500 fairly ripe eggs early in the breeding season.

When the first eggs were ready to hatch, the territorial male shut out females from his territory. The eggs hatched in two weeks. The fry were poor at swimming just after hatching and crowded behind leaves near the stem. The male guarded the eggs and fry until all the young dispersed about two days after hatching. During the guarding of eggs, if he was aware of dead eggs, he removed them with his mouth, and when he found snails climbing on the egg-holding stem, he pecked them down. After all the young dispersed, the male established a new territory or stayed *in situ*. Some males mated again during the breeding season.

Discussion

We reported (1982a, b) that in *Coreoperca kawamebari*, an intermediate color over the entire body with conspicuous eye-like spots indicates activity of one (aggressive system) of the internal agonistic systems and inactivity of the other (fear system). The male becomes more territorial during the breeding season and displays the aggressive color pattern in almost all the time. He displays this pattern also during the courting of a female. During courting, he displays *frontal display* (FD) and *tail-beating* (TB) which are behavior patterns in violent fighting. These observations suggest that the aggressive system plays an important role, as opposed to the fear system in male courtship.

Boer (1980) stated that in *Chromis cyanea* there is no need for postulating an internal sexual system for explanation of courtship behavior. According to our observation of *C. kawamebari*, however, *leading* (Ld) and *prodding* (Pd) which are never observed during agonistic encounters, appear in courting encounters, and *biting* (Bi) performed in fighting is never done in courting. Moreover, *quivering* (Qv), which is performed in the courtship sequence and also in parental care later, first takes place during cleaning of the spawning site even if females are absent. Therefore, it must be either a vacuum activity (Tinbergen, 1951) or an action released by the stimuli from the stems of plants or the walls of rocks. Qv never occurs except during the breeding season, although the plants and rocks exist in the surroundings of the fish through all seasons. These observations lead us to the view that there is an internal system which functions only during breeding season, and that the male courtship actions are closely related to the activation of the system. This view is in accordance with Morris (1958) who suggested the presence of three drives, mating, attacking and fleeing, in the courtship of fishes.

As the hatching of the eggs guarded by the male draws near, he stops performing Ld and Pd to spawning-ready females, and begins to attack them, suggesting a shift in his internal state. In explanation of this fact, although we may presume two systems, the one related to courtship actions and the other to paternal ones, it would be a rather parsimonious view that the repression of Ld and Pd is performed, not through a mediation of the activation of the paternal system, but directly by the stimuli from mature eggs and fry; the stimuli inhibit directly the subsystem of Ld and Pd and activate the aggressive system. According to this view, there is no need to assume a paternal system, although we need further studies to decide whether there is a paternal system or not.

Figure 3a is a diagram of the relation between behaviors and internal systems in the male of *C. kawamebari*. The courtship actions are probably controlled by the aggressive system and another system which we named the breeding system because it is activated only during the breeding season. *Patrolling* (Pt) seems to be an appetitive behavior caused by the activation of the aggressive and breeding systems. *Approaching* (Ap), FD and TB are released by the presence of an intruder, and Ld, Pd, *prodding around a female's genital pore* (PG) and *insemination* (Is) are performed by stimuli from a ripe female, while Qv is released by stimuli from the stems of plants and/or eggs. The occurrence of PG near her spawning suggests that the action is released by olfactory substances secreted from the female's genital pore. When the male guards his mature eggs and fry, only aggressive behaviors (FD, TB and Bi) and paternal behaviors (Qv and *fanning* (Fn)) are released probably because the stimuli from the eggs and fry inhibit courtship behaviors (Ld and Pd). The stimuli would motivate the male more aggressively.

On the other hand, a possible relationship of female actions to internal systems is represented in Fig. 3b. A spawning-ready female wanders, and in the encounter with a male she displays *dorsal-rolling* (DR) and *head-up posture* (HU), and changes her color pattern. A female not ready for spawning responds with *flight* (Fl) to the male's Ap. These facts mean that the behavior of the spawning-ready female is controlled by her breeding system activated by the ripening of her eggs. DR is displayed by defeated fish (Kohda and Watanabe, 1982a), therefore, it is presumed to be controlled by the fear system. Since the white vertex band, a component of the female color pattern, is common to defeated fish and lower-ranked fish (Kohda and Watanabe, 1982a, b), it would be a reflection of activation of the fear system. During courtship, the female never performs aggressive actions FD, TB and Bi, but often shows Fl from the male. This indicates that the aggressive system scarcely acts here. *Wandering* (Wn) is an appetitive behavior controlled by the breeding system. HU, which may be a modified DR, is highly related to the fear system. *Following* (Fw) succeeds the male's Ld, so Ld would be a releaser of Fw. As the female soon stops Qv and Tr after the male has gone to drive out intruders, these female's actions would need the plant stems plus the male's Qv, Pd or PG as a releaser. Pd by the female is released by the male's *resting* (Rs).

As soon as the male finds an intruder, he goes to drive it out even during the courting of a female. After returning to his territory, he often also drives out the female, possibly because of an increase in aggressiveness through attacking the intruder. We (1982b) reported that the fish is temporarily motivated more aggressively by a victory after fighting. Heiligenberg (1963) stated that in a cichlid *Pelmatochromis subocellatus kribensis*, the readiness to fight in-

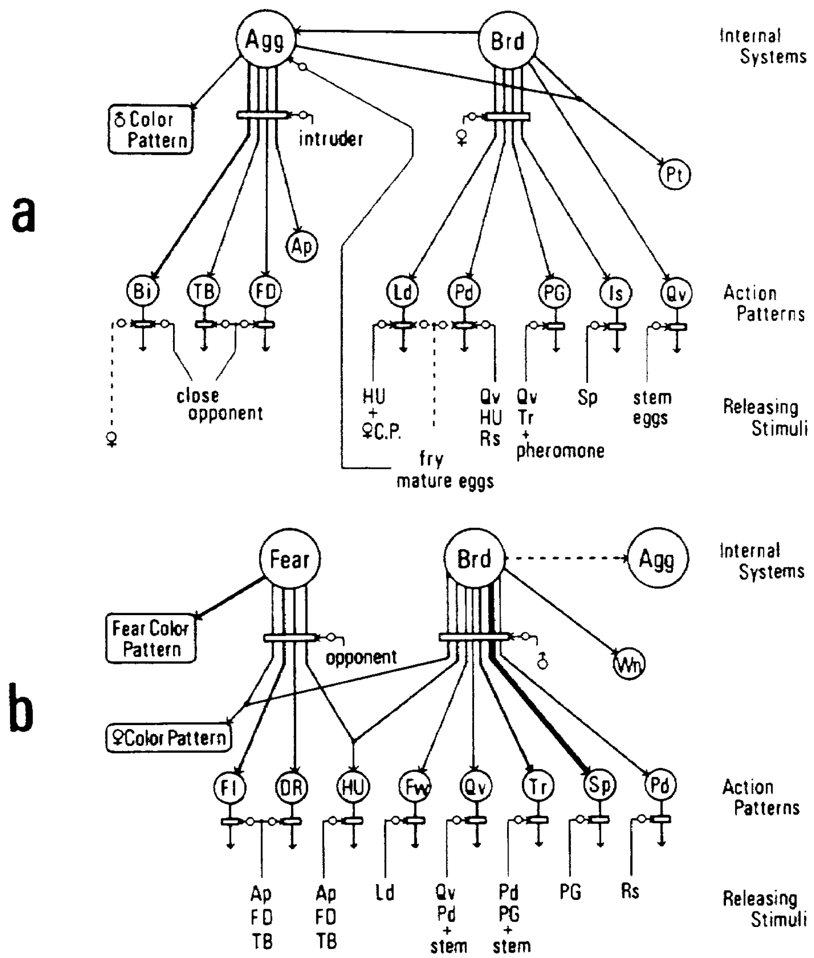

Fig. 3. The relation between internal systems and reproductive behaviors in *Coreoperca kawamebari*, based on Tinbergen's scheme (Tinbergen, 1951). A: male, B: female. Closer relations are shown by arrows; dotted arrows representing inhibition, thick arrows control in which the system concerned is more activated. Agg, Brd and Fear: Aggressive, Breeding and Fear systems respectively. For ♂ color pattern and ♀ color pattern (♀ C. P.) see Fig. 4b and c.

creased following a short fight.

Immediately after spawning, the male often drives out the courting female. This shows a temporary change of balance between the activities of the aggressive and breeding systems after his insemination. The increase of aggressiveness would not be owing to the inhibition of courting actions by newly spawned eggs, for the male often lets females spawn after a while.

Oehlert (1958) described in male cichlids that the readiness to flee suppresses the attacking as well as courting readiness, and that the latter two positively correlate, whereas in females, the attack readiness generally suppresses sexual readiness. Our conclusion, that male courtship actions are controlled by the aggressive and breeding systems and those of females done by the fear and breeding systems, is compatible with Oehlert's.

During courting and egg-caring, the male displays the same color pattern as the aggressive pattern (Fig. 4b, d). This means that in the male, the breeding system controls the color pattern, not directly, but indirectly through activating the aggressive system. In the female, the female-characteristic color pattern appears only during courtship. Therefore, the female breeding system must be responsible for the appearance of the pattern. As the white vertex band, a component of the female pattern, is also a component of fear-motivated fish (Kohda and Watanabe, 1982a, b), the fear system, too, is probably responsible for the female pattern. Figure 4 summarizes the relationship between color patterns and the three

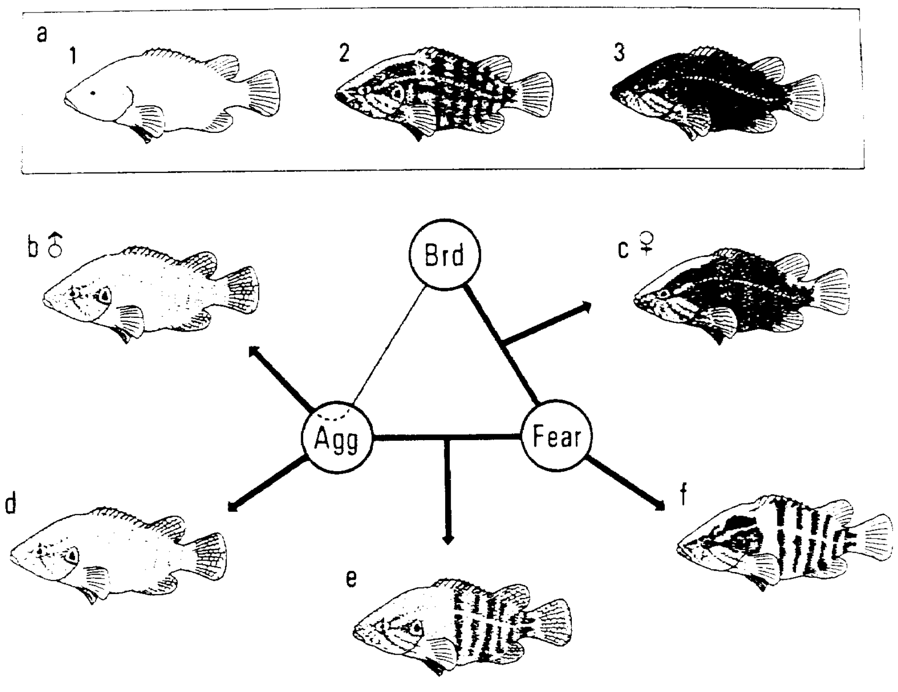

Fig. 4. Color patterns of *Coreoperca kawamebari* under various conditions. a: Patterns under solitary conditions, controlled by none of three systems, 1 —— on a white background, 2 —— on a sandy or gravelly background, 3 —— on a black background. b: Pattern of territorial male, controlled directly by the aggressive system and indirectly by the breeding one. c: Pattern of courting female, controlled by both the breeding and fear systems. d: Aggressive pattern. e: Pattern controlled by both the aggressive and fear systems. f: Fear pattern. b is more reddish than d, and is fundamentally the same as d.

internal systems, taking our previous results (1982a, b) into consideration.

The coloration of the fish would serve intraspecific communication as a sign stimulus. Moreover, the male pattern must function as a mimetic pattern against possible avian predators, because it is a quiet color on a sandy background in his territory. The mimetic function of the male pattern would be connected with his guarding and caring of eggs for a long time. On the other hand, the female-characteristic color pattern is rather conspicuous. The female displays the pattern only during courtship, and at other times, shows the obscure vertex band and obscure stripes, as non-territorial fish do. This coloration would also serve as mimesis among rocks and plants.

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