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Nocturnal Mate Recognition and Nest guarding by Female Convict Cichlids (Pisces, Cichlidae: *Cichlasoma nigrofasciatum*)

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Abstract

This study investigated the ability of nest-guarding convict cichlid (*Cichlasoma nigrofasciatum*) females to recognize their own mate and to defend their brood effectively against strangers at night. Cichlids in the laboratory bred in nesting boxes made of plexiglas. At the fry stage, various conspecific males were introduced, at night, into the nest box of brood-guarding females. Female reaction was observed with infrared equipment. If the introduced male was their own mate, females showed little reaction. If the introduced male was a stranger, females reacted by directing head shakes, tail beats, and pushes or bites at the intruder. The frequency of these acts was significantly higher in the presence of strangers than in the presence of mates; the frequency also rose significantly as the size of strangers increased. The two largest classes of strangers fought with the females. These fights included circling behaviour, but not mouth-locking. Some aspects of female behaviour suggested that mate recognition is based on short-range chemical cues and not on sound, size, or rapidly diffusing odours. Mate recognition in the nest, at night, is an example of non-visual communication in fish, and active nest defense at night shows that the convict cichlid, normally considered to be diurnal, can engage in coordinated and effective behaviour in the absence of light.

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Introduction

In cichlids, as in many other diurnal fishes, communication appears to be based largely on visual signals. Colour patterns and body movements are well documented in cichlids, and their implication in individual recognition, aggressive behaviour and sexual interaction has been comparatively well studied (NELISSEN 1991). Less well known are the acoustic, chemical and tactile means by which cichlids can communicate. It is known that some cichlids can produce sounds (MYRBERG et al. 1965) and recognize their young and conspecifics using chemical

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cues (MYRBERG 1975; CRAPON DE CRAPONA 1980; LUTNESKY 1989). Moreover, some behaviour patterns such as mouth-locking and lateral tail-beating probably convey information through tactile channels (NELISSEN 1991). In spite of this, examples of non-visual communication remain few, and it is difficult to evaluate whether this truly reflects a relative lack of use of non-visual communication by cichlids or simply the difficulty associated with studying non-visual communication in aquatic environments.

There is at least one ecological situation in which cichlids may provide a new example of non-visual communication. The situation involves individual recognition and arises at night during the parental phase. In convict cichlids (*Cichlasoma nigrofasciatum*), rainbow cichlids (*Herotilapia multispinosa*), and a few other species, parental females guard the nest and the eggs, wrigglers, or fry it contains, not only during the day but also throughout the night (REEBS & COLGAN 1991; LAVERY & REEBS 1994). The female's continuous vigilance is probably aimed at warding off nocturnal predators of her eggs and fry, such as the catfish *Rhamdia nicaraguense* (MCKAYE et al. 1979). Interestingly, the female's mate, which usually stays outside the nest at night, sometimes enters it and the female then shows little aggression towards him (REEBS & COLGAN 1991). This suggests that she can recognize her mate even in the absence of visual cues. However, to demonstrate this conclusively, it is necessary to show that the female reacts differently to her mate than to other fish, and this evidence has not yet been produced.

This study attempted to obtain such evidence by measuring the reaction of parental convict-cichlid females to the presence of unfamiliar conspecific males in their nest at night. Conspecifics were used rather than other species because conspecifics provide a more stringent test of the female's discriminative ability and because non-parental conspecifics are important predators of cichlid fry, at least during the day (KEENLEYSIDE et al. 1990; KEENLEYSIDE 1991; WISENDEN & KEENLEYSIDE 1992). The females' reactions to strangers of different sizes, and to their own mate, were compared. A secondary objective was to note whether aggressive interactions take place at night, and whether behaviour patterns that are normally performed during antagonistic encounters in daylight are also used in complete darkness.

Material and Methods

Study Species

Convict cichlids are freshwater fish native to Central America. After a courtship phase which includes much aggression, male and female form a pair bond: they stop behaving aggressively towards each other, and together they start defending a nest (usually a cavity) and a territory around it. After a period of time that may vary from several days to a few weeks, the female spawns on the substrate inside the nest and the male fertilizes the eggs. Thereafter, the male spends most of his time patrolling the territory, while the female concentrates on fanning the eggs and guarding the nest. After 3—4 days, the eggs hatch and non-mobile wrigglers (embryos) fall to the bottom of the nest, where they remain for an additional 3—4 days, guarded and fanned by the female. Then the young become mobile; this is the fry, or larvae, stage. Fry form a free-swimming school that is guarded by both the male and

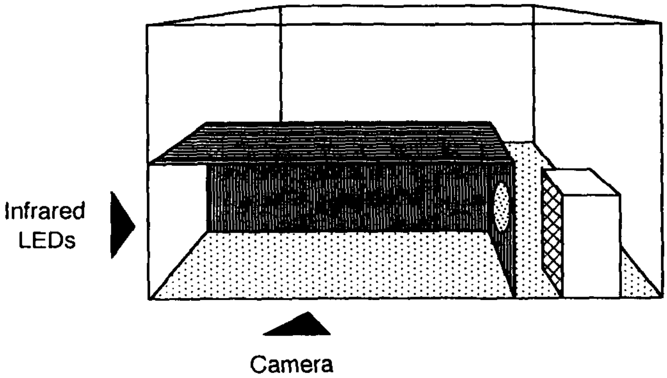

Fig. 1: Experimental setup: nest box (left) and holding box (right). During male presentation, the holding box was placed next to the entrance of the nest box. LED = light-emitting diodes

the female. At dusk and early at night, the female, aided to a certain extent by the male, 'retrieve' the fry: they repeatedly take a few young into their mouth and carry them back to the nest (REEBS 1994). Eventually, all the young are gathered up and they spend the night inside the nest under the surveillance of the female. Males also guard the nest and provide direct parental care, at all stages of the parental phase and at all times of day, but only when the female is removed (LAVERY & REEBS 1994). When the female is present, the male enters the nest only occasionally, and while inside the nest it seldom tries to care for the young.

All fish used in this study were raised in the laboratory; they were 2—3 generations removed from a stock kept in Dr. M. H. A. KEENLEYSIDE's laboratory (Univ. of Western Ontario, Canada). That stock in turn originated from wild fish caught in Costa Rica and had been back-crossed with pet-shop fish. Total length of subjects varied from 6.0—10.1 cm. All females had bred once before; males included both experienced and inexperienced breeders.

Procedures

A total of six pairs were established by placing a male and a female in each of six different aquaria (51 × 26 × 31 cm). In all pairs the female was 88—94 % smaller (total length) than her mate. Although each female was an experienced breeder, none had been paired with her present partner before. Aquaria were positioned in such a way that each pair was in visual contact with one other pair. Lighting came from overhead fluorescent bulbs and followed a schedule of 12 hr of light and 12 hr of darkness. Water temperature was maintained at 28 ± 2 °C by water heaters with disabled pilot lights to ensure total darkness at night. Each aquarium contained a 2-cm layer of gravel at the bottom, a corner filter, a plastic plant, and a 20 × 10 × 10 cm plexiglas box.

The plexiglas box was located in a front corner and had two sides removed (Fig. 1). One side next to the aquarium glass was removed to allow illumination within the box by a bank of 36 infrared-light-emitting diodes (covered with a Kodak #87B infrared-gel filter, whose transmittance below 810 nm is less than 0.1 %, to further block out visible light). The other side next to the glass was also absent to allow observation within the box using an infrared-sensitive camera connected to a remote monitor (Furhman Diversified Inc., LaPorte, Texas, USA) and a videotape recorder. A third side had a hole in it to allow fish to enter the box. The inside of the box was covered with strips of duct tape, as it seemed that convicts prefer this substrate as opposed to smooth plexiglas for egg-laying. All females spawned within the box and kept their wrigglers and fry there at night. This box will hereafter be referred to as the nest.

Experiments were conducted only after the fry stage had begun, as females are known to be more aggressive towards intruders at that time, both during the day (LAVERY & COLGAN 1991) and at night (personal observation). Within her own nest, each female was presented either with her mate, with a strange male 76—80 % smaller (in total length) than her mate, with a strange male the same size (within

3 % of total length) as her mate, or with a strange male 110—116 % longer than her mate. Each female was presented with each type of male, but only one fish was presented each night. Presentations took place from the second through to the fifth night of the fry stage and order of presentation was random for each female. Strange males came from non-breeding pairs kept in individual tanks with the same setup as the experimental tanks (by 'nonbreeding pair', a pair that defend a territory together but have not yet spawned is indicated).

Procedures for male presentation were as follows. At the beginning of the night, the female's mate was removed from the tank and put in a 5 × 8 × 8 cm plexiglas holding box immersed in a separate aquarium. If the presentation schedule called for another male to be presented to the female, then this fish was also removed from his tank, put into a holding box and immersed into the aquarium where the female's mate was kept. The holding box had one side made of wire mesh that allowed water movement and that could also be removed in the manner of a sliding door. A period of 3 hr was then allowed to elapse: enough time for the males to calm down (based on opercular opening rate) and for the female to retrieve all of her fry into the nest.

After those 3 hr, the infrared-light-emitting diodes (cichlids cannot detect infrared light; SCHWANZARA 1967; REEBS & COLGAN 1991), as well as the infrared-sensitive camera and monitor, were turned on. Using infrared goggles (The Dutchman Inc., Overland Park, Kansas, USA), I checked that the female was inside her nest. The holding box containing the male that was to be presented was then placed next to the nest, with the sliding mesh door facing the opening (Fig. 1). After a 10 min pause, the sliding door was removed and, after the male had entered the nest, the door was put back in place to force the fish to stay inside the nest. The videotape recorder was then turned on and the behaviour of both male and female was taped for 5 min. At the end of this observation period, the holding box was removed and the male was allowed to come out of the nest. He was left in the tank if he was the female's mate, otherwise he was netted and returned to his own tank and the female's mate was also returned back into his own tank.

From the videotapes, the following variables were measured: 1. Total number of head shakes by male and female (head-shaking is a behaviour that could be associated with the production of sound; ROWLAND 1978). 2. Total number of lateral tail beats by male and female (tail-beating is a behaviour in which a fish, parallel to another one, flicks its tail towards the other fish. The functions of this are unclear but it is often seen in the first stages of antagonistic encounters and may represent a tactile way of sending and receiving information about size. 3. Total number of pushes or bites by male and female (the snout of one fish makes contact with the other fish's side or head, with various degrees of force). 4. Total amount of time spent mouth-locking (the two fish grip each other by the jaw and pull or push). 5. Total amount of time spent circling (both fish swim rapidly in a tight circle in an apparent effort to bite the posterior part of their opponent's body). 6. Total amount of time spent fighting (including mouth-locking and circling, and including bouts of various instantaneous activities, such as biting and tail-beating, that were not separated by more than 2 s).

To compare female responses to the different males, Friedman tests (SPSS-PC), followed by nonparametric multiple comparisons (CONOVER 1980), were used. For each class of intruder size, sign tests (SPSS-PC) were used to compare male and female behaviour.

Results

In general, females did not react aggressively to their own mate. At most, 1—2 head shakes, tail beats, or gentle pushes were given by 1—2 of the females. Similarly, only two males responded by giving a tail beat. The males usually swam slowly throughout the nest, and sometimes attempted to push their way through the exit.

In contrast, females reacted aggressively to strange males. They directed numerous head shakes, tail beats, and pushes or bites at the intruders. The frequency of these acts was significantly higher towards strange males than towards mates; it also increased as the size of the strangers increased (Fig. 2; headshakes: $\chi^2 = 12.95$, $p = 0.005$; tail beats: $\chi^2 = 16.85$, $p < 0.001$; pushes/bites: $\chi^2 = 18.00$,

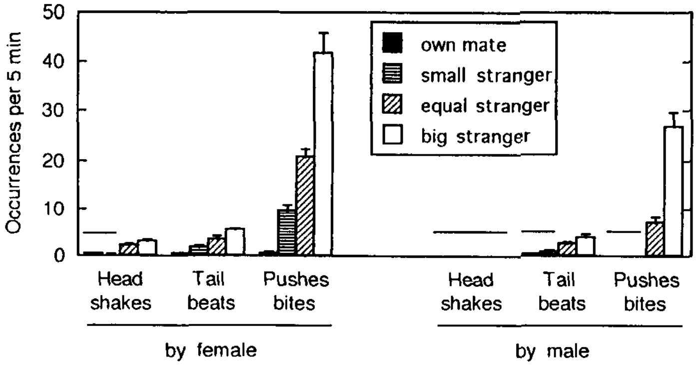

Fig. 2: Frequency ($\bar{X} \pm$ SE, n = 6) of behavioural occurrences by nest-guarding females and intruding males during 5-min nest intrusions. Within groups of bars (behavioural variables), the reaction of females to their mate, and to strange males that were either smaller, equal to, or larger than their own mate is depicted from left to right. Also within groups of bars, horizontal lines are drawn over bars that are not significantly different ($p > 0.05$)

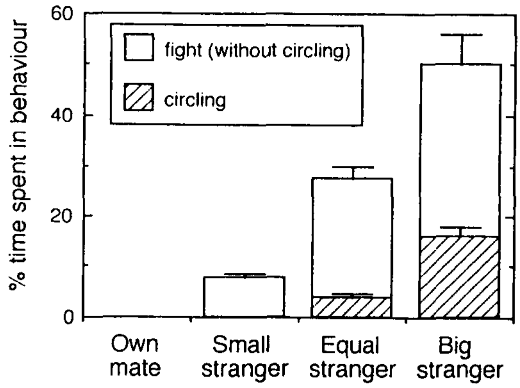

Fig. 3: Percentage ($\bar{X} \pm$ SE, n = 6) of time spent fighting by nest-guarding females and various intruding males during 5-min nest intrusions. Bars are divided in two portions, showing time spent circling and time spent in bouts of other aggressive behaviour, such as tail-beating, biting, and pushing. All between-male differences are significant ($p < 0.05$), regardless of whether the total time spent fighting or the two separate components of fighting (with exception of circling for own mate and small stranger) are considered

$p < 0.001$; multiple comparisons, $p < 0.05$). Strange males tended to respond in a similar fashion, but for almost all types of behaviour and for all size classes, male activity was lower than female activity (Fig. 2; sign tests, $p = 0.016$). The only exceptions were head shakes and tail beats in trials using small males, when too many pairs were tied at 0 or 1 to allow meaningful tests to be conducted. The percentage of time spent fighting also increased with intruder size (Fig. 3; $\chi^2 = 16.20$, $p = 0.001$), as did the circling component of these fights (Fig. 3; $\chi^2 = 18.00$, $p < 0.001$).

Females did not react immediately to the entry of intruders. Only after 14—108 s, when the male approached the female and came in contact with her snout, did the female finally react, first with a few head shakes and tail beats, and then with pushes and bites. Small males did not respond and retreated to a corner of the nesting box, where they remained motionless and unharmed by the female. Males of similar size to the female's own mate put up more of a fight, biting back and occasionally engaging in circling behaviour (Fig. 3). Eventually, however, they too broke off and retreated to corners. Sometimes they swam through the nest but did not elicit further attacks unless they came very close to the female. Larger males fought energetically, engaging in more circling behaviour (Fig. 3) and not retreating; fights in this case were punctuated by quiet bouts in which the two protagonists remained separated, but the female soon moved about and reinitiated fighting after coming into contact with the male. All of these fights were still underway at the 5-min point, when trials were stopped. No injuries could be detected the next day on the body of either protagonist.

Mouth-locking was never observed, irrespective of intruder size. To the naked eye, the other behaviour patterns (head-shaking, tail-beating, biting, circling) appeared to be performed in the same way as during the day (personal observations).

Intruding males neither attacked nor fed upon the fry. Males could not get close to the fry without encountering the female, which usually held station over the fry and fought with the males that came close to her. During fights with large males, fry were often stirred up from the bottom but no dead fry were found in the nest the next morning.

Discussion

Results show that nest-guarding females can distinguish between their mate and strange males at night, since they only reacted aggressively towards the latter. The mechanism(s) by which females recognize males as unfamiliar did not appear to operate at a distance, as females did not react immediately to the entry of intruders, and did not attack males that avoided contact. This contrasts with diurnal behaviour, in which females promptly and relentlessly attack nest intruders (personal observation). These observations confirm that convict cichlids cannot see under infra-red light, and suggest that long-distance cues such as sound, pressure waves, and rapidly diffusing odours are not of primary importance in initial recognition. In the case of sound however, one should note that the apparent lack of long-distance communication may have been caused by a lack of sound emission by one or both protagonists, and not from the lack of recognition of an acoustical signature. Males giving head shakes, a behaviour associated with sound emission (MYRBERG et al. 1965; ROWLAND 1978) were not observed. In at least one other species and one other context, sound has been shown to enable individual recognition (MYRBERG & RIGGIO 1985).

It seems unlikely that females use size as a cue to recognize their mate, as intruders of similar size to the female's mate were attacked. The different intensities of female behaviour towards males of different sizes are probably related to the willingness of males to prolong fights, and not to incomplete recognition on the part of the female. It is well known that size is the primary determinant of fighting capability in fish (KOOPS & GRANT 1993). It is not known, however, whether motivation to prolong a fight in the dark depends on a fish's knowledge of its own absolute size, or on a perception of size difference in comparison to the protagonist, based perhaps on information gained through tactile channels. It is also unclear whether the absence of visual cues at night affects a fish's perception of whether it is in its own territory or in a foreign environment, with possible repercussions on the motivation to fight (the 'prior residence effect'; FIGLER & EINHORN 1983; FIGLER et al. 1985). These uncertainties point to the potential use of darkness and night-vision equipment in studying the mechanisms of fighting and its motivation.

Chemical cues in the immediate surroundings of a fish's snout probably allowed individual recognition in this study. This view stems from the observation that fights were initiated only when the male's body came in contact with the female's snout. The importance of chemical cues in fish has already been established in other contexts (LILEY 1982; HARA 1986) including egg recognition (FITZGERALD & VAN HAVRE 1987; REEBS & COLGAN 1992), recognition of young (MYRBERG 1975; MCKAYE & BARLOW 1976), kin recognition (OLSEN 1989), sex recognition (CRAPON DE CRAPONA 1980), species recognition (CRAPON DE CRAPONA & RYAN 1990), and predator recognition (WELDON 1990; MATHIS et al. 1993). A nocturnal species, the yellow bullhead (*Ictalurus natalis*), can also discriminate between individuals on the basis of odours emanating from a mucal body covering (TODD et al. 1967). Although chemical cues can involve gustatory as well as olfactory senses (HARA 1986), it seems likely that olfaction is of primary importance. This could be tested by plugging the nose of a test fish, a difficult manipulation on a small fish like the convict cichlid, but one that has been successfully performed with at least one larger species (MCKAYE & BARLOW 1976). Unfortunately, there is a danger that such a manipulation would interfere with essential aspects of parental care, such as nocturnal fanning of eggs, wrigglers and fry (REEBS & COLGAN 1992; LAVERY & REEBS 1994) and nocturnal retrieving of fry (REEBS 1994).

With the exception of mouth-locking, all behaviour patterns normally seen during diurnal fights (BAERENDS & BAERENDS-VAN ROON 1950; KOOPS & GRANT 1993; pers. obs.) were also present at night. There is little reason why mouth-locking could not be maintained in the absence of visual cues, but it may be difficult to initiate without being able to see the opponent's jaws. Other behaviour such as tail-beating and biting can be effectively directed at any part of the body. This does not mean, of course, that visual cues are not used during biting and tail-beating in daylight; this question awaits a precise quantification of the differences between diurnal and nocturnal fights.

As opposed to the present study, KOOPS & GRANT (1993) observed no tail-beating behaviour during antagonistic encounters between convict cichlids. Their study was conducted during the day and involved only same-gender pairs.

I have often witnessed tail-beating during the day, but always during mixed-gender encounters. It is therefore possible that the occurrence of tail-beating in this species depends on the sex of the protagonists. As stated earlier, the function of tail-beating is unclear: sex recognition, size assessment, individual recognition, and even appeasement are all untested possibilities. Experiments under darkness could shed some light on this question. It would be interesting to know whether more tail-beating is given in the dark than in the light (indicating that tail-beating transmits information via tactile channels, and is used when visual cues are absent), and whether tail-beating is really limited to mixed-gender encounters, in both light and darkness (indicating that tail-beating may be related more to courtship or appeasement than to size assessment). One could therefore determine whether cichlids can discriminate between males and females in the dark.

In this study, strange males and nocturnal encounters were used as a tool to test the ability of a female to recognize her mate, and to identify some of the mechanisms used in this recognition. Nest-guarding was not the primary focus, but it could be the basis of future studies as to whether predation by conspecific convicts is as important at night as it is during the day and whether there are specialized nocturnal predators (the catfish, *Rhamdia nicaraguense*, for example) that have developed ways to minimize detection by a nest-guarding female. Furthermore such studies may help to show if, when a female is fighting with a nocturnal predator, the mate can detect the commotion and come to help the female and whether the two mates can coordinate their actions against a common enemy in the dark.

Overall, the results of the present study emphasize the non-essential nature of visual cues in several aspects of cichlid behaviour. Cichlids can both recognize their mate and fight properly against a conspecific in the dark. It is also known that they can fan their eggs (REEBS & COLGAN 1991), retrieve their young (REEBS 1994) and even spawn (NOBLE & CURTIS 1939; personal observation) in complete darkness. There is little doubt that cichlids in general, and convict cichlids in particular, are diurnal and that their behaviour can be affected by light (TOBLER & BORBELY 1985) but this should not be equated with a complete inability to be active in the dark. Because nocturnal activity is sometimes needed, such as during the parental cycle, and because the aquatic environment includes many places where light intensity is low, the diurnal cichlid has evolved ways of functioning and of recognizing conspecifics in the dark.

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