

Tidal cycling and parental behavior of the cichlid fish, *Biotodoma cupido*

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Synopsis

Parental behavior of the substrate-brooding cichlid, *Biotodoma cupido*, was studied in a small creek entering the lower Essequibo River, Guyana, where the freshwaters are affected by semi-diurnal tides. Physico-chemical variables of the tidal cycle were associated with the parental behavior of *B. cupido*. During late ebb and early flood tides, while offspring were nest dependent, parents displayed intense aggression toward brood predators, mainly characins. At low tide, when the concentration of dissolved oxygen decreased to about 4 mg l^{-1} and that of free carbon dioxide increased to 28 mg l^{-1} , parents entered a state of somnolence and brood predators vanished. Early flood tide brought an immediate and dramatic reversal of hypoxic and hypercarbic conditions and an associated renewal of aggressive and predatory activity. At very low tide, parents orally transferred the brood to a secondary nest depression in deeper water. The significance of water-level fluctuation to the evolution of this behavior, as well as that of parent-brood itineracy and the related phenomena of oral incubation and movable nests, is discussed.

Introduction

In June, 1972, while conducting extensive studies on the reproductive biology of cichlid fishes in the lower Essequibo River of Guyana, South America (Figs. 1 and 2), I made the first recorded field observations on the parental behavior of the little known

cichlid fish, *Biotodoma cupido* (Heckel). In making these observations, I took considerable advantage of a rarely encountered situation. Weeks of careful searching failed to yield additional examples. Nevertheless, the results are significant because they concern natural ecology and behavior and bear on the evolution of parental behavior in cichlids.

Biotodoma cupido (subtribe Geophagi) represents a basal offshoot of the phyletic lineage culminating in the large genera *Apistogramma* and *Geophagus* (Cichocki 1976). Mature adults are handsome fish with deep ochre flanks, a vivid dorsolateral ocellus and electric bluish-white pelvic, anal and caudal fin edges (Fig. 3). Contrary to the intimation of Wickler (1966), *B. cupido* exhibits sexual dimorphism in color pattern, with males having electric blue lines on the snout and females small, darker blue spots scattered over the snout and opercula. As in many other cichlids, within breeding pairs, the male is typically larger than the female.

Regarding the etymology of the name, *Biotodoma*, Eigenmann & Kennedy (1903) allude to an orobranchial brooding habit for *B. cupido*. This myth is still perpetuated in both popular (Goldstein 1970, 1973) and scientific (Lowe-McConnell 1969) literature despite the fact that Wickler (1966) reported it to be a substrate brooder after successful breeding in the aquarium. My field observations (Cichocki 1976) fully confirm this.

Locality and habitat

Observations were made in a small tidal creek running NW in the Essequibo River opposite Bartica,

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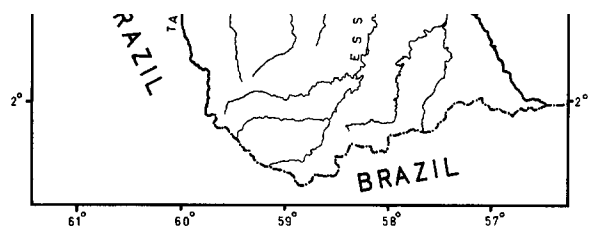
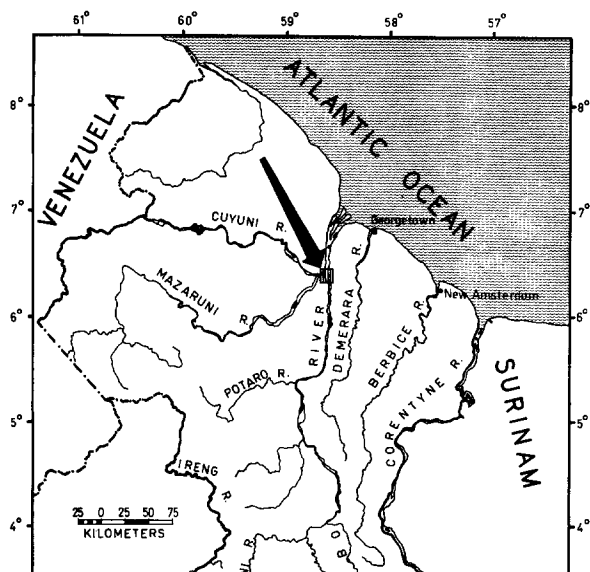


Fig. 1. Map of Guyana, South America. Arrow indicates approximate area covered by map of Fig. 2. (After a compilation by the Cartographic Division, The Lands Department, Ministry of National Development and Agriculture, Georgetown, Guyana.)

Guyana (Fig. 2). The waters of the Essequibo River, though fresh, are affected by semi-diurnal tides (ranging to 2 m) up to the first cataracts at Wineperu, some 90 km from its mouth. Present studies were conducted during the rainy season when the discharge of the Essequibo is high, resulting in rapidly rising and slowly falling tides. At Bartica, during the rainy season there is little or no upstream flow on the flood tide. However, there is flood flow up to the first cataracts during the dry season (Brown 1871). In the Essequibo currents achieve maximum velocity on the falling tide.

Largely due to its small, heavily overgrown basin and slight inland discharge, tidal conditions within the creek differed from those in the main river. The tidal cycle in the creek was marked not only by oscillation in water level but by relatively dras-

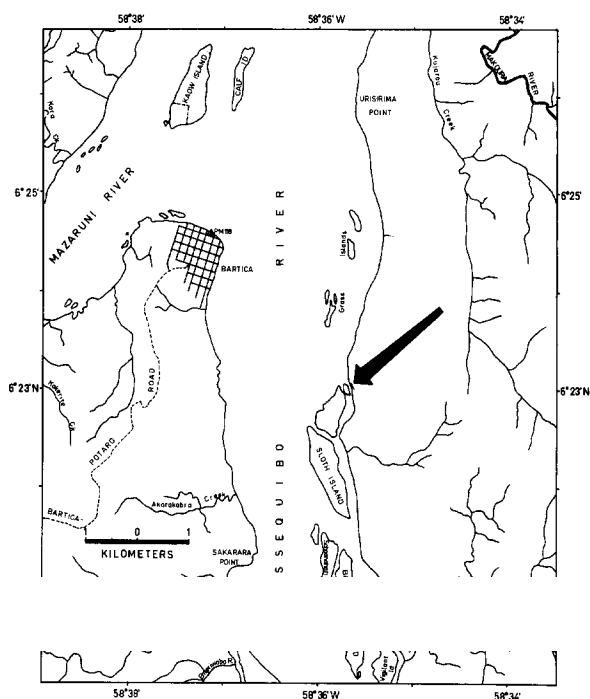


Fig. 2. Map of the Essequibo and Mazaruni region, vicinity of Bartica, Guyana. Arrow indicates location of the tidal creek in which the study was conducted. (After a compilation by the Cartographic Division, The Lands Department, Ministry of National Development and Agriculture, Georgetown, Guyana.)

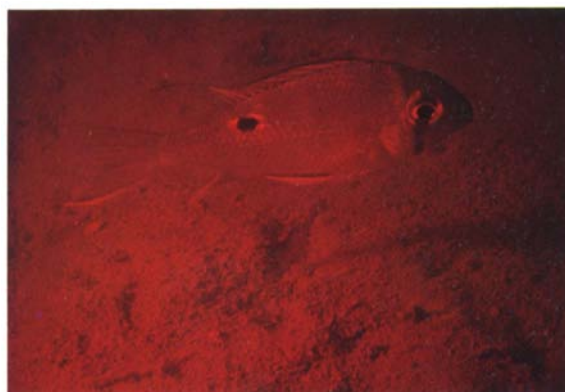


Fig. 3. Adult female *Biotodoma cupido* guarding her nest (just below the pelvic fin). Note highly visible dorsolateral ocellus and light (electric bluish-white) edging of pelvic and caudal fins. Compounds in solution selectively absorbing light of shorter wavelengths (predominantly green and blue) produce the characteristic reddish water. This absorbance, resulting in strong attenuation of radiant intensity with distance, made for less than ideal photographic conditions.



Fig. 4. a) Red mangrove (*Rhizophora mangle*) bordering the tidal creek. Similar stands of mangrove occur all along the lower Essequibo River and on many offshore islands. b) The nesting territory described in the text lies within the cluster of prop roots at the left. The task of observation was sometimes an arduous one as demonstrated by Mr. Ivan Douglas.

tic fluctuation in the direction and speed of the current and in the chemical composition of the water. Maximum current velocities in the creek occurred during the rising tide.

The lowland areas fringing the Essequibo River and the tidal creek are well populated with stands of red mangrove (*Rhizophora mangle*) (Fig. 4). Aquatic herbs are uncommon in the creek and along the banks of the Essequibo, but some barrier islands support an abundance of such plants, including sedges (e.g., *Eleocharis*) and *Sagittaria* (Fig. 5). Many offshore islands are laced with tidal channels, which held concentrations of mature *B. cupido*. The substratum of the tidal creek consists mainly of sticky, gray organic sediment overlain with easily suspended detritus.



Fig. 5. Typical "grassy" island with tidal channels and small stands of red mangrove.

Materials and methods

Observations were made on a nesting family (parents and young) and at least one older itinerant family. The nest of the former was an irregular, elongate depression in the substrate, about 30 mm in length (Figs. 3 and 6). It was situated centrally in a relatively unobstructed area about 1 m in diameter within a cluster of mangrove roots near the main channel of the creek (Fig. 4b). This constituted the territory of the family. When discovered on June 8, 1972, the nest contained embryos about to hatch. The embryos hatched by the following day, and on June 12 the young abandoned the nest and traveled with the parents. The itinerant family unit(s) consisted of parents and much older young (10–15 mm in length). They were observed briefly several times from June 15 to June 17 in another part of the creek. The parents of both the nesting and itinerant family units were comparably sized, females being 70 to 75 mm and males 80 to 85 mm in standard length.

Fish were observed under water with the aid of a face plate and snorkel and from above the surface. Underwater observations were recorded in pencil on roughened acrylic slates and later transcribed. An extensive photographic record of behavior was made using a Nikon F 35 mm camera (50 mm Micronikkor lens) encased in a Sea Glove underwater housing (Sea Research and Development Corporation, Bartow, Florida, USA) with ASA 64 and 125 Ektachrome film and auxiliary light provided by blue AGI rated flash cubes.

Several physico-chemical variables were meas-

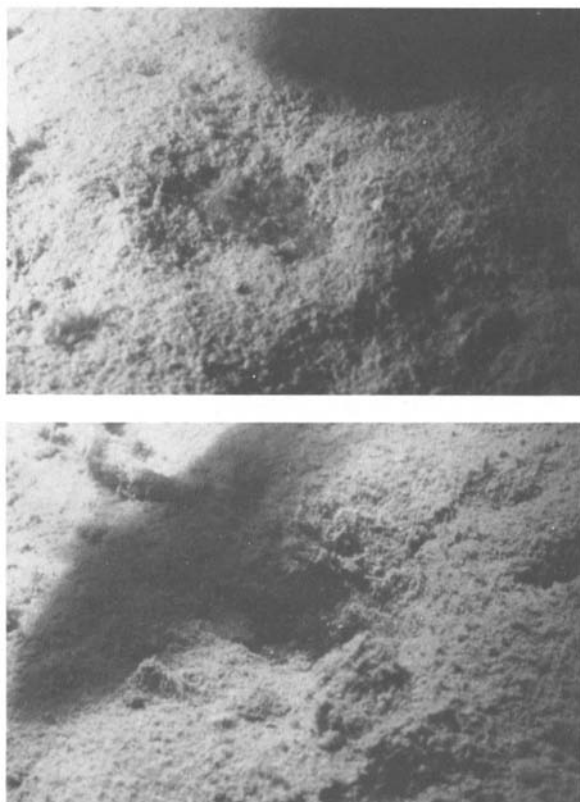


Fig. 6. a) *Biotodoma cupido* nest (center) containing wriggling free embryos (June 9, 1972). b) Same nest just before young became free swimming (June 11, 1972). Bright spots are the eyes of the young and the shadow is that of the guarding female.

ured near and just above the level of the *B. cupido* nest during various tidal stages. Water was collected with a micro-Kemmerer sampler and analyzed by standard methods using a portable field kit (Hach, AL-36-WR and 7P) with freshly standardized reagents. Water velocities were estimated by timing the drift of detritus particles over a measured distance. Water depths were established with a semi-permanent measuring rod and a standard meter stick. All but the lowest and highest levels were recorded to the nearest 5 cm. Water and air temperatures were determined by a standard mercury bulb thermometer. Times given are local (3 h and 45 min slow of G.M.T.).

Statistical hypothesis testing was limited to use of the simple t test for paired observations.

Environmental fluctuations during the tidal cycle

During the tidal cycle, the physical and chemical characteristics of the aquatic environment in the creek changed markedly (Table 1). The moon was

During the ebb tide, current velocities a few centimeters above the nest were outflowing at between 1.0 and 0.1 cm sec^{-1} gradually becoming barely perceptible at low water. With inflow on the flooding tide, current speeds increased rapidly to about 10.0 cm sec^{-1} , thereafter decreasing to hardly noticeable at high water. Strong currents during the early flood tide picked up and suspended detritus and loose sediments. These remained in suspension throughout the rising and much of the falling tide.

The relationship of dissolved oxygen and free carbon dioxide concentrations as functions of the tidal cycle were nearly enantiomorphic (Fig. 7). Dissolved oxygen approached saturation concentrations only on the rising tide, when, correspondingly, the concentration of free carbon dioxide fell to its lowest levels. Conversely, dissolved oxygen concentrations fell to low levels (about 5% of saturation) during the ebbing tide, while, at the same time, free carbon dioxide rose to high concentrations. Low tide marked the maximum free carbon dioxide and minimum dissolved oxygen concentrations. These hypercarbic and hypoxic conditions presumably are related to anaerobic processes and respiratory activity within the creek. Carbon dioxide concentration and pH were clearly and predictably associated. Chloride concentrations were always minute, never exceeding the lowest level detectable by the reagents employed (7.5 mg l^{-1}).

The portion of the tidal cycle during which observation of the nesting *B. cupido* unit was practicable and behavior could be correlated with environmental variation may be divided conveniently into three stages: 1) Approximately 2 h of falling water with an outflowing current of 1 cm sec^{-1} or less and dissolved oxygen and free carbon dioxide concentrations approaching 4 and 28 mg l^{-1} , respectively (three-quarters ebb tide to low tide). 2) One-half to one hour of lowest water with negligible outflowing current and dissolved oxygen

Table 1. Variation in the physico-chemical factors of the aquatic environment during the tidal cycle, measured at the *Biotodoma cupido* nest site. Locality: tidal creek flowing into Essequibo River opposite Bartica, Guyana.

Date (June, 1972)	Local time (hrs)	Tide	Water height (cm)	Approx. current speed (cm sec ⁻¹)	Temperature (°C) Air Water	O ₂ Conc. (mg l ⁻¹)	% O ₂ Sat.	Free CO ₂ Conc. (mg l ⁻¹)	PH	HCO ₃ ⁻¹ Conc. (mg l ⁻¹)
10	1510	low	12	< 0.1	27.5 27.0	4.4	54	28.1	5.25	6.8
10	1625	1/2 flood	80	3.0	27.0 28.0	7.0	89	8.0	5.75	—
11	1520	low	18	< 0.1	29.5 27.5	4.0	50	28.1	5.25	—
11	1700	1/4 flood	45	8.0	29.0 28.0	6.8	86	8.0	5.75	—
12	1257	1/2 ebb	80	1.0	32.0 27.0	5.8	72	14.0	5.50	—
16	0805	3/4 flood	120	3.0	26.5 27.0	7.0	86	10.0	5.50	—
16	1735	3/4 ebb	40	0.5	27.0 26.5	4.4	54	22.0	5.25	—
17	1055	high	163	< 0.1	31.5 27.0	6.4	79	12.0	5.50	—

and free carbon dioxide concentrations of about 4 and 28 mg l⁻¹, respectively (low tide). 3) One hour of rapidly rising water with an inward flow near the bottom reaching a peak of 10 cm sec⁻¹ and dissolved oxygen and free carbon dioxide concentrations becoming about 7 and 8 mg l⁻¹, respectively (low tide to one-quarter flood tide).

Parental behavior and the tidal cycle

The activity of the nesting *B. cupido* parents during much of tidal stage 1 and the early part of tidal stage 3 was dominated by aggression toward potential brood predators (Fig. 8), including characins (*Moenkhausia grandisquamis*, *Hemiodus notatus*, *Creatochanes affinis*, *Leporinus nigrotaeniatus* and *L. fasciatus*) and to a lesser extent juvenile cichlids (*B. cupido* and *Geophagus jurupari*). Parental aggression most frequently took the form of a rapid, looping dart toward, and a chase of, an antagonist ultimately bringing the parent back to, or near, its initial position. During tidal stage 2 (low tide) such parental aggression was rarely observed.

The relationship between parental aggression toward potential brood predators, expressed as the number of aggressive encounters per minute, and the tidal cycle is presented in Table 2 and Fig. 9. During brief observation under very turbid conditions when the tide was about one-half ebb (0950 h, June 10, at 85 cm depth and 1115 h, June 11, at 70 cm depth) the parents were holding their positions near the nest, and no agonistic behavior or potential brood predators were evident. Parental aggression increased as the water level fell to a depth of between 35 and 25 cm, a relationship veri-

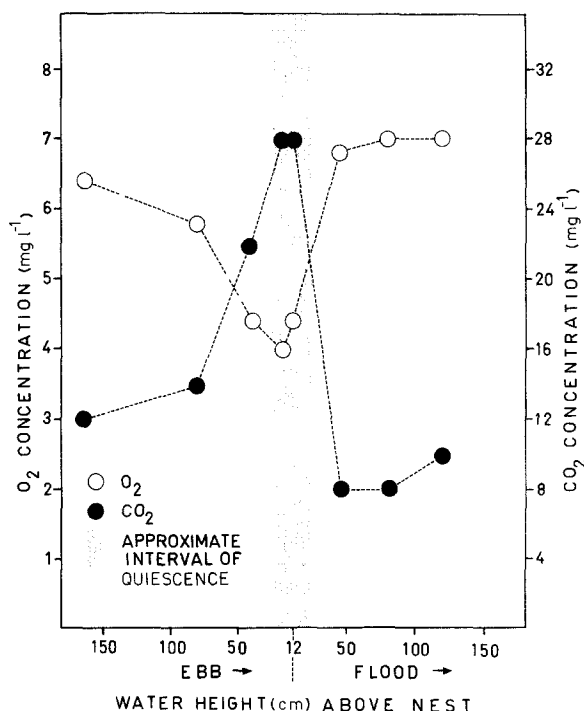


Fig. 7. Relationship between concentrations of dissolved oxygen and free carbon dioxide and the tidal cycle (quantified in terms of water height) during the period June 10 to 17, 1972 (see Table 1). All measurements taken just above the bottom near the *Biotodoma cupido* nest. Approximate interval of parental quiescence indicated.

fied by the observations of June 9 (Fig. 9). This increase was followed by a decrease in aggression as the tide ebbed further. Except for the June 8 results, little or no parental aggression occurred during low tide. Aggressive activity increased sharply



Fig. 8. *Biotodoma cupido* female chasing potential brood predators from the nest (lower center), June 9, 1972. *Moenkhausia grandisquamis* in foreground.

with the flooding tide until the water depth again reached about 25 cm and then declined as the tide continued to rise.

For June 9, 10 and 11, the differences between mean female aggression during tidal stage 2 (0.015 acts per min) and maximum mean aggression during both stages 1 and 3 (0.461 and 0.526 acts per min) achieve or approach statistical

significance ($p = 0.1$, one-tailed t test for paired observations; $t = 2.150$ and 1.704 , respectively). The corresponding differences in the means of the mean aggression values for both the male and female together for the three tidal stages (0.008 acts per min vs 0.374 and 0.295 acts per min) attain comparable significance levels ($p = 0.1$, $t = 1.656$ and 2.325 , respectively). Likewise, the low mean value for aggression of the female (0.027 acts per min) and the low mean of the mean values for both partners (0.013 acts per min) during the latter part of stage 3 approach or attain statistically significant

part of the same period ($p = 0.1$, $t = 1.733$ and 2.388). The mean values observed during tidal stage 1 and the early part of stage 3 for both female aggression and the means of male and female aggression are not significantly different ($p = 0.1$, $t = 0.160$ and 0.171).

The null values for male aggression on June 8 and 9 during tidal stage 1 and/or 2 (Table 2) were a result of the male parent spending a considerable amount of time out of sight beyond the perimeter of the nesting territory. The male's behavior while away from the nest is unknown, but no other nests

Table 2. Aggression toward potential brood predators by nesting *Biotodoma cupido* parents. Locality: tidal creek flowing into Essequibo River opposite Bartica, Guyana.

Date (June, 1972)	Local time interval (hrs)	Tide	Water depth at nest (cm)		Aggressive acts per minute		
			Range	Average	Female	Male	Mean
8	1217-1250	7/8 ebb through low	25-20	22.5	0.182	0.031	0.107
8	1251-1326	1/8 flood	20-30	25.0	0.177	0.000	0.089
8	1345-1430	1/4 flood	30-75	52.5	0.000	0.000	0.000
9	1110-1145	3/4 ebb	50-30	40.0	0.058	0.116	0.087
9	1250-1342	7/8 ebb	25-20	22.5	0.384	0.000	0.192
9	1343-1405	low	20-20	20.0	0.045	0.000	0.023
9	1406-1425	1/8 flood	20-30	25.0	1.155	0.000	0.577
9	1426-1450	1/4 flood	30-50	40.0	0.080	0.000	0.040
10	1159-1232	7/8 ebb	35-30	32.5	0.152	0.091	0.122
10	1339-1358	7/8 ebb	15-12	13.5	0.052	0.000	0.026
10	1410-1516	low	12-12	12.0	0.000	0.000	0.000
10	1518-1537	1/8 flood	12-30	21.0	0.211	0.158	0.185
10	1538-1625	1/4-1/2 flood	30-80	55.0	0.000	0.000	0.000
11	1417-1430	7/8 ebb	25-20	22.5	0.846	0.769	0.808
11	1431-1441	7/8 ebb	20-18	19.0	0.100	0.100	0.100
11	1450-1555	low	18-18	18.0	0.000	0.000	0.000
11	1600-1613	1/8 flood	18-25	21.5	0.211	0.077	0.144
11	1615-1636	1/8 flood	25-35	30.0	0.000	0.000	0.000

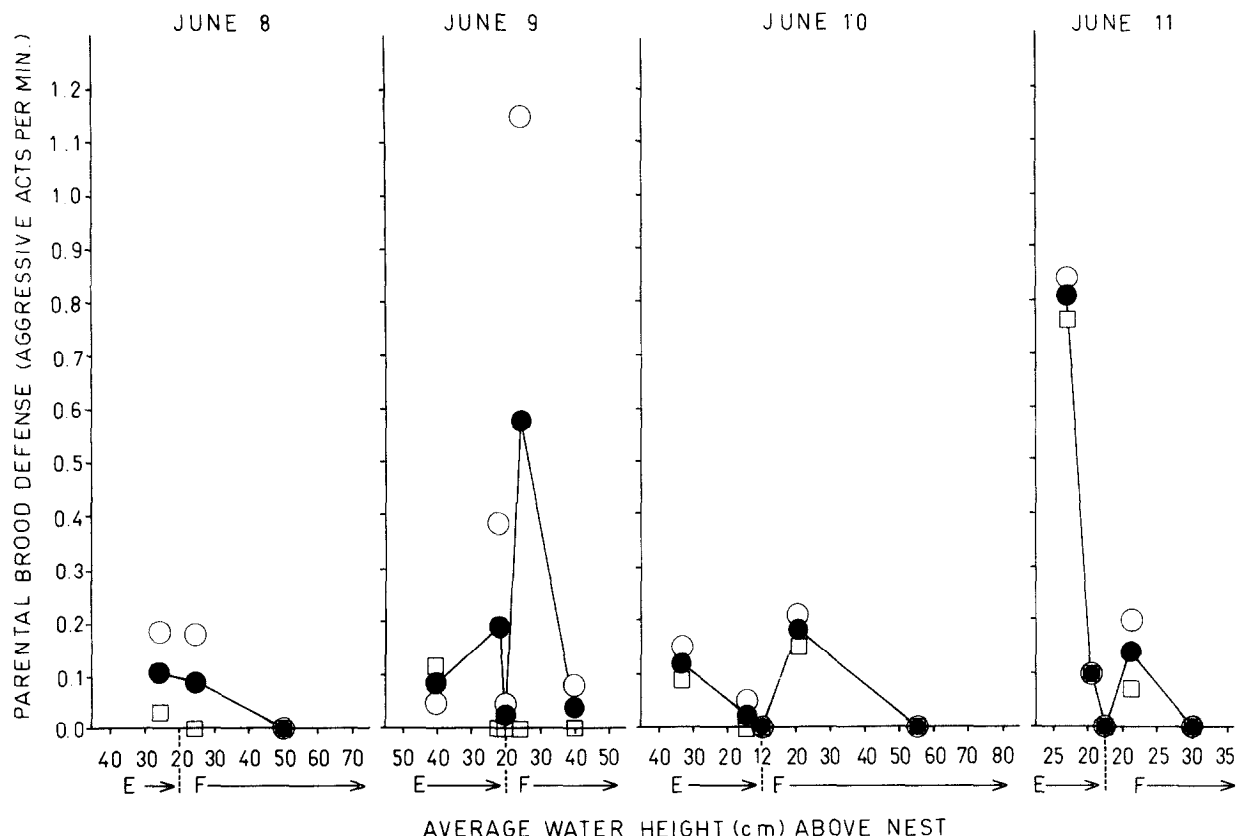


Fig. 9. The relationship between parental defense activity (against brood predators) and the tidal cycle during the period, June 8 to 11, 1972 (see Table 2). Open circles and squares indicate number of aggressive acts per min for the female and male parent, respectively. Solid circles indicate mean number of aggressive acts per min for both parents jointly. Water heights are averages or midpoints for the intervals during which aggressive encounters were recorded.

were discovered in the immediate area, and it seems unlikely that polygyny, as occurs in certain *Apistogramma* spp. (Burchard 1965), was involved.

The schedule of the agonistic activity periods was dependent on the duration of the tidal stages with an increase and subsequent decrease in parental aggression during tidal stage 1 of about 2 h, a period of inactivity during low tide of up to 1 h, and an increase and subsequent decrease in aggression during the flood tide (tidal stage 3) of less than 1 h. The activity pattern of brood predators followed the tidal cycle in a similar manner.

The period of low tide (tidal stage 2) was marked by a dramatic reduction in all activity of the *B. cupido* parents. On the afternoons of June 10 and 11 the *B. cupido* parents were actually somnolent near the nest through most of tidal stage 2. As they became quiescent they developed the noc-

turnal blotching pattern characteristic of sleeping cichlids (pers. obs.). Such diurnal somnolence has not been previously reported for cichlids. Also, during the period of somnolence, brood predators were conspicuously absent from the creek. The onset of tidal inflow brought renewed activity of both parents and predators.

The tidally related factors of water depth, current speed and the concentration of respiratory gases all probably influenced the activity patterns of the fishes. The onset and increase of aggressive activity with the low ebb tide are reasonably explained in terms of decreasing depth bringing the mid- or shallow-water characins into proximity with the *B. cupido* nest. As oxygen minimum and carbon dioxide maximum conditions were approached, activity declined. The absence of predators and quiescence in the *B.*

cupido parents are strongly associated with the oxygen minimum and carbon dioxide maximum at low tide. The flooding tide ameliorated these presumably harsh conditions leading to a corresponding renewal of activity. Rapidly mounting water velocity and depth are probably responsible for the decrease in both predatory and protective behavior which occurs during the last part of tidal stage 3. At this time characins, though present above the nest, were occupied with maintaining their positions in the current. Likewise, strong currents during the early rising tide forced the parents to swim vigorously in order to maintain their positions near the nest. Observation in the early morning (0200 h) of June 10 indicated that this activity occurs even at night.

As the water height above the nest approached barely 12 cm on the extremely low tide of June 10, the female transferred the brood, by mouth, from the primary nest to another excavation in about 20 cm of water, while the male remained by the original nest. During this lowest low tide both parents became somnolent near the second nest where the brood resided. The family remained at this nest through at least the beginning of the flood tide. When observations resumed during falling tide on the afternoon of June 11, the brood was back in the primary nest. Later, on June 11, with the approach of low tide (1440 h), the female was observed digging in the secondary excavation. This also occurred on June 12 (1443 h). On neither occasion, however, did the tide fall as low as on June 10 and no brood transfer was attempted.

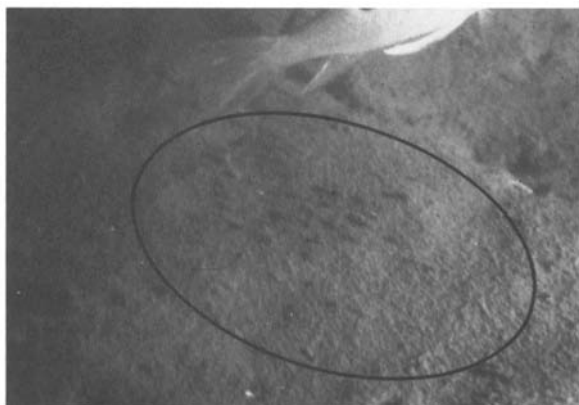


Fig. 10. Two-dimensional school (outlined) of nearly nest-independent *Biotodoma cupido* young maintaining substrate contact beneath parent (June 12, 1972). Gentle current flowed from upper left to lower right.

On June 12 the young of the nesting pair swam up from the nest and maintained themselves, facing the current, in a two-dimensional, foliate school contiguous with the bottom (Fig. 10). Between 1450 h and the beginning of the flood tide at 1625 h, the brood, flanked by their parents, foraged slowly into the slight outflowing current until they were about 2 m from the nest. At the turn of the tide they began their retreat to the nest. As the current became too strong for the young fish to swim against, the parents, in alternation, transferred them orally the remaining distance. On June 13 the territory and nest were found abandoned.

The family (or families) with older young was observed on June 15, 16 and 17 foraging near a tangle of roots several meters inland of the vacated nest. These fish were seen only on the falling tide, and I presume they retreated into shallower water and cover as the tide rose. Although the young tended to maintain themselves a short distance above the bottom, they responded to the pelvic fin flicking of one or both parents by moving into contact with the substrate. Parental fin flicking, well known in other cichlids (Cole & Ward 1969; Cichocki 1976), may be of benefit here in positioning the young in a region of minimum current. During such visual signaling, a parent's flank was turned at right angles to the direction faced by the young. In this orientation, the lateral ocellus is clearly visible to the young and may play a role in communication.

Although the rivers of South America are not generally pictured as being under strong tidal influence, the lower reaches of coastal streams, especially those between the Orinoco and Amazon, experience considerable tidal effects. Additional examples include the Demerara River in Guyana, which sustains tides up to a point 160 km from its mouth, the Commewijne River in Surinam, where 1 m tides occur at Moengo, 138 km upstream and even the Amazon, which experiences tides at Obidos over 960 km from the mouth (U.S. Naval Oceanographic office 1967). On the Pacific slope, one-half the distance between the mouth and crest of the Rio Atrato in Colombia, over 100 km, is influenced by tides (Eigenmann 1920). Therefore, in the coastal rivers of northern South

America, tides are potentially an important, but previously unrecognized (Lowe-McConnell 1975), factor affecting the reproduction and ecology of fishes.

Generally, cichlids in rivers appear to seek out relatively shallow protected areas in which to breed. Such places undoubtedly offer cover, suitable nesting substrate, minimum current conditions and other important requisites. However, under a tidal regime, inshore areas are subject to marked cyclic environmental fluctuations, which represent effectively maintained and continuously reinforced selective pressures. Consequently, specialized reproductive strategies embodying behavioral, physiological, ontogenetic and ecological adaptations are to be expected in fishes living under such conditions.

In 1973, in a paper presented before the annual meeting of the Society for the Study of Evolution, in Houston, Texas, I proposed the hypothesis that the oral incubation, nest-dragging behavior and related phenomena in certain American cichlids, especially *Geophagus jurupari* (Cichocki 1976), evolved within a selective context of cyclically fluctuating water levels, reasonably of tidal origin. Recently, Barlow (1974) and Timms & Keenleyside (1975) have suggested that mouth-brooding and/or leaf-nest dragging in the cichlids, *Aequidens paraguayensis* and *Ae. coeruleopunctatus*, would be advantageous under conditions of periodic (non-tidal) water-level changes. A relationship between water-level fluctuation and cichlid reproductive success was first clearly indicated by Ruwet (1968), who pointed out that although periodic lowering of lake levels destroys the nests of substrate-brooding *Tilapia* and leads parents to abandon free-swimming young, oral-brooding *Tilapia* (*Sarotherodon*) can breed successfully under such conditions. He viewed mouth-brooding as an adaptation reducing environmental constraints on reproduction. Similarly, I consider oral transfer of young from shallow to deep-water nests, early nest independence of offspring and the parent-brood itineracy of *Biotodoma cupido* to be related adaptations favored under conditions of tidally induced water-level fluctuations. Associated non-behavioral adaptations of *B. cupido*, which appear to have evolved within the same selective context, include relatively low fecundity, high ovum density and high female initial parental investment, both absolutely and per offspring (Cichocki 1976).

The interval between hatching and complete independence of *Biotodoma cupido* offspring from the primary nest (4 days) is shorter than that for partial nest independence in *Apistogramma trifasciatum* (5 days; Burchard 1965) and much shorter than for *Acarichthys heckeli* young under natural conditions (over 2 weeks; Cichocki 1976). Lowe-McConnell (1964, 1975) suggested that sudden water-level changes probably have selectively favored the evolution of short developmental time in some tropical freshwater fishes.

The association between the ambient levels of dissolved respiratory gases and the activity of the *B. cupido* parents, as well as that of other fishes, is striking and suggests a cause and effect relationship. Unfortunately, there appear to be no reports of similar field observations with which to compare the present results.

The effects of dissolved oxygen and, to a lesser extent, free carbon dioxide concentrations on the physiology and activity of fishes have been reviewed by Doudoroff & Shumway (1970), Fry (1971) and Davis (1975). Although little is known of the oxygen requirements of strictly aquatic tropical teleosts, comparison might be made with temperate fishes for which considerable data are available. The incipient oxygen response threshold, i.e., the lowest ambient oxygen concentration at which a homeostatic response first becomes noticeable, for non-salmonid teleosts has a mean value (pO_2) of 72.56 ± 17.44 mm Hg (95% confidence limits; Davis 1975). This corresponds closely with the pO_2 of 79 to 86 mm Hg (calculated from data of Table 1) associated with the somnolence of the *B. cupido* parents and the avoidance of low tidal conditions by predatory characins. This ambient tension may have resulted in a smaller than ordinary water-blood diffusion gradient (Randall 1970) preventing full saturation of the hemoglobin and hence adequate delivery of oxygen to the tissues (Davis 1975).

Elevated concentrations of free carbon dioxide tend to increase the oxygen requirements of fishes but acclimation is rapid and, under natural conditions, carbon dioxide is unlikely to be a limiting factor for fish activity (Powers et al. 1938; Saunders 1962; Doudoroff & Shumway 1970; Fry 1971; Davis 1975). However, if ambient carbon dioxide is raised to high levels quickly enough (as it may have been during the low falling tide), it can have considerable respiratory influence (Haskell & Davies 1958). Although the interaction is

complex (Lloyd & Jordan 1964 and Beamish 1964), the coupling of high carbon dioxide concentration with low pH and warm temperatures at low tide may have impaired the ability of fishes to extract oxygen in reduced concentration from the water. The behavioral response of characins was avoidance, but, since this was contraindicated for the *Biotodoma cupido* parents, they became quiescent.

Behavioral responses involving both increased and reduced activity have been reported for fishes exposed to hypoxic conditions (Doudoroff & Shumway 1970; Davis 1975). In one of the few studies in nature, Hubbs, Baird & Gerald (1967) reported reduced activity of warm-springs killifishes subjected to depressed midday oxygen concentrations of $1-2 \text{ mg l}^{-1}$. Apparently, through suppression of normal activity, energy can be diverted to homeostatic regulatory mechanisms (Doudoroff & Shumway, 1970; Davis, 1975). The somnolence of the *Biotodoma cupido* parents at low tide could be explainable in this way.

Interestingly, under decreasing oxygen conditions, the *Biotodoma cupido* parents failed to exhibit respiratory compensation. Increased rate or amplitude of opercular movements leading to greater irrigation of the gills are characteristic responses of fishes subjected to low ambient oxygen (Hughes, 1965; Doudoroff & Shumway, 1970; Davis, 1975). Lack of respiratory compensation in the *B. cupido* parents at low tide might be related to the high ambient pCO_2 , 15.5 mm Hg, perhaps establishing an unfavorable carbon dioxide diffusion gradient. In this case, although increased gill irrigation would have facilitated greater extraction of available oxygen, it also would have permitted carbon dioxide to diffuse more easily from the water into the fish, tending to saturate the buffer capacity of the blood. Under these conditions, increased ammonia production through limited anaerobiosis as in *Tilapia mossambica* (Kutty 1972) could be important in maintaining acid-base balance.

The somnolence of the *B. cupido* parents appears to be an appropriate behavioral and physiological response for fish constrained to endure the short-term, periodically inclement conditions of depressed oxygen, elevated carbon dioxide and low pH accompanying low tide. Detailed physiological study of the adults, juveniles and embryos of this species should prove enlightening.

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References cited

- Barlow, G. W. 1974. Contrasts in the social behavior between Central American cichlid fishes and coral-reef surgeon fishes. *Amer. Zool.* 14: 9-34.
- Beamish, F. W. H. 1964. Respiration of fishes with special emphasis on standard oxygen consumption. III: Influence of carbon dioxide and oxygen. *Can. J. Zool.* 42: 847-856.
- Brown, C. B. 1871. Report on the Kaieteur waterfall in British Guiana. *J. Roy. Geog. Soc.* 41: 77-100.
- Burchard, J. E. 1965. Family structure in the dwarf cichlid *Apistogramma trifasciatum* (Eigenmann and Kennedy). *Z. Tierpsychol.* 22: 150-162.
- Cichocki, F. P. 1976. Cladistic history of cichlid fishes and reproductive strategies of the American genera *Acarichthys*, *Biotodoma* and *Geophagus*. Ph.D. Thesis, The University of Michigan, 705 pp.
- Cole, J. E. & J. A. Ward. 1969. The communicative function of pelvic fin-flickering in *Epiplatys maculatus*. *Behaviour* 35: 179-199.
- Davis, J. C. 1975. Waterborne dissolved oxygen requirements and criteria with particular emphasis on the Canadian environment. Rep. no. 13, National Res. Council Canada, Associate Committee on Scientific Criteria for Environmental Quality. 111 pp.
- Doudoroff, P. & D. L. Shumway. 1970. Dissolved oxygen requirements of freshwater fishes. Tech. pap. no. 86, Food and Agriculture Organization, United Nations, Rome. 291 pp.
- Eigenmann, C. H. 1920. The Magdalena Basin and the horizontal and vertical distribution of its fishes. *Indiana Univ. Stud.* 7 (47): 21-34, 4 pls.
- Eigenmann, C. H. & C. H. Kennedy. 1903. On a collection of fishes from Paraguay, with a synopsis of the American genera of cichlids. *Proc. Acad. Nat. Sci. Phila.* 1903: 497-537.
- Fry, F. E. J. 1971. The effect of environmental factors on the physiology of fish, pp. 1-98. In: W. S. Hoar & D. J. Randall (eds.), *Fish Physiology*. Vol. 6. Environmental relations and behavior. Academic Press, New York.
- Goldstein, R. S. 1970. Cichlids. TFH Publications, Neptune City, New Jersey. 254 pp.
- Goldstein, R. S. 1973. Cichlids of the World. TFH Publications, Neptune City, New Jersey. 382 pp.
- Haskell, D. C. & R. O. Davies. 1958. Carbon dioxide as a limiting factor in trout transportation. *N.Y. Fish and Game J.* 5: 175-183.
- Hubbs, C., R. C. Baird & J. W. Gerald. 1967. Effects of dissolved oxygen concentration and light intensity on activity cycles of fishes inhabiting warm springs. *Amer. Mid. Natur.* 77: 104-115.
- Hughes, G. M. 1965. Comparative physiology of vertebrate respiration. Harvard Univ. Press, Cambridge. 146 pp.
- Kutty, M. N. 1972. Respiratory quotient and ammonia excretion in *Tilapia mossambica*. *Mar. Biol.* 16: 126-133.
- Lloyd, R. & D. H. M. Jordan. 1964. Some factors affecting the resistance of rainbow trout (*Salmo gairdneri* Richardson) to acid waters. *Air Water Pollution* 8: 393-403.
- Lowe-McConnell, R. H. 1964. The fishes of the Rupununi savanna district of British Guiana, South America. Part I. Ecological groupings of fish species and effects of the seasonal cycle on the fish. *J. Linn. Soc. (Zool.)* 45: 103-144.
- Lowe-McConnell, R. H. 1969. The cichlid fishes of Guyana, South America, with notes on their ecology and breeding behaviour. *Zool. J. Linn. Soc.* 48: 255-302.
- Lowe-McConnell, R. H. 1975. Fish communities in tropical freshwaters. Longman, London. 337 pp.
- National Ocean Survey. 1971. Tide tables, 1972. East Coast of North and South America including Greenland. U.S. Department of Commerce, National Oceanographic and Atmospheric Admin., Washington. 290 pp.
- Powers, E. B., H. H. Rostorfer, L. M. Shipe & T. H. Rostorfer. 1938. The relation of respiration of fishes to environment, XII. Carbon dioxide tension as a factor in various physiological respiratory responses in certain fresh water fishes. *J. Tenn. Acad. Sci.* 13: 220-245.
- Randall, D. J. 1970. Gas exchange in fish, pp. 253-292. In: W. S. Hoar & D. J. Randall (eds.), *Fish physiology*. Vol. 4. Academic Press, New York.
- Ruwet, J. C. 1968. Familial behaviour of *Tilapia* (Pisces, Cichlidae) and its implications. *Nature* 217: 977.
- Saunders, R. L. 1962. The irrigation of the gills in fishes. II. Efficiency of oxygen uptake in relation to respiratory flow, activity and concentrations of oxygen and carbon dioxide. *Can. J. Zool.* 40: 817-862.
- Timms, A. M. & M. H. A. Keenleyside. 1975. The reproductive behaviour of *Aequidens paraguayensis* (Pisces, Cichlidae). *Z. Tierpsychol.* 39: 8-23.
- U. S. Naval Oceanographic Office. 1967. Sailing directions for South America. Vol. I. East coast from Venezuelan border to and including Rio de la Plata. 6th ed. H. O. Publication 23. U.S. Naval oceanographic office, Washington.
- Wickler, W. 1966. Sexual dimorphism, Paarbildung und Verstechbruten bei Cichliden (Pisces: Perciformes). *Zool. Jahrb. Syst.* 93: 127-138.

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