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Parental egg care behavior and fanning activity for the orange chromide, *Etroplus maculatus*

Mark J. Zoran & Jack A. Ward
Department of Biological Sciences, Illinois State University, Normal, Illinois 61761, U.S.A.

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Synopsis

Physiological studies revealed that agitation (simulated fanning) of the brood results in increased oxygen consumption, increased developmental rate and general promotion of brood success. It was also found that the more intense the agitation (excursions per minute) the greater the metabolic rate is enhanced. Embryos exposed to continual agitation hatched approximately twenty hours in advance of non-agitated eggs. Temporal studies of fanning activity in *Etroplus maculatus* showed significant differences between pairs breeding in colonial situations as compared to those breeding in isolation. Parental behaviors were recorded throughout egg care until hatching. Two types of ventilatory behaviors were described: active fanning and passive fanning. Pairs breeding in isolation invested more time in long passive bouts and less time in short active bouts. Conversely, colonial parents fanned predominately with short active bouts and displayed no prolonged passive fanning. Surprisingly, no differences were apparent in either reproductive success or hatching time between isolated and colonial pairs in this study. Orange chromides readily nested in two extremely different situations. They also displayed significantly different fanning regimes, behavioral time budgets and transitions of behavior; yet they were equally successful. Parental orange chromides can modulate their ventilatory activities in response to the contingencies of their nesting situation which ultimately allows them maximization of reproductive success.

Introduction

Many fish species facilitate the early development of their offspring by ventilating the eggs in various ways. Oppenheimer & Barlow (1968) reported the details of mouthbrooding for the black-chinned mouthbrooder, *Tilapia* (= *Sarotherodon*) *melanotheron*. They reported that parents actively churn the eggs within the mouth, thereby aerating them. They also reported that the eggs were aerated in a more passive manner by holding the mouth open allowing a gentle flow of water over the embryos. They called these behaviors active respiration and passive respiration.

Many substrate-brooding species ventilate their eggs by fanning. Blumer (1979) defined fanning as the movement of the pectoral, pelvic, anal, or caudal fins over the egg mass or young thereby aerating them and removing sediments.

Preliminary observations of parental care for the orange chromide, *Etroplus maculatus*, produced qualitative evidence that brooding fish also exhibit two different modes of ventilatory behavior, active fanning and passive fanning. Daykin (1965) suggested the egg mass of a substrate brooder may act as an oxygen 'sink' in that the oxygen level at the egg's surface will always be lower than that of the surrounding water. Any means that would supply oxygen to the egg's surface would facilitate respiration.

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It can be assumed that a fanning regime is designed to maximize reproductive success (Sargent & Gebler 1980). This study is composed of four experimental approaches to the question of how a parental fish might maximize its offspring's success by fanning.

Materials and methods

First generation *E. maculatus* were imported in December 1979 from V. Perera, proprietor of Lambini Aquarium, Mt. Lavinia, Sri Lanka. Once in the laboratory, the fish were held in large stock tanks and maintained on a Tetramin and frozen brine shrimp diet (fed twice daily).

Breeding pairs of *E. maculatus* were paired in 76 liter aquaria at 27 ± 1° C. Aquaria were supplied with artificial plants and a flower pot to facilitate spawning. Aquaria were filled with deionized water containing 1 g of marine salts per liter. Aquarium water was kept at a pH of 8.0

First experiment: temporal analysis

Parents caring for eggs were videotaped. Sequences of parental behavior were replayed in slow motion, one-ninth actual speed and data were collected with an Esterline-Angus multiple-event recorder. Fanning bouts began when the egg mass movements were first detected and terminated when the eggs' movements ceased.

Two temporal properties were calculated for both active fanning and passive fanning: (1) Tempo – the number of beats of the pectoral fin per second. A beat was considered to be one complete undulatory cycle of the fin. (2) Bout duration – the mean time in seconds invested in a bout of fanning. Active and passive fanning data were collected from 10 different pairs. Mean temporal properties were compared between active and passive fanning with a Student's t-test for significant differences.

Second experiment: respirometry

Eggs were removed from 10 pairs of orange chromides. Oxygen uptake was measured under constant light conditions with a Gilson Differential Respirometer. Approximately 65 eggs were placed in individual 18 ml respirometer flasks containing 3 ml of filtered aquarium water. Five flasks containing only filtered aquarium water were used as controls. Oxgen consumption ($Q0_2$) was expressed as microliters (μl) of oxygen consumed per gram dry weight per hour at standard conditions (STPD). Eggs were dried in an oven at 60° C and then weighed to obtain the dry weight. Ascarite (A.H. Thomas Co.) was used as a carbon dioxide absorbant.

Respirometry was conducted for periods of 1 h at 27° C. Mechanical agitation could be provided by the respirometer. Oxygen consumption was measured with and without agitation at 0 and 68 e.p.m. (excursions per minute). One excursion constituted a 3 cm movement of the flasks to the left and to the right.

An additional series of measurements were conducted at increased agitation rates at 27° C. Experimental agitation rates were 0.68, 105 and 140 e.p.m.

Respirometry was also conducted on eleutheroembryos (fish between hatching and free-swimming stages) and on free-swimming juvenile fish in order to examine the effects of agitation after hatching. Approximately 30 eleutheroembryos or free-swimming juveniles were placed in respirometer flasks with 5 ml of filtered aquarium water. Control flasks were provided as described above and $Q0_2$ determinations were made as for eggs.

Mean oxygen uptake rates were graphically presented with 95% confidence intervals. Student's t-tests were used to compare $Q0_2$ means.

Third experiment: developmental rates

Eggs were removed from the spawning surface one hour after fertilization and placed into a 1:1000 formalin solution for 10 min to sterilize the chorion (Jones 1972). Groups of 30 eggs were transferred to 25 ml flasks containing 7 ml of water. Twelve flasks were then submerged into a 27 ± 1° C water bath in a Dubnoff Metabolic Shaking Incubator. Six flasks were secured to the shaker plate and six others were fixed to prevent agitation. This procedure allowed for an agitated and a non-agitated set of eggs at the same temperature. Ten eggs were removed from each flask every five hours. Each egg was then assigned a stage of development according to the system proposed by Jones (1972).

Fourth experiment: behavioral rates

Two 76 l aquaria were divided into equal halves (45.6 × 45.6 cm) by glass partitions. Both sides of the partitioned aquaria were provided with gravel (C#20, 2 cm deep), artificial green plants, a spawning surface and filter.

Twenty-four pairs of *E. maculatus* were used in the behavioral analyses. Pairs were randomly selected from stock tanks with the male always slightly larger than the female. One pair was placed on each side of the partitioned aquaria prior to the experiment. The fish were fed only once daily at 1200 h. The diet was the same as that of holding tanks.

When an initial pair spawned, an opaque divider was placed into the tank and the neighboring pair was removed. The opaque divider was used to reduce stress on the fish. Once the neighboring pair was removed, the divider was with-drawn and the isolated pair became the control.

When an initial pair spawned in a second aquarium, another opaque divider was inserted. However, the neigboring pair was not removed; the insertion and removal of an opaque divider insured consistency between the control and experimental groups. The pairs remaining in this aquarium simulated simple colonial neighbors. Both pairs had to have spawned before a colonial nesting situation existed and recordings could be made. The colonial situation in nature is certainly more complex and many neighbors often interact. This design focuses on the effect of only one neighboring pair.

Parental time budgets were calculated for both the isolated and colonial pairs. These behaviors were recorded for both the male and female depending on which was currently tending the eggs. The working definitions of these behaviors are given below. Parental behaviors were recorded twice daily from the day of spawning until the embryos hatched. Behavioral observations were recorded on a Datamyte 900 Recorder during 20 min observation periods at 1100 and 1300 h. Data were reduced to precedes/follows matrices by the computer program *reduce* (Ward et al. 1976). Time elements were produced in event frequency tables and event time tables.

Statistical analyses were used to determine differences between the time investments of the isolated parents and those of the colonial parents. ANOVA (analysis of variance) was utilized in these statistical comparisons with Tukey's H.S.D. as the follow-up test.

Reproductive success was measured for both colonial and isolated pairs by siphoning all eleutheroembryos from the brooding pit shortly after hatching. Reproductive success was estimated as the number of eleutheroembryos collected from the nest.

Hatching time was also determined as the mean time in hours from fertilization to hatching.

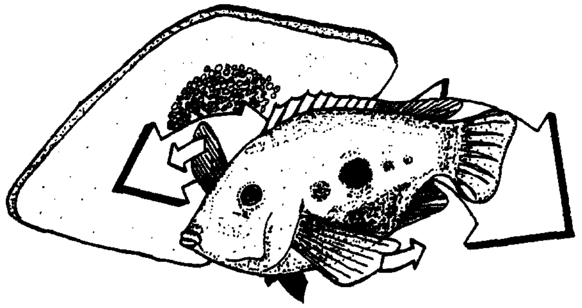
Description of behaviors

Active fanning (AF) is a rapid and intense beating of the pectoral fins causing visible movement of eggs previously attached to a spawning site. The caudal fin and the posterior portions of the dorsal and anal fins are undulated to compensate for the movements of the pectorals. A parental fish is positioned so that the distal end of the pectoral fin is within 1 cm of the egg mass. The pectoral fin often comes in contact with the surface of the eggs (Fig. 1).

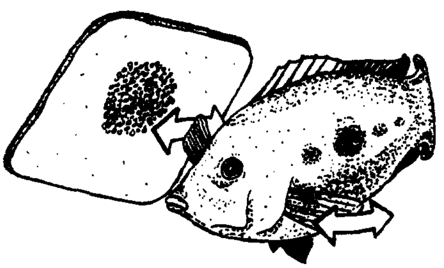
Passive fanning (PF) is a slower, less intense beating of the pectoral fins, however, still causing visible movement of the egg mass. Compensatory undulations of the caudal fin are lacking. A parental fish is positioned so that the distal end of the pectoral fin is 1 to 4 cm from the egg mass and often the caudal peduncle and fin are curved with the concave side of the curve facing the spawning site (Fig. 1).

Holding station (HS) is characterized by the guarding parent hovering near the spawn, always within view of the eggs. The parent often hovers 3–4 cm above the egg mass when holding station. This behavior caused no movements of the egg mass.

Aggressive interaction with neighbor (AN) is a general category consisting of any behavior directed



Active Fan



Passive Fan

Fig. 1. Illustration of body posture and movements during bouts of active and passive fanning. The arrows reflect the intensity of fin undulations.

towards the neighbor which is considered an aggressive modal action pattern for this species. For example chasing, ramming, biting and penduluming (Wyman & Ward 1973). Other behaviors such as frontal displays and lateral displays could also apply.

Aggressive interaction with mate (AM) is another general category consisting of behaviors identical to those of AN, however, they are directed toward the mate.

Digging (DG) is the behavior characterized by the approach, contact, and removal of substrate with the mouth; usually performed in the construction of pits.

Results

First experiment: temporal analysis

Active fanning had a mean temp of 4.34 beats sec^{-1}, significantly greater ($p < 0.05$) than the mean temp of 1.63 beats sec^{-1} for passive bouts (Table 1). Passive fanning bouts were significantly longer ($p < 0.05$) than active fanning bouts. The mean bout durations of active and passive fanning were 1.53 sec and 7.14 sec, respectively (Table 2).

Table 1. Mean tempos of active and passive fanning bouts.

	Tempo (beats per second)	
	Mean	Range
Active Fan	4.34*	1.1–6.2
Passive Fan	1.63	0.4–4.9

* Student t-test revealed significance at $p < 0.05$.

Table 2. Mean bout durations of active and passive fanning bouts.

	Bout duration (seconds)	
	Mean	Range
Active fan	1.53*	0.6–7.56
Passive Fan	7.14	1.2–40.1

* Student t-test revealed significance at $p < 0.05$.

Second experiment: respirometry

Oxygen consumption rates for eggs and eleutheroembryos gradually increased from 67.4 μl O_2 g dry wt^{-1} h^{-1} at the time of fertilization to 4290.0 μl O_2 g dry wt^{-1} h^{-1} on the ninth day. Embryos about to hatch had an oxygen consumption rate of 304.7 μl O_2 g dry wt^{-1} h^{-1}.

Newly hatched eleutheroembryos showed a mean QO_2 of 2223.0 μl O_2 g dry wt^{-1} h^{-1} which was significantly greater ($p < 0.05$) than embryos about to hatch. Oxygen consumption showed a significant increase ($p < 0.05$) from 3010.0 μl O_2 g dry wt^{-1} h^{-1}, as eleutheroembryos became free swimming, to 4290.0 μl O_2 g dry wt^{-1} h^{-1} on the following day. Agitation greatly enhanced the oxygen consumption of embryos. Oxygen consumption of agitated and non-agitated eggs differed significantly ($p < 0.05$) at 27° C (Fig. 2). These differences were significant on each day after fertilization, with the

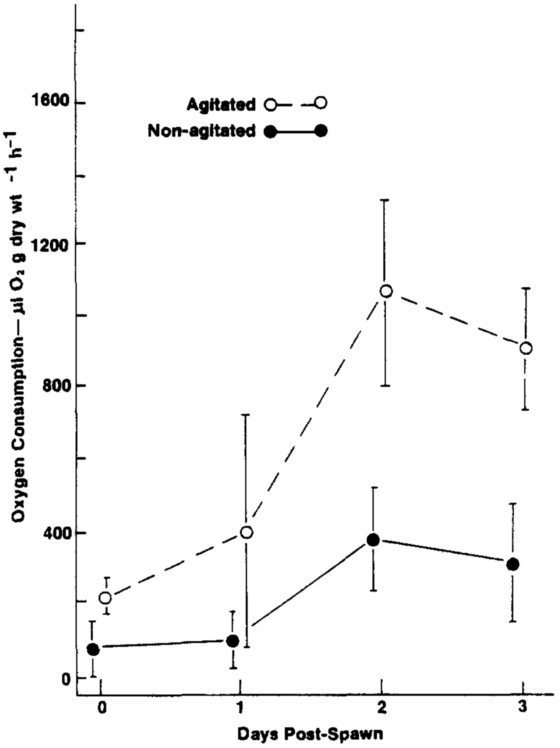


Fig. 2. The effect of agitation on oxygen consumption rate of embryos at 27° C. Vertical bars represent 95% confidence intervals.

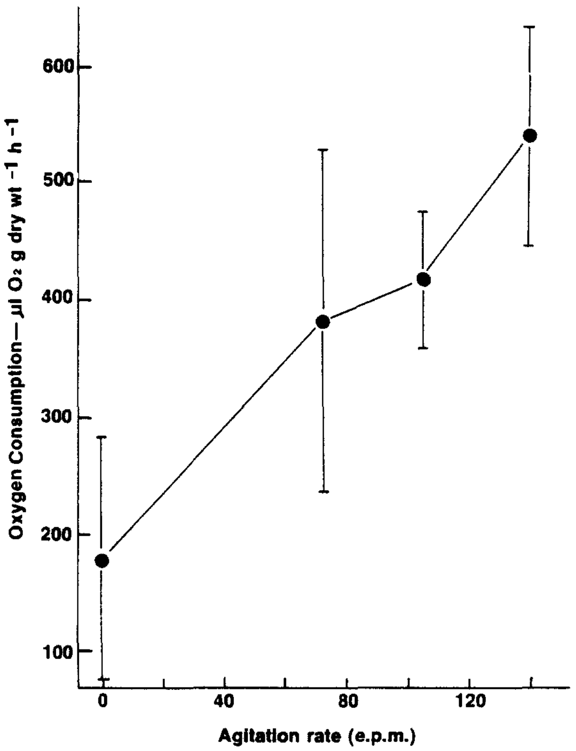


Fig. 3. The influence of agitation rate on oxygen consumption of first day after fertilization (= post-spawn) embryos at 27° C. Vertical bars represent 95% confidence intervals. The regression line calculated for these points was significantly greater than 0 ($p < 0.05$). Regression line is not included in figure.

clearest differences appearing on days 2 and 3. A decrease in oxygen consumption was apparent between the second and third day.

A linear relationship was found to exist between oxygen consumption rate and agitation rate (Fig. 3).

Fig. 4 illustrates the effect of agitation on oxygen consumption for eleutheroembryos. The effect of agitation on oxygen consumption diminished as free-swimming young developed to 20 day old fish.

Third experiment: developmental rates

Agitation of *E. maculatus* eggs accelerated the rate of embryonic development. Fig. 5 indicates that non-agitated embryos required approximately 20 hours longer to hatch (stage III$_9$, from Jones 1972) than did agitated eggs. These results indicate that the effect of agitation on developmental rate does not become evident until the end of epiboly (stage II$_{14}$, from Jones 1972). Microscopic examination of embryos revealed clear developmental differences between agitated and non-agitated eggs after 30 hours from fertilization.

Non-agitated eggs frequently developed into deformed embryos. The yolksacs of non-agitated embryos contained greater numbers of spherical droplets, probably lipids, just beneath the egg envelopes. Fishelson (1966) reported that the settling of lipids in fish eggs can disrupt normal embryonic development.

Fourth experiment; behavioral analysis

Transitions of behavior for both colonial males and females, as analyzed through kinematic graphs, were essentially identical (Fig. 6). Isolated pairs, in contrast, did not show a mirror image of transitions between males and females as did colonial nesters (Fig. 7). Kinematic graphs illustrate percentages of

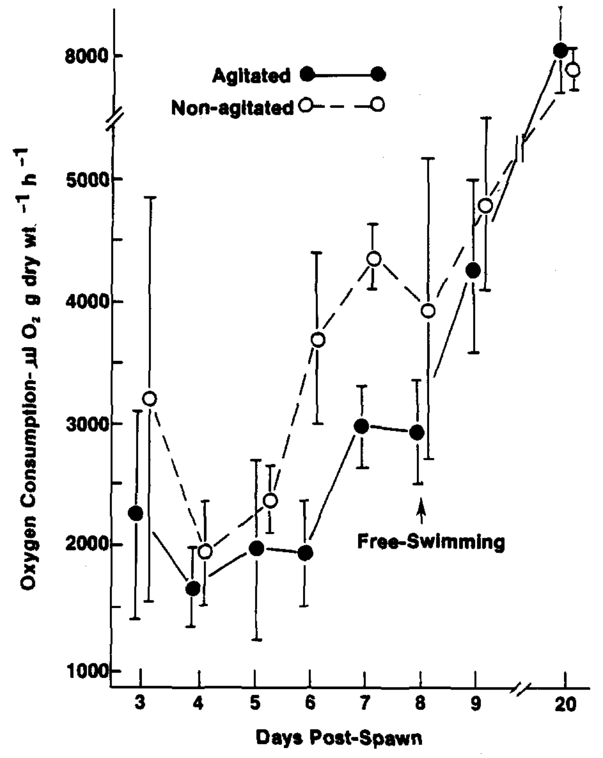


Fig. 4. The effect of agitation on oxygen consumption rates in eleutheroembryos at 27° C. Vertical bars represent 95% confidence intervals.

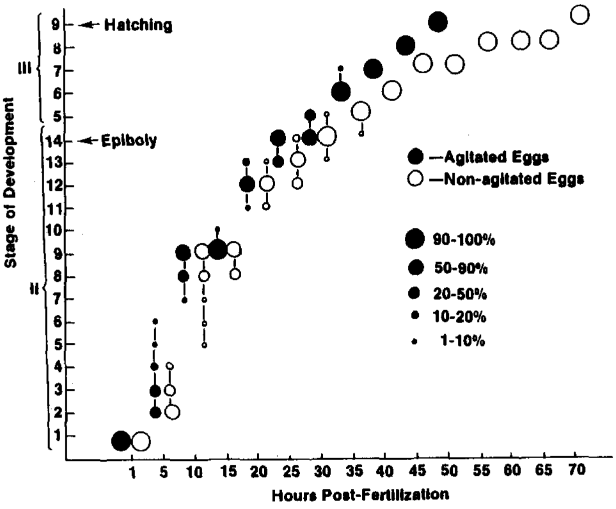


Fig. 5. The influence of agitation on the developmental rate of eggs at 27° C. Developmental stages used in this study proposed by Jones (1972). Circles represent the percentage of eggs per sample at a particular stage of development.

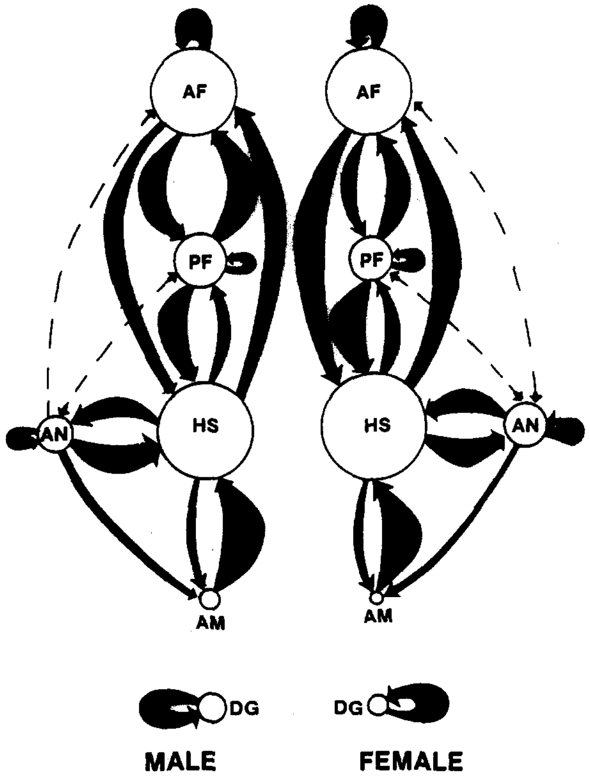


Fig. 6. Kinematic graph of behavioral transitions for colonial parents. AF = Active fanning; PF = Passive fanning; HS = Holding station; AN = Aggressive interaction with neighbor; AM = Aggressive interaction with mate; DG = Digging.

total behaviors (circles) and percentages of all following events (arrows).

Significant differences were found between the total time investments of isolated and colonial nesters for active fanning, passive fanning, and holding station (Fig. 8). Isolated males invested more time in long, passive fanning bouts and less time in short, active fanning bouts. These isolated males invested significantly more time in egg care activities (fanning) than their mates. The males' domination of these activities created a behavioral dimorphism not present in colonial nesters (Fig. 8).

Colonial nesting males invested much less time in long, passive fanning bouts (Fig. 8). Accompanying these low investments in passive fanning was a high allocation of time towards long periods of holding station.

Table 3 summarizes the analysis of fanning re-

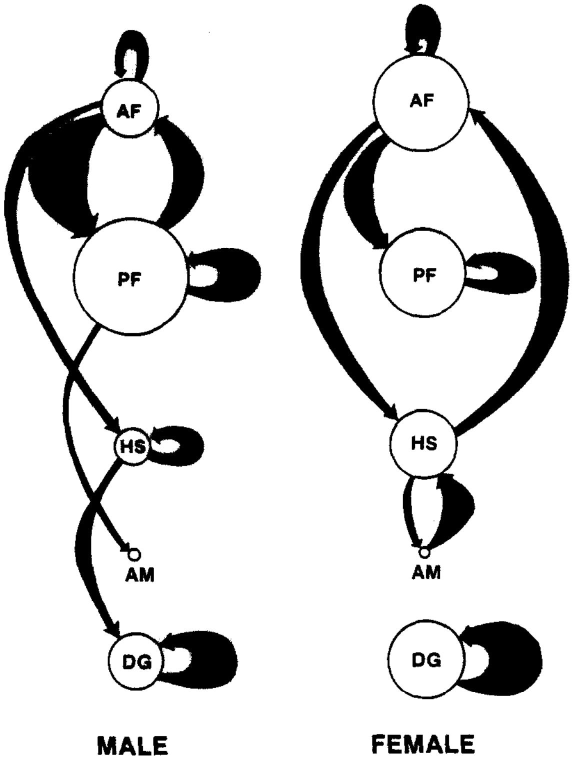


Fig. 7. Kinematic graph of behavioral transitions for isolated parents. Symbols as in Fig. 6.

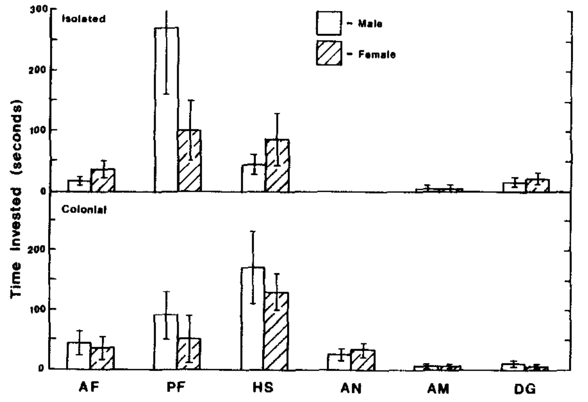


Fig. 8. Histograms of total time investments for isolated and colonial pairs. Vertical bars represent 95% confidence intervals. Symbols explained in Fig. 6.

gimes displayed by parents in the two nesting situations. Isolated males had very short bouts of active fanning; the mean duration was 1.36 sec. Colonial males had a mean active fanning bout duration of 2.05 sec. The active fanning of both isolated and colonial females were markedly similar.

Table 3. Frequency (f), mean bout duration (mbd), and total bout duration (tbd), of active and passive fanning for isolated (Iso.) and colonial (Col.) pairs.

Nesting situation	Active			Passive		
	f	mbd	tbd	f	mbd	tbd
Iso. male	8.19	1.36	14.65	16.55	15.40	267.35
Iso. female	15.29	1.71	36.60	14.00	5.72	103.29
Col. male	16.28	2.05	41.14	10.86	7.20	90.17
Col. female	16.59	1.55	34.03	8.59	3.57	47.98

Isolated males passively fanned with long, frequent bouts; the mean bout duration was 15.40 sec. Passive fanning for colonial males was significantly different ($p < 0.05$) than that of isolated males. Colonial males invested relatively little time in passive fanning; mean duration of 3.57 sec. Once again the fanning activities of the two female groups were very similar.

No significant differences ($p < 0.05$) in reproductive success or hatching time were found between isolated and colonial nesters.

Discussion

Ventilation of eggs is only one of many parental activities to which time must be allocated in order to insure success of the brood. Rechten (1980) reported that increased time invested in brood defense decreased the time available for care activities such as ventilation. Obviously, parental egg care investments must be flexible if parents are to accommodate changing environmental contingencies.

Field studies by Ward & Samarakoon (1981) revealed orange chromides breed in both isolated and colonial situations. Parents spawning in colonial aggregations invested more time in territorial defense. Conversely, it is assumed they invested less time in other unrecorded activities such as ventilation. Rechten (1980) showed in laboratory experiments that increased numbers of conspecific intruders increased the total time both parents were absent from the brood. Isolated parents spent 95% of their time with at least one parent with the brood, as compared to 50% for parents fending off potential predators (Rechten 1980).

Contrary to the prediction based on the data above, colonial nesters in nature had greater rearing success than parents spawning in isolation (Ward & Samarakoon 1981). We hypothesized that a pair nesting among colonial neighbors benefited from an early warning predator detection system. Colonial parents were alerted to the presence of intruders because of brood defense behavior exhibited by neighbors. Isolated pairs lost more broods to predation than colonial pairs presumedly because they had no alert. Natural selection should favor colonial nesting since it is the optimal reproductive tactic. However, some orange chromides in nature still breed in isolation despite the advantages of neighbors.

We initially proposed that isolated nesters, confronting fewer territorial intruders, could invest more time in ventilation than colonial nesters. Nesting alone may be disadvantageous because of predation but advantageous because parents could invest more time in caring for their brood.

Preliminary observations of orange chromide pairs in the laboratory produced evidence that their ventilation behavior was variable. Active fanning was found to be a very rapid beating of the pectoral fins (4.34 beats sec^{-1}). Passive fanning was a much more subtle behavior (1.63 beats sec^{-1}). These fanning activities caused agitation of the egg mass relative to their tempos. This suggested variations in fanning tempo might cause equally variable effects on embryonic metabolism and development. This has been suggested by previous workers (Barlow 1964, Mertz & Barlow 1966, Keenleyside 1979); however, evidence has never been presented.

The physiological study here provides clear evidence that agitation (simulated fanning) enhances embryonic metabolism and developmental rate of cichlid embryos. Eggs had peak rates of oxygen consumption on the second day after fertilization; rates more than tripled with agitation (Fig. 6). Eggs exposed to increasing agitation rates responded with increasing rates of oxygen consumption (Fig. 3).

In addition, agitated embryos of *E. maculatus* hatched approximately 20 hours before non-agitated embryos. Differences between developmental rates of agitated and non-agitated eggs became most obvious between 40 and 50 hours after fertilization (Fig. 5); a result that correlated with oxygen consumption data. Jones (1972) also reported that the eggs of five other species of substrate-spawning cichlids displayed rapid embryonic differentiation during this time. Fanning investments also peaked on the second day. Non-agitated eggs frequently contained deformed embryos and many failed to hatch. Fungal infection was not the cause of hatching failure. The yolksac of non-agitated embryos contained greater numbers of spherical droplets, probably lipids, just beneath the envelopes. Agitation may cause dispersal of the egg's lipids, thus promoting normal development (Fishelson 1966). Shaw & Aronson (1954) showed that vigorous churning by mouthbrooding cichlids also increased egg survival.

Thus, our results indicated that ventilation increased oxygen consumption, influenced developmental rate, and generally promoted brood success. Ventilation behaviors must play a very significant role in brood success for fishes in nature because ventilation is very widespread among fish families (Blumer 1979).

In addition, the manner of ventilation was different between colonial and isolated nesters in our laboratory simulations. Colonial pairs of *E. maculatus* fanned most often with short active bouts with no prolonged passive bouts (Table 3). Isolated pairs invested less time in active fanning and fanned predominately with long passive bouts; several durations were longer than 60 sec (Table 3).

Not only were fanning regimes different but behavioral investments in parental care in general differed between the two nesting situations. Kinematic graphs (Fig. 6) revealed that colonial nesters exhibited biparental behavior suggested for this species from studies in nature; that is, colonial males and females showed equal investments. The total investment of colonial parents in nature is equivalent only to the full investment of a single parent (Ward & Samarakoon 1981). Colonial males and females in our study performed identical behavior and their individual investments were 50/50 (Fig. 8).

Isolated males dominated egg care activities while their mates took a less active role (Fig. 7, 8). Keenleyside (1979) reported that biparental species usually exhibit a behavioral dimorphism; males and females display different time investments in behavior. Our study is the first to demonstrate a dimorphism of behavior for parental orange chromides. The field data collected by Samarakoon (1981) for sequence analyses were collected from only colonial nesters. He demonstrated a 50/50 investment of colonial males and females for a total parental investment of a single parent. Unfortunately, isolated pairs were fewer in numbers and a parallel analysis was not conducted. It would be of interest to determine if isolated parents display dimorphic investments in nature as we observed in the laboratory.

Surprisingly, no differences were apparent in either reproductive success or hatching time between isolated and colonial pairs in this study. Orange chromides readily nested in two extremely different situations. They also displayed significantly different fanning regimes, behavioral time budgets and transitions of behavior; yet, they were equally successful.

Colonial parents compensated for time lost in brood defense by investing more time in active fanning. Conversely, isolated parents having no brood defense investments compensated by passively fanning for long periods of time. Orians (1961) pointed out that even small differences in time budgets could affect a parent's maximization of reproductive success.

The differences between behavioral time budgets of isolated and colonial nesters illustrates the flexibility of parental investments for this species. These flexible investments allow the orange chromide to deal with extremely different nesting situations as reported in field studies (Samarakoon 1981, Ward & Samarakoon 1981).

It is obvious that a fanning regime of short, active bouts is as efficient as a regime of long, passive bouts since there were no differences for reproductive success. Parental orange chromides can modulate their parental activities in response to the contingencies of their nesting situation which ultimately allows them maximization of reproductive success.

Differential success between naturally breeding colonials and isolates no longer seems to be a paradox. Differences in parental investments cannot account for greater reproductive success of colonial nesters. Samarakoon (1981) also reported no differences for enviromental conditions between isolated and colonial nesters. The habitats selected for nesting were the same. Therefore, predation pressure is the only acceptable explanation for differential success in nature. Our studies in the laboratory then corroborate the hypothesis presented by Ward & Samarakoon (1981) that pairs nesting in colonial aggregations are more successful because the approach of predators is signaled by defensive behavior of neighbors (their early warning hypothesis), an alert isolated nesters lack.

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