DIEL ACTIVITY PATTERNS OF THE MALE SNAKESKIN GOURAMI, *TRICHOGASTER PECTORALIS* (REGAN) (PISCES, BELONTIIDAE)

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Diel activity patterns were investigated in male *Trichogaster pectoralis*. Observations on males of 12 heterosexual pairs provided data for statistical analysis. Frequency and duration of patrolling, inspiration, rest, and total activity were recorded while only frequency was recorded for agonistic behaviors. Analysis indicated discrete diel activity patterns of patrolling, inspiration, and total activity. Over half of the behaviors recorded (2,356 of 4,223) were agonistic behaviors. Agonistic behaviors including approach, bite-butt, and chase followed, generally, the same diel patterns. Analysis of relative frequency revealed that the bite-butt was the single most frequent behavior (28.91%) followed by approach (19.42%), miscellaneous behavior (17.95%) and inspiration (15.91%). These four represent 82.19% of all behaviors recorded during the study.

Many biological phenomena recur at regular intervals in both plants and animals and are referred to as biological rhythms (1). The most frequently occurring biological rhythm is the diel or circadian rhythm (1, 2). Diel rhythms of fishes have been studied by relatively few investigators (3) and most of these studies have dealt with activity periods for particular species (1, 3-7). Generally, studies on fishes have been conducted in the wild using traps of some type and extrapolating activity patterns from percentage of captured populations. There have been relatively few attempts to bring animals into the laboratory under conditions where qualitative and quantitative data on their behavior could be acquired. Under such conditions fishes have been shown to exhibit periodicity in movement (4, 8), feeding (9), and oxygen consumption (10, 11).

Diel activity patterns have recently come under investigation in anabantoid fishes. Hopkins (12) reported diurnal and nocturnal activity rhythms in aquaria for *Trichogaster trichopterus* and *Macropodus opercularis*. Wimmer (13) found a diel rhythm in *T. microlepis*. The present study was conducted to determine if a diel activity pattern exists in the Asian perciform, *Trichogaster pectoralis* (Regan) (Pisces, Belontiidae). Data reported below represent observations on activity patterns of *T. pectoralis*, the snakeskin gourami.

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METHODS AND MATERIALS

Heterosexual pairs were conditioned six months in four 15-gallon aquaria with gravel bottoms that were planted with *Vallisneria* and *Myriophyllum* and maintained on a 12-hr electronically controlled photoperiod prior to observation. The only light during the dark hours was a small, covered, downward-facing lamp which supplied light to a *Daphnia* tank. This would probably be equivalent to moonlight in the natural habitat. Hobson (7), in studies on marine fishes, concluded that total darkness was an atypical situation and this assumption is probably true in most aquatic habitats. Data were recorded for males only in each of the four tanks for a 10 min period every two hours for 24 hr. Within a period of 40 days the procedure was replicated three times. Durations (seconds) and frequencies for patrolling, inspiration, rest, and total activity were timed with stopwatches and recorded on prepared data sheets, while only frequencies of lateral displays, mouth fights, bite-butts, chases, and tail beats were recorded.

Data were subjected to an AOV analysis. Previous studies on diel behavior have used mean values for plotting frequencies or duration without regard to statistical inferences. Because the present data often showed clear-cut time effects, but not always significant differences among replicates, some graphs are plotted as mean values while others are shown as three separate replicates.

If there were no significant differences among replicates, the data were averaged and a single mean value was plotted for each observation time. Significant differences among observation times ($p < .05$) indicated that there was a time effect whereby the fish were not performing the behavior equally at all observation times, but that they exhibited definite differences in frequency or duration of the behavior at different observation times. If there were no significant differences among observation times, this indicated that the behaviors were being performed with approximately the same frequency or duration at all observation times.

Terminology for motor patterns

Motor patterns for anabantoid fishes of the genus *Trichogaster* have been described by Forselius (14), Miller (15), and Robison (16). These descriptions will serve as a basis for discussion of the motor patterns of *T. pectoralis*.

Approach. An approach is any behavior in which one fish swims directly toward a second fish. Pelvic threads are usually thrust forward with median fins slightly erected.

Lateral spread display. The lateral spread display is common during agonistic encounters. Median fins and caudal fin are spread maximally at high intensities and only slightly at low intensities. The lateral display may be expressed in the form of an S-shape (sigmoid) at maximum intensity or develop subsequently into tail beating, biting or butting, or chase (15). The displaying fish is usually in a position directly in front of or parallel to the other fish but can be oriented at any angle to the other fish. The head is directed away from the other fish at all times.

Tail beating. Tail beating consists of lateral, undulating thrusts of the caudal peduncle and fin and may vary in force and duration. Tail beating probably represents greater aggressiveness than the lateral spread display in any given encounter (15). Forselius (14) termed these "undulating movements."

Opercle spread. The inclusion of opercle spreading in the behavioral repertoire of *T. pectoralis* marks the first time it has been reported in this species. The opercles and branchiostegals of *T. pectoralis* are spread only minimally. The behavior occurs in an aggressive context while the displaying fish is lateral to and slightly behind the other fish. The head is directed toward the opponent and higher than the caudal fin while the body is positioned into a sigmoid curve with a downward concave horizontal component.

Biting and butting. Biting seems to be the most effective aggressive behavior in *T. pectoralis.* When biting, the mouth is open and is closed upon contact with the other fish. Biting may result in loss of scales and/or tearing or shredding of fins, particularly in the region of the anal fin and caudal peduncle. Butting consists of thrusting or nudging the opponent with the mouth closed and without clear attempts to bite. Due to the difficulty of differentiating between bites and butts, both were grouped under one category, bite-butt.

Fin tug. Fin tugging occurs when one fish grasps the fin of another with its mouth and holds on for a period of one to several seconds or actively pulls the fin by undulating tugging movements (15, 17). The anal fin is usually the target of attack but the pelvic, pectoral or dorsal fins may also be seized.

Mouth fight. Miller (15) described mouth fighting behavior in *T. trichopterus,* but no documentation of the occurrence of this behavior has appeared in the literature for *T. pectoralis* or other species of *Trichogaster.* A series of lunges by one or both fish seems to initiate these short, violent engagements which are extremely variable. Mouth fights do not appear to contain ritualistic elements, as they sometimes do in other teleost fishes (15), but instead seem to be a direct frontal attack and bite occurring simultaneously in both opponents.

Chase. Chasing involves the fleeing of one fish with another pursuing. The pursuing fish usually attempts to bite or butt the pursued. Pursued fish usually flee with fins folded at moderate to high speeds.

Terminology for behavioral events

The following terms are used to represent various behavioral events analyzed in this study.

Patrol. Patrolling behavior consists of slow swimming by which the fish apparently surveys the area without interacting with other fish.

Rest. A very narrow definition of rest was utilized: rest was tallied when the fish became stationary on the bottom with fins relaxed, exhibiting no movements except slight opercular opening and closing.

Inspiration. Inspiration consists of the taking in of air by the fish at the air-water interface. Wimmer (13) described two "distinctly different" methods of inspiration in *T. microlepis;* however, no such differentiation was made in this study.

Total activity. The term total activity was used to include all behaviors, except rest, occurring during a given observation period. Since rest is defined by its lack of movement, it could not be considered activity.

Miscellaneous activity. This category includes behaviors grouped under total activity but not patrolling, inspiration, rest, or any agonistic behaviors. Feeding, snapping at a snail, chaffing, yawning, and other comfort movements would be considered miscellaneous activities.

RESULTS AND DISCUSSION

Frequency of patrolling behavior showed significant differences among replicates ($p < .05$) and observation times, which indicated a definite time effect. Patrolling frequencies are thus presented for each replicate (Figure 1). Patrolling frequency

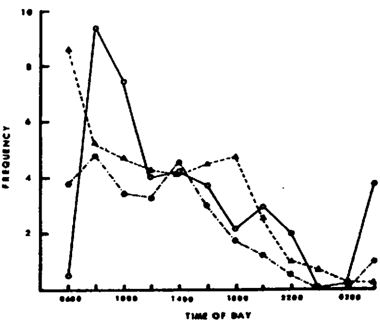

FIGURE 1. Average frequency of patrolling behavior. (Open circles = replicate 1; triangles = replicate 2; closed circles = replicate 3.)

(Figure 1) exhibited much variation between replicates in the early morning hours (0600); it varied from 0.5 patrols/10 min to 8.8 patrols/10 min. A range of 4.8 patrols/10 min to 9.5 patrols/10 min occurred at 0800. A definite decrease in patrolling activity was noted from 0800 to 1000 and continued until 1200 when followed by a slight increase from 1200 to 1400. After 1400 a general decreasing trend in patrolling frequency was seen until darkness at 1800. Patrolling was sporadic after lights-out (1800) but usually decreased until 2400. During the period of 2400 to 0200 almost no patrolling activity was recorded; patrolling increased from 0200 to 0400 as the fish was about to be exposed to "daylight" at 0600. This general increase at 0400 seems to indicate that the fish anticipates the approach of light at 0600.

AOV analysis of patrolling duration indicated a significant time effect ($p < .05$) over the 24-hr period analyzed but no significant difference among replicates occurred, *i.e.,* the pattern of these replicates was generally the same. Mean values, therefore, could be calculated for patrolling duration

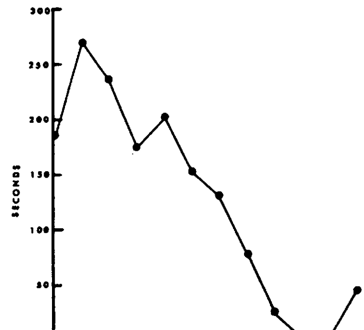

FIGURE 2. Average duration of patrolling behavior.

and are shown in Figure 2. A definite increase in patrolling duration from 187.3 sec to 270.9 sec occurred from 0600 to an 0800 peak, followed by a rather sharp decrease at 1000 which continued until 1200. From 1200 until 1400 an increase from 175.2 sec to an afternoon peak of 205.4 sec was reached. A reduction of patrolling duration followed this slight increase until 1800 (darkness) and continued until a low of 0.6 sec was recorded at 0200. This period of decreased patrolling duration was accompanied by a decrease in patrolling frequency (Figure 1). After 0200 duration of patrolling increased until lights were turned on.

Frequency of inspirations subjected to AOV analysis revealed no significant differences among replicates; there was a definite significant difference ($p < .05$) among observation times. Mean values for the rep-

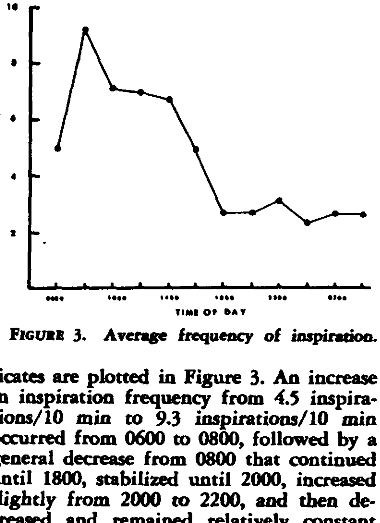

FIGURE 3. Average frequency of inspiration.

licates are plotted in Figure 3. An increase in inspiration frequency from 4.5 inspirations/10 min to 9.3 inspirations/10 min occurred from 0600 to 0800, followed by a general decrease from 0800 that continued until 1800, stabilized until 2000, increased slightly from 2000 to 2200, and then decreased and remained relatively constant until 0400. The data suggest a morning peak in inspiration frequency of 9.3 inspirations/10 min which is followed by relatively lowered inspiration frequencies throughout the remainder of the 24-hr cycle.

Durations of inspiration are shown in Figure 4. The significant difference noted ($p < .05$) among observations and replicates ($p < .05$) necessitated plotting values for each replicate. Generally, high variability occurred in inspiration duration from 0600 until 1200, after which a general increasing trend became evident from 1200 until 1400, followed by a general decrease to 1600. This decreasing trend continued until 2000 when flucuations again occurred to cause difficulty in interpretation.

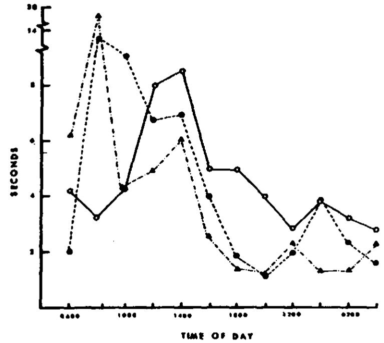

FIGURE 4. Average duration of inspiration. (Closed circles = replicate 1; open circles = replicate 2; triangles = replicate 3.)

Due to its infrequency, rest behavior was not analyzed statistically. Because of the narrow definition employed for rest behavior, *i.e.*, no movement by the fish, true rest was rarely seen and, as expected, occurred primarily after 1800 and increased, generally, until about 0400. Rest duration presented much the same pattern, with highest values after 1800, but variability was high.

Analysis of frequency of total activity (*i.e.*, all behaviors, except rest, occurring during a given observation period) probably is a better overall indicator of the daily activity pattern of *T. pectoralis* than

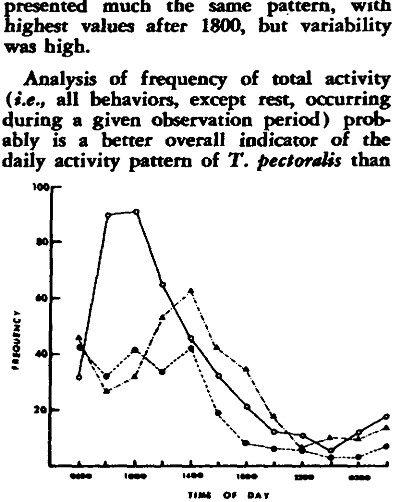

FIGURE 5. Average frequency of total activity. (Open circles = replicate 1; triangles = replicate 2; closed circles = replicate 3.)

any single parameter; however, individual replicate variation clouded the importance of this measure as an indicator of biological rhythm. AOV analysis of the frequency of total activity revealed significant differences ($p < .05$) among replicates, while also revealing significant differences ($p < .05$) among observation times. There was, therefore, a definite replicate and time effect (Figure 5). Variability of total activity frequency in the morning hours, from 0600 to 1000, among replicates made interpretation difficult. However, from 1400 until 1800 a definite decrease in frequency of activity occurred. The decrease continued after the lights were turned out (1800) until about 2400, after which a slight increasing trend in total activity occurred until 0400.

Duration of total activity represents another useful indicator of fish activity during the 24-hr period. Analysis of duration of total activity indicated no significant differences among replicates, but significant differences did exist among observation times ($p < .05$). Mean values are plotted in Figure 6. From a mean of 369.8

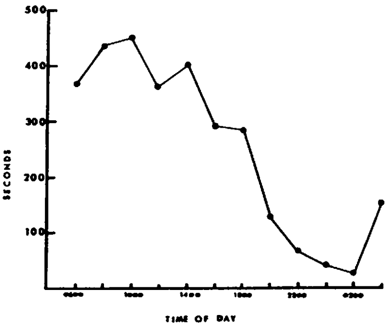

FIGURE 6. Average duration of total activity.

sec total activity duration at 0600, duration increased to a peak of 457.4 sec at 1000 when it was followed by a decrease to 368.7 sec at 1200, and then there was another increase at 1400 to 404.8 sec. This second peak was followed by a rapid decrease to 294.6 sec at 1600 and further decreases throughout darkness until 0200. From 0200 to 0400 total activity duration increased from a daily low of 30.8 sec to 158.5 sec.

Hourly percentages of total activity (percentage of the sum of behaviors in a 24-hr period) of *T. pectoralis*, based on observa-

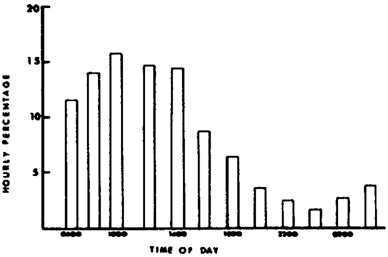

FIGURE 7. Hourly percentages of total activity.

tions of 12 males, are presented in Figure 7. Again the general increase in activity which occurred from 0600 to 0800 and reached a peak at 1000 is seen. After 1000 a nearly continuous decrease occurred until 2400. After 2400 there was a gradual increase in total activity until 0400.

Relative frequency of behaviors

To provide an indication of the relative frequency of behaviors shown by *T. pectoralis* during a 24-hr period, the relative frequency of each behavior, expressed as a percentage of total activity recorded during the experiment, was calculated and is

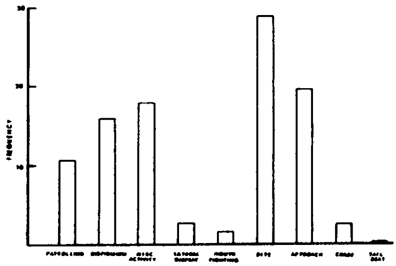

FIGURE 8. Frequency of individual behaviors expressed as percentage of total activity.

shown in Figure 8. A total of 4,223 behaviors were recorded.

The most frequent single behavior was biting and butting. Bite-butts represented 28.91% of all behaviors recorded; it appears to be the most prevalent behavior in heterosexually paired situations. Approach accounted for 19.42% of total activity; it was very common in aquaria and seems to be used as a threat behavior. The grouping termed miscellaneous activity constituted 17.95% of the total activity. Inspiration accounted for 15.91% of all recorded activity.

These four behaviors or groups of behaviors represent a combined percentage of 82.19% of behaviors recorded during the experiment. The remaining behaviors are represented, in decreasing percentage frequency, by patrolling (10.35%), chase (3.34%), lateral display (2.25%), mouth fight (1.54%) and tail beating (0.33%).

Agonistic behavior

Of 4,223 behaviors recorded during the study, 2,356 were agonistic behaviors. Percentage frequency of each behavior is shown in Figure 9.

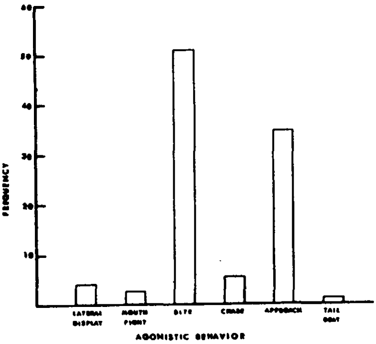

FIGURE 9. Frequency of agonistic behaviors expressed as percentage of total activity.

Bite-butt and approach represented 86.63% of all agonistic behaviors. Bites alone accounted for 51.83% and thus represented over half of all agonistic behaviors recorded. Approach constituted 34.80% of agonistic behaviors. After approach, in decreasing order of magnitude, came chase (5.98%), lateral display (4.03%), mouth fight (2.76%), and tail beats (0.59%).

Diel rhythm of agonistic behavior

AOV analysis of all agonistic behaviors except tail beating (which was not analyzed because of too few observations) revealed no significant differences among replicates; therefore, replicates were lumped and means plotted. All agonistic behaviors exhibited significant differences among observation times ($p < .05$), *i.e.*, a definite time effect was observed.

Mouth fights exhibited a slight peak at 0800, followed by fluctuations throughout the 24-hr period (Figure 10).

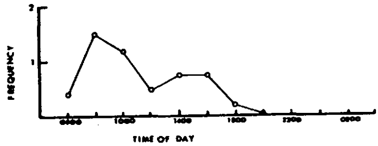

FIGURE 10. Average frequency of mouth fight behavior.

Lateral display frequency of 0.75/10 min was recorded at 0600; a slight decrease followed at 0800, with subsequent fluctuations at 1000 and 1200 (Figure 11). A peak of 2.4 lateral displays/10 min occurred at 1400. A notable decrease in lateral displays took place after 1400 until 1600. From 1600 until 1800 a slight increase occurred, after which no lateral displays were ever seen in darkness.

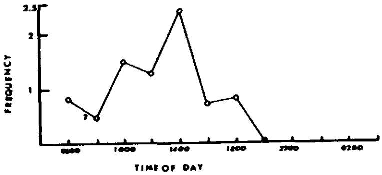

FIGURE 11. Average frequency of lateral display behavior.

Peaks of biting-butting occurred at 1000 (22.8 bite-butts/10 min) and at 1400 (21.3 bite-butts/10 min) and were followed by a decline to a low of 0.08 bite-butts/10 min at 2400 (Figure 12). Some biting and

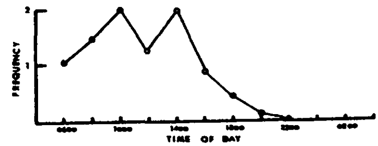

FIGURE 12. Average frequency of bite behavior.

butting occurred throughout the 24-hr period even in darkness.

Approach frequency remained fairly constant in the morning hours but displayed the same (1400) afternoon peak as for previous behaviors; this peak was followed by a gradual decline until 2400 (0.17 approaches/10 min) (Figure 13). The gradual decline was in turn followed by a slight increase at 0200 (0.42 approaches/10 min), and continued to increase until 0400 (0.75 approaches/10 min).

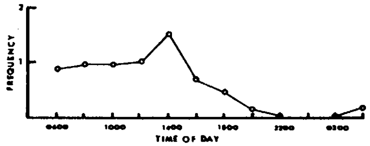

FIGURE 13. Average frequency of approach behavior.

Frequency of chase dipped at 0800 (0.83 chases/10 min) after being 1.42 chases/10 min at 0600. A gradual increase occurred after 0800 to a peak at 1400 of 2.42 chases/10 min; this peak was followed by a steady decline to no chases at 2400. A slight increase was observed at 0200 and 0400.

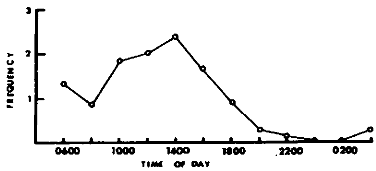

FIGURE 14. Average frequency of chase behavior.

Approach, bite, and chase frequencies all follow the same general patterns. Typical agonistic encounters between a dominant male and subordinate female are characterized by the sequence of approach, bite, and chase; therefore, the same patterns for the three behaviors might be expected. Overall, the data suggest a pattern of agonistic activity in male *T. pectoralis*. From an intermediate level in the morning hours (0600), a general increase occurs until an afternoon peak is reached at 1400. This afternoon high is followed by a decrease until lights out, after which a continued decrease until 2400 is seen. A gradual increase from 2400 until 0400 follows.

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