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Day–night alternation prevails over food availability in synchronising the activity of *Piaractus brachypomus* (Characidae)

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Abstract — Pirapatinga given submaximal rations grow faster when fed at night than when fed during daylight hours. It was hypothesised that these fish were day–night conformers, with a nocturnal acrophase, and expended more energy during daytime feeding. In order to test this hypothesis, telemetry was applied to study the behaviour of cultured pirapatinga (stocking biomass of 40 $kg \cdot m^{-3}$; 27 ± 1 °C; 6 mg $O_2 \cdot L^{-1}$; 13.5 L/10.5 D) under three feeding schedules (diurnal versus nocturnal feeding [12 $g \cdot d^{-1} \cdot fish^{-1}$ over 10 h] versus fasting) that were evaluated in succession over 1 week each. This implied a feasibility study to test the adequacy of tagging fish with surgically implanted transmitters (ventrolateral incision, posterior to the pelvic girdle). There was no mortality or tag loss over 12 months following surgery, and abdominal incisions healed within 4 weeks. Under all three feeding schedules, activity increased at dawn, peaked during daytime, decreased at twilight and reached a minimum during the late night. Diurnal and twilight activity levels were similar under all three schedules, whereas nocturnal activity was significantly lower with daytime feeding. These observations indicate that pirapatinga have a diurnal activity acrophase, which is little influenced by food availability, and imply that the higher growth of fish fed at night does not originate from lower energetic expenditures. © 2000 Ifremer/Cnrs/Inra/Ird/Cemagref/Éditions scientifiques et médicales Elsevier SAS

Activity rhythm / activity entrainment / meal timing / fish telemetry / tagging / aquaculture / South America

Résumé — Synchronisation de l'activité locomotrice de *Piaractus brachypomus* (Characidae) : prédominance de l'alternance jour-nuit sur la disponibilité de la nourriture. La croissance du pirapatinga en aquaculture est nettement plus élevée lorsque l'aliment est exclusivement distribué au cours de la scotophase. L'hypothèse testée dans cette étude est que le pirapatinga avait un type d'activité typiquement nocturne, synchronisé par l'alternance jour-nuit, et que la distribution d'aliment au cours de la photophase impliquait des dépenses énergétiques supplémentaires. Pour tester cette hypothèse, l'activité locomotrice du pirapatinga a été étudiée par télémétrie en milieu contrôlé (biomasse de 40 $kg \cdot m^{-3}$; 27 ± 1 °C ; 6 mg $O_2 \cdot L^{-1}$; 13,5 L/10,5 N), dans trois contextes d'alimentation (diurne opposée à nocturne [12 $g \cdot j^{-1} \cdot poisson^{-1}$ pendant 10 h] versus à jeun) évalués successivement pendant une semaine chacun. L'étude a requis la mise au point et l'évaluation d'un protocole d'implantation abdominale d'émetteurs de télémétrie adapté à des poissons compressés latéralement (incision ventrolatérale, postérieure à la ceinture pelvienne). Aucune mortalité ou perte de marque n'est survenue pendant les 12 mois suivant le marquage, l'incision abdominale étant cicatrisée en quatre semaines. Quel que soit le schéma d'alimentation évalué, l'activité locomotrice des pirapatingas était typiquement diurne, augmentant à l'aube, atteignant un maximum pendant la journée, diminuant au crépuscule et devenant minimale en fin de nuit. Les niveaux d'activités diurnes et crépusculaires (aube et crépuscule) étaient comparables, alors que l'activité nocturne était significativement plus élevée quand aucun aliment n'avait été distribué pendant la photophase (poissons à jeun et nourris de nuit versus nourris de jour). Ces observations révèlent que l'activité locomotrice du pirapatinga est quasi indépendante de la disponibilité de la nourriture, et que la croissance plus élevée des poissons nourris la nuit ne provient pas d'une diminution des dépenses énergétiques consenties pour la locomotion. © 2000 Ifremer/Cnrs/Inra/Ird/Cemagref/Éditions scientifiques et médicales Elsevier SAS

Rythme d'activité / horaire des repas / télémétrie / marquage / aquaculture / Amérique du Sud

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1. INTRODUCTION

Meal timing has been shown to influence feed intake, growth and/or conversion efficiency in several fish species. There may be differences when single meals are distributed at different times of the day or night [10, 12, 40], or when food is available for longer periods of the daily cycle (day or night [24, 33]). Hypotheses to explain the growth differences include the correspondence between meal timing and fish activity pattern [2, 11], the alleviation of density-dependent growth under low light conditions [8, 23], and differences in food processing and nutrient deposition [18, 19, 24, 34].

The South American pirapatinga *Piaractus brachypomus* (Characidae, Serrasalminae) grows well when fed during the day [31], but fish fed at night may grow 35–50 % better (300–400 g fish [5]). Examination of oxygen consumption by pirapatinga [37] raises the possibility that pirapatinga grow at a slower rate when fed during the day because they are nocturnally active and may expend additional energy under daytime feeding. The aim of the present study was to test this hypothesis by investigating the behaviour of pirapatinga under different feeding schedules (fasting, optimal food ration during the day or night). Because fish behaviour had to be monitored in large scale enclosures, similar to those during the growth study (see [41]), independently of illumination or water clarity, and ideally at the individual level, this was accomplished through the use of telemetry techniques.

Surgical implantation is the most frequently used technique to attach telemetry tags in fish [4, 28, 39], and it is heavily recommended for investigations in intensive culture, where other tagging techniques (intragastric insertion, dorsal attachment) may have more numerous adverse effects. However, surgical tagging may be more difficult in laterally compressed fish such as pirapatinga. Studies on fish species with similar body shapes (American crappies *Pomoxis* sp. [25, 35]; bluegill *Lepomis macrochirus* [26]) indeed reported high mortality rates, irregular healing progress and frequent tag shedding when surgically implanted tags were used. Hence, a preliminary feasibility study was needed to evaluate the adequacy of surgical tagging in pirapatinga.

2. MATERIALS AND METHODS

2.1. Evaluation of surgical tagging

A feasibility study to test tagging was conducted on 2-year-old hatchery-reared fish (1 378–2 227 g) using epoxy dummies that mimicked actual radio transmitters (72 × 12.5 mm in diameter, 13–14 g in the air). The fish were anaesthetised with tricaine (100 mg·L^{-1}), and placed in a V-shaped support. Pirapatinga have a midventral cartilaginous ridge, and have rigid flanks, supported by long thick ribs. Hence surgical tagging was carried out via a ventrolateral incision made parallel to the sagittal axis of the fish, and posterior to the pelvic girdle. Because the ribs anterior to the pelvic girdle are much longer than those posterior to it, only the latter site was considered.

The incision was circa 2.5 times as long as the diameter of the transmitter to enable its insertion and horizontal positioning inside the body cavity. Forceps with a smooth surface were necessary to temporarily enlarge the incision for tag passage. Penicillin (5 000 U·kg^{-1}) was injected into the body cavity, and the incision was closed with four or five stitches, using either non-absorbable sterile braided silk (Ethicon 2/0) or polyamide monofilament (Ethilon® 2/0) affixed to 23-mm cutting needles (15 fish for each suture material evaluated). Each fish was also tagged with a passive integrated transponder (PIT) tag (Indexel) inserted into its dorsal musculature for individual identification.

After recovery, fish were stocked together with 20 control (PIT-tagged only) fish in a 1.5 m^3/4 m^2 flow through tank (natural photoperiod, 27 ± 1 °C; 6 mg O_2·L^{-1}). Formulated feed (4 mm in diameter, 45 % protein, 11 % lipid; 12 g·d^{-1}·fish^{-1}) was distributed during daytime by an automatic belt feeder. Fish were examined for healing progress and weight gain at weekly intervals for 6 weeks, and then once every 4 weeks over 12 months. Possible long-term effects of suture filaments were examined by removing the stitches from 18 tagged fish on day 21, whereas they were left in place in the other fish.

2.2. Study of fish behaviour

The experiment was conducted in August (same time of the year as growth study [5]) when day length varied from 14L:10D to 13L:11D. The rearing environment, food composition, ration and distribution were as above, and stocking density was circa 40 kg·m^{-3} (30 fish of circa 2 kg in a 1.5-m^3 tank, including two radio-tagged fish). Water turbidity never exceeded 15 FTU over the entire study. Three feeding schedules (diurnal, nocturnal and fasting) were evaluated. During the first week, food was exclusively distributed during daytime (10 h per day, starting from 09:30 hours). During the second week, food was provided during night-time only (10 h per day, starting from 21:30 hours). The diurnal feeding schedule was then restored over 1 week, and then fish were deprived of food over an entire week.

Four weeks before the experiment started, two fish (1 625 and 1 782 g) were surgically implanted with radio transmitters, using braided silk sutures (see justification in results). Transmitters were motion-sensible units, the pulse rate of which shifted in between 42 ± 1 and 84 ± 1 pulses per min (ppm), depending on the orientation of a mercury tilt connected to an activity circuit. Fish activity was measured using the same protocol as described previously [3, 42]. Briefly, radio signals were detected using a dipole antenna and a Lotek SRX-400 data-collecting receiver (processor W-18), which automatically switched from one individual fish to the other after an interpulse interval had been detected. About 4 000 records of five interpulse intervals each were recorded daily for each fish, and were downloaded with Lotek Host™ software. Records were ranked as activity, rest or non-valid records, depending on transmitter pulse frequency and signal strength variations [3]. The activity level was calculated as the proportion of time when fish were active, and was calculated at hourly, periodic (diurnal, nocturnal and twilight) and daily (24-h) levels. Activity levels were compared by multiple analysis of variance (MANOVA) against the feeding schedule (n = 3), the fish (n = 2) and the day of the experiment (n = 7).

3. RESULTS

3.1. Evaluation of surgery procedures

There was no mortality or tag loss over the 12 months following surgery. Surgically tagged fish lost 2–4 % of their body weight over the first 2 weeks, and grew slowly over the next 4 weeks. Control fish also grew slowly over the first 6 weeks, suggesting that most adverse effects were due to repeated handling and anaesthesia. All incisions closed with braided silk were healed and covered by scales within 4 weeks, whereas sutures with polyamide filaments caused deeper cuts to the muscles, which required an additional week to heal. The early removal of the suture filaments had no effect on healing, growth or infection. Gross necropsy revealed no internal damage to the viscera, transmitters being encapsulated in connective tissue, which was partly or totally embedded in abdominal fat.

3.2. Fish behaviour

Activity was significantly influenced by feeding schedule (MANOVA; $P < 0.01$), but did not differ ($P > 0.10$) between days or between fish. When fed during daytime, the pirapatinga were more active during the day than at night (*figure 1a*). Activity started increasing at dawn, reached a maximum before food was distributed in the morning and decreased slightly during the afternoon. Activity decreased steeply at dusk and was at a minimum between 02:00 and 05:00 hours.

The transition to nocturnal feeding did not cause a shift to a predominantly nocturnal activity pattern (*figure 1b*), activity still being highest during daytime, and decreasing at dusk even though food was offered at night. However, night-time activity was significantly ($P < 0.01$) higher than when food was provided during the day (*figure 2*).

When fish were deprived of food for seven consecutive days, there was also a consistent diurnal activity pattern (*figure 1c*). Night-time activity levels were similar to those observed under nocturnal feeding, and significantly ($P < 0.01$) higher than when food was offered during the day (*figure 2*).

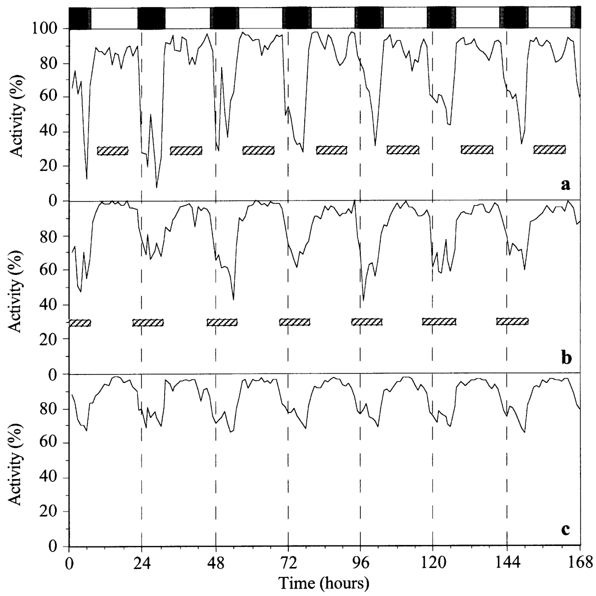

Figure 1. Locomotor activity patterns of pirapatinga (40 kg·m^{-3}) at 27 ± 1 °C under different feeding schedules. Activity is the proportion (%) of time spent swimming per hour (mean of two 1.7-kg individuals tagged with motion-sensitive radio transmitters). Open, grey and closed bars above the graph stand for day, twilight and night, respectively. Dashed bars represent the periods when food (12 g·d^{-1}·fish^{-1}) was distributed by an automatic feeder. a) diurnal (09:30–19:30 hours); b) nocturnal (21:30–07:30 hours); and c) fasting.

4. DISCUSSION

Surgical tagging was more successful in pirapatinga than in other laterally compressed fish (bluegills or crappies [25, 26, 35]), and no long-term adverse ef-

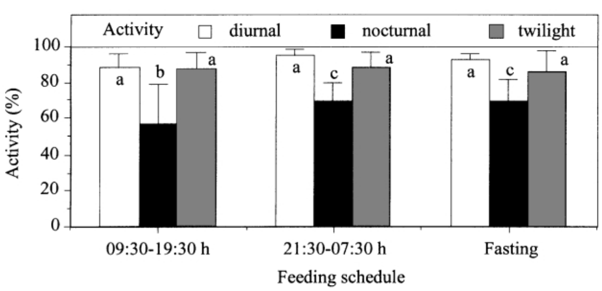

Figure 2. Activity of cultured pirapatinga by day (12.5 h·d^{-1}), night (9.5 h·d^{-1}) and twilight (2 h·d^{-1}), depending on the feeding schedule. For each schedule and period of the day, values are means of hourly activity levels of two 1.7-kg fish over seven consecutive days [see *figure 1*; no significant differences ($P > 0.10$) between days or between fish]. Error bars are the standard deviations of estimates. Values with different superscripts differ at $P < 0.01$, whereas others comparisons are not significantly different ($P > 0.10$).

fects were observed. Long-term fouling of braided silk sutures was observed, but this did not cause the problems encountered in studies with tilapia that grazed algae developing on this suture material, and this interfered with the healing progress of tagged fish [42]. Implant encapsulation has been reported as a compulsory step in body wall and anal exit mechanisms [9, 27, 29, 30]. All tags implanted into pirapatinga became encapsulated in connective tissue but none was expelled, and this is a further example that implant encapsulation is not synonymous with expulsion risk [4, 9, 42].

These different elements indicate that a reliable technique has been developed to tag pirapatinga. However, due to the limited distance between the pelvic girdle and the ano-uro-genital papilla, only low tag to body weight ratios (< 0.7 %) can be used in pirapatinga. These drawbacks caused no inconvenience in this experimental study, where the activity of large fish was monitored at close range over a limited period of time, but could prove to be limiting factors for smaller fish or for tracking studies of wild fish, where reception range or tag endurance matters. Also, the observation that tagged individuals lost weight soon after tagging indicates that the collection of telemetry data should be postponed for a few weeks, until the fish have recovered their physical integrity.

The incision had completely healed for both tagged individuals when the study started, and the risk that their behaviour was altered by the tagging procedure or tag presence is deemed to be minimal. They showed a consistent diurnal behaviour under all three feeding schedules, and the early morning peak of activity persisted under all three feeding schedules, suggesting this was no anticipation of a daily meal [1]. This indicates that patterns of locomotor activity were chiefly entrained by day–night alternation and were little influenced by food availability and consumption. The prevalent influence of day–night alternation on the activity of pirapatinga was initially expected [5]. However, pirapatinga fed at night were expected to expend less energy than those fed during the day, whereas this study demonstrated the opposite. As a corollary, the faster growth of pirapatinga fed at night does not originate from lower energetic expenditures.

It could be argued that the consistency of the diurnal activity of pirapatinga throughout this short-term experiment was related to some feeding of the fish during the day over long periods prior to the start of the study [38]. However, this also applied to studies that showed marked differences between growth rates under different meal timings even though they were run over a few days ([5]; Baras and Mélard, unpublished). Pirapatinga given submaximal rations were never observed wasting food, neither during the day nor at night ([5, 31]; Baras and Mélard, unpublished). Since pirapatinga fed during the day apparently do not waste food and spend less energy than those fed at night, their slower growth originates presumably from time-dependent energy use (e.g. capacity for protein synthesis and fat storage [18, 19, 24, 34]). Energy use is influenced by fish behaviour, and notably by swimming activity [21, 22]. Fish exercising in moderate water velocities frequently show less agonistic interactions [13, 17] and greater deposition of protein [14, 20] or glycogen [15, 17] in the swimming muscles than those held in standing water. Because the locomotor activity of pirapatinga during daylight hours is essentially entrained by day–night alternation, and is little influenced by food availability and consumption, fish fed at night would exercise almost continuously after feeding, and would thus achieve a higher weight gain per unit of food consumed.

This hypothesis still needs to be tested in the course of behavioural studies coupled to proximate analyses of body composition of fish fed at different times of the day. In any case, the observation that pirapatinga grow faster when forced to feed outside of their genuine acrophase is of particular concern to fish well being and to the use of self-feeders in aquaculture. It suggests that unrestricted access to food over the daily cycle is not always the best way to obtain the best growth or feed conversion efficiency, even though no food is wasted. Similar arguments have been put forward with respect to feeding charts including fasting days, after it was demonstrated that fish could positively trade off periods of denutrition through compensatory growth [16, 32, 36]. Comparisons between studies suggest that time-restricted access to food is better for day–night conformers such as pirapatinga than for food-conformers such as the blue tilapia, *Oreochromis aureus*, which adapt their daily activity pattern to meal timing experienced the previous day [7], and show similar growth rates under different meal timings [6].

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