ORIGINAL PAPER

Reproductive behavior of the Amazonian dwarf cichlid *Apistogramma hippolytae* Kullander, 1982: offsetting costs and benefits

**Raoni Rosa Rodrigues · Jansen Zuanon ·
Kleber Del-Claro · Lucélia Nobre Carvalho**

Abstract The reproduction trade-off for an animal is a
conflicting choice in which resources (e.g., time and/or energy)
allocated to one reproduction trait (e.g., parental care) become
unavailable to other traits (e.g., future reproduction events).
Here, we tested three hypotheses related to the parental care of
the Amazonian dwarf cichlid *Apistogramma hippolytae* in its
natural habitat of Central Amazonia: (1) brood-caring females
have a lower feeding frequency than individuals that are not
involved in this behavior; (2) females that spend more time
on nest defense have lower feeding rates; and (3) females can
recognize the species that present the greatest danger to its
offspring and move farther from the nest to chase away these
piscivorous fishes. We also described for the first time the
reproductive behavior (including courtship) and parental care
of this species. The results showed that maternal care
produces a reduction in the rate of feeding of mothers, a
greater amount of time is spent chasing invaders away from
the nest, and reproductive females are able to distinguish
species-specific predators. These observations support the
hypotheses of this study and also suggest a trade-off between
current and future reproduction events.

Keywords Trade-off · Feeding behavior · Parental care ·
Reproduction · Cichlidae

R. R. Rodrigues (✉)
Centro de Transposição de Peixes–ICB, Universidade Federal
de Minas Gerais (UFMG),
Av. Antônio Carlos, 6627, Bloco E2, Sala 180,
31270–901 Belo Horizonte, Minas Gerais, Brazil
e-mail: raonirosa@yahoo.com.br

R. R. Rodrigues · K. Del-Claro
LECI–Laboratório de Ecologia Comportamental e de Interações,
Universidade Federal de Uberlândia,
Caixa Postal 593,
38400–902 Uberlândia, Minas Gerais, Brazil

K. Del-Claro
e-mail: delclaro@ufu.br

J. Zuanon · L. N. Carvalho
Coordenação de Pesquisas em Biologia Aquática (CPBA),
Instituto Nacional de Pesquisas da Amazônia (INPA)
and Biological Dynamics of Forest Fragments Project (BDFFP),
Smithsonian Tropical Research Institute,
CP 478, 69011–970 Manaus, Amazonas, Brazil

J. Zuanon
e-mail: zuanon@inpa.gov.br

L. N. Carvalho
e-mail: carvalholn@yahoo.com.br

Present Address:
L. N. Carvalho
Instituto de Ciências Naturais, Humanas e Sociais (ICNHS),
Universidade Federal de Mato Grosso (UFMT),
Campus de Sinop, Avenida Alexandre Ferronato, 1200,
Setor Industrial,
78550–000 Sinop, Mato Grosso, Brazil

Introduction

In the balance between the costs and benefits that regulate
animal actions, all investments in a specific life history trait
represent the time and/or energy that is unavailable to
another trait (i.e., a trade-off) (Trivers 1972; Cuthill and
Houston 1997). The concept of a trade-off has been
identified as one of the main pillars of an evolutionary
approach to animal behavior (Cuthill and Houston 1997),
whose roots are deeply fixed in animal physiology (Daan
and Tinbergen 1997). Trade-offs can be related to many
aspects of a species' life history, such as predation risk
assessment and foraging activities (e.g., Werner and Hall
1988; Carvalho and Del-Claro 2004; Cresswell 2008).
Several examples of trade-offs related to reproductive

behavior, including decisions involving energetic, temporal, or mechanistic limitations, are known (Stiver and Alonzo 2009). For instance, trade-offs may involve the decision to protect current offspring or leave the offspring and mate a second time in the same breeding season (e.g., Székely and Cuthill 2000), to produce a lot of offspring or fewer with a better reproductive value (e.g., Daan and Tinbergen 1997), or even whether to mate or not at a given moment depending on the number of sneaker males in the area (e.g., Alonzo and Warner 1999).

Reproductive trade-offs have been documented for many animal taxa (e.g., Sadras 2007; Stiver and Alonzo 2009; Székely and Cuthill 2000; Tallamy and Denno 1982) including fishes (Steinhart et al. 2004; Steinhart et al. 2008; see review by Kolm and Ahnesejo 2005). Cichlid fishes are remarkable for their complex behavioral repertoire that includes elaborated forms of parental care (Keenleyside 1991) and sophisticated breeding systems (Baerends and Baerends-van Roon 1950; Desjardins et al. 2008; Nakazawa and Yamamura 2009; Nelissen 1991). Therefore, cichlids constitute good models for testing hypotheses related to reproductive trade-offs.

Dwarf cichlids of the genus *Apistogramma* Regan, 1913 are small fishes (typically 20 to 60 mm, standard length (SL)) that generally present marked sexual dimorphism: males are bigger, more colorful, and more adorned than females (Römer 2001). Previously published studies have indicated that these fishes are omnivorous, feeding on plant debris, algae, and small terrestrial and aquatic arthropods (Henderson and Walker 1990; Silva 1993; Sánchez et al. 2003). *Apistogramma hippolytae* is a small fish that is common in clear and black water streams and in the rivers of Central Amazonia. In contrast to the majority of the species of this genus, *A. hippolytae* does not show a marked sexual dimorphism; however, it does have an elaborate parental care behavior, which is typical of this family (Römer 2001). During field studies developed in a pond near Manaus in the Brazilian Amazon, we had the opportunity to investigate the behavioral aspects of the life history of an *A. hippolytae* population, including the color changes related to social and environmental settings (Rodrigues et al. 2009), foraging activity and the reproductive behavior of breeding and nonbreeding individuals. Several females in the pond were engaged in brood care, alternating between foraging and nest defense, which allowed us to detect a possible trade-off involving feeding and breeding activities by the dwarf cichlid in its natural environment.

Here, we describe the reproductive behavior of *A. hippolytae* under natural conditions at a pond in Central Amazonia, including courtship and parental care. We tested three hypotheses, two of which potentially involve trade-offs in parental care: (1) females engaged in parental care have a lower feeding frequency than individuals that are not involved in this behavior; (2) there is a negative relationship between the number of fishes that females chase away from the nest and the feeding frequency (i.e., females that spend more time on nest defense have lower feeding rates); and (3) females recognize fish species that pose a greater risk to their offspring and move farther from the nest to chase away these piscivorous fishes.

Materials and methods

Study area

The study was conducted between April and September of 2005 in a pond near the Dimona Farm research station (2°20′25.5114″S/60°6′5.7594″W) in the Biological Dynamics of Forest Fragments Project (BDFFP) area. This area is part of the Cuieiras River basin, a tributary of the Negro River, which is 70 km north of Manaus, Brazil. The area receives rainfall that varies from less than 100 mm in the dry season (June to November) to 2,500 mm in the rainy season (December to May; Gascon and Bierregaard 2001). For a map and additional information about the study area, see Bührnheim and Cox-Fernandes (2001) and Gascon and Bierregaard (2001).

The studied pond (approximately 40 m long×14 m wide×0.5 m deep) is part of a forest streamlet (locally known as an *igarapé*) with a bottom consisting of submerged dead leaves (~80%) and trunks and twigs (~20%), covered by a layer of fine sediments. The pond is surrounded by primary and secondary tropical rain forests, which form a mosaic of trees and shrubs that overhang the pond margins and contribute organic matter to the aquatic system. The physicochemical characteristics of the water were stable during the study period (range: dissolved oxygen, 3.5 to 4.7 mg L^{-1}; pH 4.9 to 5.0; and conductivity, 8.6 to 8.8 $\mu S\ s^{-1}$) and the water temperature also were stable throughout the day (ranging from 24.4°C to 26.2°C). Despite the large amount of forest debris that had accumulated at the pond bottom, the water was clear and allowed for ideal underwater visualization conditions. For images of the study pond, see Rodrigues et al. (2009).

Data collection

Feeding and reproductive behavior data were acquired from direct observations in the natural habitat. We conducted 15 h of observation, which were divided into 8 h of underwater observation (snorkeling; cf., Sazima 1986) and 7 h of supra-aquatic observation (in places where the depth was less than 0.50 m). The "focal animal" and "all occurrences" sampling methods were used for all sessions
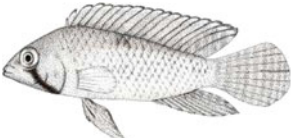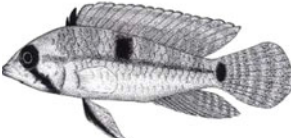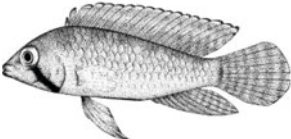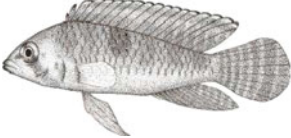
(Lehner 1996). The color patterns used in the behavioral descriptions followed Rodrigues et al. (2009; Table 1).

The foraging intensity was determined from direct observations of individuals ("focal animal" sampling) where the observer recorded the number of feeding bites at the substratum. Individuals were observed at 1-min intervals between 06:00 hours and 18:00 hours, and the average number of feeding bites per minute per individual and hour of observation were determined. Fishes were divided in two groups: females caring for offspring ($n=10$ individuals per hour; $n_{total}=120$) and individuals that were not involved in this behavior ($n=10$ individuals per hour; $n_{total}=120$).

Parental care was analyzed during 17 snorkeling sessions with 30 min of continuous observation during each session ("all occurrences" sampling). During these sessions, the number of feeding bites and the attacks by brood-caring females on other fishes that approached its offspring were recorded. The identity of the attacked species and the distance covered by the female to drive away the intruder (measured from the point where the first attack was initiated) were recorded.

Table 1 Description of the color patterns related to different behavioral contexts for *A. hippolytae* individuals

Color pattern	Description	Behavioral context
Shining	Individuals are characterized by a general increase in the intensity and contrast of the body colors, especially in the ventral region. The suborbital stripe has different degrees of conspicuousness, and the eyes become brighter.	Males during courtship
Stripe-spot	Individuals present a dull background color over the entire body with a conspicuous lateral stripe, lateral blotch and caudal spot. The eyes become darker, the suborbital stripe turns faint or absent, and the lateral bars become visible.	Females during courtship
Females	The first rays of the pelvic and dorsal fins are strongly colored in black. The lateral blotch, suborbital stripe, and caudal spot are very conspicuous. An intense yellow ground color is seen.	Females during brooding care
Painted-face	Individuals have a silver-gray background color with no spots or stripes, except for the conspicuous suborbital stripe.	Individuals engaged in agonistic behavior
Plain	This pattern is similar to "painted-face" but with a faint or absent suborbital stripe.	Females after fry desertion

The figures and descriptions were adapted from Rodrigues et al. (2009)

Voucher specimens of *A. hippolytae* were preserved and deposited in the Fish Collection of the National Institute of Amazon Research (INPA) under catalog numbers 26,114 (males) and 26,115 (females).

Data analysis

Differences in foraging frequency, in individuals with or without offspring, throughout the day were evaluated using a two-way ANOVA (hypothesis 1). The relationship between feeding frequency and attacks on intruders was analyzed using a Pearson's correlation test (hypothesis 2). Differences in the distances covered by brood-caring females to attack different target fish species were analyzed using a Kruskall–Wallis test followed by a Dunn's multiple comparisons test (hypothesis 3). Statistical tests were performed using the software Statistica 7.0 with a significance level of 0.05.

Results

Adult *A. hippolytae* males were always larger than the females and exhibited the "shining" color pattern at the beginning of the courtship behavior (Table 1). We observed five courtship sequences when the male positioned its body perpendicular to the front of the female, spread all fins, and waved its body (i.e., a lateral display followed by tail beating; cf., Baerends and Baerends-van Roon 1950). The female remained with its fins partially closed and exhibited the "stripe–spot" pattern (Table 1); the females performed tail-beating movements but without moving perpendicularly to the male. These displays were never simultaneous but were performed alternately. After one or two exhibition cycles, the couple always moved to a hidden place that precluded further observation.

Only *A. hippolytae* females were observed taking care of the offspring. Brood-caring females were found either congregated in small groups with other brood-caring females or were isolated (Fig. 1). Brood-caring females showed a unique color pattern with a vivid yellow background and conspicuous jet-black marks in the first rays of the ventral and dorsal fins (Fig. 1a; Table 1). Areas occupied by two or more brood-caring females frequently had a large male (>50 mm SL) swimming nearby. On five occasions, brood-caring females in the same area showed territorial disputes; these confrontations started with agonistic displays and sometimes escalated to direct attacks and biting (i.e., butting; cf., Baerends and Baerends-van Roon 1950). These females changed colors to the "painted-face" pattern (Table 1) but maintained an overall yellow tone that increased in intensity.

No nests with eggs or wrigglers were found during our surveys; however, one female with a light yellow coloration was observed defending a location covered by dead leaves, which suggested that nesting occurred under leaves near the edge of the pond. Females kept the free-swimming juveniles grouped around them (Fig. 1c). Rarely, the female positioned itself above the fry, keeping its pelvic and dorsal fins extended and showing its

Fig. 1 Selection of reproductive behaviors and parental care by *A. hippolytae* females. **a** Conspicuously colored individuals engaged in brood care, **b** a female sheltered under dead leaves at the bottom of the pond (*arrow*), **c** a cryptically colored fry that is stationary near the edge of a dead leaf (*arrows*), and **d** fry in an aquarium. A female is located at the *top left* (the photos were taken from the surface: **a**, **b**, **c** by R.R. Rodrigues; **d** by F. Mendonça)
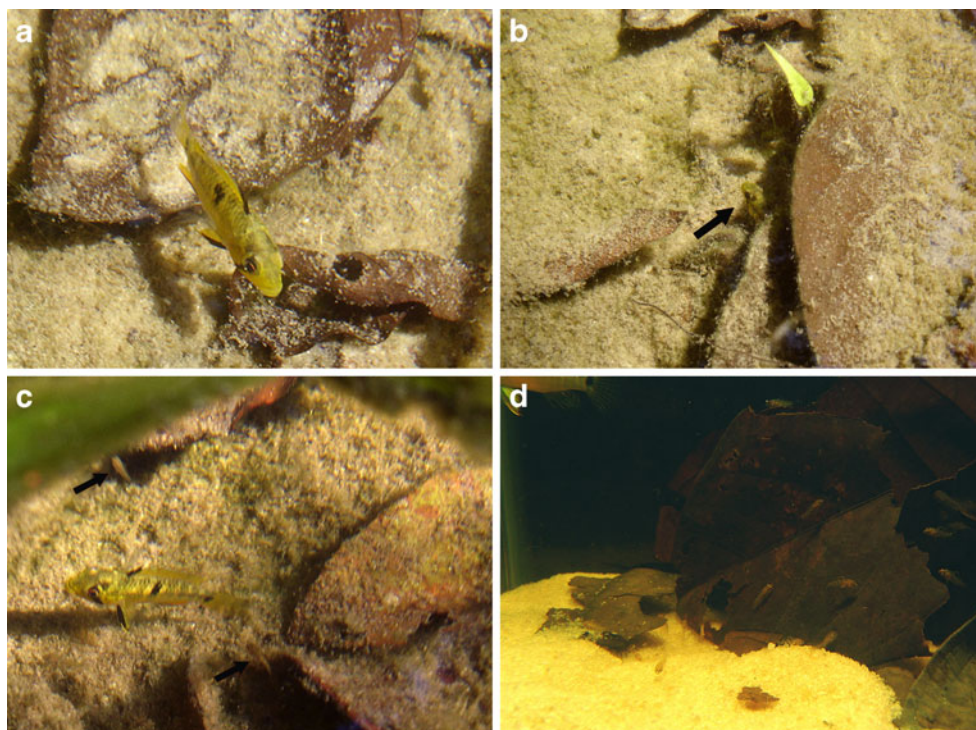
conspicuous black marks (i.e., calling young; cf., Baldaccini 1973; Fig. 1). Pelvic fin flickering by these females was also apparently used to stimulate the grouping of fry around them. One brood-caring female was observed to always occupy the same area for four consecutive weeks. At the beginning of the observations, there were 30–40 younglings (~1 mm SL with brownish coloration) that were commonly seen near or under the edges of submerged leaves. The fry occasionally split into smaller groups but never ventured out alone, swimming up to 3 cm between nearby leaves (Fig. 1d). The leaves were also used as hiding places by the fry and its mother when disturbed and at night (Fig. 1b). At the end of the fourth week, the female resumed the "plain" coloration (Table 1) and started to chase and drive away the juveniles that followed her.

We observed females that chased all 163 fishes that approached their offspring, quickly moving away from their brood toward the intruder with their mouths closed (i.e., chasing; cf., Baldaccini 1973) or wide open (i.e., butting and biting; cf., Baerends and Baerends-van Roon 1950). Most of the attacks were directed toward other *A. hippolytae* individuals (65%), and the distance covered by females to attack intruders varied between species (Kruskall–Wallis test, $P=0.026$; Fig. 2). Approaching *Crenicichla* sp. individuals (pike cichlid) elicited a different behavior: the female moved away from the nest (as far as 60 cm) and toward the intruder, performing a lateral display. When this procedure failed to drive away the pike cichlid, the *A. hippolytae* female bit the flanks of the intruder once or twice and quickly returned to her offspring. This behavior was observed on three occa-
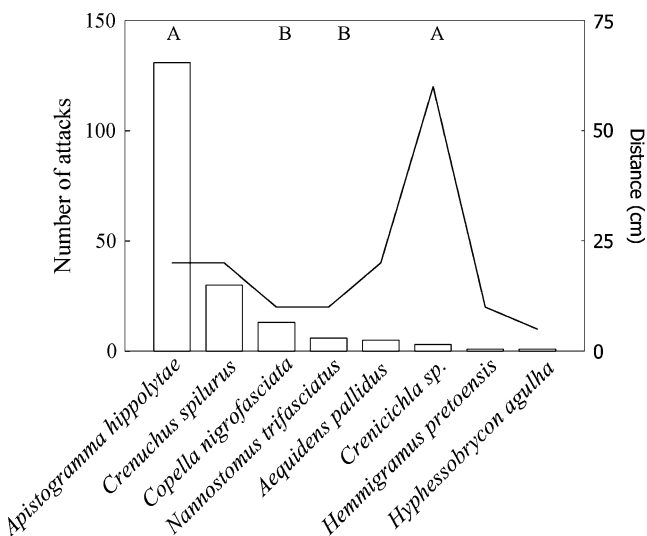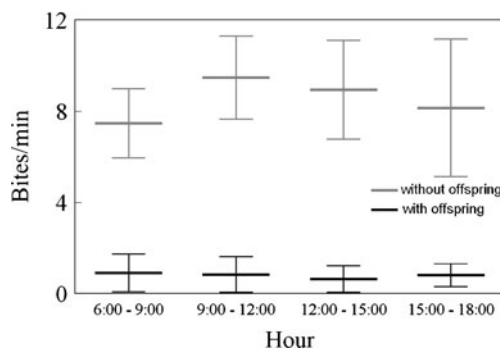

Fig. 3 Foraging frequency (mean±SD) throughout the day of *A. hippolytae* individuals with and without offspring

sions: in one instance, a display alone was enough to drive away the intruder; the combination of a lateral display and a biting attack was needed to drive away medium-sized pike cichlids (~150 mm SL) in the other two cases. Large *A. hippolytae* males (>50 mm SL) were rarely attacked.

Females in parental care presented a lower frequency of foraging compared to other individuals, independent of the time of day (two-way ANOVA, $F_{1,36}=415.30$, $P<0.05$; Fig. 3). A negative relationship was also observed between the foraging frequency and the number of attacks directed against invaders during the observation sessions (Pearson correlation test, $r=-0.66$, $P=0.005$; Fig. 4).

Discussion

Our results support the three hypotheses that were tested: *A. hippolytae* females engaged in parental care forage less than

Fig. 2 Frequency of attacks by *A. hippolytae* targeted toward different species (*bars*) and the mean distance covered by the female to attack the intruding fish (*line*). Values for *Hemigrammus pretoensis* and *Hyphessobrycon agulha* represent single observations. Different *letters* indicate significant differences in the distance covered during the attacks ($P<0.05$)
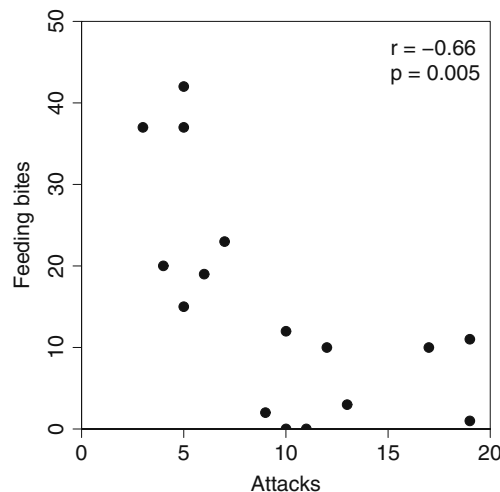

Fig. 4 Correlation between the number of feeding bites and the number of attacks performed by brood-caring *A. hippolytae* females ($n=17$)

individuals that are not involved in this behavior, the decrease in foraging frequency is proportional to the increase in the number of intruders that are chased away by the females, and females can discriminate between fish species that offer a greater risk to their offspring and travel farther distances to drive away such fishes.

Due to the high costs that are typically involved in reproductive activities, animals are faced with important situations during their life history (Bell 1980), including the timing of reproduction during the seasonal cycle and the amount of time and energy invested in each reproductive event. Such situations may influence the success of future spawning, or even the survival probability of the parents, and constitute crucial decisions for an individual. According to Williams' principle (Williams 1966; q.v., Sargent and Gross 1993), an individual invests in parental care at the cost of future reproduction, potentially reducing its individual fitness (Bell 1980). The conflict between current and future reproduction, or other life traits such as growth, characterize the trade-off in reproduction (Trivers 1972). Our results suggest that this type of trade-off occurs in *A. hippolytae* where brood-caring females showed a lower foraging frequency than individuals that were not involved in parental care. The energy spent during brood care is possibly balanced by a specific behavioral mechanism, such as an increase in the feeding rate immediately after fry desertion. The negative relationship between feeding frequency and attacks on intruders also suggests that nests that are more exposed may compromise the nutritional status and reproductive potential of females (e.g., Steinhart et al. 2004; Desjardins et al. 2008). This set of conditions could result in a preference for *A. hippolytae* females to mate with males with better or more sheltered territories, which may produce the observed female aggregations and ultimately the evolution of a harem-style reproductive behavior. Römer and Beisenherz (2005) have suggested that the characteristics of the male territory may be important in mate choice by *Apistogramma cacatuoides* individuals (other examples are presented by Burchard (1965), Keenleyside (1991), and Walter and Trillmich (1994)).

Römer (2001) kept groups of *A. hippolytae* in aquaria for 8 years and observed the formation of stable couples but did not document a single case of polygamy. However, our study corroborates the observations of Schmettkamp (1982 *apud* Römer 2001) that documented polygamy as the usual mating system for *Apistogramma* species and reported the first reproduction of *A. hippolytae* in captivity. In fact, polygamy is the breeding system adopted by most dwarf cichlids (Baerends and Baerends-van Roon 1950; Burchard 1965; Barlow 1974; Römer 2001). The concentration of females in a small area, with only one large male patrolling nearby, suggests the existence of a harem-like reproductive system for *A. hippolytae*, at least under certain conditions.

In addition, the observed high availability of shelters along the pond shore may facilitate the protection and reduce the risk of offspring predation, which can predispose males to desertion and therefore contribute to the prevalence of exclusively maternal care in the population (Barlow 1991). Variations in the mating system of cichlids have been documented for other species (e.g., Townshed and Wootton 1985; Keenleyside et al. 1990; Barlow 1991), although additional studies are needed to determine how particular situations may produce mating system variability among cichlid species.

The analysis of the distance covered by *A. hippolytae* females to attack intruders suggests that females have the ability to perceive potential predators and variable levels of risk to their offspring, as previously observed for African (Ochi and Yanagisawa 1998) and Neotropical cichlids (Barreto et al. 2003). Moreover, the high frequency of intraspecific attacks may be related to the high abundance and aggregated distribution of *A. hippolytae* in the pond (based on our personal observations).

Trade-offs play a crucial role in explaining many ecological and evolutionary patterns among animals. Our results indicate that *A. hippolytae* females may face contradictory demands between parental care and feeding such that the costs of a lower foraging frequency can reduce the energy available for the next spawning. The hypothetical energetic deficit can be even more pronounced if the females must chase frequent predators away from the nest. However, not all brood-caring behaviors are indicative of trade-off situations (Stiver and Alonzo 2009). Therefore, studies that quantify the energetic costs of parental care duties and test the consequences of this cost on future reproduction events can elucidate the evolutionary pressures that have shaped these behaviors among species of the dwarf cichlid genus *Apistogramma*.

support to the Igarapés Project. This is contribution number 573 of the BDFFP and number 18 of the Igarapés Project.

References

Alonzo SH, Warner RR (1999) A trade-off generated by sexual conflict: Mediterranean wrasse males refuse present mates to increase future success. Behav Ecol 10:105–111

Baerends GP, Baerends-van Roon JM (1950) An introduction to the study of the ethology of cichlid fishes. Behav Supplement 1:1–243

Baldaccini NE (1973) An ethological study of reproductive behaviour including the colour patterns of the cichlid fish *Tilapia mariae* (Boulanger). Monitore Zool Ital 7:247–290

Barlow GW (1974) Contrasts in social behavior between Central American cichlid fishes and coral-reef surgeon fishes. Amer Zool 14:9–34

Barlow GW (1991) Mating systems among cichlid fishes. In: Keenleyside MHA (ed) Cichlid fishes: behavior, ecology and evolution. Chapman & Hall, London, pp 173–190

Barreto RE, Luchiari AC, Marcondes AL (2003) Ventilatory frequency indicates visual recognition of an allopatric predator in nave nile tilapia. Behav Proc 60:235–239

Bell G (1980) The costs of reproduction and their concequences. Am Nat 116:45–76

Bührnheim CM, Cox-Fernandes C (2001) Low seasonal variation of fish assemblages in Amazonian forest streams. Ichthyol Explor Fresh 12:65–78

Burchard JE (1965) Family structure in the dwarf cichlid *Apistogramma trifasciatum* Eigenmann and Kennedy. Zeit Tierpsychol 22:150–162

Carvalho LN, Del-Claro K (2004) Effects of predation pressure on the feeding behaviour of the serpa tetra *Hyphessobrycon eques* (Ostariophysi, Characidae). Acta Ethol 7:89–93

Cresswell W (2008) Non-lethal effects of predation in birds. Ibis 150:3–17

Cuthill IC, Houston AI (1997) Managing time and energy. In: Krebs JR, Davies NB (eds) Behavioural ecology: an evolutionary approach, 4th edn. Blackwell Science, London, pp 97–120

Daan S, Tinbergen JM (1997) Adaptions of life histories. In: Krebs JR, Davies NB (eds) Behavioural ecology: an evolutionary approach, 4th edn. Blackwell Science, London, pp 311–333

Desjardins JK, Fitzpatrick JL, Stiver KA, Van Der Kraak GJ, Balshine S (2008) Costs and benefits of polygyny in the cichlid *Neolamprologus pulcher*. Anim Behav 75:1771–1779

Gascon C, Bierregaard RO (2001) The Biological Dynamics of Forest Fragments Project: the study site, experimental design, and research activity. In: Bierregaard RO, Gascon C, Lovejoy TE, Mesquita R (eds) Lessons from Amazonia: the ecology and conservation of a fragmented forest. Yale University Press, New Haven, pp 31–42

Henderson PA, Walker I (1990) Spatial organization and population density of the fish community of the litter banks within a central amazonian blackwater stream. J Fish Biol 37:401–411

Keenleyside MHA (1991) Parental care. In: Keenleyside MHA (ed) Cichlid fishes: behavior, ecology and evolution. Chapman & Hall, London, pp 191–208

Keenleyside MHA, Bailey RC, Young VH (1990) Variation in the mating system and associated parental behaviour of captive and free-living *Cichlasoma nigrofasciatum* (Pisces, Cichlidae). Behav 112:202–221

Kolm N, Ahnesejo I (2005) Do egg size and parental care coevolve in fishes? J Fish Biol 66:1499–1515

Lehner PN (1996) Handbook of ethological methods. Cambridge University Press, Cambridge

Nakazawa T, Yamamura N (2009) Theoretical considerations for the maintenance of interspecific brood care by a Nicaraguan cichlid fish: behavioral plasticity and spatial structure. J Ethol 27:67–73

Nelissen MHJ (1991) Communication. In: Keenleyside MHA (ed) Cichlid fishes: behavior, ecology and evolution. Chapman & Hall, London, pp 225–239

Ochi H, Yanagisawa Y (1998) Commensalism between cichlid fishes through differential tolerance of guarding parents toward intruders. J Fish Biol 52:985–996

Rodrigues RR, Carvalho LN, Zuanon J, Del-Claro K (2009) Color changing and behavioral context in the Amazonian Dwarf Cichlid *Apistogramma hippolytae*. Neotrop Ichthyol 7:641–646

Römer U (2001) Baensch/Mergus Cichlid atlas. Mergus Publisher, Berlin

Römer U, Beisenherz W (2005) Intra- and interspecific mate choice of female *Apistogramma cacatuoides* (teleostei: Cichlidae). Ichthyol Explor Fresh 16:339–345

Sadras VO (2007) Evolutionary aspects of the trade-off between seed size and number in crops. Field Crops Resear 100:125–138

Sánchez RM, Galvis G, Victoriano PF (2003) Relacion entre caracteristicas del tracto digestivo y los habitos alimentarios de peces del rio Yucao, sistema del rio Meta (Colombia). Gay 67:75–86

Sargent RC, Gross MR (1993) William's principle: an explanation of parental care in teleost fishes. In: Pitcher TJ (ed) Behaviour of teleost fishes. Chapman & Hall, London, pp 332–361

Sazima I (1986) Similarities in feeding behaviour between some marine and freshwater fishes in two tropical communities. J Fish Biol 29:53–65

Schmettkamp W (1982) Die Zwergcichliden Südamerikas. Landbuch-Verlag GmbH, Hannover

Silva CPD (1993) Alimentação e distribuição espacial de algumas espécies de peixes do igarapé do Candirú, Amazonas. Brasil Acta Amazon 23:271–285

Steinhart BG, Sandrene ME, Weaver S, Stein RA, Marschall EA (2004) Increased parental care cost for nest-guarding fish in a lake with hyperabundant nest predators. Behav Ecol 16:427–434

Steinhart GB, Dunlop ES, Ridgway MS, Marschall EA (2008) Should I stay or should I go? Optimal parental care decisions of a nest-guarding fish. Evol Ecol Res 10:351–371

Stiver KA, Alonzo SH (2009) Parental and mating effort: is there necessarily a trade-off? Ethol 115:1101–1126

Székely T, Cuthill IC (2000) Trade-off between mating opportunities and parental care: brood desertion by female Kentish plovers. Proc Biol Sci 267:2087–2092

Tallamy DW, Denno RF (1982) Life history trade-offs in *Gargaphia Solani* (Hemiptera: Tingidae): the cost of reproduction. Ecol 63:616–620

Townshed TJ, Wootton RJ (1985) Variation in the mating system of a biparental cichlid fish, *Cichlasoma panamense*. Behav 95:181–197

Trivers RL (1972) Parental investment and sexual selection. In: Campbell B (ed) Sexual selection and the descent of man. Aldine-Atherton, Chicago, pp 136–179

Walter B, Trillmich F (1994) Female aggression and male peace-keeping in a cichlid fish harem: conflict between and within the sexes in *Lamprologus ocellatus*. Behav Ecol Sociobiol 34:105–112

Werner EE, Hall DJ (1988) Ontogenetic habitat shifts in bluegill: the foraging rate-predation risk trade-off. Ecol 69:1352–1366

Williams GC (1966) Natural selection, the costs of reproduction, and a refinement of Lack's Principle. Am Nat 100:687–690