Breeding behaviour and distribution of the tucunaré *Cichla* aff. *monoculus* in a clear water river of the Bolivian Amazon

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The breeding behaviour and distribution of tucunaré *Cichla* aff. *monoculus* were studied for 2 months during the breeding season in the Paraguá River, Bolivia. Tucunaré were more abundant in the old remnant channels and isolated lakes than in the main river channel. The breeding period was delayed for *c.* 1 month in the river compared to the old remnant channels and lakes. The batch fecundity ranged between 3712 and 10 355 for females weighing 460 and 1380 g, respectively. Gonad analysis of egg-guarding or juvenile-guarding females showed that a female was able to spawn more than once during the breeding season. Nests were significantly larger and deeper in the isolated lakes than in the old remnant channels and in the main river. The maximum depth of the nests also differed significantly, being deeper in the isolated lakes than in the river channel and in the old remnant channels. © 2006 The Authors

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INTRODUCTION

The genus *Cichla* belongs to the Cichlidae. Members of this genus are known as 'pavón' in Venezuela and as 'tucunaré' in the rest of South America (Winemiller, 2001). Five species of *Cichla* are currently recognized (Kullander, 2003), but other taxa need description in the Amazonian basin (Kullander, 1986). Kullander & Nijssen (1989) suggested the existence of 11 taxa in the genus *Cichla*. The five formally described species are: *Cichla ocellaris* Schneider, *Cichla temensis* Humboldt, *Cichla orinocensis* Humboldt, *Cichla intermedia* Machado and *Cichla monoculus* Spix. Recent studies, however, revealed the existence of hybrids between *C. monoculus* and *C. temensis* (Brinn *et al.*, 2004; Teixeira & da Silva de Oliveira, 2005). In Bolivia, the local species was first referred to as *C. ocellaris* (Lauzanne & Loubens, 1985), and eventually as

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C. monoculus (Kullander, 1986). Given the uncertainty about its systematic status in the Bolivian Amazon, however, the species will be referred to as *Cichla* aff. *monoculus* in the present study.

Fishes of the genus *Cichla* are among the most widespread predators of tropical South America and are the largest cichlid predators of South America (Winemiller *et al.*, 1997; Winemiller, 2001). Owing to their voracity and tenacity they are very popular as sport fishes, which have motivated their introduction in several tropical and subtropical countries (Winemiller, 2001). They also play an important role in subsistence fisheries and, in some places, in commercial fisheries.

Although the biology of *Cichla* species in their natural environments remained poorly known for a long time, recent studies in the Venezuelan waters have brought much information about the ecology, trophic and spatial segregation, and growth patterns of *C. temensis*, *C. orinocensis* and *C. intermedia* (Jepsen *et al.*, 1997, 1999; Winemiller *et al.*, 1997; Winemiller, 2001). The other two species are still poorly studied apart from some ecological aspects in the rivers of Guyana (Lowe-McConnell, 1969) and Brazil (Goulding, 1980; Goulding *et al.*, 1988) for *C. ocellaris* and in Colombia-Peru and Brazil (Cala *et al.*, 1996; Riofrio *et al.*, 2000) for *C. monoculus*.

Even less is known about their breeding behaviour in natural environments. The information available concerns *C. ocellaris* and comes from pond studies in Brazil (Fontenele, 1950; Braga, 1952) and from introduced populations in Hawaii (W. S. Devick, unpubl. data) or in the man-made Lake Gatún, Panama (Zaret, 1980). This last study provided invaluable knowledge on *C. ocellaris* in 'natural conditions' and stands as the reference for the breeding behaviour of all *Cichla* species.

In the present paper, the breeding behaviour of *C.* aff. *monoculus* (Fig. 1), one of the least studied *Cichla* species (Winemiller, 2001), was investigated in
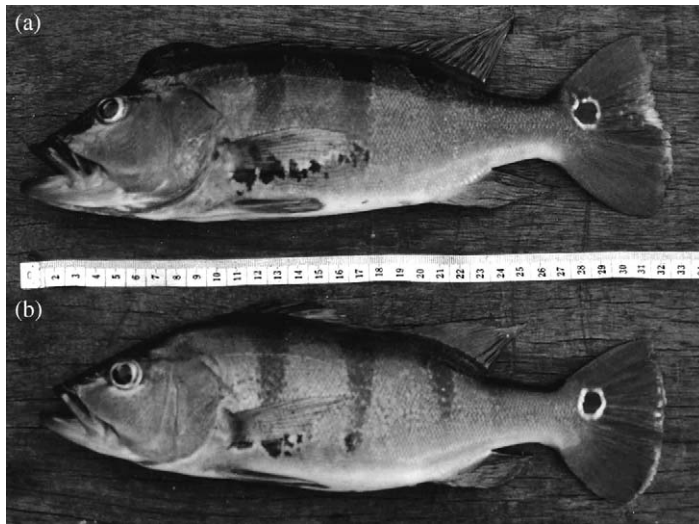

FIG. 1. *Cichla* aff. *monoculus* (a) male and (b) female from the Paraguá River, Bolivia.

its native environment in the Amazon drainage of Bolivia. Emphasis was placed on aspects of breeding behaviour: comparison of nest sites, distribution, size, shape, structure and depth between the main river channel, old remnant channels and isolated lakes in a clear water river of the Bolivian Amazon.

MATERIALS AND METHODS

STUDY AREA

The present study was conducted in the Paraguá River, close to the community of Piso Firme (13°34′57″ S; 67°1′49″ W to 13°39′19″ S; 67°1′26″ W, extremes of the study area), border river between the Noel Kempff National Park and the Indigenous Territory Bajo Paraguá, in the province Velasco (Department of Santa Cruz, Bolivia) (Fig. 2).

The Paraguá River is a clear water river characterized by a mono-modal flood pulse. The river and the old remnant channels are bordered by riparian forest, whereas the aquatic vegetation consists of floating macrophytes (*Paspalum repens* and *Eichornia* sp.) (Sarmiento & Killen, 1998). Fieldwork was carried out between the end of the dry season (October 2001) and the beginning of the rainy season (November 2001), which corresponded to the breeding season of the species in the Paraguá River, based on previous observations (P. Van Damme, unpubl. data).
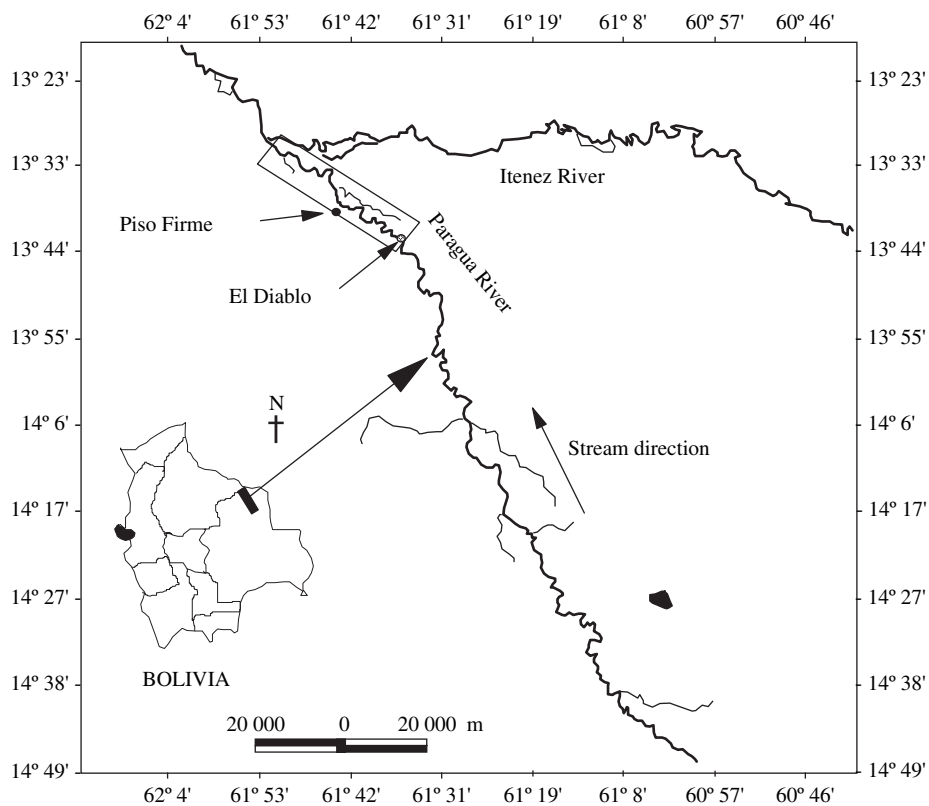

FIG. 2. Study area, delimited by the rectangle, in the Paraguá River, Bolivia.

HABITAT DESCRIPTION

A portion of 68 km of the River Paraguá was studied (Fig. 2). The river depth was measured every kilometre across a transversal transect of five points from one border to the other for the river and at six points for the old remnant channels. Water depth was measured with the help of a wire and weight graduated every 1 cm. In the river, the maximum depth varied between 1 and 6 m, with a mean $\pm$ s.d. of 1.83 ± 0.90 m. In the old remnant channels and lakes, the maximum depth varied between 0.9 and 5 m, with a mean $\pm$ s.d. of 0.87 ± 0.35 m. Transparency was measured with a Secchi disk. Mean $\pm$ s.d. water transparency was 1.2 ± 0.4 m in the river and in the old remnant channels and lakes 1.3 ± 0.3 m. The water level was measured daily during the study period using a limnimetric ruler. The sandy bottom of the river, old remnant channels and lakes was covered with large quantities of organic material, mainly made up of tree leaves. The river had virtually no current velocity, and its general appearance was that of a lake.

FISH SAMPLING AND OBSERVATION

Nocturnal counts of *C.* aff. *monoculus* were performed in the river channel, in old remnant channels temporarily connected with the river channel and in isolated lakes (all lakes visited had a fluvial origin). The counts were carried out with a halogen reflector along three transects of 300 m each in each type of environment. Transects were made along the border of the river or lakes, not transversally. Isolated individuals, nest-guarding or egg-guarding individuals, and juvenile-guarding individuals were visually distinguished. Some individuals were captured using a trident harpoon or hook and line for determination of total length (L_T; cm), mass (M; g), sex, sexual maturity stages and to check for the presence of a nuchal hump. Thirteen nest-guarding or juvenile-guarding females were also captured with harpoon to check their L_T, M and gonadal development. This traditional capturing method was used, as it is efficient and specific in catching only the observed females guarding their eggs or juveniles.

The maturity stage of the female gonads was determined using the maturity scale described in Legendre & Ecoutin (1989). Briefly, stage 1 comprises immature gonads, stage 2, gonads in early recrudescence phase and stage 3, the early vitellogenic stage. Stage 4 is characteristic of females that are shortly to reproduce (end of vitellogenesis), stage 5 of gonads with ovulated oocytes (ovules) and stage 6 of postspawning gonads. Stage 6-2 describes gonads of resting females and stage 6-3 of recovering females. Stage 6-3 is characterized by a few atretic follicles still visible, some remaining empty spaces and a new batch of vitellogenic oocytes developing.

Batch fecundity (number of eggs laid per spawning event) was determined for 37 females in final maturation stage (stage 4).

Nest sites, distribution, size, shape, structure and depth were recorded and compared between the main river channel, old remnant channels and isolated lakes.

Nest morphology was described by a transversal section of the nest measured in seven points. The diameter of the nest was taken from one border of the cleaned area to the other (always at the maximum width of the cleaned area).

STATISTICAL ANALYSIS

Comparisons of fish size and abundance and nest characteristics were carried out using *t*-test or one-way ANOVA and Tukey's *post hoc* test when the normality of distributions and homoscedasticity were respected. When these conditions of application were not met, a Mann–Whitney *U*-test or Kruskal–Wallis test on ranks and Dunn's *post hoc* test were used.

Given the narrow size range of fish caught, the comparison of L_T and M relationships was carried out on the ln-transformed data using an ANCOVA applied to regression lines.

RESULTS

SIZE DISTRIBUTION AND ABUNDANCE

The density of tucunaré was 10.4 ± 11.3 individuals km^{-1} (mean $\pm$ S.D.) in the river channel, 25.3 ± 17.1 individuals km^{-1} in the old remnant channels and 28.3 ± 18.8 individuals km^{-1} in the isolated lakes (Fig. 3). Fish density was significantly different between the old remnant channels and the river channel (Kruskal–Wallis test, d.f. $= 2$, $P < 0.01$). Both old remnant channels (Dunn's *post hoc* test, $n = 31$, $P < 0.05$) and isolated lakes ($n = 19$, $P < 0.05$) had significantly higher densities of tucunarés than the river channel.

Of the 182 individuals caught for sex and maturity determination, 55% ($n = 101$) were males and 45% ($n = 81$) females (Table I). Eighty per cent of the captured specimens had empty stomachs. There was no difference in the mean L_T of females (Mann–Whitney U-test, $n = 59$, $P > 0.05$) or males ($n = 68$, $P > 0.05$) between the old remnant channels, the lakes and the river channel. Pooling the individuals caught in the different environments (isolated lakes, old remnant
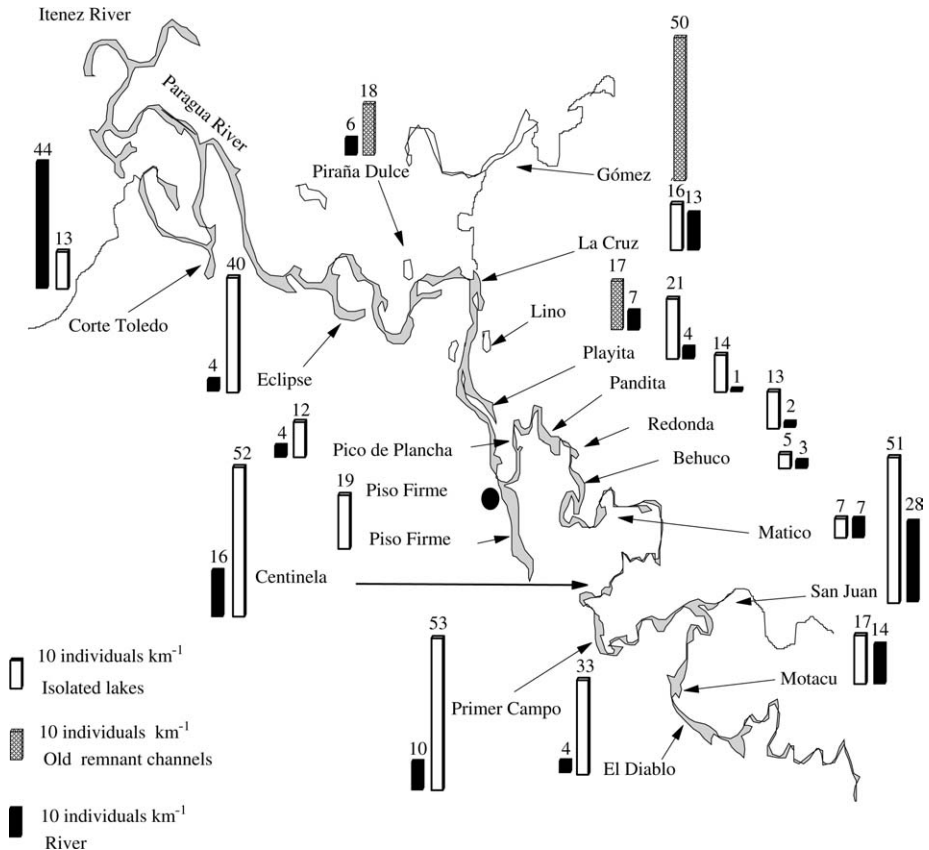

FIG. 3. Density of *Cichla* aff. *monoculus* (individuals km^{-1}) in the river channel of the Paraguá River, in the old remnant channels and isolated lakes. Numbers above the bars indicate the number of individuals observed. The portion of river corresponds to the rectangle in Fig. 1.

TABLE I. Total length and mass of male and female *Cichla* aff. *monoculus* in the Paraguá River

	n	Mean $\pm$ S.D. L_T (minimum–maximum) (cm)	n	Mean $\pm$ S.D. mass (minimum–maximum) (g)
Females	81	35.0 ± 4.8 (15·0–46·0)	77	667.0 ± 228.0 (40·0–1380·0)
Males	101	39.0 ± 5.9 (19·0–55·0)	101	998.0 ± 429.4 (70·0–2650·0)

channels and river channel), however, males reached larger sizes than females. A comparison of the ln-transformed L_T and M relationships of females ($M = 0.017 \, L_T^{2.965}$; $r^2 = 0.951$, $n = 77$) and males ($M = 0.003 \, L_T^{3.449}$; $r^2 = 0.963$, $n = 101$) showed a significant slope difference (ANCOVA, d.f. $= 3, 174$, $P < 0.001$).

REPRODUCTION

The study period coincided with the breeding season of *C.* aff. *monoculus*. All the females captured were mature and sexually active (maturity stages 3, 4 and 6-3) (Fig. 4), with the exception of one immature individual with a L_T of 15 cm (stage 2). All, but two, of the males captured were sexually mature. Every mature male caught was characterized by a nuchal hump on the forehead, whereas females lacked this morphological trait. A single female was observed
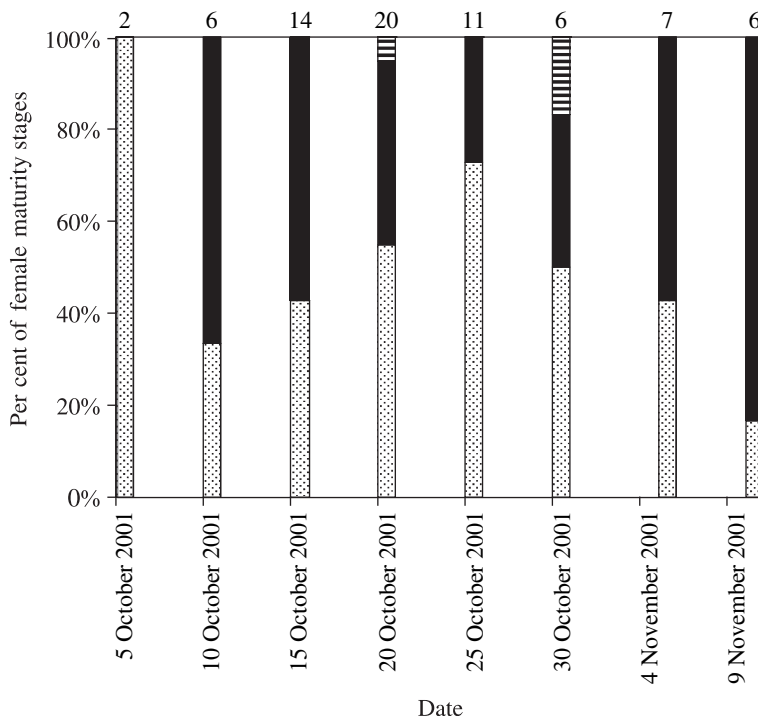

FIG. 4. Sexual maturity [(stages 3 (▨), 4 (■) and 6-3 (▤)] of female *Cichla* aff. *monoculus* caught in the Paraguá River in October and November 2001. Above the bars is the number of females observed at each month.

with a slightly developed hump. Both sexes presented an intense orange colour in the lower part of the head close to the operculum.

The nesting period was similar in the isolated lakes and old remnant channels and nest-guarding individuals were recorded from the beginning of October [Fig. 5(a)]. Their number increased at the end of October and through November, together with an increase of egg-guarding and juvenile-guarding individuals. The nesting period appeared slightly postponed in the river channel compared to the isolated lakes and old remnant channels. In the river, nesting or guarding individuals appeared only in the last days of October [Fig. 5(b)].

All 13 females caught in their nest, guarding either eggs or fingerlings, presented signs of being sexually active anew, suggesting that a female might reproduce more than once during the breeding season. The five females guarding eggs were found in stage 6-3, which corresponds to a postspawning female with a new batch of vitellogenic oocytes developing. The eight females guarding fingerlings were observed in stage 4, hence in final gonadal maturation. All of these stage 4 gonads and those observed on fry-guarding females had oocytes in two to four distinct development stages (including vitellogenic stages).

There was a significantly positive correlation between batch fecundity (F) and female M ($F = 4 \cdot 179\ M^{2826 \cdot 7}$, $r^2 = 0 \cdot 514$, $n = 37$). The smallest number of oocytes produced by *C.* aff. *monoculus* during the study period was 3712 for a female of 460 g and the maximum number was 10 355 for a female of 1380 g.

BREEDING BEHAVIOUR

During the 2 months of field observation, the courtship behaviour could not be observed precisely. Once the pairs were formed, however, both the male and the female participated in digging the nest and cleaning the ground of the abundant organic matter. They dug a circular nest of <2 m in diameter, with a central depression of 20–100 cm. In total, 291 nests were observed. Of these, 279 were dug around a slender (between 3 and 30 cm diameter) branch or wood stick, sometimes buried at one extremity. The branch rarely exceeded the nest diameter. Although isolated nests were observed in each environment (river, old remnant channels or isolated lakes), the nests were often dug close to each other, forming aggregations of maximum 18 nests (in a 50 m^2 area), with inter-nests distances of 1 m minimum. This pattern was less frequent in the river than in the other two environments. In the river channel as in the old remnant channels and isolated lakes, nests were dug in the shallow zones, between 1 and 10 m of the water edge. Of the 90 nests measured in the three environments, not a single one was found below 1 m depth (Fig. 6).

The nests presented different characteristics in the river channel and in the old remnant channels and isolated lakes (Fig. 6). The mean diameters of the nests differed significantly between the three environments (one-way ANOVA, d.f. = 2, 27, $P < 0 \cdot 001$). They were smaller in the river channel than in the isolated lakes (Tukey's *post hoc* test, $P < 0 \cdot 01$) and old remnant channels ($P < 0 \cdot 01$) and larger in the isolated lakes than in the old remnant channels ($P < 0 \cdot 01$).

The minimum depth at which the nests were dug did not differ between the three types of environments (one-way ANOVA, d.f. = 2, 32, $P > 0 \cdot 05$). But the maximum depth of the nests differed significantly (d.f. = 2, 32, $P < 0 \cdot 001$),
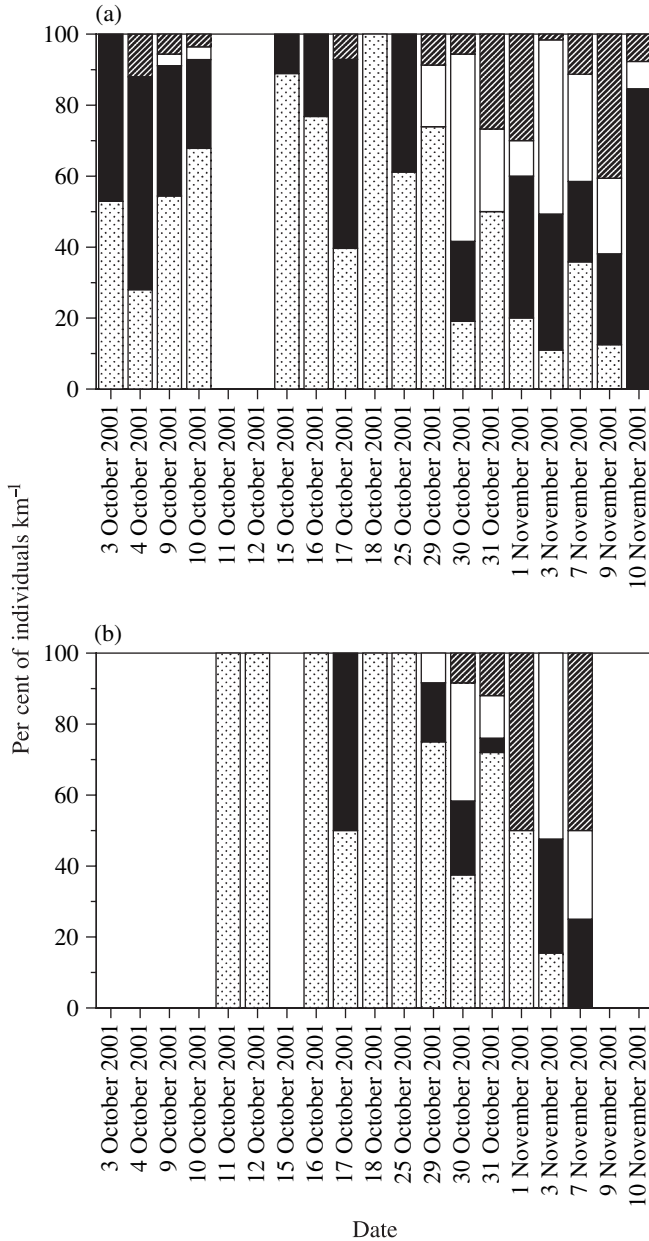
FIG. 5. Percentage of *Cichla* aff. *monoculus* in different breeding stages [alone (▦), in nest (■), with eggs (☐) and with fingerlings (▨)] in (a) the old remnant channels and isolated lakes and (b) in the river channel of the Paraguá River, Bolivia.

being deeper in the isolated lakes than in the river channel (Tukey's *post hoc* test, $P < 0.01$) and in the old remnant channels ($P < 0.01$). The maximum depth of the nest, however, did not differ significantly between the old remnant channels and the river channel ($P > 0.05$).
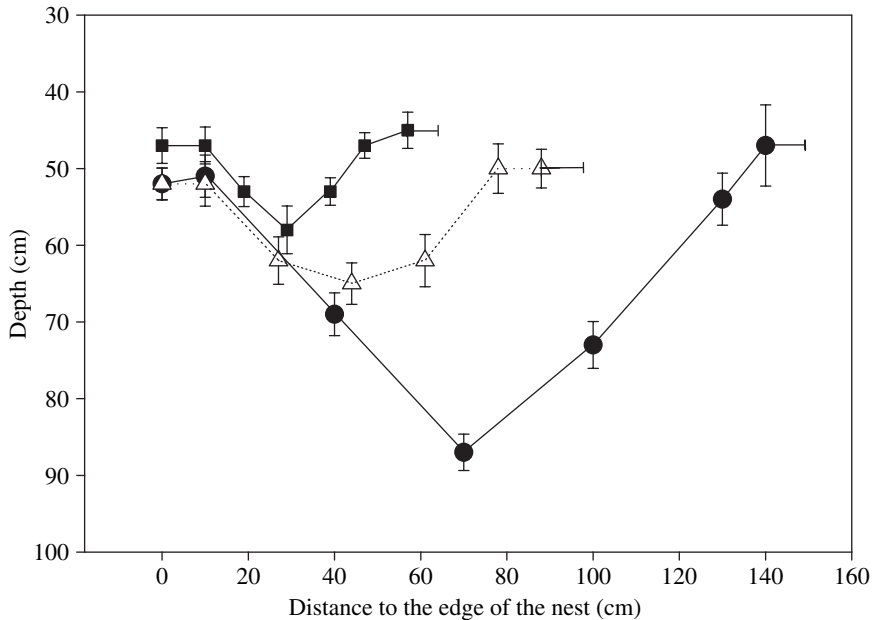
FIG. 6. Nest morphology (transversal section, means ± S.E.) of *Cichala* aff. *monoculs* in the river channel ($n = 23$; ■), old remnant channels ($n = 47$; △) and isolated lakes ($n = 20$; ●) of the Paraguá River, Bolivia. The horizontal error bars are the S.E. of the mean nest diameters.

Once the nest was completed, the female spawned her eggs on the upper part of the branch, covering it completely when the branch was small. After fertilization by the male, both parents took care of the eggs, chasing away any fishes getting close to the nest. During daytime, however, when approached within *c.* 2 m, the parents started to leave the nest. The female was always ($n = 50$) the last to leave the nest (when the observer was at a distance of *c.* 1 m) and the first to come back afterwards. As soon as the female left the nest, small characids started to feed upon the eggs, but immediately left when the female came back. On the other hand, during the nocturnal observations with the light reflector, the parents usually did not leave the nest, at least not both of them.

After hatching, the fingerlings usually stayed in the deeper part of the nest, below the branch, under the close protection of both parents. Out of the 291 nests observed, 40 contained fry. Of these 40 nests with fry, 12 did not have the typical branch. They were usually of the same size than normal nests but located in more protected zones: closer to the water edge, often in between submerged macrophytes (*Elodea* sp.) or branches.

DISCUSSION

SIZE DISTRIBUTION AND ABUNDANCE

The sexual dimorphism between males and females in species of *Cichla* is well documented (Lowe-McConnell, 1969; Zaret, 1980; Jepsen *et al.*, 1997,

1999) and was confirmed for *C.* aff. *monuculus* in the Bolivian Amazon. Males grow larger than females. The introduced population of *C. monoculus* in Campo Grande Reservoir in north-east Brazil also displayed this characteristic (Chellappa *et al.*, 2003). In contrast, in the lagoons and lake populations of *C. monoculus* studied by Cala *et al.* (1996), males and females had comparable L_T and M relationships. Riofrio *et al.* (2000) reached the same conclusion for *C. monoculus* in the Ucayali River, Peru. In contrast, here in the Paraguá River, there was a significantly different L_T and M relationship between males and females. The M increment was faster than the L_T increment in males, whereas females had a more isometric growth. This might be a reflection of the sampling period, centred on the breeding period, where female energy expenditure is probably higher than that of males.

As in most cichlid species (Lowe-McConnell, 1987), species of *Cichla* tend to prefer lentic habitats (Winemiller, 2001), apart from *C. intermedia*, which essentially occupy the running part of the river channel (Jepsen *et al.*, 1997; Winemiller *et al.*, 1997). The populations of *C. monoculus* studied by Cala *et al.* (1996) were also from lakes or lagoons, their preferred habitat according to the authors. In the Paraguá River, the water velocity was close to zero during the study and the general conditions resembled more that of a lake, but *C.* aff. *monoculus* nevertheless was more abundant in the still waters. Indeed, Novoa (1993) emphasized the littoral habits of *Cichla* species, which frequently use the shallow zones, at least for spawning (Winemiller *et al.*, 1997).

REPRODUCTION

The presence of a nuchal hump on the forehead is a well-known secondary sexual characteristic in *Cichla* sp. males (Lowe-McConnell, 1969; Zaret, 1980; Jepsen *et al.*, 1999; Winemiller, 2001), and in *C. monoculus* as well, both in natural (Cala *et al.* 1996) and introduced populations (Chellappa *et al.*, 2003). Males in the Paraguá River also displayed the nuchal hump. In one case, however, a female having a nuchal hump was observed, although less developed than that of males. The same was observed on a few females, usually large ones, in the San Martin River, another affluent of the Itenez (F. Duponchelle, F. Carvajal, J.-F. Renno & J. Nuñez, unpubl. data). The presence of this secondary sexual characteristic in some females, albeit infrequent, can lead to inaccurate sex determination and it is recommended to cross-check the genital papilla for confirmation.

During the study period, which coincided with the breeding season, both sexes had an intense orange colour in the lower part of the head close to the operculum, as already reported for other species of *Cichla* (Lowe-McConnell, 1969; Zaret, 1980; Jepsen *et al.*, 1999; Winemiller, 2001). It has also been reported that species of *Cichla* usually do not feed during the breeding period (Jepsen *et al.*, 1997, 1999) and the guarding phase (Zaret, 1980). The observations in the Paraguá River tended to partially confirm these reports, as 80% of the tucunaré caught during the study period had empty stomachs.

Although this study coincided with the breeding season of *C.* aff. *monoculus*, a delay in reproduction of *c.* 1 month was observed between the river and the old remnant channels and lakes. Nest-guarding activities had already started at

the beginning of October in the old remnant channels and lakes, whereas nest-guarding only begun at the end of October in the river. This might be due to the shallower borders, more adapted nesting conditions of the old remnant channels and lakes. In the river, the water level started to increase after mid-October, which might have made available more favourable breeding zones.

The batch fecundity of *Cichla* sp. is positively correlated to the female body M and L_T (W. S. Devick, unpubl. data; this study), as in many fishes and most cichlid species (Lowe-McConnell, 1987; Winemiller & Rose, 1992; Duponchelle *et al.*, 2000). The present results provide the first batch fecundity and M relationship of a species of *Cichla* in its native fluvial environment. Nevertheless, the mean values observed by Cala *et al.* (1996) and Chellappa *et al.* (2003) for *C. monoculus* were within the range of the present observed values. The fecundity of *Cichla* species holds another subject of debate: whether the same female spawns more than once during the breeding season. Although many authors have observed several size of developing oocytes in ripe gonads of introduced (Zaret, 1980; Chellappa *et al.*, 2003) or natural (Cala *et al.*, 1996; Riofrio *et al.*, 2000) populations, Jepsen *et al.* (1999) stated 'it is not clear if individual fish are capable of multiple spawns under natural conditions'. It was also reported that female *C. ocellaris* spawned only once a year in Hawaiian reservoirs (W. S. Devick, unpubl. data). The present observations of eggs or fry-guarding females with developing or ripe gonads, of stage 6-3 females (recently spent females in another vitellonenic cycle) and of several batches of developing eggs in ripe gonads, clearly showed that the same *C.* aff. *monoculus* female will be able to and do spawn several times during the same breeding season under natural conditions.

BREEDING BEHAVIOUR

The breeding behaviour of *C. ocellaris* was described by Braga (1952) in cultured conditions, then by W. S. Devick (unpubl. data) and more recently and extensively by Zaret (1980), on introduced populations. This study aimed at confirming the general breeding patterns for *C.* aff. *monoculus*, and at providing some complementary information on the breeding behaviour of *Cichla* sp. particularly nest sites, shape, depths and structure in a natural environment. As observed for *C. ocellaris*, both male and female *C.* aff. *monoculus* participate in nest-digging and cleaning the ground of organic matter. Two types of nests were described for *C. ocellaris*: small depressions on soft clay of *c.* 15 cm depth and up to 20–25 cm in diameter at a depth of 1·5 m, or deeper nest (4–6 m) made of a natural depression around a branch (Zaret, 1980). Branch-type nests at depth below 1 m were found to be the most common for *C. ocellaris* in Hawaii (W. S. Devick, unpubl. data). Out of the 291 nests of *C.* aff. *monoculus* observed in the Paraguá River, nearly all of them were located beneath a branch. The only nests without a branch contained fry, and were dug in shallower, more protected areas. All the nests observed for *C.* aff. *monoculus* in the Paraguá River were dug at depths shallower than 1 m. It would be interesting to investigate whether this pattern still stands during the high water period, but the extent of the flooded area (up to 150 000 km^2; Denevan, 1966) would make observation of large number of individuals nearly impossible. Similar nests dug

in shallow water (30 cm) were reported for *C. orinocensis* in Venezuela, but these were dug on rocky substrata (Winemiller, 2001).

Cichla orinocensis was observed nesting in isolated pairs in several rivers and reservoirs, but also forming aggregations in some lagoons of Venezuela (Winemiller, 2001). Winemiller (2001) also reported that '*C. temensis* formed nesting aggregations as a function of limited suitable nesting habitat rather than social instinct'. Similar nesting aggregations were also observed for *C.* aff. *monoculus* in the Paraguá River. It is likely, however, that nest aggregation is a protective measure against eggs and fingerlings predation given the wide suitable nesting sites available in the Paraguá River. Aggregations in shallow littoral zones are likely to diminish the potential angles from which predatory fishes can attack the nests.

This study lasted only 2 months and it is known that the breeding season of this species lasts *c.* 5–6 months in the Itenez basin (F. Duponchelle, F. Carvajal, J.-F. Renno & J. Nuñez, unpubl. data). It coincided, however, with the peak breeding period (F. Duponchelle, F. Carvajal, J.-F. Renno & J. Nuñez, unpubl. data) as attested by the maturation stages of all the specimens analysed. Also of interest were the important size and depth differences observed between the nests dug in the river, in the connected and the isolated lakes. Although actual differences were not measured, the ground (below the organic matter) in the lakes and in a lesser extent in the old remnant channels, was covered by a thicker layer of fine sediments than in the main river channel. The observed differences might be due to the necessity of digging deeper and over a larger area (to avoid the border of the depression to collapse) in the lakes and the old remnant channels. Although the reasons for these differences remain to confirm, they indicate that breeding patterns in tucunaré may be more complex than supposed so far and open the way for further ecological studies of these fascinating and economically important neotropical cichlids.

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