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Reproductive biology of *Eretmodus cyanostictus*, a cichlid fish from Lake Tanganyika

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Synopsis

One of the most widely accepted explanations for monogamy is the need for biparental care. However, the occurrence of monogamy combined with biparental care is extremely rare in oral incubating (mouthbrooding) cichlid fishes. Few studies have been performed on cichlid species that exhibit this behaviour, and therefore the ecological factors that favour monogamy in these cases remain obscure. Here we present new information on the natural history and reproductive biology of *Eretmodus cyanostictus* (Boulenger 1898), a monogamous biparental mouthbrooder from Lake Tanganyika. The populations studied consisted of territorial pairs and a male-biased non-territorial population of smaller ‘floater’ individuals. We present the first detailed description of spawning in this species, show that breeding does not appear to be synchronised within the population, and provide evidence that parental care is costly. We discuss the implications of this information for our understanding of monogamy.

Introduction

The spiny-rayed freshwater fishes of the family Cichlidae are indigenous to tropical rivers and lakes across South America, Africa, Madagascar and the Indian subcontinent (Lowe-McConnell 1975, Stiassny 1991). All cichlids show parental care, but there is variation in the form of care exhibited and the sex of the caretaker (Baerends & Baerends-van Roon 1950, Breder & Rosen 1966, Fryer & Iles 1972, Keenleyside 1991a). Two distinct forms of care are found among cichlids: substrate guarding in which fertilized eggs and young are cared for at a nest site (e.g. directly on the substrate, in a crevice, or in an empty mollusc shell) and mouthbrooding in which the young are protected within the buccal cavity of the parent for all or part of the care period. Mouthbrooding is derived from substrate brooding (Goodwin et al. 1998), and various intermediate forms, which combine guarding and mouthbrooding, are known (Myers 1939, Lowe-McConnell 1959, 1969, Oppenheimer 1970, Fryer & Iles 1972).

Biparental care is the ancestral state in cichlids (Goodwin et al. 1998) and is commonly thought to be maintained because two parents are required to successfully raise the brood (Barlow 1974, Perrone & Zaret 1979, Keenleyside 1991b). However, if ecological conditions change, e.g. if predation pressure is reduced or remating opportunities increase, monogamy can become destabilized and one partner, usually the male, may desert their mate and the young (Barlow 1974, Keenleyside 1983, Keenleyside 1985, Townshend & Wootton 1985, Wisenden 1994). A number of biparental species have been reported to be facultatively polygamous (Kuwamura 1986, Keenleyside et al. 1990, Gashagaza 1991, Wisenden 1994), presumably made possible by the division of labour between the parents. In general, females tend to provide direct brood care, guarding and tending the fertilized eggs and newly hatched young, while males defend the periphery of the territory (Barlow 1974, Smith-Grayton & Keenleyside 1978, Dupuis & Keenleyside 1982, Mrowka 1982, Itzkowitz 1984, Itzkowitz 1985, Townshend &Wootton 1985, Rogers 1988, Lavery & Keenleyside 1990, Barlow 1991, Lavery & Reebs 1994, Annett et al. 1999). The different parental roles mean that the female is tied more closely to the young while the male has a greater opportunity to assess alternative mating options (reviewed by Keenleyside 1991b). Thus it has been argued that the need for biparental care can select for monogamy.

Utilising the mouth in brood care dramatically reduces predation pressures on the young (Oppenheimer 1970, Baylis 1981), allowing one parent to become emancipated from care (Gross & Sargent 1985). This explains the dramatic predomination of uniparental care in mouthbrooders (80% of these genera show female-only care). As argued above, males have a greater opportunity to desert, and also usually have more to gain by deserting because, in most species, their potential reproductive rate is higher; that is males can replenish their gametes more quickly than females and have shorter interspawn intervals (Sevenster-Bol 1962, Polder 1971, Fryer & Iles 1972, Wooton 1974, Baylis 1981, Clutton-Brock & Vincent 1991, Balshine-Earn 1996). Thus, the reduced predation pressure on the young of mouthbrooders sets the stage for male desertion; hence mouthbrooding species tend to show exclusively female care. In contrast, substrate brooding in cichlids is generally associated with biparental care and monogamy (Fryer & Iles 1972, Keenleyside 1991a, Goodwin et al. 1998). The occurrence of biparental mouthbrooding is rare and not easily explained.

Biparental mouthbrooding is thought to be an intermediate state between biparental substrate guarding and uniparental mouthbrooding (Keenleyside 1991a, Balshine-Earn & Earn 1998), and is usually associated with defence of young after mouthbrooding, or clutches that are too large for a single parent to incubate (see Kuwamura 1986). However, there are a small number of species that have clutches that are small enough to fit into the mouth of a single parent, and where the parents do not guard the fry after oral incubation has ceased. Thus, neither defence of free-swimming fry nor clutches too large for uniparental care can explain the continued presence of biparental care in these species. Consequently, these species provide perfect opportunities to investigate alternative factors involved in the maintenance of biparental care and monogamy.

Eretmodus cyanostictus is one such species. It is one of the 15 mouthbrooding species from Lake Tanganyika (East Africa) that perform a female-to-male shift in brood care, i.e. sequential biparental care. The female initially incubates all the fertilized eggs and newly-hatched young and the male takes over the parental role as the young grow (Kuwamura 1986, Yanagisawa 1986, Konings 1988, Kuwamura et al. 1989, Kuwamura 1997). *E. cyanostictus* does not show post-release guarding of young and so parental care ends when the male finishes mouthbrooding. *E. cyanostictus* is socially monogamous (long term observations in the field during two field seasons), and a recent study confirms that they are also genetically monogamous (unpublished observations). Pairs defend territories that provide them with shelter and food, in the form of algae that the fish scrape from rocks using their teeth (Yamaoka et al. 1986, Yamaoka 1997). Pairs appear to remain on their territories all year, but to date there is no firm data on how long pairs inhabit their territories or how territories are established. In our study site, pairs remained together on their territories without producing young, and territorial individuals only left their territories when chasing away conspecifics or being chased by heterospecifics (pers. obs.).

In this study, we investigated the potential costs of parental care in terms of loss of feeding and mating opportunities. First, we compared the gut contents of mouthbrooding individuals with non-mouthbrooding individuals to test the prediction that mouthbrooding fish have fewer opportunities to feed. Second, we monitored sex ratio, ovarian development and breeding synchrony, to test whether lack of alternative females was a potential constraint on male desertion. We used a combination of population census methods and targeted studies on individuals to gather new natural history and reproductive information on *E. cyanostictus*, and to understand the unusual combination of biparental care mouthbrooding and monogamy found in this species.

Methods

We conducted a total of 105 days of fieldwork over 2 consecutive years at two separate sites on the southern coast of Lake Tanganyika, in Zambian waters (Figure 1). In 1998, we conducted work from 4 February to 14 April at a site north-west of Mpulungu

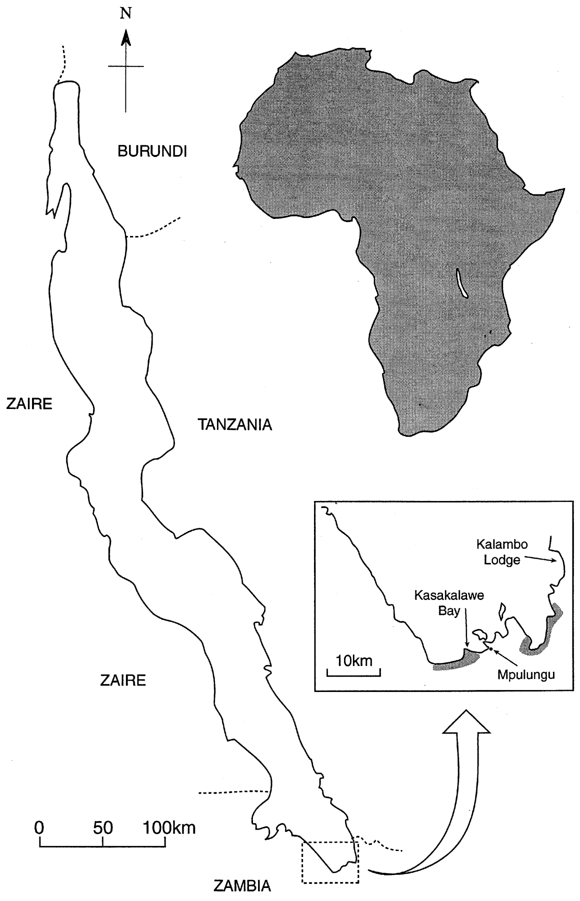

Figure 1. Map showing Lake Tanganyika, Africa, and the location of the field sites used in this study.

in Kasakalawe Bay (KB), 100 m east of Kasakalawe Village. In 1999, we conducted additional fieldwork from 12 February to 20 March at Kalambo Lodge (KL), north-east of Mpulungu, near the Tanzanian border (for a detailed description of these sites see Morley 2000).

Observations were made using snorkel or SCUBA at depths of 1–3 m, where *E. cyanostictus* was abundant, wave action was less intense than in shallower surge-zone regions (<1 m) and there was plenty of light.

Fish capture

Population census

We conducted a population census of *E. cyanostictus* in February 1998 at KB. The area from which the samples were taken was separated from other experimental sites by at least 100 m.

Every 2–3 days, between 08:30 and 11:00, we caught a sample of *E. cyanostictus* by using snorkel equipment and a monofilament fence-net (6 m long, 1 m high, mesh size 6 mm) that had weights along the bottom edge and floats along the top, so that it stood upright in the water. On each sampling day, we set the fence-net parallel to and approximately 5 m from the shoreline, in water approximately 1 m deep (the height of the net). To minimize the chance of collecting the same individual twice, each new sampling area began 5 m further down the shore from the point where the net had ended on the previous sampling occasion. Over a 2 h period, two researchers identified all the fish within 1.5 m of each side of the fence-net (i.e. in a 6 m (net length) by 3 m area), captured them using hand-held nets, and quickly transferred them to collection bags. Individuals smaller then 45 mm were immediately released because accurate sexing was not possible below this size. In this manner, a total of 342 adult fish, including 16 mouthbrooders, were caught over a 4-week period.

Study of territorial individuals

In a completely separate area of the study site (3 m depth, 25 × 10 m area), 18 breeding pairs were specifically targeted by taking advantage of the territorial nature of *E. cyanostictus*. Mouthbrooding individuals were systematically searched for, and when a mouthbrooding *E. cyanostictus* was discovered it was observed for a minimum of 10 min to estimate its territory boundaries and identify its mate. All mouthbrooding individuals located in this way stayed within a defined territory and had an identifiable mate.

Once we had identified a breeding pair we captured both individuals, non-brooder first, using a tent-net (a conical net consisting of a round piece of fine mesh with weights at the perimeter and floats tied in the centre). Of the 18 breeding pairs caught, the mouthbrooding individual was the male in all but one pair. This method was also used to capture 45 non-breeding territorial pairs: 20 at KB and 25 at KL. We brought all the fish that we caught to the surface for measurement and determination of sex (by examination of the genital papilla; males have small, conical genitalia, females have a rounder opening with a distinctive slit). Standard length measurements were taken with a ruler to the nearest 1 mm, and mass was recorded to the nearest 0.01 g on a battery-operated balance.

We coaxed mouthbrooding individuals (16 from the population census and 18 from the capture of breeding pairs) into releasing their young by gently dipping the fish's head into a container of water. We counted the young and measured the maximum length of 10 offspring. We noted the developmental stage of the young and gave a score from 0 to 4 as follows: (0) developing young prior to hatching; (1) newly-hatched young (head and tail just visible); (2) yolk sac between 1 and 2 times body width; (3) yolk sac less than one body width; (4) no/small yolk sac still visible.

We returned most individuals captured during the population census to the collection site, but an average of eight females from each sample (total $N = 115$) were permanently removed for examination of gonad development. To examine how mouthbrooding affects feeding and interspawn intervals, we sacrificed an additional 15 pairs of breeding territorial animals to allow analysis of gut contents and ovarian development. We killed the fish with an overdose of MS-222 anaesthetic (tricaine methanesulphonate) and then dissected them. We removed the guts of individuals of both sexes and measured the total length of the gut using a ruler, to the nearest milimetre. We estimated the length of the gut that contained food. We weighed ovaries, noted oocyte colour and approximate size, and assigned a numerical classification to the developmental stage of the oocytes. This classification followed Neat & Balshine-Earn (1999) so that the results were directly comparable: (0) small white oocytes, total ovary mass <0.01 g; (1) mixture of small white, yellow and orange oocytes, total ovary mass 0.01–0.05 g; (2) mainly medium sized orange oocytes, total ovary mass 0.06–0.1 g; (3) oocytes large and orange, total ovary mass >0.1 g.

In two cases parents spat out or swallowed their young, and one other fish escaped before it could be brought to shore and dissected. Thus, we could not include these three individuals in the analyses and the final sample sizes are given with the statistics.

Statistical methods

We used parametric statistics wherever possible. We tested data for normality using a Kolmogorov-Smirnov test and employed a square-root transformation in some cases to improve normality of the data. We confirmed homogeneity of variance with an F_{MAX}-test (Sokal & Rohlf 1995, p 397). We performed parametric tests using StatView 5, calculated all other test statistics by hand and found significance using tables from Siegel & Castellan (1988). When we performed multiple tests on a single data set, we used sequential Bonferroni tests to determine the significance of each contrast, such that the overall probability of type I error was $\alpha = 0.05$ (Sokal & Rohlf 1995, p 240). All p-values presented are two-tailed unless otherwise stated.

Results

Territoriality

Both the KB and the KL populations consisted of territorial pairs and solitary, non-territorial individuals. Territorial status was apparent after only a few minutes of observation. Non-territorial individuals were solitary, moved over large distances and were chased regularly. These solitary fish were never observed to defend a territory. In contrast, territorial individuals were confined to a defined area and defended this area against conspecifics.

Mouthbrooding fish were always territorial. The mouthbrooding fish from the population census were similar in size to known territorial fish at both other sites: KB and KL. However, non-mouthbrooding individuals from the population census were smaller than both the mouthbrooding individuals from the census samples and the known territorial fish (Figure 2, Kruskal-Wallis: males, $H = 123.43$, $n_{\text{census\_non-brooding}} = 210$, $n_{\text{census\_brooding}} = 13$, $n_{KB} = 39$, $n_{KL} = 25$, $p < 0.0001$; females, $H = 62.87$, $n_{\text{census\_non-brooding}} = 116$, $n_{KB} = 39$, $n_{KL} = 25$, $p < 0.0001$, for both sexes comparisons are significant between non-mouthbrooding individuals from the population census and all the other groups). Note: statistical comparison was not possible for the mouthbrooding females from the population census because the sample size was too small.

Male-biased sex ratio

The population of *E. cyanostictus* at KB was male-biased. Of the total sample of 342 fish captured, 223 (65.2%) were male. Twelve of the 15 samples were male biased and the other three had equal numbers of males and females. The male-biased samples contained significantly more males than females (Wilcoxon signed rank test: $T^+ = 78$, $N = 12$, $p = 0.0002$). There was no correlation between sample date

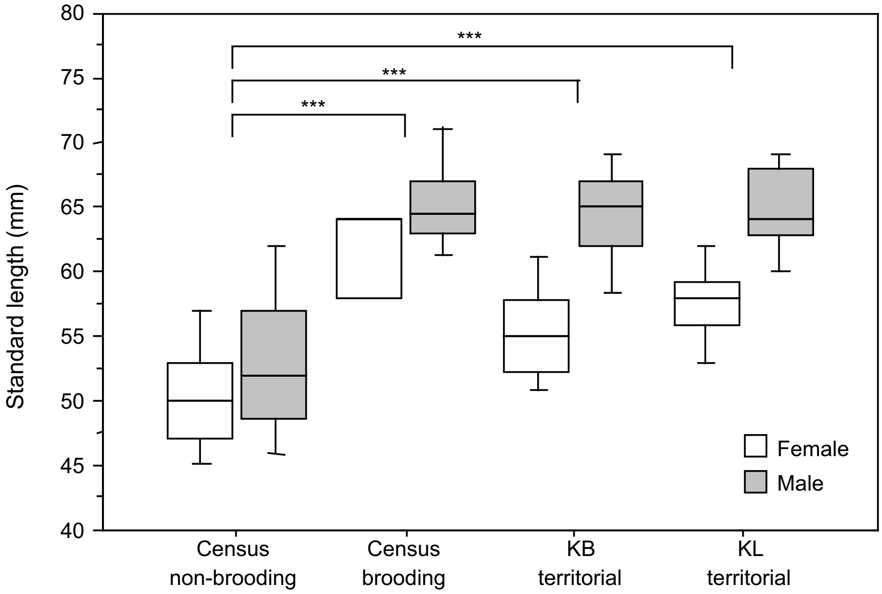

Figure 2. Standard length (in mm) of territorial versus non-territorial male (grey) and female (white) *E. cyanostictus*: Census non-brooding = non-mouthbrooding individuals from the population census; Census brooding = mouthbrooding individuals from the population census (presumed territorial); KB territorial = known territorial individuals from KB, KL territorial = known territorial individuals from KL. The whiskers and boxes represent the 10th, 25th, 50th, 75th and 90th percentiles. $^{***}p < 0.0001$.

and proportion of males (Spearman rank correlation: $r_s = 0.483$, $N = 15$, $p > 0.05$), so the removal of some females did not appear to affect the sex ratio of later samples.

The fence net would have passed through approximately eight territories (calculated using the median territory size at 1 m depth, see Morley 2000). The samples collected contained, on average, eight females and 15 males. Our behavioural observations suggested that these extra male individuals were non-territorial. Thus, the population appeared to comprise a male-biased floater population and an equal-sex-ratio territorial group. It is not known how far non-territorial individuals roam and so it remains possible that some non-territorial individuals were captured more than once. However, given the massive total area of habitat available, this is unlikely to be a major factor affecting the results.

Assortative mating

Pairs were always heterosexual ($N = 63$), and paired males were always larger than their mates (standard length, mean diff. = 8.4 mm, t-test: $t = 15.7$, $df = 63$, $p < 0.0001$). Strong assortative mating was observed; the standard lengths of the male and female in a pair were strongly correlated (Pearson correlation: $r = 0.596$, $N = 63$, $p < 0.0001$).

Ovarian development

More females had immature (stage 0 and 1) than mature ovaries (stage 2 and 3) in every population census sample collected (Wilcoxon signed ranks: $T^+ = 101.5$, $N = 15$, $p < 0.02$). Ovary weight increased with body length (to control for differences resulting from egg size, only females with fully developed, stage 3, ovaries were considered, Spearman rank correlation: $R_s = 0.636$, $N = 16$, $p < 0.01$). Females with further developed oocytes in their ovaries were heavier, for a given standard length, than those with undeveloped oocytes (Kendall partial correlation: SL as a covariate, $N = 115$, $T_{(stage)(weight).(SL)} = 0.248$, $p < 0.002$).

There was significant variation among samples in the proportion of females with mature ovaries (Chi-square: $\chi^2 = 29.4$, $df = 14$, $p < 0.01$). However, there was no synchronization of ovary maturation within the population and no consistent changes with the lunar cycle, as has been reported previously for this species and for other Tanganyikan cichlids (Figure 3). Similarly, and in contrast to previous reports, we found no differences in the proportion of mouthbrooding individuals captured

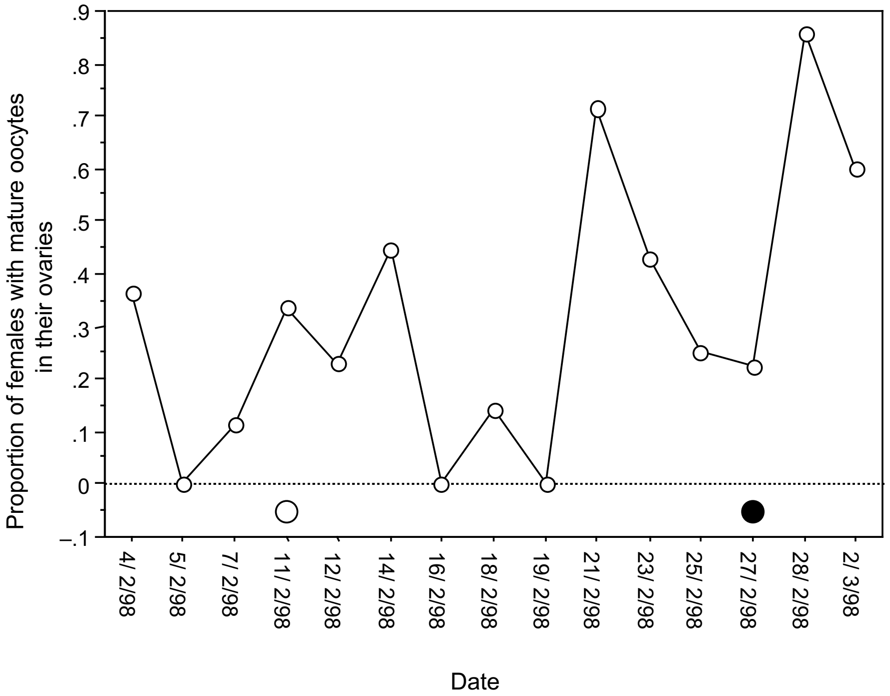

Figure 3. The proportion of females in a sample with mature oocytes in their ovaries, over a period of 1 month. The corresponding lunar cycle is shown by an open circle (full moon) and a filled circle (new moon).

around the full and new moons. In the two weeks around full moon we caught 7 mouthbrooders and 88 non-mouthbrooders, and in the two weeks around new moon we caught 9 mouthbrooders and 145 non-mouthbrooders (Chi-square: $\chi^2 = 0.044$, $N = 249$, $p > 0.8$). Similarly, mouthbrooding females did not appear to be more common in a particular phase of the moon; two of the female mouthbrooders were caught around a full moon and two around a new moon.

Spawning behaviour

Spawning was observed twice during this study (08/03/98 at 13:05 and 23/03/98 at 14:10), 2 days before a full moon and 3 days before a new moon. On both occasions the territorial pair was at 3 m depth. Initial courtship behaviours included circling, shaking and performing S-bends (these displays were regularly observed in non-spawning pairs). At varying intervals one fish would bring its mouth to the flank or genital region of its partner (nuzzling) and the partner would respond with a tail quiver in head-up position. These behaviours continued, becoming more and more intense, until the female swam forward and scraped her genital region over the surface of a flat rock. She swam in a small circle and repeated this movement until a single egg was spawned. The female immediately turned and picked the egg up in her mouth. The male then took a head-up position, quivering his tail, and the female nuzzled his genital region. At this point the male probably releases sperm and the eggs are fertilised inside the female's mouth (as suggested by Mrowka 1987). The cycle of pseudospawning (when no egg was produced) and spawning continued, with the female nuzzling the male after every one or two eggs were laid. In one case 15 eggs were spawned and in the other 3, but it is probable that more eggs were laid because the female had a slightly enlarged buccal pouch when observations began.

Spawning was often interrupted; for example in one case nine eggs were laid in 2 min with a slight interruption during which the spawning site changed. The pair was then disturbed by a *Mastacembelus* eel and the female swam out of sight. She returned after 7 min to lay an additional six eggs in two batches. Thus, a total of 15 eggs were laid in a period of 19 min. At the end of oviposition the female continued to pseudospawn intermittently for 5 min, she nuzzled the male twice more but no other eggs were spawned. Both males fed during courtship and spawning, whereas the females did not feed at all after the first egg had been produced.

Parental care

Size and number of young

Females were found brooding eggs and very small young (stages 0–3), while males were brooding larger young (stages 2–4). The median standard length of young found in the care of females was 6.6 mm (range 3.8–9.6 mm), and in the care of males was 10.5 mm (range 6.4–11.9 mm) (Mann-Whitney: $z = -2.95$, $N_m = 27$, $N_f = 4$, $p = 0.0032$). This is consistent with the reported female-to-male shift in brood care (Yanagisawa 1986, Kuwamura et al. 1989).

The median number of young mouthbrooded by females was 17 (range 14–24) while the median number of young mouthbrooded by males was 15 (range 9–25). There was no difference between the sexes in the number of young brooded (Mann-Whitney: $z = -1.43$, $N_m = 24$, $N_f = 5$, $p = 0.15$). The number of young incubated by a male was related to his female mate's body size, but not to his own size (Kendall partial correlations: $T_{(\text{no.} * \text{female SL}).(\text{male SL})} = 0.41$, $P < 0.05$; $T_{(\text{no.} * \text{male SL}).(\text{female SL})} = 0.17$, $P > 0.4$). The number of young decreased with mean size of young in the clutch (Figure 4, correlation: $r = -0.466$, $N = 28$, $p = 0.01$).

Duration of parental care

The duration of parental care was estimated from six pairs that bred in the field in 1998. Females cared for the young for 8–10 days and then the males took over for an additional 12–14 days, so the total period of care is 20–24 days.

Costs of parental care

Costs of care were examined using three indices: gut fullness, degree of oocyte development and body mass. In 15 out of 15 cases mouthbrooding males had completely empty guts while their partners' were between 51.1% and 98.6% full (sign test: $x = 0$, $N = 15$, $p < 0.0005$). Comparisons were made between individuals and their partners to control for territory quality differences. These results are unlikely to be confounded by sex because all sixteen mouthbrooding fish (including 4 females) from the population census also had completely empty guts, implying that the lack

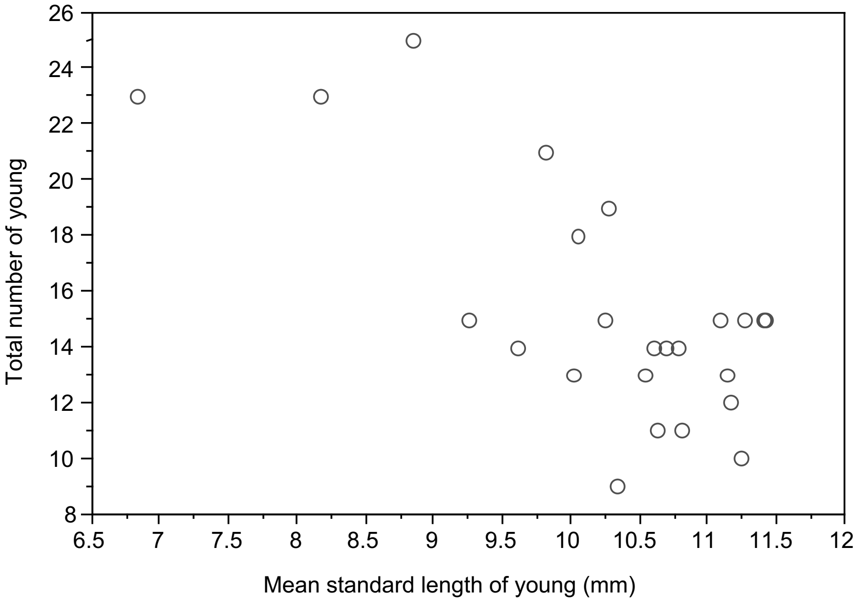

Figure 4. Total number of young per clutch versus the mean body length of the young in the clutch.

of food is more likely to be a result of mouthbrooding than gender.

Females with mouthbrooding partners had immature oocytes (stages 0 or 1) in their ovaries in all 15 cases, indicating that they were not ready to breed again immediately after completing parental care. This is significantly different from the ratio of immature to mature oocytes found in the population in general (82 immature: 36 mature, Fisher's exact test: $p = 0.0064$).

There was no difference in body length between territorial individuals that were mouthbrooding (or whose partners were mouthbrooding) and territorial individuals from pairs that were not mouthbrooding (unpaired t-test: females, $t = 0.22$, $N_{\text{no young}} = 45$, $N_{\text{with young}} = 22$, $p = 0.63$; males, $t = 0.22$, $N_{\text{no young}} = 45$, $N_{\text{with young}} = 32$, $p = 0.83$). However, for a given standard length, mouthbrooding males were heavier than non-mouthbrooding males (unpaired t-test: $t = -3.42$, $N_{\text{non-mouthbrooding}} = 28$, $N_{\text{mouthbrooding}} = 31$, $p = 0.0012$), and there was a tendency for mouthbrooding females to be heavier than non-mouthbrooding females (Mann-Whitney: $z = -1.94$, $N_{\text{non-mouthbrooding}} = 28$, $N_{\text{mouthbrooding}} = 4$, $p = 0.052$).

Discussion

The results of this study are consistent with the hypothesis that *E. cyanostictus* is monogamous and exhibits a female-to-male switch in mouthbrooding with no parental care after release. The populations studied consisted of territorial pairs and smaller non-territorial solitary individuals that were mostly males. The first detailed description of spawning behaviour in this species is presented. These observations are similar to those of Kuwamura et al. (1989) for a related species, *Tanganicodus irsacae*. This study also provides support for the existence of costs of parental care. Mouthbrooding fish had empty guts, indicating that individuals do not feed when mouthbrooding, which may affect growth and survival. In addition, females that had recently finished mouthbrooding had immature oocytes in their ovaries, indicating that they were not ready to breed again at the end of the parental care period. However, our results suggest that females with mature oocytes are continually available in the population and so staying with a mate that is not ready to reproduce represents a cost to males in terms of lost breeding opportunities.

It is possible that the observed bias in the sex ratio of samples was the result of behavioural differences. Male *E. cyanostictus* exhibit higher rates of conspicuous behaviour (aggression towards con- and heterospecifics and courtship) than females, but the general activity of both sexes is similar (Morley 2000). Thus, at first sight, males are more conspicuous than females, but after several minutes the females can easily be observed, so it is unlikely that over a 2 h sampling period many females would have been missed. However, because so few territories were crossed compared with the total number of males caught in each sample, even if some territorial females were missed and all the territorial males were caught there would still be a male bias in the non-territorial sex ratio.

Territorial pairs were mated assortatively by size, and the males were always bigger than their mates. This result fits well with the current theory on monogamy and mutual mate choice (Johnstone 1997). Males will benefit from mating with a fecund female, and the fecundity of female *E. cyanostictus* increased with body size (as recorded for many species of fish, Fryer & Iles 1972, Bagenal & Braum 1978, Wootton 1979, Wootton 1990). Larger females had heavier ovaries and the number of young brooded by a pair was positively correlated with the size of the female. Conversely, a female should not accept a male whose buccal cavity is too small to contain her clutch. The young found in the care of males were larger and developmentally more advanced than those carried by females, thus the mouth of the male would need to be larger than that of his mate. It is interesting to note that there is a sexual dimorphism in mouth size in *E. cyanostictus*; controlling for body size, males have larger mouths than females (Neat & Balshine-Earn 1999).

Lunar synchrony occurs in various lamprologine cichlids (Nakai et al. 1990) and has been suggested as a factor influencing the maintenance of monogamy (Knowlton 1979, Neat & Balshine Earn 1999). We did not find evidence to support the hypothesis of lunar synchrony in either ovary maturation or spawning (contrary to earlier results of Neat & Balshine-Earn 1999).

Monogamy in cichlids is generally associated with biparental care (Barlow 1974, Barlow 1984). Monogamous mouthbrooders can be divided into three categories: those where the clutch is too large for one parent to brood alone (e.g. *Chromidotilapia guentheri*, *Sarotherodon galilaeus*, Perrone & Zaret 1979), those in which the female, or the female then the male, mouthbroods and the pair guard the free-swimming young (e.g. *Perissodus microlepis*, Yanagisawa & Nshombo 1983; *Xenotilapia flavipinnis*, Yanagisawa 1986), and those in which mouthbrooding is switched between the female and male in a pair but no subsequent guarding occurs (e.g. *T. irsacae*, Kuwamura et al. 1989; *Microdontochromis* sp., Yanagisawa et al. 1996).

E. cyanostictus falls into the last and most intriguing category. The small clutch size and the absence of parental care after release make the evolutionary persistence of biparental care curious because we might expect these to be ideal conditions for male desertion. Further, in the laboratory, a mouthbrooding female whose mate has been removed will continue to care until the young reach the normal size at independence, implying that biparental care is not essential for offspring survival (*E. cyanostictus*, Morley 2000; *T. irsacae*, Kuwamura et al. 1989). In addition, biparental care is not necessarily more efficient than uniparental care; Kuwamura et al. (1989) showed that the number of young in the mouth of two other related goby-like cichlids (*Spathodus marlieri*, a maternal mouthbrooder and *T. irsacae*, a biparental mouthbrooder) decreased significantly as they grew, down to 70% or less of the original brood size.

The same pattern was found for *E. cyanostictus* in this study. The value of the correlation coefficient between size and number of young did not differ significantly from those found by Kuwamura et al. (1989) for *Spathodus marlieri* and *T. irsacae* ($\bar{z} = -0.379$, $p > 0.5$). That is, the extent of the decrease in clutch size was similar in all three species, implying that biparental care may be no more efficient, in terms of clutch survival, than female-only care. Thus, biparental care does not satisfactorily explain the maintenance of monogamy in these species. In fact the converse is likely to be true and it may be that monogamy (maintained for other reasons, see Morley 2000) favours biparental care (see Kuwamura et al. 1989).

When a pair of animals breeds repeatedly, the reproductive success of both individuals is limited by the rate at which the female can produce a new clutch. Therefore, we might expect a division of labour between the pair members (in terms of parental care, territory defence or territory maintenance), which allows the female to feed so that she may return to breeding condition sooner (e.g. *Xenotilapia flavipinnis*, Yanagisawa 1986; butterflyfish, Hourigan 1989; *Valenciennea longipinnis*, Takegaki & Nakazono 1999).

Mouthbrooding *E. cyanostictus* were never observed feeding and had no food items in their guts ($n = 31$), suggesting a large cost to parental care in terms of lost body condition and potentially reduced survival. Additionally, the partners of mouthbrooding males always had immature oocytes in their ovaries, implying that their gonads would not mature during the mouthbrooding period. To confirm that the costs of mouthbrooding in terms of lost feeding opportunities affect weight loss, individuals would need to be repeatedly sampled before and after mouthbrooding.

It appears that the costs of caring are high for a male *E. cyanostictus*, while the benefits may be low. However, if other factors were making desertion unfavourable the male may be increasing his own reproductive success by contributing to parental care and allowing his mate to begin feeding sooner, thus decreasing the time until she can produce another clutch and enhancing her fecundity (larger females produced bigger clutches) (Yanagisawa 1986; Kuwamura et al. 1989). Thus, it seems that in *E. cyanostictus* monogamy may be maintaining biparental care rather than vice versa.

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