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ORIGINAL ARTICLE

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Faithful fish: territory and mate defence favour monogamy in an African cichlid fish

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Abstract Monogamy is thought to occur when the opportunities for polygyny are constrained by strong intra-sexual competition, or when two individuals are needed to defend a territory, or to feed or defend their young. In *Eretmodus cyanostictus*, a monogamous cichlid from Lake Tanganyika, parents do not feed young and each sex is capable of caring for all the offspring alone. We used a series of field-based removal experiments to investigate what other factors may select for monogamy. We found that single individuals usually retained their territory and gained new mates quickly. Thus, it does not seem to be mate availability or the need for a pair to defend a territory per se that maintains monogamy in this species. However, the new mates of widowed individuals were smaller than the original mates had been, and single fish were not capable of taking over empty territories. Single females remated faster than males and had to significantly increase their defence behaviour as singletons. Thus we argue that monogamy results from the need to guarantee a high quality mate and territory in a competitive environment.

Keywords Biparental care · Cichlidae · Competition · *Eretmodus cyanostictus* · Mate removal

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Introduction

Monogamy in cichlid fishes is usually considered to be the inevitable outcome of essential biparental care; species that care for large clutches directly on the substrate are biparental and monogamous, while those that utilise safer breeding sites are uniparental and polygamous (Keenleyside 1991a). Oral incubation provides one of the safest possible brooding sites, thus the vast majority of mouthbrooding species are uniparental and the occurrence of monogamous mouthbrooders is peculiar (Fryer and Iles 1972; Keenleyside 1991b). Especially large clutch sizes or post-release guarding of young have been cited as factors that may perpetuate the necessity of biparental care, and hence monogamy, in mouthbrooders (Kuwamura 1986; Balshine-Earn 1995).

In certain species, however, clutches are small enough to fit into a single parent's buccal cavity and parents do not guard newly released young (Kuwamura 1986). Biparental care appears to be neither essential nor more efficient than uniparental care in these cases and alternative explanations for monogamy must therefore be sought (Kuwamura et al. 1989; Morley 2000). *Eretmodus cyanostictus* (Cichlidae) is one such species: the female lays a small clutch of eggs (range 14–25, Morley 2000) that she mouthbroods alone for 8–10 days before transferring the growing young to her mate. The male mouthbroods for a further 12–14 days and then the independent young are released and they leave the territory, and no additional parental care occurs (Morley 2000). This mating system precludes simultaneous polygyny because the male would be unable to mouthbrood the young of two females at once; however, it is intriguing that the male does not desert his mouthbrooding partner and search for other mates. Male emancipation from care and subsequent desertion has been suggested as the evolutionary origin of uniparental female care (Gross and Sargent 1985), and appears to have happened many times in the cichlids (Goodwin et al. 1998). Thus, in *E. cyanostictus*, factors other than the need for biparental care must be maintaining the evolutionary stability of the mating system.

The relative pay-off from staying versus deserting determines whether individuals remain with their partner or desert to find another mate (Trivers 1972; Maynard-Smith 1977; Grafen and Sibly 1978; Lazarus 1990). Conspecific competition for limited resources (food or a breeding site) may reduce the relative pay-off from desertion. It has been suggested that monogamy may be maintained if a solitary individual is unable to defend a territory alone (Fricke 1986; Wisenden 1994, 1995). Similarly, desertion may be unfavourable if alternative partners are not available because of synchronous breeding, low densities or intense intrasexual competition (Knowlton 1979; Wittenberger and Tilson 1980; Wickler and Seibt 1981; Nakai et al. 1990).

To understand how monogamy might be adaptive, two questions must be addressed: (1) Why do individuals stay and defend the current mate and/or territory and (2) Given that they stay, why do individuals not mate multiply within their territory? In this study we concentrated on the first of these questions by investigating mate and territory availability as two potential factors that may affect the costs of desertion in *E. cyanostictus*.

E. cyanostictus is endemic to Lake Tanganyika. It inhabits shallow rocky zones, to which it is restricted by its sensitivity to oxygen depletion and its poor swimming ability (Brichard 1989). The species is fairly common and has been documented at various locations around the lake (Boulenger 1898; Hori et al. 1983; Kuwamura 1986; Brichard 1989; Kuwamura et al. 1989; Khoda et al. 1996; Verheyen et al. 1996). *E. cyanostictus* feeds by scraping epilithic algae from rocks using its teeth (Yamaoka et al. 1986; Yamaoka 1997).

Pairs of *E. cyanostictus* aggressively defend territories, which provide them with food and shelter, and only leave their territories to chase away conspecific intruders or if chased by heterospecifics (Morley 2000). Fish appear to inhabit these territories year-round; territories are commonly occupied by pairs without young.

Removal experiments can help resolve the relative benefits and costs of desertion. In the first experiment we removed one member of a pair of *E. cyanostictus* to investigate whether monogamy was enforced either through limited remating opportunities or by the necessity of a pair for territory defence. If low availability of replacement partners prevents polygyny, an individual that loses its mate would not be expected to remate easily. In addition, if there is competition for partners it might be expected that high quality individuals could remate while others could not, and that the new partners would be of lower quality than the original ones. Likewise, if two individuals were required for territory defence, it would be anticipated that an individual that loses its mate would also lose all or part of its territory, or be forced to increase investment in territorial defence. A second experiment was performed, in which both members of a pair were removed, to establish whether single individuals are capable of taking over empty territories.

Methods

The experiments were conducted at two field sites on the southern coast of Lake Tanganyika, in Zambian waters. In 1998 fieldwork was conducted at Kasakalawe Bay (north-west of Mpulungu, 100 m east of Kasakalawe Village). As a result of logistic constraints, fieldwork was moved to Kalambo Lodge in 1999 (north-east of Mpulungu, near the Tanzanian border). Detailed descriptions of these sites can be found elsewhere (Morley 2000). All observations were conducted underwater at depths of 2.7–3.0 m using SCUBA equipment.

Pairs of *E. cyanostictus* were located by swimming along a transect line. Pairs could be identified by courtship behaviour and joint defence against conspecific neighbours. Once a pair was located each member of the pair was observed for 10 min; we recorded the frequency of courtship and defence behaviours and the length of time spent hiding under rocks. In addition, a brief sketch of each individual was made, outlining the unique pattern of blue spots on its head and dorsal surface (see Morley 2000 for details). Based on these initial 20 min of observation, a numbered rock was positioned on the presumed territory boundary to assist rediscovery of the territory; the fish could then be reliably identified by their location and the unique pattern of blue spots on their body. None of the pairs used for this study were providing parental care for young, and it was unknown whether the pairs had produced young prior to the study.

We observed the pairs on a further 2–3 occasions for a total of 30–60 min, and then drew a map of each pair's territory. Territory boundaries were assessed using data collected on range of movement and aggressive interactions with conspecifics. Range of movement was considered to be a good indicator of territory boundaries because ranges of different pairs did not overlap and neighbour contests always occurred at the edges of the pairs' movement ranges. The assumed territory boundaries were further tested by presenting to pairs a large male *E. cyanostictus* in a transparent cage. One or both members of the pair would attack this 'intruder' when the cage was placed at or within the boundary defined by the range of movement, but not when the cage was presented outside (Morley 2000). Each pair's territory size was measured using a tape measure. The number of neighbours was recorded, as well as the position and approximate size and shape of neighbouring territories. We also estimated the standard lengths (SL) and noted the pattern of blue dots of all neighbours.

A tent net (a conical net comprising a round piece of fine mesh with weights at its perimeter and floats at its centre, which cause it to float upward) was used to capture individuals, and colour-coded net collection bags were used for transporting individuals to the surface. The removed fish were weighed (to the nearest 0.01 g) and measured (SL to the nearest 1 mm) on land. During the experiment the removed fish were kept in large plastic containers (at Kasakalawe Bay) or concrete ponds (at Kalambo Lodge). At the conclusion of the experiment all removed fish were returned to their original territories.

Mate removal experiment

This experiment was carried out between 16 March and 14 April 1998 at Kasakalawe Bay, and 18 February and 16 March 1999 at Kalambo Lodge. A total of 19 pairs was used at Kasakalawe Bay, and a further 20 at Kalambo Lodge. All observations were conducted between 0700 and 1030 hours.

Pairs were identified as described above and were chosen so that there was a minimum of 10 m between the experimental territories. One member of each pair was captured, measured with a flexible ruler (SL in mm) and marked by excising a spine from one of four positions along the dorsal fin. These fin-clips healed after 4–5 weeks, and we detected no related deleterious effects on fish health or behaviour. Marked individuals were immediately released back onto their territories and the pair was left undisturbed for at least 3 days before the experiment began. In total, ten females and nine males were marked at Kasakalawe Bay and ten females and ten males were marked at Kalambo Lodge.

On the first day of the experiment a 10-min focal watch was conducted on each fish in a pair. Immediately after these observations the unmarked fish was captured. Another 10-min focal observation was performed, 15 min after the removal, on the remaining, marked fish. Individuals and territories were then monitored daily until a new pair formed or the marked fish disappeared. If a new mate was present on the territory both fish were observed for 10 min and, whenever possible, the SL of the new mate was measured. If remating did not occur the experiment ended after 3 days, although on 17 of the territories at Kalambo Lodge monitoring continued for 5 days. Where data from both years were analysed together only matings within the first 3 days were considered because of the difference in experimental duration.

Territory vacancy experiment

This experiment was conducted between 1 February and 10 March 1999 at Kalambo Lodge. All observations took place between 0700 and 1100 hours.

Ten pairs of *E. cyanostictus* (located at 5-m intervals along a transect line) were identified and observed as described above. Territory maps were made and then both fish in each pair were captured, and measured on the surface.

The empty territories were checked daily for the presence of new *E. cyanostictus*. Individuals discovered on the territories were observed for 10 min to determine whether they were strangers or known neighbours. Monitoring continued until the new individuals were consistently observed on the territory for 5 or more days.

In most cases the assumptions of parametric tests were not met so the closest nonparametric alternative was used (Siegel and Castellan 1988). All tests were two-tailed unless otherwise stated.

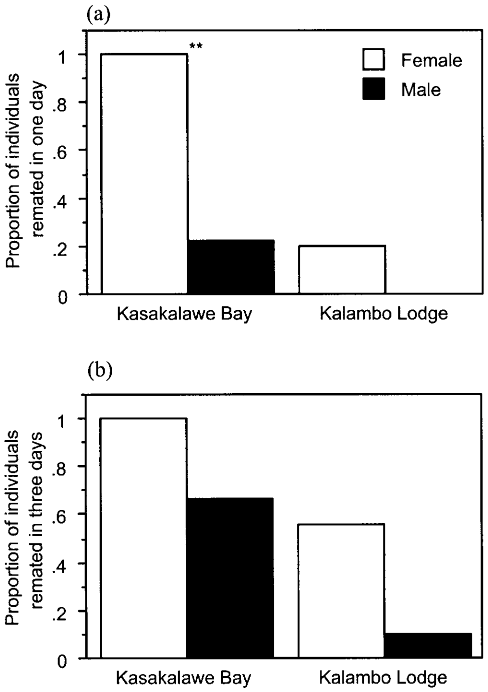

Fig. 1 Proportion of individual *Eretmodus cyanostictus* remating within **a** 1 and **b** 3 days of mate removal, for females (*white bars*) and males (*black bars*) at two separate field sites. ** $P<0.005$

Results

Mate removal experiment

Of the 39 widowed fish, all except four females remained on their territories. Two females at Kasakalawe Bay lost their territories in less than 24 h and two at Kalambo Lodge lost their territories after 3 and 4 days, respectively. Males were not, however, more likely than females to hold their territories alone (Fisher's exact test: $P=0.06$). Neither SL nor aggressive behaviour after mate removal differed between those females that kept their territories and those that lost them (Mann-Whitney tests: SL $z=0.61$, $n=4,16$, $P=0.54$; aggression $z=0.19$, $n=4,16$, $P=0.85$).

Only those fish that remained on their territories are considered in the following analyses.

Females were more successful at attracting new mates than males

On the third day after mate removal, 13 of the 17 remaining females had found new mates, compared with 7 of the 19 remaining males. A further three males remated at Kalambo Lodge (two by day 5 after mate removal and one by day 7). At both sites the females remated more quickly than the males (Fig. 1). Large individuals or those with large territories may have been expected to be among the quickest to remate. However, neither SL nor territory size differed between individuals that remated quickly or slowly relative to the median remating time (to account for differences caused by sex and site, deviations from the median of each variable, i.e. SL and territory size) were compared between groups of individuals that gained new mates in more or less than the median remating time; Mann-Whitney U tests, SL $U=9$, $n=5,5$, $P=0.79$; territory size, $U=11$, $n=5,5$, $P=0.65$).

Mating success was greater at Kasakalawe Bay than at Kalambo Lodge

Overall mating success after 3 days was greater at Kasakalawe Bay (14/17 remated) compared to Kalambo Lodge (6/19 remated). Females remated faster at Kasakalawe Bay than at Kalambo Lodge (Fisher's exact test: after 1 day $n=18$, $P=0.001$; after 3 days $n=17$, $P=0.05$). There was no difference between the sites in the proportion of males that had remated after 1 day (Fisher's exact test: $n=19$, $P=0.21$), but after 3 days a greater proportion of the males at Kasakalawe Bay than at Kalambo Lodge had remated ($n=19$, $P=0.02$). These differences in mating success between the field sites are probably a result of the higher densities of *E. cyanostictus* at Kasakalawe Bay than at Kalambo Lodge, exemplified by smaller territories and a larger population of non-territorial individuals (Morley 2000).

Single females increased their defence rate but males did not

Single females increased their defence behaviour against conspecifics while single males showed no change in

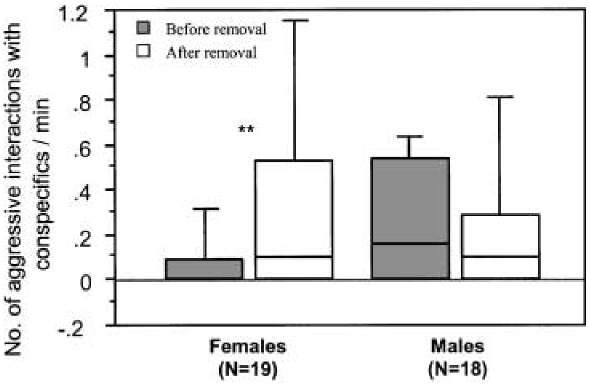

Fig. 2 Defence behaviour of males and females before mate removal (*grey boxes*) and 15 min after mate removal (*white boxes*). *Whiskers* and *boxes* represent the 10th, 25th, 50th, 75th, and 90th percentiles. ** $P<0.01$

frequency of defence (Wilcoxon signed ranks test: females, $z=-2.67$, $n=19$, $P=0.008$; males, $z=-0.97$, $n=18$, $P=0.33$, Fig. 2). The rate of defence by lone individuals was not significantly different to the combined defence by the pair prior to removal (Wilcoxon signed ranks test: conspecific aggression, $z=-1.49$, $n=37$, $P=0.14$), that is individuals increased their rate of defence to compensate for the loss of their mate.

New mates may be of lower quality than the original mates

Eleven of the 13 new male mates and all 10 of the new female mates were measured. Overall, new mates were smaller than the original mates were (Wilcoxon signed ranks test, one-tailed: $z=-1.61$, $n=21$, $P=0.05$). However, there was no clear pattern as to what determined whether a widowed individual gained a new mate that was smaller, larger or of an equivalent size to the old mate (Fig. 3a, b).

The original pairs used for this experiment showed the strong assortative mating for size (Spearman rank correlation: $r_s=0.43$, $n=39$, $P=0.007$) that is typical of *E. cyanostictus* (Morley 2000). However, the newly formed pairs were not as strongly matched by size as the original pairs ($r_s=0.261$, $n=21$, $P>0.20$; Fig. 4). There was a weak relationship between old and new mate size (remated females, $r_s=0.228$, $n=11$, $P>0.5$; males, $r_s=0.512$, $n=10$, $P>0.10$). That is, if an individual had had a large original mate they were likely to gain a large new mate and vice versa, although this was not always the case (Fig. 3a, b).

New mates performed more courtship than the previous mate did (Wilcoxon signed ranks test: $z=-3.36$, $n=22$, $P=0.0008$). The remated (previously widowed) fish displayed more to their new mates than to their original mates ($z=-3.07$, $n=22$, $P=0.002$). This increase in courtship might relate to the establishment of pair bonds. No other differences were found in any of the behaviours measured.

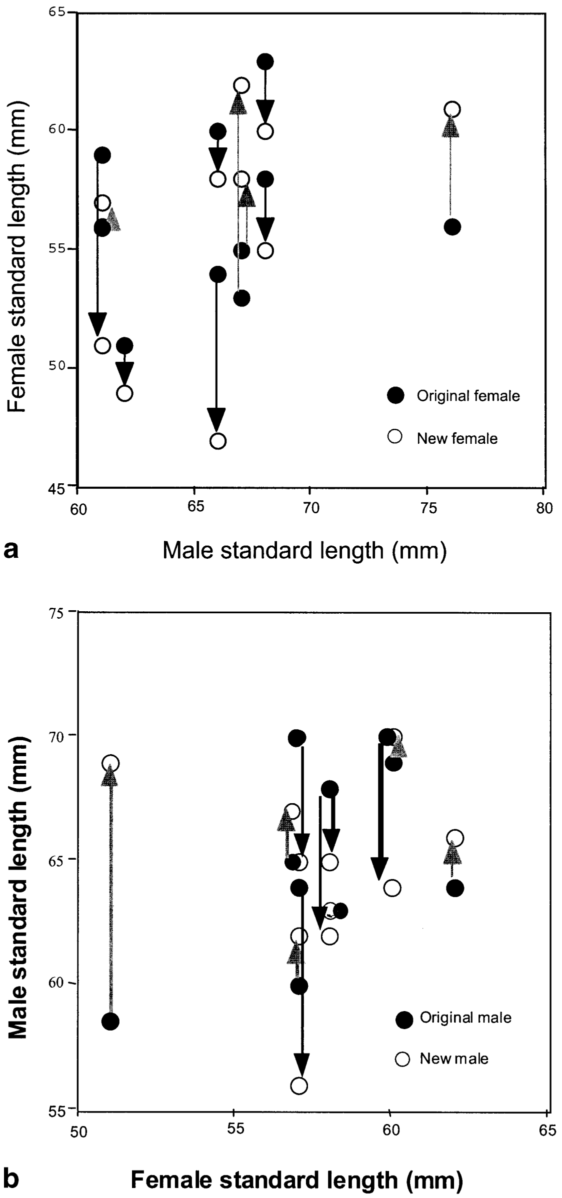

Fig. 3 Difference between standard length (mm) of original mate (*black circles*) and that of new mate (*white circles*) for **a** female and **b** male mate removals

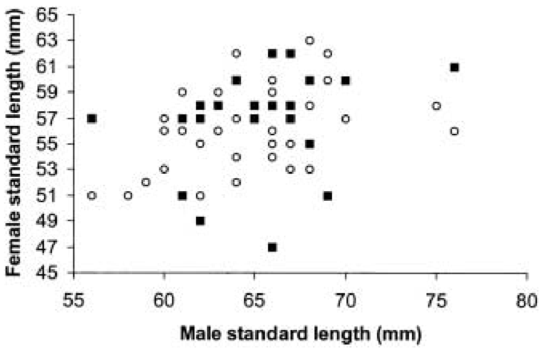

Fig. 4 Male and female standard length in pairs before manipulation (*circles*) and in pairs where a widowed individual had gained a new mate (*squares*)

Pair removal experiment

In all ten experimentally created vacancies, neighbours gradually invaded the empty territories. In every case this resulted in the division of the vacated territory between the neighbouring pairs that bordered it.

Discussion

Monogamy confers different benefits to male and female *E. cyanostictus*. The results of this study suggest that intrasexual competition makes desertion costly for males, while slow reproductive rates, energetic territory defence and dispersal risks make desertion costly for females.

A deserting individual benefits if it can acquire additional matings. For male fish this benefit is potentially high because they are ready to breed again in a relatively short period compared to the duration of brood care (Wootton 1976; Balshine-Earn 1995). So male *E. cyanostictus* are presumably ready to breed again before the brood care is complete, provided they can find a new mate. The most accurate way to assess remating opportunities is directly, by mate removal (Székely et al. 1999). Our removal experiments showed that males are capable of remating in an interval considerably shorter than the average brood care period (20–22 days, Morley 2000). Thus a deserting male could potentially find a new mate and breed again in less time than it would take to complete the brood cycle with the current mate.

However, the benefits of desertion are substantially reduced if alternative partners are not available, and many of the males in our study were unable to find new mates during the course of the experiment. In addition, deserting males would have to acquire a new territory, unlike the males in our experiments. When pairs were removed the resulting vacancies were filled quickly by neighbouring pairs. Single individuals never took over previously occupied territories. Thus empty territories are probably not commonly available and a deserting individual (male or female) is unlikely to be able to take over a territory alone. All else being equal, residents have an advantage in territorial conflict (Maynard-Smith and Parker 1976; Davies 1978; Itzkowitz et al. 1998) and so intruders are unlikely to win unless they are larger than the territorial individual (Barlow et al. 1986; Koops and Grant 1993; Turner 1994; Itzkowitz et al. 1998), or the same-sex resident has been depredated.

There was some evidence that the new mates were smaller than the original mates had been. Body size in *E. cyanostictus* is an important correlate of quality for both sexes (Morley 2000). Female fecundity is directly related to body size, and male size is crucial because the male's buccal cavity must be large enough to accommodate the developing brood (Morley 2000). The strong assortative mating seen in the unmanipulated population was less pronounced in the new pairs. Widowed individuals would benefit from accepting a new mate, regardless of size, and the costs associated with searching for a size-matched mate are likely to be high, especially if alternative partners are indeed limited. Similarly, if the new mates were previously non-territorial then they will benefit from gaining a territory and a breeding situation, regardless of the size of their partner. Thus, it is not surprising that some initial pairings are mismatched. However, the mismatches in pairing are unlikely to be stable because individuals should strive for the largest possible mate (e.g. *Valenciennea longipinnis*, Takegaki and Nakazono 1999), and if observations had continued it is possible that further changes in partners would have been observed (as in Red Sea butterflyfish, Fricke 1986).

Combined, these results suggest that there is strong competition between males for breeding vacancies, as demonstrated by the rapidity with which removed males were replaced. Competition between males will be further exacerbated if the population is male-biased, as appears to be the case among the non-territorial individuals at Kasakalawe Bay (Morley 2000; a sex ratio survey was not conducted at Kalambo Lodge). Thus, for males the costs of desertion are high due to intrasexual competition.

Solitary females rapidly secured new mates in both sites, suggesting that alternative male partners were readily available. However a female would only benefit from deserting if she were able to produce another clutch before her partner had completed the brood care of the first one. The inter-clutch interval in the field was long (more than 5 weeks, Morley 2000), and under laboratory conditions, where food was plentiful, females did not produce a new brood before their partners had completed care (Morley 2000). These observations suggest that the slow reproductive rates of females limit the benefits of desertion.

Moreover, although defending a territory alone may have been costly for both sexes, it was arguably more costly for females. Lone females were usually able to defend their territories at a level equivalent to that shown by the pair before removal, although this involved a significant increase in the female's defence effort. As the majority of territory defence in unmanipulated pairs was undertaken by males (Morley 2000), single males were capable of territory defence without increasing their defence rates. These findings may explain why some females but no males lost their territories. They also imply that one benefit of monogamy for females is territory defence by their partners.

Observations ceased before all the fish had remated and it is possible that those that did not find a mate within a few days would not be able to continue defending their territory alone. Anecdotally, this seems to be true for females. At Kalambo Lodge, where remating was slow, a female lost its territory 5 days after mate removal, possibly because it was unable to continue defending alone.

In *E. cyanostictus* territories provide food and shelter and non-territorial individuals are chased away as soon as they are detected on a territory (Morley 2000). Thus searching for a new mate, and hence not being territorial, is likely to be an energetically costly strategy for both sexes. This is especially true for females, which are less aggressive and require longer to regain breeding condition than males (Morley 2000). Similarly establishing a pair bond is potentially costly because new pairs were observed to court at a much higher rate than established pairs. Conspicuous courtship behaviour may attract predators, potentially representing an additional survival cost associated with changing partners. Thus, for females the benefits of monogamy are likely to be high, and the costs low.

Given that monogamy is the best option for both partners, the maintenance of biparental care may be explained because the reproductive success of the pair will be limited by the rate at which the female can produce eggs. The male may therefore be able to increase his reproductive success by relieving the female of parental care, thus allowing her to begin feeding sooner than if she had brooded the young to independence. To conclude, these results provide strong support for the hypothesis that intense intra-sexual competition (for females and territories) in males, and the high costs of dispersal and defence for females help to explain monogamy in *E. cyanostictus*.

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