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Bigamy and mate choice in the biparental cichlid fish *Cichlasoma nigrofasciatum*

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Summary. Sixty percent of *C. nigrofasciatum* males showed bigamous behaviour when held in small, outdoor ponds at an adult sex ratio of 5 males to 10 females. No male held more than two pair bonds simultaneously. Bigamy had reproductive benefits; bigamous males, on average, fathered more broods that survived well into the free-swimming fry stage than did monogamous males. In ponds where adult size varied, no positive correlations were found, for either sex, between adult size and frequency of spawning or success of brood-rearing, despite predictions that larger size would confer reproductive benefits on both sexes. A significant positive correlation was found between the sizes of mated individuals in the pond where both sexes varied in size. On theoretical grounds this relationship is likely to be more strongly influenced by female than by male choice of spawning partner.

Introduction

Polygyny, defined as the prolonged association and essentially exclusive mating relationship between one male and two or more females at the same time (Wittenberger 1981), is rare among freshwater fishes. It has been described for a few species in the family Cichlidae. For example, in the South American genus *Apistogramma* (Burchard 1965) and the African genus *Lamprologus* (Wickler 1965) one male may establish a large territory within which several females, with each of whom he has spawned, protect their offspring in separate small territories. However, these observations were made on aquarium-held fishes; they have apparently not been confirmed in nature.

Field observers of supposedly monogamous, biparental cichlids in Central America have seen a few cases of a single male sharing his time between two brood-rearing females, each reacting to the male as though he is her mate. Examples are *Aequidens coeruleopunctatus* in Panama (Barlow 1974) and *Cichlasoma nigrofasciatum* in Costa Rica (Meral 1973; personal observation 1984).

Thus, there appears to be a tendency for males of presumed monogamous species to seek additional breeding opportunities, even while cooperating with a mate in raising a brood. This should not be surprising, given that male animals in general attempt to maximize their reproductive output by fertilizing as many eggs as possible, while females do so by concentrating on maximum egg production (Williams 1975; Dawkins 1976; Wittenberger 1981). However, a male cichlid, in a typically biparental species, who divides his parental defence effort between two or more females runs the risk of losing all his offspring to predators (Barlow 1974). In many tropical waters the young of non-mouthbrooding cichlid species appear to need both parents to protect them from predators (Barlow 1976; Keenleyside and Bietz 1981), and in some regions predation pressure is so heavy that a high proportion of broods is completely lost before reaching independence from their parents (McKaye 1984). Thus, a tendency to attempt polygynous mating is likely to be countered by the high risk of predation on a brood left with only one parent.

C. nigrofasciatum is a promising species in which to examine the tendency of males to breed polygynously, as well as the eventual reproductive consequences of doing so. Bigamous males have occasionally been seen in its natural habitat (Meral 1973; personal observation 1984) and it breeds readily in captivity, where the survival of broods can be monitored. In a pilot study we saw some cases of apparent bigamy by males in a shallow outdoor pond. However, we had no information on survival of broods with bigamous fathers. Therefore, the first two objectives of the present study were to document the mating relationships among groups of adult *C. nigrofasciatum* in small ponds, and to compare the reproductive success of monogamous and polygynous males.

The probability that males would mate polygynously was increased by using experimental populations of 10 females and five males in each of four ponds. This also allowed me to search for evidence of mate choice. I predicted that if there was size variation among the males, larger males would breed more often and would have greater reproductive success than smaller males. This is based on the assumption that females will choose larger mates as better defenders of their brood against predator attacks, as documented by Perrone (1978) and Noonan (1983). I also predicted that larger females would breed more often and have greater reproductive success than smaller females because fecundity is directly related to female size in fishes (Bagenal and Braum 1978). Males should prefer to breed wth larger females, who can produce more offspring per spawning.

Methods

Four outdoor ponds at the University of Western Ontario (described in Keenleyside 1983) were used for the experiment. Clay flower pots, 20 cm in top diameter, were cut in half and placed concave side down on the substrate to serve as spawning sites. Ten of these half-pots were distributed in a regular pattern in each pond, with 1.5 m between adjacent pots. Of 72 spawnings during the study, 65 (90.3%) occurred inside flower pots; most of the others were on a pond wall.

Ten female and five male *C. nigrofasciatum* were released into each pond. They were from a large population maintained for several years in the laboratory. Some may have had previous breeding experience; none had any experience as adults in the ponds. The influence of size on mate choice and breeding success was examined by selecting fish for each pond that were, within sexes, either almost identical or different in total length when the experiment began. The four ponds allowed one replicate of each possible combination of same-sized or different-sized males and females. Size ranges of males and females within a pond did not overlap except in Pond A (different-sized males and females) where slight overlap occurred between the two smallest males and the four largest females. Males are typically larger than females within mated pairs of *C. nigrofasciatum* and other biparental cichlids in nature (McKaye 1977; Perrone 1978; Keenleyside and Bietz 1981; Neil 1984).

Fish were individually identified by fastening two coloured embroidery beads into the dorsal musculature with stainless steel wire. They were placed in the ponds on 5 July 1982 and removed on 25 August. Water temperatures ranged between 20° C and 30° C during that period. No other fish were in the ponds. Supplementary food was not provided. *C. nigrofasciatum* is omnivorous in nature (Meral 1973) and adults and young actively foraged on the pond substrate. Most adults increased in weight and length during the experiment, indicating that adequate food was available.

Each day an observer recorded which fish were pair-bonded and the location and developmental stage of all broods of young. Broods hidden in flower pots, or in pits excavated in the substrate by the parents, were checked by an observer wearing face mask and snorkel. The offspring of a *C. nigrofasciatum* pair pass through three developmental stages before becoming independent of their parents. These are the egg, wriggler (non-free-swimming hatchling or free embryo: Balon 1984) and free-swimming fry stages. They lasted for 2 to 3 days, 4 to 7 days and 2 weeks or more, respectively, in this study.

A male was classed as polygynous if he maintained a pair bond simultaneously with more than one female. Since few spawnings were observed, the existence of pair bonds was confirmed by observing the behaviour of brood-guarding adults. Monogamous pairs were obvious; both adults remained near their brood except for brief excursions by one of them to forage or attack approaching fish. On that fish's return the two adults "greeted" each other with brief bouts of mutual opercular flaring and tight circling. Polygyny was assumed when a female was found guarding a brood alone, with occasional visits by a male who also spent some time with another female and her brood. The reaction of a lone brood-guarding female to approaching males clearly showed which male was her mate. If she immediately attacked and drove him away I assumed he was not the father of her brood. However, if she "greeted" him in the standard way, and especially if she left the brood in his care while she foraged or chased away other fish, I concluded he was her spawning partner.

A Reproductive Success score was used to quantify the reproductive performance of the fish. Each breeding attempt was classified as Successful or Failed and was assigned a score of 1 or 0 respectively. A *Successful* attempt was one in which the young remained with one or both parents until they had been at least 8 days at the fry stage. Broods abandoned by both parents before that age were usually eaten (by other adults and older juveniles); older fry appeared to survive without guarding adults. A *Failed* attempt was one in which the family unit (brood with one or both parents) did not remain intact until 8 days into the fry stage. Some breeding attempts beginning in mid to late August were ended by the closure of the experiment on 25 August. I classed these as *Interrupted* if the young were not 8 days into the fry stage and gave them a score of 0 because there was no way to predict the longer-term success of these attempts. I did not count individual offspring surviving to independence because a pilot study showed that attempts to catch fry were inefficient and seriously disturbed nearby family units. Brood sizes probably ranged between 100 and 250 (FitzGerald and Keenleyside 1978) but numbers of fry could not be estimated accurately by eye.

Results

Size data for the fish placed in each pond, together with the frequency and fate of all spawnings, are presented in Table 1. Approximately equal numbers of spawnings occurred in all ponds. A 4 × 2 contingency table analysis of Successful vs. Failed spawnings showed no significant differences among ponds ($\chi^2 = 4.02$, $P > 0.05$). However, Pond B (where there was little variation in size of males or females) had the highest proportion of Successful and the lowest proportion of Failed

Table 1. Frequency and fate of spawnings in ponds with four size treatments. Sizes shown are total lengths in cm (means and ranges) of fish at start of experiment. Percentages are in italics

Pond	♂ size (cm) $n=5$ Mean range	♀ size (cm) $n=10$ Mean range	Number of spawnings	Number of spawnings		
				Successful	Interrupted	Failed
A	9.9	7.4	16	8	3	5
	7.5–13.2	6.0–9.2		*50.0*	*18.8*	*31.3*
B	9.1	7.4	19	12	3	4
	9.0–9.2	7.2–7.5		*63.2*	*15.8*	*21.1*
C	9.8	6.6	17	8	4	5
	7.1–12.8	6.5–6.9		*47.1*	*23.5*	*29.4*
D	9.9	7.5	20	7	3	10
	9.7–10.1	6.0–9.4		*35.0*	*15.0*	*50.0*
		Totals	72	35	13	24
				48.6	*18.1*	*33.3*

Table 2. Stability of pair bonds among the 35 successful breeding attempts. E, W and F represent egg, wriggler and fry stages. Subscripts represent day within that stage when male parent deserted his mate and brood. Numbers in brackets are percentages

Pond	n	No. reaching age F_8 with		Brood age when deserted
		pair bond intact	desertion	
A	8	6 (75.0)	2	E_2, F_5
B	12	6 (50.0)	6	E_1, E_2, W_1, W_1, F_1, F_9
C	8	7 (87.5)	1	F_3
D	7	6 (85.7)	1	E_1
Total	35	25 (71.4)	10 (28.6)	

spawnings, while Pond D (where males were similar and females variable in size) had the reverse. A 2×2 analysis of the Successful vs. Failed data of these two ponds showed they were significantly different ($\chi^2=3.89$, $P<0.05$).

Twenty-one of the 72 spawnings during the experiment, involving 12 of the 20 males, were bigamous, that is, the male had previously spawned with another female and he continued to collaborate in brood-rearing with her as well as with his new mate. No male had more than two simultaneous mates, although some bigamous males spent short periods in non-aggressive interactions with unattached females. Bigamy was the only form of polygynous mating seen in this study.

The duration of the bigamous relationships ranged from one to 20 days ($\bar{x}=5.57$, SE$=1.19$). Some males maintained two bonds until one brood developed to independence and the family unit dispersed; they then continued a monogamous relationship with the other female. Other males were bigamous for one or more days, then deserted one mate and brood and continued as a monogamous mate with the other. In the latter cases the male's second spawning partner was deserted more often than the first (10 cases to 4, respectively), but this difference is not significant ($\chi^2=2.57$, $P>0.05$).

The time interval between the two spawnings by bigamous males was highly variable, ranging from zero to 17 days ($\bar{x}=7.19$, SE$=1.11$, $n=21$). In only two cases did a male spawn with two females on the same day. The developmental stage of a bigamous male's first brood did not seem to influence the timing of his second spawning. The 21 cases of bigamy occurred when the male's first brood was at the egg, wriggler or fry stages 8, 4 and 9 times respectively.

The reproductive consequences of bigamous behaviour were reasonably clear. The mean Reproductive Success score for the 12 males that showed bigamous behaviour was 2.17 (SE$=0.21$), and for the 8 strictly monogamous males was 1.25 (SE$=0.16$). This difference is significant (Mann-Whitney $U=4$, $P<0.001$, one-tailed test), indicating that bigamy was a successful reproductive option in the conditions of the experimental ponds.

The records of the 35 successful spawnings were examined to see if there was any correlation between success in raising a brood and stability of the bond between the guarding parents. In 25 of these cases (71.4%) the male-female bond remained intact at least until the fry were 8 days free-swimming (the criterion for a successful spawning) (Table 2). In the other 10 cases (28.6%) the male deserted his mate before the brood had reached the criterion age, and the female continued to rear them alone. Success for these single female parents was not clearly related to age of their brood when the male deserted, which ranged from the day after spawning to day 9 of the fry stage (Table 2).

Among the 72 spawnings overall, 24 (33.3%) produced broods that did not survive at least 8 days into the fry stage, i.e. they were classed as failed, (Table 1). More of these failures occurred when the progeny were at the egg stage than when they were wrigglers or fry, and more occurred when both parents were with the brood than when the male had deserted, leaving the female as the lone parent (Table 3). However, these differences

Table 3. Relationship between developmental stage of the brood and state of parental pair bond when breeding attempts failed

Stage	Pair intact	Alone	Totals
Egg	8	6	14
Wriggler	4	2	6
Fry	3	1	4
Totals	15	9	24

were not great and contingency table analysis of the data is inappropriate because there are small Expected values in too many cells (Siegel 1956). The causes of brood mortality are uncertain, although predation is the most likely candidate. Predation attempts by adults and large juveniles were common, and brood-guarding adults consistently attacked other fish that approached their young. *C. nigrofasciatum* about 2 cm in total length are known to prey on younger conspecifics in the wild (Hay 1976).

The influence of size of adults on their spawning frequency and reproductive success was examined by Spearman rank correlation analysis. For the different-sized males (Ponds A and C) and females (Ponds A and D) none of these correlations was significant ($P > 0.05$ in all cases).

One indication of female size effects was that of the 40 females used in the study only the smallest female in Pond D and the second smallest in Pond A did not spawn.

The clearest evidence of the influence of size on mate choice came from Pond A (the only pond in which both male and female size varied), where there was a strong positive correlation between the total length of the partners within mated pairs ($r = 0.777$; $P < 0.001$).

Discussion

A tendency towards polygynous behaviour by males of typically monogamous, biparental cichlids, as described by field observers in tropical America (e.g. Meral 1973; Barlow 1974), was clearly demonstrated in this study. Twelve of the 20 male *C. nigrofasciatum* maintained a pair bond and collaborated in raising a brood with two females at the same time. No male was ever found with more than two simultaneous mates. Apparently the time and energy requirements associated with effective brood care set an upper limit of two on the number of pair bonds a male can maintain at once.

The bigamous behaviour was no doubt facilitated by the 2:1 female:male sex ratio in the experimental population. However, there are two reasons for arguing that the imposed female surplus was not the sole cause of bigamy. First, during a field study in Costa Rica in 1984 I saw three cases of bigamous breeding in a natural, undisturbed population of *C. nigrofasciatum*. The adult sex ratio at that study site did not appear to be unbalanced; several collections made by seining produced many dozens of mature adults, with an approximate 1:1 sex ratio. Second, in an earlier study in the same experimental ponds using *Herotilapia multispinosa*, another supposedly monogamous, biparental Central American cichlid, a female-biased sex ratio was frequently accompanied by a parental male permanently deserting his mate and brood and spawning with another female (Keenleyside 1983). Bigamy was never observed. Thus, bigamous behaviour is not the inevitable result of imposing a female surplus on a captive population of a biparental cichlid species. Rather it appears that *C. nigrofasciatum* males are not obligately monogamous, but may attempt to increase their reproductive output by facultative bigamy, especially if the local adult sex ratio facilitates it by having a female surplus.

Bigamous males had a higher average Reproductive Success score than monogamous males, indicating that bigamy was a successful option for increasing reproductive output. No doubt the success of polygynous mating attempts depended on the extent to which both parents were needed to protect the brood. Biparental care has presumably evolved because of the reproductive advantages of having both parents constantly available to guard their offspring against predators. Perhaps predation pressures were low in the experimental ponds compared to some natural situations (e.g. McKaye 1984). However, in the later stages of the two-month study there were large numbers of subadult fish (survivors of earlier spawnings) in the ponds. Lone female parents (whose mates had deserted them) actively defended their broods, and at least some of them were successful (Table 2). However, it is clear that intact pairs (whether the male was periodically away with another mate or not) were more likely to be successful than were deserted females.

On the other hand, mate-fidelity did not ensure reproductive success (Table 3). Failed breeding attempts occurred in all ponds, when broods were at the egg, wriggler or fry stages, and whether both parents or the female alone were in attendance. Sixteen of the 24 failures (66.7%) occurred during the first 2 weeks of the 8-week long study, suggesting that inexperience with brood-rearing in the pond environment by tank-held fish may have contributed to some initial breeding failures.

The second part of this study involved the role of size of adults on their reproductive frequency and success. No positive correlations were found for either sex. However, since the ratio of successful to failed spawnings was highest in Pond B and lowest in Pond D, it is possible that size differences were partially responsible for this variation. Pond B had similar-sized fish of both sexes, perhaps contributing to relative stability of male-female interactions during courtship and competition for mates. Pond D had similar-sized males but variable females, which might have resulted in more vigorous competition among males for the larger females and less pair bond stability during rearing of young. It is also interesting that all five Pond B males were bigamous at some time, whereas in the other three ponds the number of males showing bigamous behaviour was either two or three.

The lack of correlation between adult size and either spawning frequency or reproductive success score, for both sexes, suggested that mate choice on the basis of size did not occur in this experiment. On the other hand, Noonan (1983) found that when two male *C. nigrofasciatum* of different sizes were confined by clear partitions to opposite ends of a large aquarium, a female in the central section consistently spawned near the larger male. Perhaps in our outdoor ponds, where the 15 adults in each pond were free to interact with each other at all times, any underlying size preferences in spawning partners were overshadowed by other features, such as vigour and persistence of courtship. And variation in these behaviours may not have been directly related to body size. However, the positive correlation in size between spawning partners in Pond A, where both sexes were variable in size, indicates that size did play a role in the choice of spawning partner.

The question of which sex has the greater influence on choice of mate cannot be answered clearly by pond experiments like this one. On two grounds I would expect female *C. nigrofasciatum* to be more selective of a spawning partner than males. First, because of anisogamy, females (and their eggs) are a limited resource for which males compete (Williams 1975). Second, even though both sexes care for the young, females are more heavily involved than males, especially during the early stages of brood development (Mertz 1967; Weber 1970; Williams 1972). This imbalance should be accompanied by greater emphasis on mate choice by females (Trivers 1972; Halliday 1983). The results of Noonan's (1983) study suggest that the positive correlation in size within breeding pairs in Pond A was caused primarily by females exercising choice of spawning partner.

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References

Bagenal TB, Braum E (1978) Eggs and early life history. In: Bagenal TB (ed) Methods for assessment of fish production in fresh waters. IBP Handbook, no 3. Blackwell, Oxford, pp 165–201

Balon EK (1984) Patterns in the evolution of reproductive styles in fishes. In: Potts GW, RJ Wootton (eds) Fish reproduction: strategies and tactics. Academic, London, pp 35–53

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

Barlow GW (1976) The Midas cichlid in Nicaragua. In: Thorson TB (ed) Investigations of the ichthyofauna of Nicaraguan lakes. University of Nebraska, Lincoln, pp 333–358

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

Dawkins R (1976) The selfish gene. Oxford University Press, New York Oxford

FitzGerald GJ, Keenleyside MHA (1978) The effects of numerical density of adult fish on reproduction and parental behavior in the convict cichlid fish *Cichlasoma nigrofasciatum* (Günther). Can J Zool 56:1367–1371

Halliday TR (1983) The study of mate choice In: Bateson P (ed) Mate choice. Cambridge University Press, Cambridge p 3–32

Hay TF (1976) Effects of age and experience on responses of *Cichlasoma nigrofasciatum* fry to parents and predators (Pisces: Cichlidae). PhD dissertation, University of California, Berkeley

Keenleyside MHA (1983) Mate desertion in relation to adult sex ratio in the biparental cichlid fish *Herotilapia multispinosa*. Anim Behav 31:683–688

Keenleyside MHA, Bietz BF (1981) The reproductive behaviour of *Aequidens vittatus* (Pisces, Cichlidae) in Surinam, South America. Environ Biol Fish 6:87–94

McKaye KR (1977) Competition for breeding sites between the cichlid fishes of Lake Jiloa, Nicaragua. Ecology 58:291–302

McKaye KR (1984) Behavioural aspects of cichlid reproductive strategies: patterns of territoriality and brood defence in Central American substratum spawners and African mouth brooders. In: Potts GW, RJ Wootton (eds) Fish reproduction: strategies and tactics. Academic, London, pp 245–273

Meral GH (1973) The adaptive significance of territoriality in New World Cichlidae. PhD dissertation, University of California, Berkeley

Mertz JC (1967) The organization and regulation of the parental behavior of *Cichlasoma nigrofasciatum* (Pises: Cichlidae), with special reference to parental fanning. PhD thesis, University of Illinois

Neil SJ (1984) Field studies of the behavioral ecology and agonistic behavior of *Cichlasoma meeki* (Pisces: Cichlidae). Environ Biol Fish 10:59–68

Noonan KC (1983) Female mate choice in the cichlid fish *Cichlasoma nigrofasciatum*. Anim Behav 31:1005–1010

Perrone M (1978) Mate size and breeding success in a monogamous cichlid fish. Environ Biol Fish 3:193–201

Siegel S (1956) Nonparametric statistics for the behavioral sciences. McGraw-Hill, New York

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

Weber PG (1970) Visual aspects of egg care behaviour in *Cichlasoma nigrofasciatum* (Günther). Anim Behav 18:688–699

Wickler W (1965) Neue Varianten des Fortpflanzungsverhaltens afrikanischer Cichliden (Pisces, Perciformes). Naturwissenschaften 52:219

Williams GC (1975) Sex and evolution. Princeton University Press, Princeton

Williams NJ (1972) On the ontogeny of behaviour of the cichlid fish *Cichlasoma nigrofasciatum* (Günther). PhD thesis, University of Groningen

Wittenberger JF (1981) Animal social behavior. Duxbury, Boston