

Reproductive behaviour of free-ranging convict cichlids, *Cichlasoma nigrofasciatum*

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Synopsis

Cichlids are unusual among fishes because they have prolonged care of their young. Convict cichlids, *Cichlasoma nigrofasciatum*, are monogamous and have biparental care of their young. This species has been studied extensively in the laboratory, however, little is known of their reproductive habits in nature. Four populations of convict cichlids were studied in Costa Rican streams during the long dry season in 1990 and 1991. Basic physical and chemical parameters of the study sites are described. In the study area breeding fish paired size assortatively; large males with large females and small males with small females. A comparison of the size distribution of breeding fish to that of non-breeding fish showed that small males and in some cases, small females were excluded from breeding. This suggests competition among males for nest sites and mates or female-female competition. Further evidence of intrasexual competition in females is provided by the black colour phase adopted by some females. Some of these females were active in courtship and had mature ova. Cave guarding behaviour and reuse of caves show that a ready-made spawning site is an important resource shaping the mating system of this species. This description of basic natural history can serve as a source of testable hypotheses for future research and allow the results from laboratory studies on this and related species to be interpreted within the ecological context of the natural habitat.

Introduction

Cichlids have attracted interest because, unlike most fishes, they have prolonged parental care of their eggs and free-swimming young (Keenleyside 1991). Many of these freshwater fishes are small and adapt well to aquaria and thus make ideal subjects for the laboratory study of reproductive behaviour.

The convict cichlid, *Cichlasoma nigrofasciatum*, is a substrate brooding species native to lakes and streams in Central America, ranging from Guatemala to northern Panama (Bussing 1987). Adults form monogamous pair bonds and jointly care for

their eggs, newly-hatched free embryos and free-swimming juveniles for four to six weeks. Eggs are laid on the ceiling of small caves which the pair prepare by excavating sand from under large stones. Helpless free embryos emerge from the egg envelopes in about three days. After another three days, the yolk sac is absorbed and the fins become differentiated more fully, allowing the young to become free-swimming and begin exogenous feeding (Noakes 1991). Young emerge from their cave during daytime and form a dense school close to the substrate. Both parents guard the young, aggressively chasing away potential brood predators. The

young forage on the substrate, assisted periodically by parental fin digging and leaf lifting that uncover food items otherwise unavailable to the young (Wisenden et al. 1994).

Convict cichlids are commonly used in laboratory studies of parental care and social behaviour in fishes. However, few studies have examined the behavioural ecology of convict cichlids in nature (Meral 1973, McKaye 1977, 1986, Keenleyside et al. 1990) and none in detail. Observations of convict cichlids in their natural habitat will permit researchers to interpret convict cichlid behaviour observed in the laboratory within the context of the fish's natural habitat.

This paper describes mating behaviour of convict cichlids in Costa Rican streams during the long dry seasons of 1990 and 1991. Convict cichlids bred throughout the long dry season from December to June. Breeding phenology and the mating system are described in Wisenden (1994a). The number of pairs guarding broods increased to a peak in early March, then declined to a minimum in June. Males had a higher seasonal breeding frequency than females.

Here, I present data on positive size-assortative mating as evidence for intersexual selection. Then, I present data on the size of breeding fish compared to non-breeding fish, and the presence of different colour phases in females. I look to these data for evidence of intrasexual selection. Finally, I present

data on the use of spawning caves, and cave guarding behaviour, to argue that cave possession may play an important role in sexual selection and the mating system in this species.

Materials and methods

Study sites

Four sites were used in this study (Table 1) located in, or adjacent to, Lomas Barbudal Biological Reserve in Guanacaste Province, northwestern Costa Rica (10° 30' N, 85° 23' W). Two sites were in the río Cabuyo: one was a wide, deep pool, referred to as the 'Cabuyo Pool' site (CabP); the other was a section of the río Cabuyo consisting of a series of small, shallow interconnected pools, referred to as the 'Cabuyo Stream' site (CabS). These sites were approximately 750 m apart. The same two habitat types were represented by two sites in the Quebrada Amores, a tributary of the río Cabuyo. These two sites were approximately 100 m apart and are referred to as the 'Amores Pool' (AmP) and 'Amores Stream' (AmS) sites. AmP was closed to immigration and emigration during the dry season by a 53 cm high waterfall at the inlet and a dense mat of leaf litter at the downstream edge. The AmS site contained three main pools separated from each other and adjacent pools by small outfalls and

Table 1. Physical and chemical descriptors of the study sites. SA = surface area; Vol = volume; \bar{Z} = mean depth; δZ = difference between seasonal extremes in water depth; DMax = mean daily maximum water temperature; DMin = mean daily minimum water temperature; pH; Alk = alkalinity; Hard = total hardness; D.O. = dissolved oxygen. Values are means for both years of the study.

	Quebrada Amores		río Cabuyo	
	Pool	Stream	Pool	Stream
SA (m ²)	345.7	319.3	286.4	227.1
Vol (m ³)	107.2	54.5	119.7	24.8
\bar{Z} (cm)	31.0	19.2	37.5	13.4
δZ (cm)	2.90	10.25	6.90	6.82
DMax (° C)	28.5	29.2	28.5	30.2
DMin (° C)	25.5	25.5	26.0	26.6
pH	6.6	7.0	7.8	7.7
Alk (ppm CaCO ₃)	127	121	107	110
Hard (ppm CaCO ₃)	77	73	64	63
D.O. (ppm)	7.7	8.5	9.8	9.6

a steep cascade. Both sites at the río Cabuyo were open to immigration and emigration.

The forest at Lomas Barbudal is a tropical dry forest, where four seasons are recognized based on seasonal fluctuations in rainfall: a long dry season (November to May); a long wet season (May to July); a short dry season (July and August) and a short wet season (August to October) (Frankie et al. 1974). Data for this study were collected during two long dry seasons, from January to June 1990, and December 1990 to June 1991.

Water conditions throughout the long dry season were stable. Water level, measured by benchmarks at each site, indicated daily water fluctuation (mean \pm SE) of only 0.1 ± 0.53 cm over the season. Fluctuations in daily maximum and minimum water temperatures were similarly stable among sites and over time. Typically, mean water temperatures cycled 3.2°C between a daily maximum of 29.0°C and a nocturnal minimum of 25.8°C (Table 1).

Sampling procedure

Each site was sampled at regular intervals (usually 5–7 days). At the beginning of the day, a complete survey of the site was conducted. The location of each spawning site (cave) was noted and marked with flagging tape or a painted stone. All breeding pairs were captured and marked after their young reached 5 mm standard length (SL), about three days after emergence from the spawning cave. A 10 m bag seine, dyed black to make it less conspicuous, was placed around the parents and the brood. The male was captured first by chasing him into the seine with a small hand net. Next, all the young were captured, using small hand nets, face-mask and snorkel. The female parent remained with the brood, often attacking the net or my hands. Any young that strayed always returned to the female. When all the young had been captured, the female was captured with a hand net.

I anaesthetized each parent with MS222 (tricaine methanesulfonate), measured its SL and gave it a unique mark by excising two dorsal spines in varying combinations (Rinne 1976). In the second season an anal spine was also removed to distinguish

fish marked in each season. The vertical dark bar patterns on the sides of convict cichlids are variable and sketches served as a quick and reliable method for identifying adults in subsequent samples without handling the fish. I counted the number of young in each brood and arbitrarily chose 15 which I anaesthetized with MS222 and measured their SL to the nearest 0.5 mm. When all fish had recovered from the MS222, the parents were gently released within the seine corral at the point of capture. Within 30 s, the female (and occasionally the male) began to search for the young. A clear plastic cylinder (diameter = 105 mm) was placed vertically with one end on the substrate. The young were released into the tube and they immediately swam to the substrate. The female and the young could see each other through the walls on the cylinder and responded by approaching each other. I gently raised the cylinder so that the female could join her young. Normal parental defence resumed immediately. The seine was then removed. The male parent often joined the female when the cylinder was lifted, or waited several minutes after the seine was removed. Controls testing for mortality caused by handling showed a loss of 0.78 ± 0.28 young (range 0 to 2, $n = 9$ broods) per sample.

Parental convict cichlids were captured once per brood cycle for marking. I recognized individual broods by the body markings of the parents, the location of the brood in the stream and the state of brood development. In 1990 and in 1991 I also collected 100 and 295 non-breeding adult convict cichlids at CabS and AmP, respectively. The SL of each fish in the sample was recorded. Sex was determined by examination of external features. Females have gold flecking on their abdomen and a yellow-orange flash on the dorsal fin located near the posterior of the fin. It was not possible to collect enough fish at AmS or CabP to adequately describe non-breeding fish at those sites.

Female convict cichlids adopted one of three colour phases: parental (contrasting black and white vertical bars), cryptic (dull olive background and grey vertical bars), and black (vertical bar patterns obliterated leaving other body pigments of yellow, orange and blue on a black background). Females of each colour phase were collected from the río Ca-

Table 2. Standard lengths (mm) of breeding female convict cichlids.

Site	Mean	SE	Min	Max	Range	n
1990						
AmP	54.7 ^a	0.55	48	61	13	34
CabP	42.3 ^b	1.33	34	63	29	27
AmS	54.4 ^a	0.95	49	59	10	13
CabS	51.1 ^a	1.30	44	61	17	13
1991						
AmP	52.6 ^d	0.69	47	62	15	24
CabP	44.6 ^f	0.67	37	53	16	42
AmS	52.4 ^d	0.59	45	60	15	34
CabS	49.1 ^e	0.67	41	59	18	57

Shared superscripts denote means that do not differ ($p > 0.05$) within each year (Student-Newman Keuls multiple comparison test).

buyo in March 1990 outside the study areas, and the developmental state of their ovaries were examined.

Variation is always expressed as standard error (SE) of the mean.

Results

Size of breeding fish

In both years, SL of breeding females was significantly smaller at the río Cabuyo sites (ANOVA 1990: $F = 36.15$, $p < 0.001$; 1991: $F = 27.35$, $p < 0.001$), particularly at CabP (Table 2). Overall, the difference between the smallest and largest breeding females averaged 13.25 ± 1.18 mm ($n = 4$, 2 years \times 2 sites) at Quebrada Amores and 20.0 ± 3.03 mm ($n = 4$) at río Cabuyo. There were no significant differ-

ences in SL of breeding males among sites in 1990 (ANOVA, $F = 1.52$, $p = 0.216$), but in 1991 males at AmP were significantly larger than males at the other three sites (ANOVA, $F = 4.82$, $p < 0.001$; Table 3). The mean size range of breeding males was 12.75 ± 1.31 mm ($n = 4$) in sites at Quebrada Amores, and 17.25 ± 1.55 mm ($n = 4$) in sites at río Cabuyo.

Size-assortative pairing was evident at three of the four study sites (Fig. 1). The regression of \ln female SL on \ln male SL was significant at CabP ($df = 67$, $r^2 = 0.29$, $p < 0.001$), AmS ($df = 42$, $r^2 = 0.21$, $p = 0.002$) and CabS ($df = 65$, $r^2 = 0.22$, $p < 0.001$) but not at AmP ($df = 53$, $r^2 = 0.03$, $p = 0.199$). In all but one pair ($n = 249$), male SL was larger than female SL (Fig. 2). On average, males were 13.2 ± 0.4 mm larger than their mates, ranging from -1 mm to $+31$ mm with a mode at 10 mm, except at CabP site where the small size of breeding females resulted in

Table 3. Standard lengths (mm) of breeding male convict cichlids.

Site	Mean	SE	Min	Max	Range	n
1990						
AmP	63.3 ^a	0.54	57	70	13	34
CabP	63.8 ^a	0.89	55	74	19	29
AmS	63.7 ^a	0.74	60	69	9	11
CabS	66.1 ^a	1.14	60	73	13	11
1991						
AmP	65.0 ^b	1.04	58	73	15	21
CabP	62.6 ^c	0.76	51	71	20	43
AmS	60.6 ^c	0.59	55	69	14	33
CabS	61.9 ^c	0.52	54	71	17	57

Shared superscripts denote means that do not differ ($p > 0.05$) within each year (Student-Newman Keuls multiple comparison test).

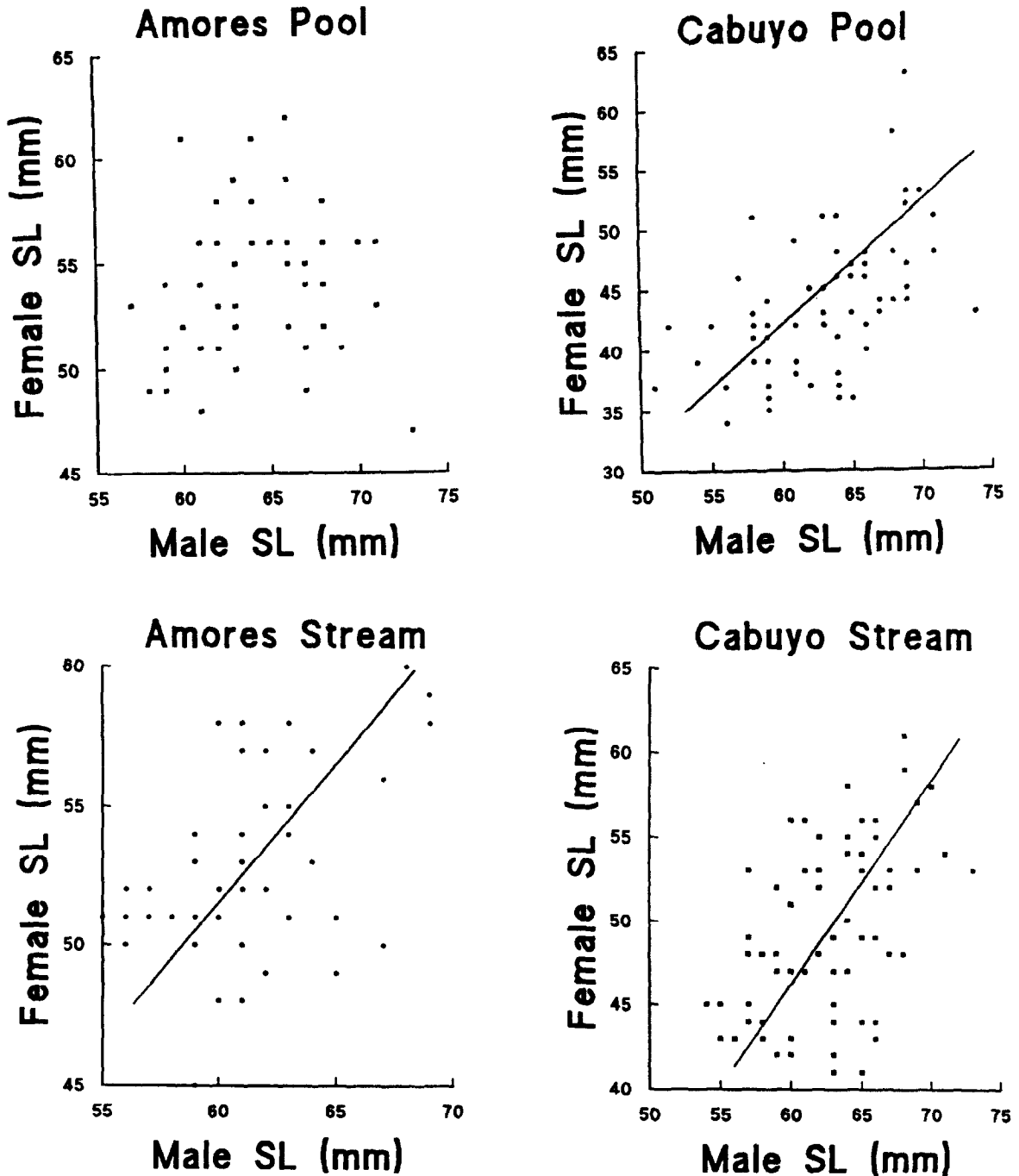


Fig. 1. Standard length of male and female convict cichlids within mated pairs at the four study sites. Data from 1990 and 1991 are combined.

a modal intra-pair size difference of 18 mm (ANOVA, $F = 61.50$, $p < 0.001$). A multiple comparison of mean intra-pair size difference among sites showed CabP > CabS > AmP = AmS (Student-Newman Keuls, $p < 0.05$). There were no consistent seasonal

trends in the size of breeding males or females at any site.

Breeding females were significantly larger than females in the non-breeding stock at AmP ($t = 8.48$, $p < 0.001$; Fig. 3) but not at CabS ($t = 1.61$, $p = 0.109$).

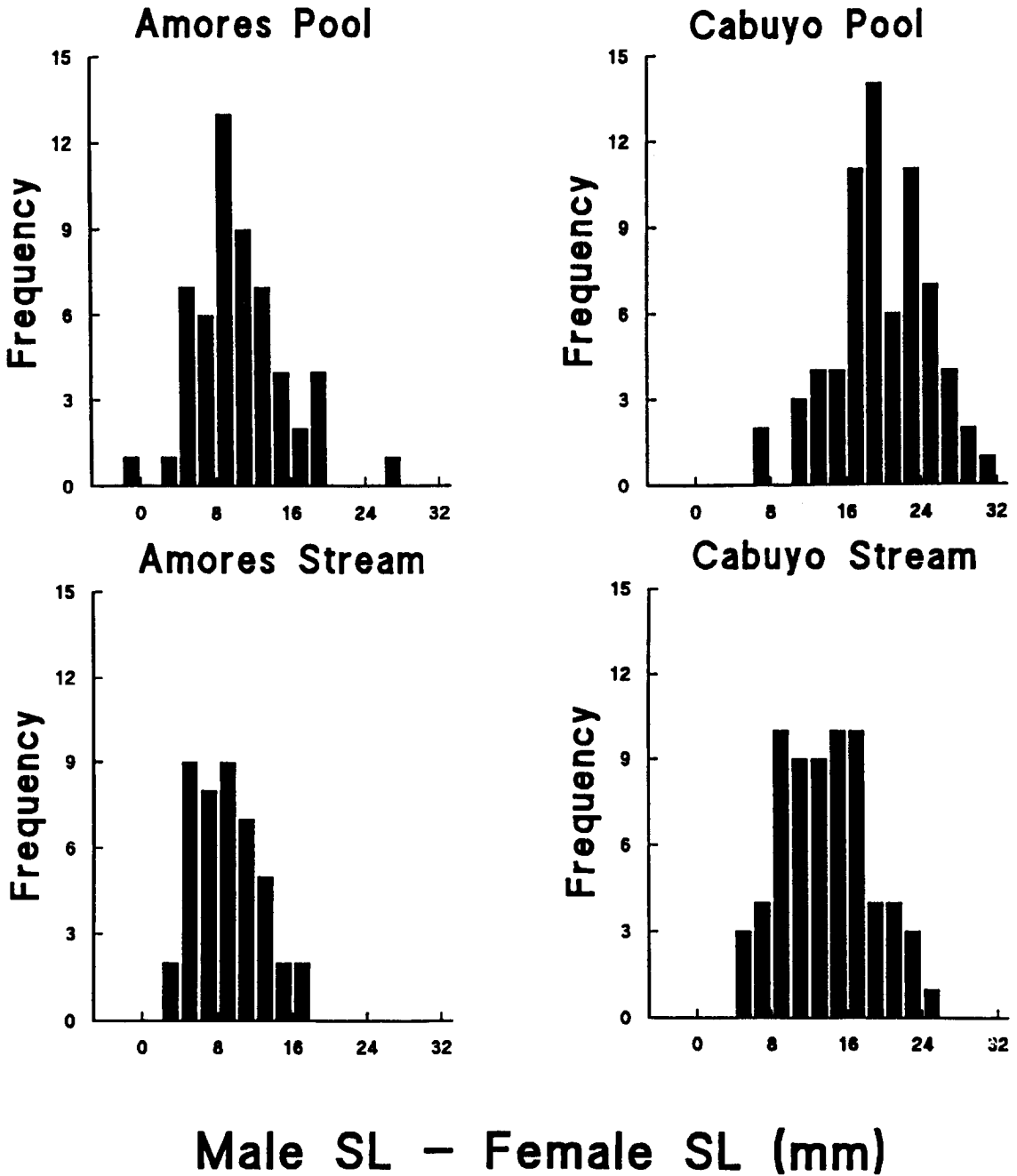


Fig. 2. Frequency-distribution of intra-pair size differences (male SL minus female SL) for each site. 1990 and 1991 data combined.

At AmP and CabS, breeding males were significantly larger than males in the non-breeding stock (AmP: $t = 11.53$, $p < 0.001$; CabS: $t = 8.50$, $p < 0.001$) indicating that small males did not breed (Fig. 4).

Seasonal mating frequencies

There was a significant sex difference in seasonal mating frequencies. Breeding males attempted 1.34 ± 0.05 ($n = 175$) broods within a season compared to 1.05 ± 0.01 ($n = 230$) broods by breeding females ($t = 5.95$, $p < 0.001$). Males attempted up to

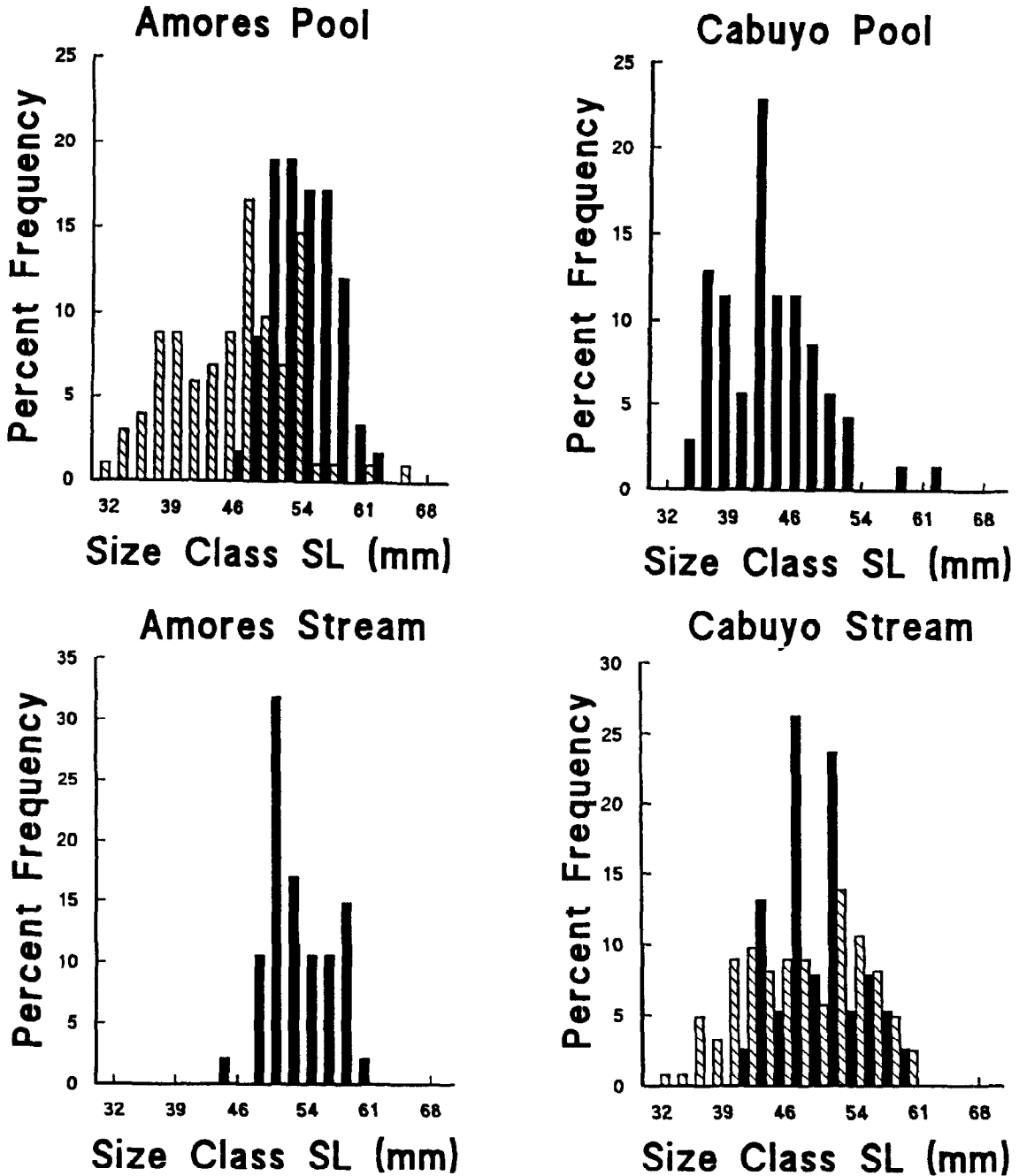


Fig. 3. Length-frequency distributions of breeding (solid bars) and non-breeding (hatched bars) female convict cichlids.

four broods within a season; 28% of breeding males bred more than once. Generally, breeding females attempted a single brood per season; only 5% attempted a second brood. For 58 out of a total of 59 repeat spawning attempts, males and females re-spawned with a new partner.

Females that bred twice within a season were sig-

nificantly larger than those that bred only once for 5 out of 5 site-years in which females spawned more than once (Table 4; one-tailed binomial test $p = 0.031$). Among males there was no significant difference (ANOVA, $p > 0.05$) in SL, either overall or within each site, between males that remated within a season and males that did not. During the second

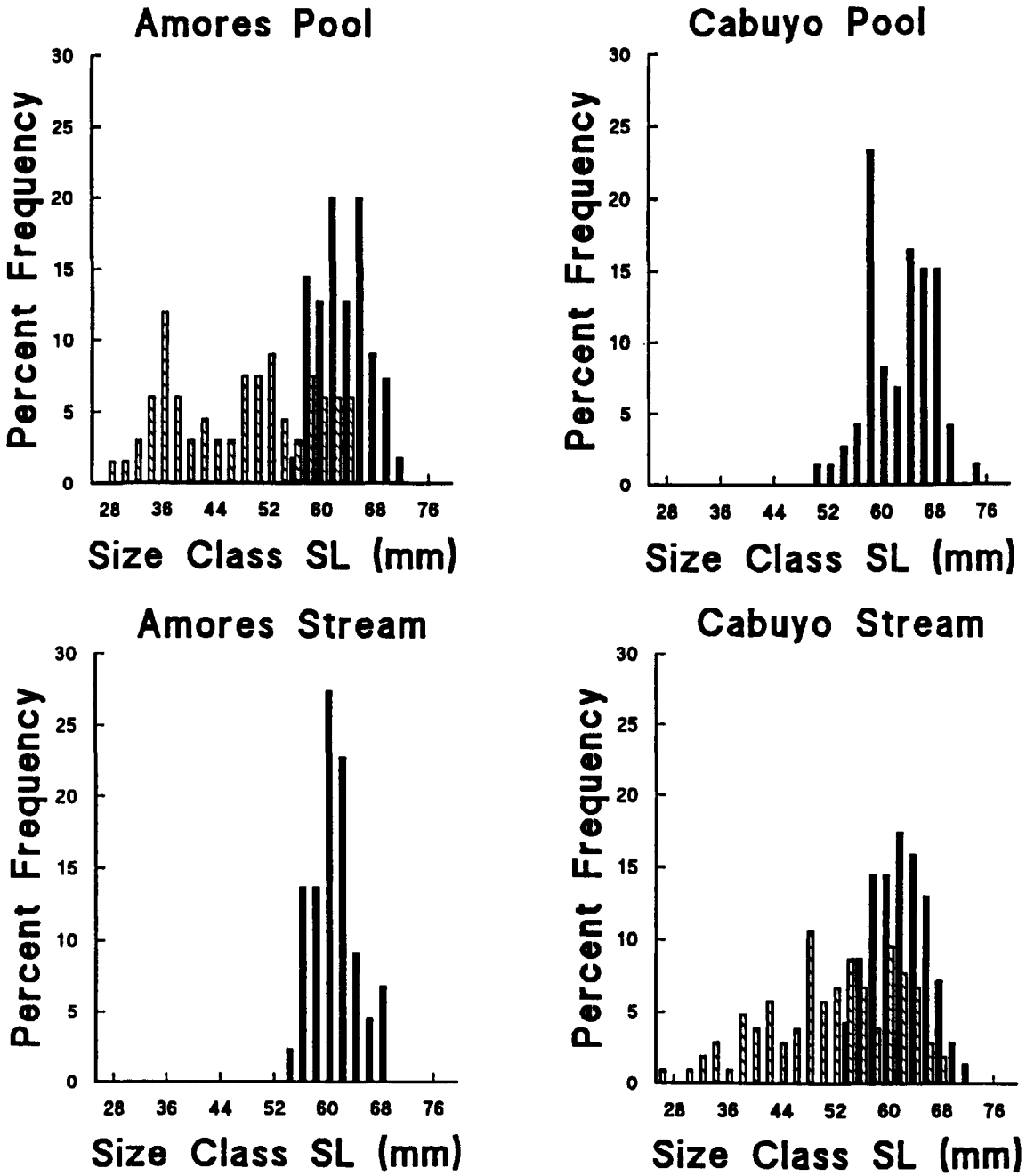


Fig. 4. Length-frequency distributions of breeding (solid bars) and non-breeding (hatched bars) male convict cichlids.

field season 15.6% of breeding males and 13.0% of breeding females had dorsal spines that were clipped the previous year. The spines had partially regenerated by the second year of the study. Thus, estimates of the proportion of the breeding stock that bred in more than one season may be conservative because spines that had completely regenerat-

ed may not have been recorded. However, these data establish that at least some members of both sexes breed in at least two successive dry seasons, within the same section of stream. The number of seasons in which individual convict cichlids are reproductively active remains unknown.

Interspawning intervals were significantly longer

Table 4. Mean standard length (mm) of males and females by breeding frequency (BFR) at each site within a season.

	AmP			CabP			AmS			CabS		
	\bar{X}	SE	n	\bar{X}	SE	n	\bar{X}	SE	n	\bar{X}	SE	n
BFR	1990 Males											
1	62.3	0.8	16	63.3	1.5	16	64.0	1.4	6	65.3	1.5	8
2	63.8	1.0	6	62.6	1.7	5	63.0	0	1	–	–	0
3	64.5	2.5	2	66.0	0	1	63.0	0	1	67.0	0	1
	1991 Males											
1	62.9	1.3	10	61.2	1.2	22	61.6	1.3	13	63.5	1.1	17
2	65.3	3.5	3	63.2	2.0	6	59.6	1.1	5	60.1	4.0	9
3	71.0	0	1	–	–	0	–	–	0	61.8	1.7	5
4	–	–	0	64.0	0	1	59.5	1.5	2	–	–	0
	1990 Females											
1	54.6	0.6	30	42.3	1.3	27	54.4	1.0	13	50.8	1.5	11
2	56.0	0	1	–	–	0	–	–	0	52.0	0	1
	1991 Females											
1	52.6	0.7	24	43.2	0.7	30	52.4	0.7	30	49.0	0.7	53
2	–	–	0	47.5	1.5	6	52.5	0.7	2	53.0	0	1

for females than for males and longer in 1991 than in 1990 for both sexes (ANOVA, sex: $F = 42.48$, $p < 0.001$; year: $F = 4.42$, $p = 0.037$; site: $F = 1.24$, $p = 0.300$; Table 5). There was no effect of site and there were no significant interactions. Male interspaw-

Table 5. Mean interspawning intervals (ISI) in days for male and female convict cichlids.

Year	Site	Males			Females		
		Mean	SE	n	Mean	SE	n
1990	AmP	34.1	5.0	10	78.0	0	1
	CabP	39.8	7.4	7			0
	AmS	40.3	1.5	3			0
	CabS	32.0	1.7	2	64.0	0	1
	Total	36.5	3.2	22	71.2	7.2	2
1991	AmP	46.0	12.9	5			0
	CabP	45.7	6.6	11	96.1	8.9	6
	AmS	39.6	5.1	11	96.6	1.5	2
	CabS	59.0	6.3	17	100.6	0	1
	Total	49.4	3.6	44	96.7	5.8	9

ISI	1 st → 2 nd brood			2 nd → 3 rd brood			3 rd → 4 th brood		
	Mean	SE	n	Mean	SE	n	Mean	SE	n
Males	47.1	3.3	49	40.2	4.6	14	34.7	12.7	3
Females	92.1	5.7	11						

ing intervals for each interval (from first to second, second to third, and third to fourth broods within a season) were not significantly different (ANOVA, $F = 0.86$, $p = 0.427$).

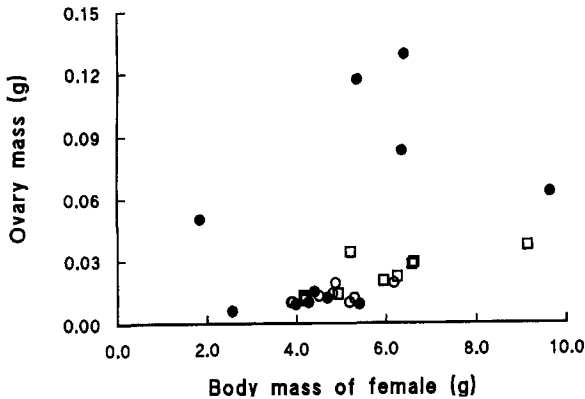


Fig. 5. Ovary mass compared to total body mass for females of three colour phases. Open squares = brood guarding females with contrasting black and white pattern; open circles = non-breeding females with dark grey bars on grey background; solid circles = non-breeding females in black colour phase.

Female colour phases

Convict cichlids do not conform to the most common pattern of sexual dichromatism in fishes in which males are more brightly coloured than females. Non-breeding adult convict cichlids of both sexes have dark grey or black vertical bars on each side against a light grey background. In addition, females have gold flecks on the abdomen, and iridescent blue, orange and yellow hues on the throat and chin, dorsal and anal fins (Bussing 1987). Among females there were three variations in intensity of the grey and black patterns. Parental (i.e. brood-guarding) females had a white background and intense black bars, producing a pattern of starkly contrasting black and white vertical bars on each side. Most non-breeding females had dark grey bars on a pale olive-grey background.

Some non-breeding females were black overall, with no visible lateral bars. The bright colours on their abdomen and fins were displayed to full effect when contrasted against a solid black background. Black phase females actively courted males, including mated males guarding a brood with another female. When black phase females formed a pair bond with a male and spawned, their colouration changed to the black and white parental pattern. Males were never observed in the black colour phase.

Ovary mass, in relation to total body mass, of about half of the black phase females sampled, was

much higher than that of females of the other two colour phases (Fig. 5).

Data on seasonal variation in the prevalence of black colour phase females were collected at four sites in 1991: AmP, CabS and at the río Tenorito and río Potrero. The Tenorito and Potrero rivers are part of the same watershed as the study sites (río Tempisque). On average, black phase females represented 21.5% ($n = 195$) of non-breeding adult females, declining during the dry season from 27.1% in January to 14.9% by late May.

Influence of spawning site

Possession of a good spawning cave may be important to breeding pairs long after the embryos have hatched. Convict cichlid families consistently returned to their spawning cave to take shelter during the night (Wisenden 1994a). Typically the male was stationed just outside the entrance and the female was further inside, close to the young. This behaviour is presumably an anti-predator tactic that makes it more difficult for the young or parents to be captured by nocturnal predators.

Both sexes participated in cave guarding behaviour during the day. Throughout the day, parental convict cichlids shepherded their school of young along the stream bottom, moving up to 13.7 m (mean = 1.48 ± 0.04 m, $n = 429$) from the cave in which the brood had been incubated. One parent often left the vicinity of the brood to chase off brood predators, forage, or to return to the cave where the brood was deposited. Parents took turns leaving the brood so that it was never left unguarded. While visiting the cave the parent chased away all conspecifics that were in or near it. Visits to the spawning cave were performed 0.67 ± 0.05 ($n = 155$) times per 10 min by male parents and 0.44 ± 0.04 ($n = 161$) times by female parents. Cave visiting frequency differed by site but not by sex in 1990 (ANOVA, site: $F = 3.06$, $p = 0.030$; sex: $F = 3.19$, $p = 0.076$) and 1991 (ANOVA, site: $F = 7.96$, $p < 0.001$; sex: $F = 0.33$, $p = 0.566$).

In addition to providing shelter for the brood at night, spawning caves were often reused by individual fish in subsequent breeding attempts (Fig. 6a).

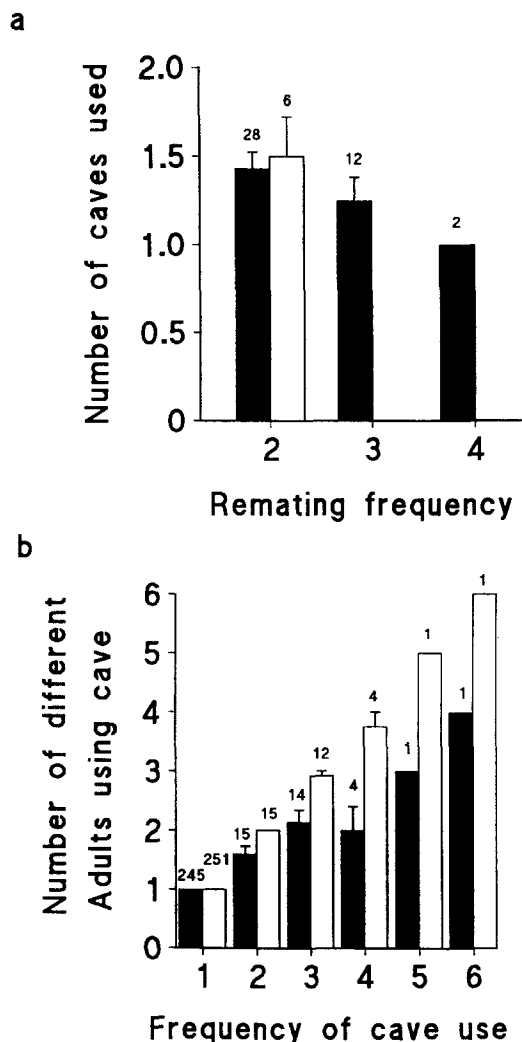


Fig. 6. a – Mean number (+ SE) of different spawning caves used by females (open bars) that attempted two broods, and by males (solid bars) that attempted two, three and four broods within a 5–6 month breeding season. Numbers above bars, sample size. b – Mean number (+ SE) of different adult convict cichlids spawning in caves that were used up to six times within a breeding season. Females, open bars; males, solid bars. Numbers above bars, sample size.

Some caves were used up to 6 times by different pairs of convict cichlids within a season (Fig. 6b).

Discussion

Size of breeding fish

The mean size of breeding convict cichlids reported

here was larger than those breeding in Lake Jiloá, Nicaragua (McKaye 1986). Mean SL of breeding males and females at the sites in Lomas Barbudal was 62.8 ± 0.3 mm (51–74, $n = 239$) and 49.6 ± 0.4 mm (34–63, $n = 244$) respectively, compared to 55.1 mm (34–66 mm, $n = 36$) and 33.1 mm (17–47 mm, $n = 36$) in Lake Jiloá. There may be greater food availability or greater competition for nesting sites in Costa Rican streams than in Lake Jiloá. Alternatively, intense predation pressure on adults in Lake Jiloá may select for individuals that become sexually mature and breed at a relatively small size. This phenomenon occurs among populations of Trinidadian guppies that differ in predation pressure (Reznick 1982). Unfortunately, the age distribution and size at maturity of convict cichlids in these two populations are not known.

Size assortative pairing occurs in a variety of Central American cichlids in Lake Jiloá, Nicaragua (McKaye 1986), Gatún Lake, Panama (Perrone 1978) and in outdoor experimental ponds (Keenleyside 1985). In the laboratory, female convict cichlids prefer to mate with large males (Noonan 1983, Keenleyside et al. 1985) and males prefer large females over small females when both are gravid, and ignore size when choosing gravid females over non-gravid females (Nuttall & Keenleyside 1993). Large females have more eggs than small females (Bagenal & Braum 1978, Perrone 1978, Townshend & Wootton 1984, 1985) and may be more effective at brood defence. An analysis of the factors affecting reproductive success in these populations showed that large females start with more young than small females and that large parents of both sexes are more effective defenders of young than small parents (Wisenden 1994b). Thus, there are fitness benefits for males mating with large females.

There are also fitness benefits for females that mate with large males (see Turner 1993, his Table 10.1 for review of noncichlids). Small males were excluded from breeding at both sites where data are available for comparison, suggesting that male-male competition occurred. Small firemouth cichlids, *Cichlasoma meeki*, of both sexes do not breed in Laguna Bacalar, Mexico (Neil 1984). Large male *Herotilapia multispinosa* and *Cichla ocellaris* get the best spawning sites (Baylis 1974, Zaret 1980)

and large *Cichlasoma maculicauda* secure the best feeding territories (Perrone 1978).

Generally, males are larger than their mates within pairs of biparental cichlids (Barlow 1974, Perrone 1978, Itzkowitz & Nyby 1982, Neil 1984, McKaye 1977, 1986). It is not clear if the consistent intra-pair size difference observed in pairs of convict cichlids in this study confers some selective advantage to one or both sexes. Neil (1984) observed an intra-pair size difference in pairs of *C. meeki* of about 10 mm, closely matching the intra-pair size differences of convict cichlids at three of the four sites in this study. Cave spawning precludes sperm competition as a selective force promoting sexual dimorphism in this species and biparental care should select for sexes of similar size (Parker 1992). Other factors that may influence sexual dimorphism such as growth and mortality rates for each sex are not known for this species. Future research into these phenomena would be rewarding.

Seasonal mating frequencies

Only five percent of females bred more than once within a season and the maximum was twice (Table 4, 5). In contrast, females in laboratory aquaria breed repeatedly, with interspawning intervals as short as 12–13 days (Wisenden 1993). Food limitation could constrain female reproduction in the field. Although food in the field may be of lower quality than commercial cichlid pellets fed to fish in the laboratory, pairs of convict cichlids are capable of bringing two broods to independence within 9 weeks in the University of Western Ontario outdoor experimental ponds where no supplemental food is provided (Keenleyside personal communication). Convict cichlids in Lake Jilóá do not appear to be food limited (McKaye 1977) however, seasonal mating frequencies from this location are not known. A food supplementation experiment in the field would provide an interesting test of this hypothesis.

Social factors are probably at least partially involved in constraining female reproduction in nature. Females take longer to replace their gametes than males because eggs are energetically more ex-

pensive than sperm (Baylis 1981). When a brood cycle is completed (i.e. either the young reach independence and disperse or the brood fails), a male achieves higher reproductive success by pairing with a new female that is reproductively ready rather than waiting for his current mate to produce a second clutch of mature ova.

The overall sex ratio was significantly different from 50:50 in favour of females at AmP (total of three samples = 66M:103F, $X^2 = 8.101$, $p = 0.005$) but not at CabS (total of five samples = 104M:123F, $X^2 = 1.590$, $p = 0.221$; Wisenden 1994a). If the operational sex ratio was female-biased or the number of males available to breed was limited by male-male competition, then male choice for large females, or female-female competition could be responsible for the smallest females not breeding. In this study, small females (< 50 mm SL), which presumably were physiologically capable of breeding, were excluded from doing so at the site where females were more abundant than males. Small females bred at the sites in the río Cabuyo (especially CabP) but they were not well represented in the breeding stock at sites in Quebrada Amores (Fig. 3). Female-female competition occurs in convict cichlids in Lake Jilóá (McKaye 1986). The breeding system of Midas cichlids, *Cichlasoma citrinellum*, seems to be driven by female choice (Rogers & Barlow 1991). Male Midas cichlids do not exercise mate choice on the basis of size, aggression or experience, either because they do not have the opportunity or because there is no benefit to choosiness.

Female colour phases

About half of the black phase females collected from the field did not have mature ova (Fig. 5). I did not observe the behaviour of these females prior to capture. Perhaps some females adopt the black colour phase before their ova are fully mature. The presence of mature ova in only those females in the black colour phase but not in females of other colour phases, the seasonal decline in the proportion of females in black colour phase and the enhancing effect of a black background on other body pigments all suggest that the black colour phase plays a

role in courtship. Colour change corresponding with reproductive readiness occurs in females of many fish families in addition to the Cichlidae, usually in species in which the male provides care for the young (for review see Turner 1993, his Table 10.2). Other examples of female nuptial colouration not listed in Turner (1993) are the cichlids: *Hemichromis fasciatus* (Burchard 1967), *Tilapia zillii* (Fryer & Iles 1972), *Herotilapia multispinosa* (Baylis 1974), *Cichlasoma citrinellum* (Baylis 1975), *Aequidens portalegrensis* (Baerends 1984), *Chromidotilapia guentheri* (Baerends et al. 1986), and sunfishes (Centrarchidae): *Lepomis gibbosus* (Stacey & Chiszar 1977), *Micropterus dolomieu* (Ridgway et al. 1989), and a stickleback (Gasterosteidae) *Culaea inconstans* (Winn 1960, McLennan 1994).

Influence of spawning sites

Suitable spawning sites may limit reproduction in cichlids (McKaye 1977, Zaret 1980, Itzkowitz & Nyby 1982). Cave guarding behaviour by both sexes and the use of spawning caves for night shelter and later breeding efforts (Fig. 6) suggest that suitable spawning caves may be an important resource affecting the mating system of this species. The mating system appears to be monogamous (but see Keenleyside et al. 1990, Wisenden 1994a), tending towards resource defence (serial) polygyny (Emlen & Oring 1977). Males may establish territories first before beginning to court females (Baylis 1974, Perrone 1978), or pairs may form first then obtain a breeding territory together (McKaye 1977, Itzkowitz & Nyby 1982, Mackereth & Keenleyside 1993), or a combination of these two styles may occur (Neil 1984, Zaret 1980, Rogers & Barlow 1991, this study).

The size distribution of breeding and non-breeding females, the colourful courtship phase and the differential seasonal mating frequency between the sexes suggest that females compete for access to large males because large males that possess good nest sites may be limiting, skewing the operational sex ratio. Females may be attracted to mated males because males often reuse the same spawning cave with a new female after the current brood cycle.

Other cichlid researchers working in the field have observed that mated males court unmated females in convict cichlids (Meral, cited in Barlow 1974), *Aequidens coeruleopunctatus* (Barlow 1974) and *Cichlasoma panamense* (Townshend & Wootton 1985). Males may accept females that indicate their readiness to spawn by their dark nuptial colouration.

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