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Effect of Mate Removal on Current and Subsequent Parental Care in the Convict Cichlid (Pisces: Cichlidae)

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Abstract

In most biparental, substrate-brooding species of cichlid fishes, female and male roles differ. Females are usually more involved in direct care of the young while males spend more time away patrolling the territory. This study tested the flexibility of these sex roles with removal experiments in the convict cichlid, *Cichlasoma nigrofasciatum*. When males were removed, female fanning activity increased. When females were removed, males spent more time fanning and less time away from the brood. Other behavioural variables (frequency of digging, mouthing, foraging and retrieving) were not affected. Being alone or paired during a first breeding episode did not affect parental behaviour during a subsequent episode in which all fish were paired. Observations were carried out during the day and at night, and nocturnal fanning of fry is reported here for the first time. Female role appears less flexible than male role, as befits the more direct care normally given by females.

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Introduction

Among fishes, the family Cichlidae distinguishes itself by the prolonged care given to embryos and larvae (KEENLEYSIDE 1991). In substrate brooders (as opposed to mouthbrooders), this care is almost invariably biparental, that is both male and female care for the young. Male and female roles differ, however. Usually, females are more involved with direct care of the eggs while males spend more time away from the brood, patrolling the brood-rearing territory (KEENLEYSIDE 1991). Although this pattern is generalized across species, there is still little information about the flexibility of sex roles within a given species (exception: MROWKA 1982), yet there are situations in nature where flexibility in parental care may be required.

Several studies have shown that the mating systems of biparental cichlids are flexible (Barlow 1991). Generally monogamy is the rule, but a female-biased sex ratio (*Herotilapia multispinosa* and *Cichlasoma nigrofasciatum*, Keenleyside 1983, 1985; *Cichlasoma panamense*, Townshend & Wootton 1985) and low predation rates (Townshend & Wootton 1985) can lead to polygyny. Cichlid males can either desert their mate and respawn with a new female (sequential polygyny) or breed with two females at the same time (bigamy: simultaneous polygyny; Keenleyside et al. 1990). Such a system arises because females are limited by time and energy constraints and males are only limited by the number of matings they can achieve (Barlow 1991). Therefore, males may achieve higher reproductive success if they desert their first brood and start another with a new female than if they remain monogamous. Keenleyside (1985) has shown that bigamous males fathered more offspring than monogamous males. However, the benefits of mate desertion may only exist if the first brood survives; therefore, males should only desert if environmental pressures are minimal (e.g. low predation) and the first brood is likely to survive under the care of a lone mother.

If the male deserts, the male may benefit but females may suffer a cost in future reproduction (Williams' principle; Sargent & Gross 1986). Townshend & Wootton (1985) have shown that deserted *C. panamense* females spent less time away from the brood, chased more intruders and lifted more leaves for their young than mated females. Similarly, deserted convict cichlid females attacked intruders more and spent less time away from the brood; consequently they spent less time foraging than paired females (Keenleyside et al. 1990). Because deserted females spend more energy caring for the current brood, they may suffer higher mortality or a decrease in somatic growth and future reproduction than paired females.

The purpose of this study is to investigate the effects of mate removal on current and future parental care by male and female convict cichlids. Although females are deserted more than males in the wild, males may also be deserted if their mate is taken by a predator or is killed while defending the brood. Because males generally do not participate in direct care (i.e. fanning), we were interested in determining if lone males would compensate for the absence of the female.

We also observed the behaviour of the lone parents during a subsequent breeding episode (in which they remained paired with their partner) to determine whether sex roles could be affected by a fish's previous experience as a lone or paired parent. If males and females increase their effort during a breeding attempt, they may become more committed to future broods because of a potential decline in future reproduction. As recent evidence has been discovered about the importance of nocturnal care in cichlids (Reebs & Colgan 1991), we observed the behaviour of parents during the day and night.

Methods

Fish and Aquaria

Initially all fish used in this study were inexperienced breeders. The stock originated in Costa

Table 1: Parental weight (g), total length (cm) and number of fry in each experimental group. x̄ ± SE
are presented (n = 10)

		Control	Male removal	Female removal
Male				
	Weight	8.4 ± 0.7	8.2 ± 0.7	9.9 ± 0.7
	Length	7.9 ± 0.2	7.7 ± 0.2	8.2 ± 0.2
Female				
	Weight	5.7 ± 0.7	5.7 ± 0.5	5.8 ± 0.3
	Length	6.8 ± 0.2	6.7 ± 0.1	6.8 ± 0.1
No. of fry				
	Episode 1	227 ± 24	171 ± 29	186 ± 27
	Episode 2	232 ± 36	184 ± 22	261 ± 24

Rica, was 5–6 generations removed from the wild, and had been outcrossed with fish from local pet stores. The fish were held in large holding tanks ($122 \times 46 \times 46$ cm) before being put in the observational tanks.

The observational tanks measured $52 \times 26 \times 30$ cm (41 l). Each tank contained an airstone, a clay flower pot for spawning and gravel. The water was kept at 26 °C by a room heater and lighting was provided by incandescent bulbs on a 12:12 h light:dark cycle.

To facilitate pair formation, females were added to the observational tanks 3–4 d before males. After being weighed to the nearest mg and measured to the nearest mm (total length), males and females were randomly assigned to each other and to each group. Each fish was fed a pellet of food a day (Tropic Aquaria Ltd, stock no. A149).

Experimental Groups

We had three groups with 10 pairs in each: male removal (MR), female removal (FR) and control (C). One day after spawning, males (MR) and females (FR) were removed and their mates remained alone with the brood for the rest of the breeding episode. Control males and females were disturbed by placing a net in their tank, after which they were left together. Episode 1 lasted until 6 d into the fry stage, at which time the parent(s) and fry were removed and fry were counted. Approximately 1 wk later, males and females in the removal groups were given a new partner that had bred once before. Control males and females were also given a new partner, but the partner was previously in the control group; in effect, males and females in the control group were swapped. All these new pairs were left intact throughout the ensuing breeding episode (2). The experiment was stopped after 6 d into the fry stage of episode 2. All fry were removed and counted.

There were no significant differences between lone and paired parents in body size (male weight: $F = 2.10$, $p = 0.142$; male total length: $F = 1.58$, $p = 0.225$; female weight: $F = 0.024$, $p = 0.976$; female total length: $F = 0.24$, $p = 0.785$; Table 1). Brood size also did not differ among groups (first breeding episode: $F = 1.16$, $p = 0.328$; second breeding episode: $F = 1.91$, $p = 0.167$, Table 1).

Observation Periods and Defence Test

For each group and breeding episode, we videotaped parents during the day and night at four different stages of the breeding cycle: egg (embryo), wriggler (free-embryo), d 2 fry (larvae), d 5 fry (larvae). From the 15-min observation periods, we quantified the following behaviour patterns: time spent two body lengths away from the brood; time spent fanning; and the frequency of digging, of mouthing eggs and wrigglers, of foraging and of retrieving fry (KEENLEYSIDE 1991). While fanning, the parent rhythmically beats the caudal, soft dorsal, and pectoral fins while positioned less than one body length from young. The amplitude of the fin beats is unmistakably larger than when the fish is merely stationary.

Night observations were made using infrared light (a bank of 36 light-emitting diodes) and an

infrared-sensitive camera (Sony CCD, Fuhrman Diversified Inc., LaPorte, TX). Convict cichlids cannot see infrared light (SCHWANZARA 1967). Observations took place 3 h after night onset (at the fry stage, this gave the parent(s) enough time to retrieve all their young in a central place, usually the flower pot, where they were cared for). No digging, mouthing, foraging or retrieving took place at night, so only fanning and time spent away from young were scored.

During the day on day 6 for both breeding episodes, we presented a model predator, *Gobiomorus maculatus*, 12.6 cm long, to all groups. The predator was a preserved specimen that had been filled with silicone and later covered with clear enamel; glass eyes were glued into the eye sockets. It was suspended from the top of the aquarium and presented 10 cm away from the brood for 1 min. We videotaped the defensive behaviour of the parents during this minute and later scored the following behaviour patterns: time spent two body lengths away from the brood and predator, bites, total displays (frontal displays and headshakes) and the latency to display at the model predator (LAVERY & COLGAN 1991).

Data Analysis

We used ANOVAs with two repeated measures to analyse the behavioural data. For each breeding attempt, our independent factor was group (control, male and female removal). The two repeated factors were time of day (day vs. night) and stage (egg, wriggler, day 2 fry, day 5 fry). Because of the number of factors and a problem of independence, we analysed the sexes separately for each of the above factors. For each breeding episode, lone males and females were compared with control males and females, respectively.

Time of day was added to the statistical model only for behaviour patterns that occurred during both the day and night, i.e. time away from brood and time fanning. Moreover, because fry were never fanned during the day, the fry stage was not included in the statistical comparisons of day and night fanning.

Defensive behaviour was analysed with t-tests within each breeding episode and between episodes.

Results

Effect of Mate Removal on Care: Episode 1

During the first breeding episode, lone females fanned more than paired females (F = 6.26, p = 0.024, Fig. 1a). No other differences were found between lone and paired females. The two groups did not differ in time spent away from the brood (F = 4.05, p = 0.063, Fig. 2a). For the behaviour patterns that only occurred during the day (frequency of digging, foraging, mouthing eggs and wrigglers, and retrieving fry), lone females did not differ from paired females (Table 2 gives p values). During the defence test, lone females did not differ from paired females in any of the behaviour patterns measured (Table 3 gives p values).

Lone males fanned more (F = 12.52, p = 0.003, Fig. 3a) and spent less time away from the brood than paired males (F = 6.60, p = 0.021, Fig. 4a). However, they did not differ in the frequency of digging, foraging, mouthing eggs or wrigglers, and retrieving fry (Table 4 gives p values). During the defence test, lone males did not differ from paired males in the frequency of displays, the latency to display, and the time spent away from the brood and predator (Table 5 gives p values). However, whereas none of the paired males bit the predator model, 4 of the 10 lone males did.

Effect of Mate Removal on Subsequent Care: Episode 2

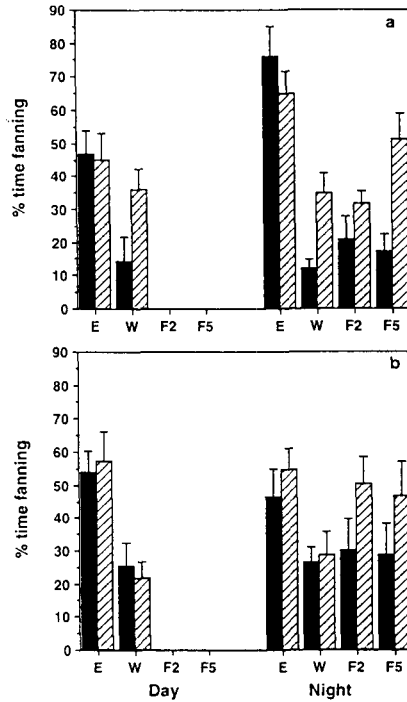Mate removal during episode 1 had little effect on female and male care during

Fig. 1:   Mean (±SE, n = 10) % time spent fanning by females during breeding episodes 1(a) and 2(b). Both day and night data are presented. Black bars = control (paired) females; hatched bars = lone females. E = egg, W = wriggler, F2 = d 2 fry, F5 = d 5 fry

episode 2. Females and males that were previously alone did not differ from previously paired females and males, respectively, in time spent fanning (females: F = 0.08, p = 0.785, Fig. 1b; males: F = 0.45, p = 0.511, Fig. 3b) and in time spent away from the brood (females: F = 0.00, p = 0.983, Fig. 2b; males: F = 2.14, p = 0.162, Fig. 4b). They also did not differ in behaviour patterns that occurred only during the day: digging, foraging, mouthing eggs and wrigglers, and retrieving fry (female p values in Table 2; male p values in Table 4). Control and ex-lone parents also did not differ in defensive behaviour (females: Table 3; males: Table 5).

Day–night and Stage Effects for Each Episode

There was a significant interaction between time of day and stage in the time females and males spent away from the brood for episode 1 (females: F = 11.57, p = 0.001, Fig. 2a; males: F = 22.05, p = 0.001, Fig. 4a) and episode 2 (females: F = 7.54, p = 0.001, Fig. 2b; males: F = 42.55, p = 0.001, Fig. 4b); during the day, females and males spent less time away from the brood as it aged but stage had no effect on the time spent away during the night. During episode 1, females and males fanned more at night than during the day (females: F = 6.37, p = 0.023,
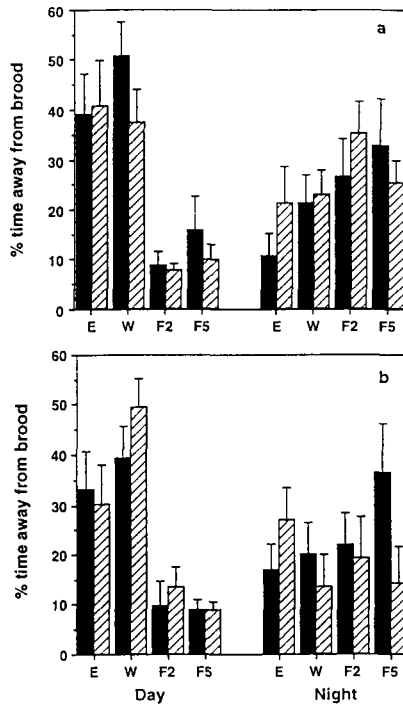
Fig. 2: Mean (±SE, n = 10) % time spent away from brood by females during breeding episodes 1(a) and 2(b). Both day and night data are presented. Black bars = control (paired) females; hatched bars = lone females. E = egg, W = wriggler, F2 = d 2 fry, F5 = d 5 fry

Fig. 1a; males: F = 10.40, p = 0.005, Fig. 3a). During episode 2, only males fanned more at night than during the day (F = 8.71, p = 0.009, Fig. 3b). However during both episodes, fanning levels of both sexes changed with stage; the time spent fanning decreased for females (episode 1: F = 28.36, p = 0.001, Fig. 1a; episode 2: F = 25.39, p = 0.001, Fig. 1b) and increased for males (episode 1: F = 18.79, p = 0.001, Fig. 3a; episode 2: F = 5.08, p = 0.037, Fig. 3b) with brood age (remember that the fry stage was not included in this analysis). For the behaviour patterns that only occurred during the day, stage had effects on the frequency of foraging and retrieving larvae. During both episodes, females and males retrieved fewer larvae as the young aged (Tables 2, 4 give p values). Except for female foraging during episode 1, both sexes increased their foraging with brood stage (Tables 2, 4).

Episode Effects for Each Experimental Group

The only effect breeding episode had on control pairs was that control males spent more time away during episode 1 than during episode 2 (F = 4.49, p = 0.050, Fig. 4a, b). Females in the male removal group did not alter their behaviour from episode 1 (without a mate) to episode 2 (with mate). However, breeding

Table 2: Frequency (per 15 min) of diurnal behaviour patterns in paired and lone female parents during the first breeding episode, and in ex-paired and ex-lone females during the second breeding episode ($\bar{x} \pm$ SE, n = 10). P values for group (paired female vs. lone or ex-lone female) and stage effects are presented for each behaviour pattern during each breeding episode

Behaviour	Stage	Paired female	Lone female	Group p	Stage p
Episode 1					
Dig	Egg	8.2 ± 4.8	1.4 ± 0.9	0.658	0.485
	Wriggler	6.2 ± 2.7	1.9 ± 1.0		
	Fry 2	1.2 ± 1.1	1.6 ± 0.6		
	Fry 5	2.0 ± 0.7	6.5 ± 4.0		
Forage	Egg	4.7 ± 2.0	2.6 ± 1.4	0.686	0.158
	Wriggler	3.2 ± 1.2	3.6 ± 1.0		
	Fry 2	1.4 ± 0.9	5.2 ± 2.0		
	Fry 5	11.0 ± 7.4	12.1 ± 8.3		
Mouth	Egg	2.2 ± 1.4	9.2 ± 5.6	0.894	0.104
	Wriggler	9.1 ± 3.8	6.0 ± 2.2		
Retrieve	Fry 2	19.2 ± 4.4	27.8 ± 5.2	0.773	0.001
	Fry 5	0.7 ± 0.4	0.3 ± 0.3		
Episode 2					
Dig	Egg	2.4 ± 1.3	1.0 ± 0.7	0.252	0.337
	Wriggler	5.7 ± 3.0	0.7 ± 0.3		
	Fry 2	2.7 ± 1.7	1.1 ± 0.5		
	Fry 5	5.5 ± 3.2	5.4 ± 3.4		
Forage	Egg	0.9 ± 0.3	7.2 ± 4.9	0.179	0.015
	Wriggler	2.5 ± 1.1	7.6 ± 2.8		
	Fry 2	15.3 ± 6.8	30.8 ± 16.9		
	Fry 5	12.0 ± 5.1	13.4 ± 4.9		
Mouth	Egg	9.2 ± 5.0	1.7 ± 0.9	0.616	0.168
	Wriggler	12.0 ± 6.1	6.7 ± 3.0		
Retrieve	Fry 2	27.3 ± 11.6	21.3 ± 6.9	0.892	0.001
	Fry 5	1.0 ± 0.7	0.6 ± 0.4		

episode had significant effects on male behaviour. When males were alone (episode 1), they fanned more (F = 12.73, p = 0.002, Fig. 3a, b) and spent less time away from the brood (F = 6.62, p = 0.020, Fig. 4a, b) than when paired with a female (episode 2).

Male and female defensive behaviour did not differ between breeding episodes (Tables 3, 5, p values not presented).

Discussion

Effect of Mate Removal on Current Care

The only significant effect of male removal on female behaviour was an

Table 3: Female behaviour during the defence test for episodes 1 and 2 ($\bar{x} \pm$ SE, n = 10). P values
for group effects (paired female vs. lone female (episode 1) or ex-lone female (episode 2)) are presented
for each behaviour pattern. Unless otherwise indicated, data are frequency in 1 min

Behaviour	Paired female	Lone female	Group p
Episode 1			
Bites	0.3 ± 0.2	3.8 ± 2.4	0.123
Displays	12.7 ± 4.2	9.5 ± 3.9	0.579
% Time away	11.7 ± 6.7	28.8 ± 13.8	0.609
Latency to display (s)	18.4 ± 5.8	38.9 ± 8.4	0.059
Episode 2			
Bites	1.7 ± 1.0	2.5 ± 1.2	0.616
Displays	8.1 ± 2.3	17.2 ± 4.3	0.077
% Time away	20.3 ± 11.2	12.8 ± 9.7	0.618
Latency to display (s)	16.3 ± 6.2	8.3 ± 4.0	0.292

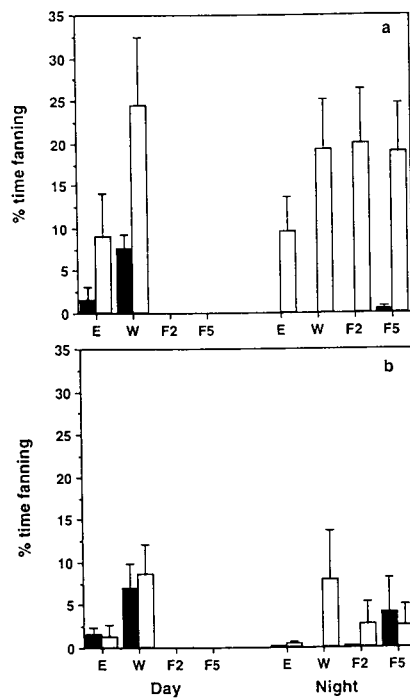*Fig. 3:* Mean ($\pm$SE, n = 10) % time spent fanning by males during breeding episodes 1(a) and 2(b).
Both day and night data are presented. Black bars = control (paired) males; open bars = lone males.
E = egg, W = wriggler, F2 = d 2 fry, F5 = d 5 fry

increase in levels of fanning. This result was unexpected because it cannot be
considered a compensatory response, as male convicts generally show no or very
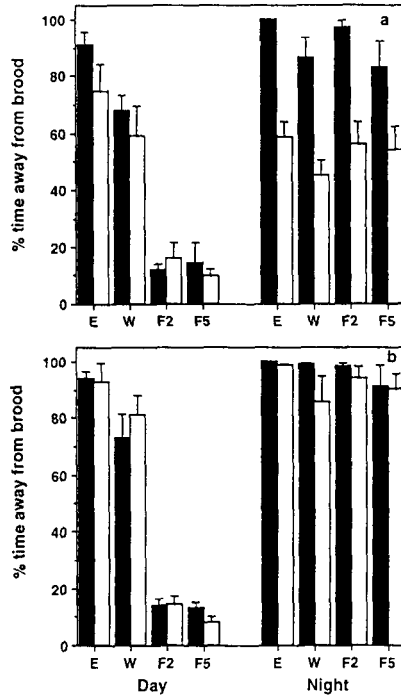
Fig. 4: Mean (±SE, n = 10) % time spent away from brood by males during breeding episodes 1(a) and 2(b). Both day and night data are presented. Black bars = control (paired) males; open bars = lone males. E = egg, W = wriggler, F2 = d 2 fry, F5 = d 5 fry

little fanning. One possible explanation for this result is that when paired, a fanning female is occasionally disturbed by her mate, at which time she displays at him and thus interrupts fanning. In the cichlid *Aequidens paraguayensis*, MROWKA (1982) also found increases in female fanning when males were removed, but in this case the increase was compensatory and corresponded to the amount of fanning the male normally gave.

Lone females did not compensate for the lack of male territory patrolling by increasing their time away from the brood. Observations on deserted convict females in outdoor ponds and in natural streams also failed to detect an increase in time away from the brood; in fact, lone females spent more time with the brood at all development stages (KEENLEYSIDE et al. 1990). Similar findings have been reported for the cichlid *C. panamense* (TOWNSHEND & WOOTTON 1985). If the ultimate function of territory patrolling is to protect the brood from predators, then a lone parent may be more successful if it defends the brood close to it rather than away from it, as the latter option leaves the brood open to attacks from additional predators.

Although active desertion by females is unlikely to occur in the wild, females could be killed or eaten by predators. Our results show that males in this case are

Table 4: Frequency (per 15 min) of diurnal behaviour patterns in paired and lone male parents during the first breeding episode, and in ex-paired and ex-lone males in the second breeding episode ($\bar{x} \pm$ SE, n = 10). P values for group (paired male vs. lone or ex-lone male) and stage effects are presented for each behaviour pattern during each episode

Behaviour	Stage	Paired male	Lone male	Group p	Stage p
Episode 1					
Dig	Egg	2.3 ± 1.6	2.3 ± 2.3	0.890	0.104
	Wriggler	1.5 ± 1.0	1.9 ± 1.6		
	Fry 2	0.5 ± 0.4	0.1 ± 0.1		
	Fry 5	1.6 ± 0.9	5.7 ± 4.3		
Forage	Egg	2.6 ± 1.5	1.1 ± 0.8	0.812	0.001
	Wriggler	1.7 ± 0.5	1.4 ± 1.4		
	Fry 2	2.2 ± 0.7	19.1 ± 15.5		
	Fry 5	6.2 ± 3.0	7.0 ± 1.7		
Mouth	Egg	0.1 ± 0.1	3.2 ± 2.0	0.076	0.645
	Wriggler	0.2 ± 0.1	1.0 ± 0.5		
Retrieve	Fry 2	8.7 ± 3.3	5.7 ± 1.9	0.242	0.001
	Fry 5	3.1 ± 2.1	0.0 ± 0.0		
Episode 2					
Dig	Egg	1.0 ± 0.9	0.2 ± 0.2	0.457	0.074
	Wriggler	1.7 ± 1.2	0.8 ± 0.5		
	Fry 2	2.1 ± 1.8	0.2 ± 0.2		
	Fry 5	2.4 ± 1.0	3.6 ± 1.9		
Forage	Egg	1.3 ± 0.9	3.0 ± 3.0	0.277	0.001
	Wriggler	1.7 ± 0.9	2.2 ± 1.5		
	Fry 2	10.5 ± 3.8	1.9 ± 1.0		
	Fry 5	11.7 ± 5.8	4.0 ± 1.7		
Mouth	Egg	0.0 ± 0.0	0.0 ± 0.0	–	–
	Wriggler	0.1 ± 0.1	0.3 ± 0.2		
Retrieve	Fry 2	4.9 ± 2.7	1.6 ± 0.6	0.294	0.001
	Fry 5	0.9 ± 0.5	0.0 ± 0.0		

capable of performing direct care. In particular, lone males performed more fanning, especially at night (Fig. 3a). At the egg stage, this increase was not fully compensatory for the absence of female fanning, but at the other stages it was (Figs 1, 3). Lone males also spent less time away from the brood, again most notably at night. Here the effect appeared to compensate in half for the absence of the female (Figs 2, 4). Thus the flexibility of the male parental role seems partial: direct care is given, but not always at the same level as given by the female. (MROWKA 1982 gives an example of full compensatory response by lone males of *A. paraguayensis.*)

Interestingly, no differences could be detected between lone and paired parents in terms of defensive behaviour (as opposed to KEENLEYSIDE et al. 1990,

Table 5:   Male behaviour during the defence test for episodes 1 and 2 ($\bar{x} \pm$ SE, n = 10). P values for group effects (paired male vs. lone male (episode 1) or ex-lone male (episode 2)) are presented for each behaviour pattern. Unless otherwise indicated, data are frequency in 1 min

Behaviour	Paired male	Lone male	Group p
Episode 1			
Bites	0.0 ± 0.0	3.7 ± 1.6	–
Displays	3.6 ± 1.8	9.2 ± 4.1	0.378
% Time away	33.0 ± 12.8	29.3 ± 11.8	0.837
Latency to display (s)	25.9 ± 7.9	24.7 ± 7.6	0.914
Episode 2			
Bites	2.0 ± 1.3	0.9 ± 0.4	0.678
Displays	6.1 ± 2.6	3.2 ± 1.3	0.447
% Time away	31.3 ± 13.0	58.5 ± 14.7	0.182
Latency to display (s)	26.9 ± 8.0	40.7 ± 8.0	0.237

although one may see a trend in our data on 'bites' Tables 3, 5). Individual parents may show almost maximum response to predators whether they are alone or not; it would therefore be impossible for a parent to compensate for the absence of its mate. This point emphasizes how superior biparental care, being the sum of two individual efforts, is at the fry stage, a point underlined by laboratory and field observations of lone parents being unable to protect their fry from predators (BARLOW 1974; McKAYE 1977). KEENLEYSIDE (1978) has shown that predation decreases the reproductive success of lone rainbow cichlid parents, *Herotilapia multispinosa*.

Effect of Mate Removal on Subsequent Care

In their second breeding episode, parents that had previously been alone did not differ in their parental behaviour from parents that had previously remained paired. Thus sex roles do not seem to be affected by previous experience as a lone or paired parent, at least for the first two breeding episodes. COLGAN & SALMON (1986) have shown that parental experience has little influence on behaviour such as fanning and time spent with young, although foraging by females and aggression by males may increase with successive breeding attempts.

Although fanning is considered energetically costly (COLEMAN & FISCHER 1991), the increase in its levels by lone parents in episode 1 had no effect on parental care during episode 2. The lack of predation and the presence of good feeding conditions in the observation tanks may have overshadowed any detrimental effects of increased effort during the first breeding cycle. In the field where predation is high (McKAYE 1977), mate desertion might affect the survival of the brood and lone parent (KEENLEYSIDE & MACKERETH 1992). Wild deserted females are more aggressive than their paired counterparts (KEENLEYSIDE et al. 1990). Therefore deserted parents may suffer higher fitness costs in terms of future reproduction than paired parents, given that investment in a current brood reduces future reproductive expenditures (SARGENT & GROSS 1986).

Stage and Day–night Effects

In this study, stage and time of day had the largest effects on care in both breeding episodes. Stage effects have been documented before (ROGERS 1988; LAVERY & KEENLEYSIDE 1990) and are largely due to parents adjusting care to the needs of their offspring. For instance, retrieving larvae occurs more frequently when the young are relatively small and weak swimmers (Tables 2, 4).

As previously reported (REEBS & COLGAN 1991), parents fanned eggs more at night than during the day. However, the observations of nocturnal fanning given to wrigglers and fry are novel. During this nocturnal fanning, both male and female swam 'on the spot' 1 cm above the mass of wrigglers or fry, using large-amplitude movements of the pectoral and caudal fins. The difference between this fanning and simply holding station above the young (which the parent often did) was obvious. It is unclear whether this nocturnal fanning is necessary: the wriggling motion of wrigglers' tails and the locomotory autonomy of fry can already contribute to water movement within the nest.

Experiments on the survival of wrigglers and fry in the presence or absence of parental fanning at night remain to be carried out, but the possibility also exists that motivated parents are simply doing 'the next best thing' at a time when vigilance is still necessary but not much else, besides fanning, can be done effectively. Whatever the answers, the presence of relatively high levels of night fanning at all brood stages shows that nocturnal energy expenditure extends over a long period of time, at least in the laboratory, making it all the more important to consider nocturnal activity when assessing energy and activity budgets.

Summary

Lone males and females performed more fanning than paired males and females, respectively. These differences in behaviour had no effects on the roles of males and females during a second breeding attempt. Although studies have shown that lone parents provide more care than their paired counterparts, there is no evidence to suggest that mate desertion has any significant effects on care given during a later reproductive episode.

Acknowledgements

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