Fin digging and leaf lifting by the convict cichlid, *Cichlasoma nigrofasciatum*: examples of parental food provisioning

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Abstract. In fish, the predominant form of parental care is brood defence. The convict cichlid, a biparental fish native to Central America, also engages in two types of brood provisioning: fin digging and leaf lifting. These behaviour patterns were studied in the field, and in outdoor experimental ponds and laboratory aquaria. In the ponds, females fin dug 51 times more often when guarding fry than when unmated; males fin dug three times more frequently when guarding fry than when unmated. After the young became free-swimming, females performed four times (field) and two times (pond and laboratory) more fin digging and twice as many leaf lifts (field) as males. Females in the field increased leaf lifting with brood age but males did not. Fin digging frequency by parental females and males increased with brood age. Frequency of adult feeding bites at the substrate did not change with brood age except in the field, where female feeding bites increased with brood age. In the field, females performed more feeding bites than males but in the laboratory males fed more often than females. Thus changes in fin digging frequency with brood age do not seem to be strongly linked to the feeding requirements of the parents. In the laboratory, fin digging frequency was influenced by substrate quality ($P=0.08$) but not by ration ($P>0.10$). Taken together, these data support the hypothesis that parental fin digging and leaf lifting help increase food availability to their young.

Typical components of parental care in mammals and altricial birds are protection of the offspring from predators and the elements, and the provisioning of food to the young. Both patterns of behaviour increase offspring survival (Trivers 1972; Clutton-Brock 1991) and ultimately increase the fitness of the parents (Hamilton 1964). Parental care in fish is uncommon, occurring in about 20% of fish families (Blumer 1982), and differs in form from that of other vertebrate groups (McKaye 1981). The most common form of parental care in fish is for the male parent to aerate and defend one or more clutches of eggs in a nest until the eggs hatch and the young disperse (Blumer 1982). There is generally no provisioning of food to the young, even in species that defend their free-swimming young for some time after hatching (Perrone & Zaret 1979). However, there are a few exceptions. Parental discus cichlids (*Symphysodon* spp.) produce copious amounts of

protein-rich mucus along the sides of their bodies upon which their young feed (Hildemann 1959). In several other species, the young nip at the sides of their parents and ingest mucus (Ward & Barlow 1967; Noakes & Barlow 1973; Robertson 1973; Ward & Wyman 1977). Females of two cichlid species (*Tropheus* sp.) in Lake Tanganyika, Africa, browse while orally brooding their young (Yanagisawa & Sato 1990). Bagrid catfish, *Bagrus meridionalis*, in Lake Malawi, provide food for their young directly (McKaye 1986). Unfertilized eggs produced by the female and benthic invertebrates foraged by the male are fed to the young.

Cichlids are unusual among fish because parental care continues for several weeks after their young have begun free-swimming (Keenleyside 1991). Convict cichlids are small freshwater fish native to Central America, ranging from Guatemala to Panama (Miller 1966; Bussing 1987). These fish are substrate brooders, which lay their eggs inside small caves they excavate under stones. Convict cichlids have cooperative, biparental care of their eggs, wrigglers (non-swimming hatchlings) and fry (free-swimming

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young) for about 6 weeks. During the fry stage of brood development (3–4 weeks) both parents actively defend their fry against potential brood predators. In addition, they occasionally perform two activities that have been called fin digging (Williams 1972) and leaf lifting (Keenleyside et al. 1990).

During fin digging, a parent fish settles onto the substrate and stirs up loose material by a short bout of vigorous rapid beating of its pectoral fins. During leaf lifting, a parent grasps the edge of a sunken leaf and, with a series of backward tugs and forward pushes, raises the leaf off the substrate and then releases it. As the leaf sinks it often turns over, exposing the underside. Parental fin digging has been observed in Costa Rican streams, performed by convict cichlids (Keenleyside et al. 1990) and *Cichlasoma alfari* (B. D. Wisenden, personal observation). It has also been reported for a few other biparental cichlids in the aquarium literature (Loiselle 1985; Azas 1992). Leaf lifting has been reported from the field for convict cichlids (Meral 1973; Keenleyside et al. 1990) and for *C. panamense* (Townshend & Wootton 1985a).

When parental fish perform fin digging or leaf lifting, their fry immediately converge to feed on suspended or newly exposed food items. Thus, these two activities appear to assist the young in feeding (Keenleyside 1991). Parental food provisioning may increase survival of their offspring by increasing fry growth and thus decreasing the time during which fry are vulnerable to brood predators (Perrone 1978).

Non-breeding convict cichlids occasionally fin dig and leaf lift while foraging for themselves. However, both acts appear to be performed more often by breeding pairs, especially when their young are free-swimming fry (Williams 1972). Because both adults and fry feed primarily on algae and microfauna in the benthos (B. D. Wisenden, personal observation), fin digging, especially on silty substrates, and leaf lifting, should make more food available for the fry.

The aim of this research was to explore the possibility that fin digging and leaf lifting by parental convict cichlids are acts of food provisioning for their free-swimming young. We did this in two ways. First, we recorded the frequency of both behaviour patterns by breeding adults in their natural habitat, and of fin digging in outdoor experimental ponds and in the laboratory. We

also recorded adult feeding rates in the field and adult feeding rates in the laboratory. Second, we measured the influence of substrate quality (clean versus silty) and adult food ration (two levels) on fin digging in a laboratory experiment. Fin digging should be of greatest potential benefit when the substrate is silty because small organisms hidden in the silt may be exposed to foraging fish. Therefore fin digging activity should increase on silty substrate and decrease on clean substrate. Parents may use their own nutrient status to judge ambient food availability for their young. When food for the parents is limited, parents may perceive food to be limited for their fry and increase the frequency of fin digging behaviour to provide more food for their young. Therefore, rates of fin digging should be higher for parents on a low food ration than for those on a high food ration.

METHODS

Field Study

Parental care behaviour was monitored during two breeding seasons, January–June 1990 and December 1990–June 1991. Data were collected from two study sites in the río Cabuyo, and two sites in the quebrada Amores at Lomas Barbudal Biological Reserve in Guanacaste province, northwest Costa Rica, 10°30′N, 85°23′W. Quebrada Amores is a small headwater stream and a tributary of the río Cabuyo.

We monitored pairs of convict cichlids breeding at each site regularly at intervals of 3–10 days (usually 7) throughout brood development from oviposition to fry independence. We identified individual broods and identified attending parents on subsequent sampling dates using sketches of parental body markings, stage of brood development and location in the stream. After a 5-min acclimation period, we recorded the frequency of parental behaviour patterns performed by each parent, including fin digging and leaf lifting, for 10 min. Observations were made from shore or while wading nearby, with the aid of polarized sunglasses to reduce surface reflection. Altogether, we made 840 10-min recordings on 195 brooding pairs; 115 in 1990, 80 in 1991; 102 in quebrada Amores, 93 in río Cabuyo. Immediately after the behavioural recordings, we captured each brood using hand nets, a face mask and snorkel. We

arbitrarily anaesthetized 15 fry with MS222 (tricaine methanesulphonate) and measured their standard length (SL) to the nearest 0·5 mm. We allowed the fry to recover from the anaesthetic and returned them to their parents using a clear plastic tube (Wisenden & Keenleyside 1992). Because the exact date of spawning was often not known, we used fry size to classify brood development into five stages: (1) cave; when the brood was still concealed inside the spawning cave as either eggs or wrigglers; (2) fry less than 6 mm SL; (3) fry 6–8 mm SL; (4) fry 8–10 mm SL; and (5) fry greater than 10 mm SL. Fry first emerged from their cave at 4–4·5 mm SL and began dispersing soon after reaching 10 mm SL (personal observation).

Pond Observations

We used four outdoor ponds measuring 7 × 10 m at the University of Western Ontario (43°01′N, 81°17′W). The ponds had sloping bottoms; water entered at the shallow end (depth 65 cm) and drained by a vertical standpipe at the deep end (depth 100 cm). Pond substrate was 10 cm of fine sand over 5 cm of coarse gravel. Scattered clumps of algae (*Chara* sp.) grew in all ponds and a layer of organic debris, detritus and algae accumulated on the substrate during the experimental period. Clay flower-pots (20 cm top diameter) were cut in half and placed concave side down on the substrate to serve as spawning sites. Eight half-pots were placed in each pond in a regular pattern, separated by 1·5 m.

All experimental fish were obtained from the University of Western Ontario laboratory stock, composed of fish purchased from local aquarium dealers back-crossed with fish captured in Costa Rican streams in 1984 and 1990. Past breeding experience of the fish was unknown. Each fish was anaesthetized with MS222, weighed, measured and tagged with a unique combination of coloured beads attached to the dorsal musculature with stainless steel wire. We observed six males and six females in each pond from 28 June to 6 September 1990. Fish fed on accumulated detritus and algae on the substrate; additional food was not provided.

Each day between 0900 and 1500 hours we recorded the mating status of all adults and the location and developmental stage of each brood being guarded. We visually checked broods inside flower-pots using a face mask and snorkel. We recorded 10-min observations of each parent of 14 pairs consecutively for each of the following stages of brood development: (1) 1 day after the fish spawned (egg stage); (2) 1 day after the eggs hatched (wriggler stage); (3) 3 days free-swimming (fry stage); (4) 10 days as fry; and (5) 17 days as fry. The fifth stage corresponded with the 8–10 mm SL fry stage of the field study. We recorded the number of fin digs performed with the brood (within two body lengths) and away from the brood during each 10-min observation period. We also recorded the frequency of fin digging behaviour by randomly selected unmated males ($N=13$) and females ($N=13$) for comparison with fin digging by parental fish. Because of the limited number of adults in the experimental ponds, the behaviour of some fish was recorded while parental and non-parental, some fish were recorded only while parental, others only while non-parental. In the analyses, these data were treated as independent points. Leaf lifting did not occur in the ponds because very few leaves fell into them during the experimental period.

Laboratory Experiment

Pairs of convict cichlids from the laboratory stock were placed into 96-litre aquaria (80 × 40 × 30 cm high) with 3 cm of naturally coloured gravel, a clay flower-pot cut in half placed at one end, and a plastic plant in the centre. Water temperature was maintained between 27 and 29°C by aquarium heaters and the photoperiod was a 14:10 h light:dark cycle. Each pair was in visual contact with one neighbouring pair.

Two factors were tested for their effect on fin digging: substrate quality and food availability. We used two levels of substrate quality (enriched; clean) and two levels of ration (high; low) to form a 2 × 2 factorial design. Trials with 'clean' substrate started with freshly cleaned gravel. Trials with 'enriched' substrate had 250 ml (506·6 ± 21·2 g) of detritus and sand added to a tank with clean gravel, forming a 0·25-cm layer of fine material on top of the gravel. Sand and detritus were collected from the experimental ponds. We fed each pair of adults in the low-ration treatment 1 g of commercial cichlid pellets (Tropic Aquaria, Brampton, Ontario) three times per week and those in the high-ration treatment daily. Fry were fed 0·1 g of FryFeedKyowa B-250 (BioKyoma,
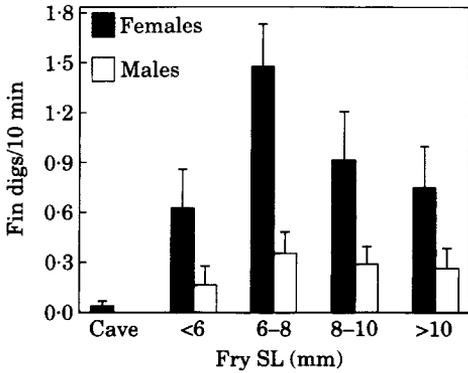
Figure 1. Mean (+se) fin digging frequency per 10 min by parental female and male convict cichlids in Costa Rica at each of five stages of brood development. Data from both watersheds combined.
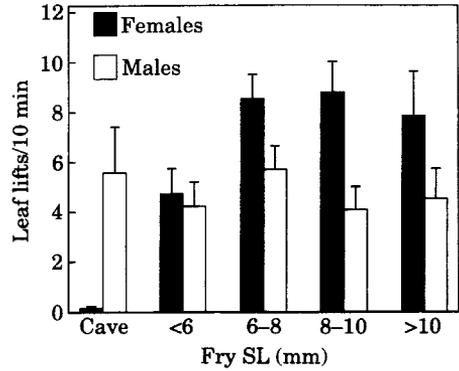

Figure 2. Mean (+se) leaf lifting frequency per 10 min by parental female and male convict cichlids in Costa Rica (both watersheds) at each of five stages of brood development.

Chesterfield, Missouri) three times per week in all treatments. We recorded the frequencies of fin digging (within two body lengths and away from the brood), and of feeding bites at the substrate for each parent during consecutive 10-min observations. Seven pairs were used for each treatment combination, for 28 pairs.

RESULTS

Field Study

Fin digging was performed significantly more often by female convict cichlids than by males (repeated-measures ANOVA, $P<0.001$) and changed significantly with brood age for both sexes (repeated-measures ANOVA, $P<0.001$; Fig. 1). There was no significant interaction between sex and brood age (repeated-measures ANOVA, $P=0.464$). In females, fin digging frequency increased from the cave stage to a peak at the 6–8 mm SL fry stage, then declined towards fry independence. In males, fin digging increased from the cave stage to the 6–8 mm SL fry stage, then levelled off.

Leaf lifting by females increased from the cave stage to an asymptote at the 6–8 mm fry SL stage (Fig. 2). Leaf lifting by males showed no significant change in frequency with brood development, resulting in a significant interaction between sex and brood stage (repeated-measures ANOVA, $P<0.001$). In the later stages of fry development (6–8 mm fry SL to independence) females leaf lifted more than males.
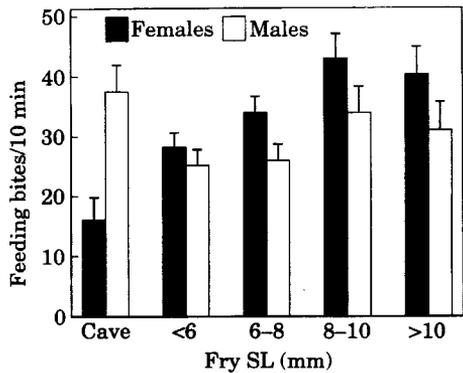

Figure 3. Mean (+se) frequency of feeding bites at the substrate per 10 min by parental female and male convict cichlids in Costa Rica (both watersheds) at each of five stages of brood development.

Feeding bites at the substrate by females increased with brood stage (repeated-measures ANOVA, $P<0.001$) but male feeding frequency did not (repeated-measures ANOVA, $P=0.766$; Fig. 3). Males fed more frequently than females at the cave stage (ANOVA, $P=0.037$) but females tended to feed more often during later stages of brood development, reaching statistical significance only at the 6–8 mm stage (ANOVA, $P=0.042$).

Pond Observations

Fin digging near the brood (within two body lengths) was significantly higher than fin digging
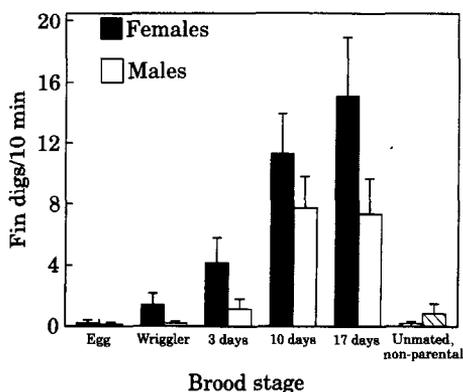
Figure 4. Mean (+SE) fin digging frequency per 10 min in outdoor ponds by parental female and male convict cichlids at five stages of brood development, and by unmated, non-parental females (▨) and males (▧). Fin digging near and away from the brood is combined.
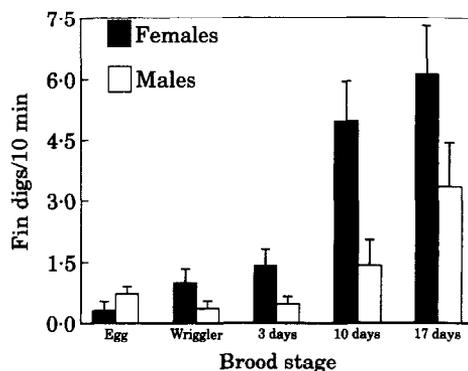

Figure 5. Mean (+SE) fin digging frequency per 10 min in aquaria by parental female and male convict cichlids at five stages of brood development.

away from the brood (parental females: $t=5.31$, $P<0.001$; parental males: $t=2.93$, $P=0.004$). When away from the brood, parental females and males performed 0.20 ± 0.11 ($N=132$) and 0.54 ± 0.30 ($N=132$) fin digs per 10 min; near the brood they performed 5.23 ± 0.94 and 2.36 ± 0.54 fin digs per 10 min, respectively. Unmated, non-parental adults fin dug at rates similar to parental fish away from their broods (females: 0.23 ± 0.05; males: 1.00 ± 0.26 per 10 min).

Fin digging frequency while away from the brood was not influenced by stage of brood development; neither sex nor brood stage had a significant effect (repeated-measures ANOVA: sex: $P=0.990$; stage: $P=0.550$). Repeated-measures ANOVA on total fin dig frequency (near and away from brood combined) showed significant sex ($P<0.001$) and stage effects ($P=0.007$) with no significant interaction ($P=0.277$). Females fin dug more than males and fin digging by both sexes increased with brood age (Fig. 4). Fin digging frequency did not decline in late fry stages in the experimental ponds or the laboratory because data collection ended well before fry independence and corresponded approximately to the 8 mm SL fry (i.e. when fin digging rates began to decline in the field study).

Laboratory Experiment

Fewer than 30 out of 560 fin digs occurred away from the brood over all trials; therefore, fin digs performed near and away from the brood were combined for the analyses. Sex of the parent and brood stage had the same effects on fin digging frequency in the laboratory setting as in the outdoor ponds and the field. After the young became free-swimming, females fin dug more than males (repeated-measures ANOVA, $P=0.010$) and both sexes increased fin digging frequency with brood age (repeated-measures ANOVA, $P<0.001$; Fig. 5). There was no significant interaction between sex and stage (repeated-measures ANOVA, $P=0.071$).

Although not statistically significant (repeated-measures ANOVA, $P=0.084$), fin digging tended to be performed more frequently on enriched substrate than on clean gravel, especially in late fry stages (Fig. 6). There was no significant interaction between substrate and either brood stage (repeated-measures ANOVA, $P>0.100$) or ration (repeated-measures ANOVA, $P>0.100$). The ration treatment failed to produce a statistically significant effect (repeated-measures ANOVA, $P>0.100$). Fin digging tended to occur more frequently in trials with the low food ration except at the 10-day fry stage where this trend was reversed (Fig. 7), producing a significant interaction between stage and ration (repeated-measures ANOVA, $P=0.010$). We have no explanation for this reversal at the 10-day fry stage. However, taken together, the treatments of ration and substrate affected mean fin digging frequency in the predicted directions (Fig. 8).

Feeding bites at the substrate by parents in the laboratory were much less frequent overall than by parental convict cichlids in the field and did
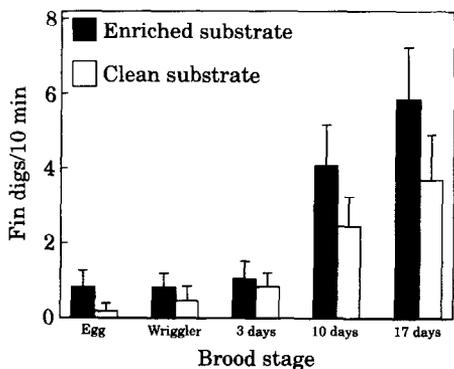
Figure 6. Effect of substrate quality on frequency of fin digging ($\bar{X}$+SE) per 10 min by parental convict cichlids (sexes combined) in aquaria at five stages of brood development.

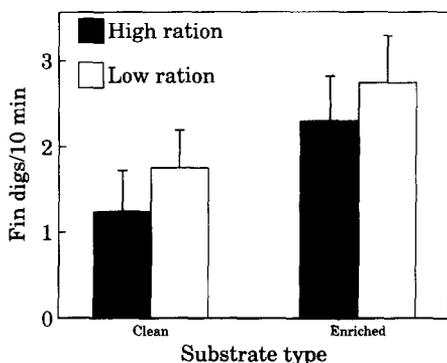**Figure 8.** Overall effects on fin digging ($\bar{X}$+SE) per 10 min, of the substrate and ration treatments used in the laboratory experiment. Sexes and brood stages are combined.

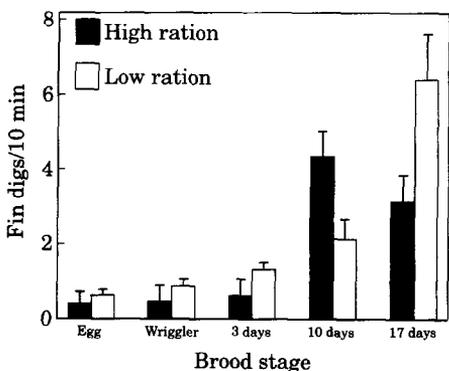**Figure 7.** Effect of food ration on frequency of fin digging ($\bar{X}$+SE) per 10 min by parental convict cichlids (sexes combined) in aquaria at five stages of brood development.
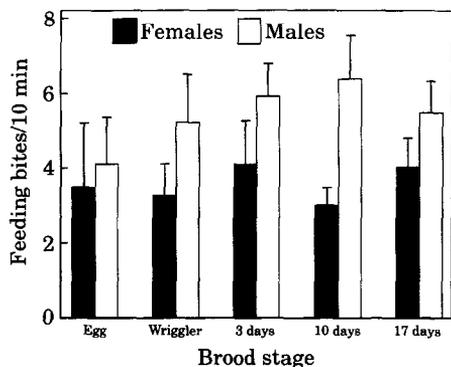

Figure 9. Frequency of feeding bites ($\bar{X}$+SE) per 10 min by parental female and male convict cichlids in aquaria at five stages of brood development.

not follow the same pattern (Fig. 9). In the laboratory, the feeding frequency of females was lower than that of males (repeated-measures ANOVA, $P=0\cdot023$) and neither sex changed feeding frequency with brood stage (repeated-measures ANOVA, $P=0\cdot906$).

Within each sex, rates of feeding bites were uniformly high except for the combination of clean substrate and high ration, when feeding activity was significantly reduced in both sexes (Fig. 10). Consequently there was a significant interaction between substrate and ration (repeated-measures ANOVA, $P=0\cdot046$). Fin digging events were not closely associated with adult feeding activity (fewer than 30 feeding bites occurred within 1 s of a fin dig

during 280 observation periods or 1261 feeding events).

DISCUSSION

Fin digging data from the field, experimental ponds and laboratory, and leaf lifting data from the field, indicate that parental convict cichlids use these two behaviour patterns to assist their young in feeding. The strongest evidence that these are methods of food provisioning is that in all parts of the study, fin digging by both parents seldom occurred when their young were at the egg and wriggler stages, and were thus incapable of exogenous feeding, but increased in frequency with increasing age of their free-swimming young. Also, in the ponds, unmated, non-parental adults,
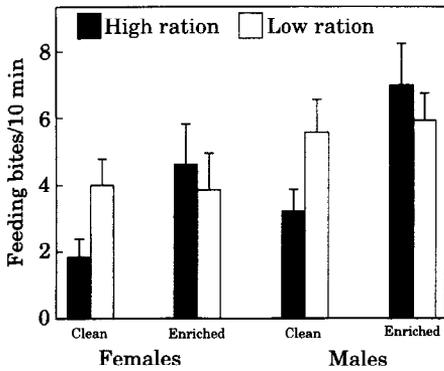
Figure 10. Frequency of feeding bites ($\bar{X}+$SE) per 10 min by parental female and male convict cichlids in aquaria during trials differing in substrate and ration treatments.

and parents away from their brood, seldom performed fin digging. In addition, the frequency of leaf lifting by parental females in the field increased with offspring age. This corresponds with the data on leaf lifting by parental convict cichlids in Costa Rican streams by Keenleyside et al. (1990).

In the field, ponds and laboratory, after the young became free-swimming, females performed more fin digging, and in the field more leaf lifting than males. This finding concurs with other reports of parental fin digging (Krischik & Weber 1974; Lavery & Keenleyside 1990) and leaf lifting by convict cichlids (Keenleyside et al. 1990).

Parental care duties among biparental cichlids are usually not divided equally between the sexes (see Keenleyside 1991 for a review). Females are more directly involved in the care of the eggs and wrigglers than are males, and generally spend more time closely associated with the young throughout the brood-rearing period than do males. Males patrol the breeding territory and then join the female in active brood defence when the young become free-swimming. The sex differences in fin digging and leaf lifting in this study were consistent with this pattern. Females rarely left the spawning cave when the brood was at the egg and wriggler stages (especially in the field where brood predators were abundant), and consequently fin digging and leaf lifting by females occurred infrequently at the cave stage. During these early brood stages, males were not constrained by egg and wriggler care and used leaf lifting to forage for themselves. However, parental males did not fin dig when their broods were at the

egg or wriggler stage. This suggests that leaf lifting is an important foraging technique for adult convict cichlids and is not solely a form of food provisioning for their young.

In general, parental investment should increase with offspring age because the probability of offspring survival and thus the potential value of the offspring to parental fitness increase with offspring age (Clutton-Brock 1991). Parental investment often declines towards the end of the period of parental care as the young become self-sufficient and their survival is less dependent on parental care. This pattern of increasing then decreasing levels of parental investment with increasing offspring age has been modelled (Sargent & Gross 1993) and supported by empirical studies of brood defence in fish, birds and some mammals (reviewed in Montgomerie & Weatherhead 1988; Clutton-Brock 1991; Sargent & Gross 1993).

Parents may have increased fin digging frequency with brood age because the food requirements of the fry increase as they grow. Unfortunately we were not able to collect data on fry foraging rates to confirm this. Williams (1972) and Krischik & Weber (1974) found an increase in fin digging frequency by male and female parental convict cichlids as their fry developed, followed by a gradual decline over the next 10 days. Glancing behaviour and associated micronipping at the parents' body, by fry of the Asian cichlid, *Etroplus maculatus*, increased significantly between the ages of 9 and 19 days free-swimming (Ward & Barlow 1967).

The decline in female fin digging at late fry stages in the field may be related to the increasing abilities of young convict cichlids to forage independently on the substrate as they grow and develop, even though they are still being guarded by their parents (Williams 1972). However, the decline in fin digging is also associated with increased feeding rates of females. This raises an alternate hypothesis, that the increase in fin digging frequency with brood age by parental females is partially attributable to a general increase in female feeding activity, perhaps in response to gonad exhaustion from spawning or somatic exhaustion from the metabolic demands of brood defence. This hypothesis is countered by data from the pond study where fin digging frequency by females and males did not change with brood stage while they were away from the brood,

presumably when they were feeding only for themselves, and there was also a low level of direct temporal association between feeding bites and fin digging. Furthermore, the frequencies of feeding bites by females and males in the laboratory (Fig. 9), and males in the field (Fig. 3) were not influenced by brood age. In addition, an earlier study of convict cichlid parental behaviour in the same ponds found that the feeding frequency of male and female parents did not change with increasing age of the brood (Keenleyside et al. 1990). The feeding frequency of non-parental convict cichlids in the field is more than three times higher than that of parental fish (Keenleyside et al. 1990).

In the laboratory, fin digging was somewhat reduced on clean, silt-free substrates regardless of ration level (Fig. 8), while the frequency of parental feeding bites on clean substrate was reduced for the trials with high ration (Fig. 10). Substrate type had a weak effect on parental fin digging ($P=0.084$) and food ration had no effect. Adult hunger levels may have been satisfied by the high food ration and thus adults were less motivated to forage on sterile substrate. An alternate hypothesis, that the low food ration may have limited the amount of energy available to parents to invest in their offspring (Townshend & Wooton 1985b), was not supported by the results of the ration treatment.

Fin digging occurred most frequently in the experimental ponds and least frequently in the field. This was probably because the substrate in the ponds contained more silt and detritus than the field sites where convict cichlids reared their broods. The relatively low fin digging frequency in the field may also reflect the greater availability of alternate food sources in the benthos. Alternatively, benefits from high rates of fin digging in the field could be offset by potential brood predators that are attracted by this conspicuous activity.

In this paper we have presented data on fin digging and leaf lifting by convict cichlids from the field, outdoor ponds and laboratory aquaria, and we propose that these patterns of behaviour are examples of parental food provisioning in fish. Females performed more fin digging and leaf lifting than males. Fin digging frequency increased with brood age and was more frequent on a silty substrate than a clean substrate in the laboratory.

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