Parental brood provisioning in cichlid fishes by means of stirring up of the loose material of bottom substrate: a brief review

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Parental brood provisioning in cichlid fishes by means of stirring up the bottom substrate: a brief review

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ABSTRACT

Although parental care in fishes does not usually include food provisioning of offspring after hatching, various types of this kind of investment have been documented in some bony fishes, and particularly, in cichlids. However, brood provisioning in cichlid fishes has been studied much less than other forms of their parental care. One example of such poorly understood patterns of parental behaviour in cichlids is stirring up the bottom substrate containing detritus, zoo- and phytobenthos (SUBS). During SUBS parents release the loose material and reveal benthic animals, in all probability assisting their young in feeding. Four features are typical for cichlid fishes exhibiting this form of parental provisioning: (1) most of them are taxonomically closely related and are included in the monophyletic subfamily Cichlasomatinae (Kullander, 1998). (2) most of these cichlids reside in Central America and only one species, *Guianacara owroewefi* does not live in this region. (3) most of them inhabit small lakes, rivers and streams but not large reservoirs. (4) the adult food in all these species is mainly zoobenthos.

Main forms and features of this parental behaviour were considered. The adaptive functions of stirring up the substrate is most probably associated with increasing food availability for the offspring. It is also suggested that, because SUBS is associated with both own feeding of adults and parental food provisioning, the immediate nutritive status of adults and their offspring would correlate and satiation of parents may be the primary mechanism regulating SUBS. A possible scenario of the evolution of SUBS may involve an expansion and/or a shift of adaptive function from adults own foraging to parental brood provisioning.

INTRODUCTION AND DEFINITIONS

The most magnificent feature that characterises the family Cichlidae (Teleostei: Labroidei) is the long (3-4 weeks, and in some species considerably longer) period of parental care. In all of more than 1400 cichlid species, one or both parents protect the offspring from predators and promote their normal growth and development (Keenleyside, 1991). Moreover, though parental care in fishes does not usually include provisioning of offspring after hatching, various types of brood provisioning have been documented in cichlids.

Parental food provisioning of young after birth or hatching is an important component of parental care in many viviparous as well as oviparous animals (Clutton-Brock, 1991). This is beneficial because it increases offspring survival and ultimately fitness of the parents (Hamilton, 1964; Trivers, 1972). Many types of provisioning of young after birth or hatching have been documented in insects (Wilson, 1971), spiders (Kaston, 1965), crabs (Diesel, 1989), leeches (Kutschera, 1992), birds (Lack, 1966), mammals (Ewer, 1973) and in other animals.

Various forms of this kind of investment are also known in cichlid fishes. In at least 30 species it may occur with ectodermal mucus (Noakes, 1979; e.g. in *Symphysodon discus*, Hildemann, 1959; *Etroplus*

maculatus, Ward and Wyman, 1977), partly chewed food (e.g. in *Astatheros longimanus*, Konings, 1989; *Pelvicachromis pulcher*, Martin and Taborsky, 1997), by means of buccal feeding (e.g. in *Oreochromis alcalicus*, Coe, 1966; *Tropheus duboisi*, Yanagisawa and Sato, 1990; *Cyphotilapia frontosa*, Yanagisawa and Ochi, 1991), pasture of brood, that is movements of parents and the young to more profitable feeding areas (e.g. in *Vieja maculicauda*, Perrone, 1978; *Boulengerochromis microlepis*, Kuwamura, 1986).

Several New World substrate brooding cichlids increase food availability for their fry by means of stirring up the bottom substrate containing detritus, zoo- and phytobenthos (SUBS). There exist several different kinds of this form of parental food provisioning. However, two types of parental SUBS are most typical. These are leaf lifting and fin digging (see e.g. Keenleyside, 1991; Wisenden et al., 1995). During leaf lifting, a cichlid uses leaves that have fallen from trees and are laying on the substrate. The fish grasps the edge or petiole of a leaf in the mouth and, with a series of rapid pushes and oscillatory movements by its body, lifts the leaf off the substrate and then releases and stirs it up. Fin digging occurs when the fish settles its body onto the substrate and stirs up detritus and other loose material by a short bout of rapid, vigorous beating of its pectoral fins and undulating movements of the body, revealing benthic animals.

Keenleyside (1978) described one more type of parental provisioning in cichlid fishes, that may be also considered (with the proviso which will be made below) within the framework of SUBS. This is the plunge feeding which is most characteristic of the geophagine cichlids (genus *Geophagus sensu lato*). The fish plunges its snout into substrate, takes up a mouthful of that, and after withdrawing its head, ejects the collected material from the mouth and gill opening. The loose material, like detritus and benthic animals, sinks slowly onto the surface of the substrate. After that, adult and fry consume (sometimes selectively) this food. Additional separation of organic material from inorganic substrate is achieved because geophagines chew the mouthful before spitting it, and

thus cleans off soft fragments from inorganic particles of substrate (Allgayer, 1983, 1988; Zworykin, 1990). Unfortunately, there exists much less reliable information on parental plunge feeding than on leaf lifting and fin digging. One of the few scientific publications, in which adults foraging and brood provisioning through plunge feeding in *Satanoperca jurupari* was outlined, is rather an old article of Reid and Atz (1958).

Actually, foraging behaviour like plunge feeding is widespread among benthophage cichlids (see Fryer and Iles, 1972; Yamaoka, 1991 for reviews). Among New World cichlid fishes, similar behaviour has been observed during feeding (but not brood provisioning) in *Bujurquina vittata* (Timms and Keenleyside 1975, note that the old name of this species, *Aequidens paraguayensis*, was used by the authors) and in *Herotilapia multispinosa* (Smith-Grayton and Keenleyside, 1978), although in these species plunging before taking up the substrate portion is not well expressed. In these papers, however, plunge feeding was not considered as a component of parental care. Moreover, one of the most important peculiarities distinguishing this behaviour from all other forms of the stirring up the substrate is that SUBS (as will be shown below) usually have substantially higher importance as brood provisioning rather than feeding of adults. On the contrary, plunge feeding is mainly used by various cichlids during their own foraging. Its provisioning function, as noted above, has been described in only few species and is poorly investigated. Thus, I assume that plunge feeding is, first of all, an element of the foraging activity of adults in some cichlid species. Because of lack of reliable information on the provisioning function of plunge feeding, I excluded, with few exceptions, this behaviour from further review.

Finally, some cichlids, particularly the convict cichlid, *Archocentrus nigrofasciatus*, stir up the substrate in a way combining elements of plunge feeding and fin digging. The fish takes up a portion of substrate into the mouth and ploughs the bottom pushing the snout forward and making simultaneously horizontal movements with its head. After that, the fish withdraws its head and ejects the collected material from the mouth. In the convict cichlid this behaviour often precedes fin digging (Zworykin, personal observations). Thus, this behaviour pattern could be named as head digging or mouth digging.

My observations on *Aequidens coeruleopunctatus*; Jack Dempsey, *"Cichlasoma" octofasciatum; Geophagus steindachneri* and the convict cichlid under laboratory conditions showed that effect of SUBS is considerable enough to dig not only soft material like detritus and silt, but also firm substrate, for example sand and even fine gravel. Some data on cichlid species exhibiting the various types of SUBS are given in Table 1.

The first reports on SUBS in cichlids have appeared in the literature in the seventies (Williams, 1972; Meral, 1973; Barlow, 1974; Krischik and Weber, 1974). Since then, stirring up of the substrate have been a priori considered as both foraging activity of adults and an element of parental care. However, this assumption has not been tested directly.

SUBS AS A FORM OF PARENTAL CARE

One of the most obvious problems regarding SUBS is whether this behaviour is really a component of parental care in cichlid fishes. This hypothesis was confirmed by Wisenden et al. (1995), who showed that adult convict cichlids fin dig much more frequently when guarding fry than when unmated. Parental convict cichlids performed fin digging not only near the brood but also away from it. However, the frequency of digging in the former case was much higher than in the latter. Moreover, the pattern and frequency of fin digging activity away from the brood were similar to those in non-breeding fish. Unlike parental fin digging, the frequency of non-parental fin digging was influenced neither by stages of brood development, nor by the sex of the parent (Wisenden et al., 1995). Thus, fin digging without offspring (both in breeding and non-breeding cichlids) differs from fin digging with brood both in frequency and dynamics. My observations showed that Jack Dempsey fin dig during parental care quite often, whereas non-parental fish exhibit this behaviour extremely rarely (Zworykin, 1998).

Many investigations have shown that, in the field, in experimental ponds and in laboratory aquaria, parental females of the convict cichlid and Jack Dempsey fin dig significantly more often than males (Figure 1; Krischik and Weber, 1974; Lavery and Keenleyside, 1990; Wisenden et al., 1995; Zworykin, 1998; Zworykin et al., 2000). The same trend has been observed in leaf lifting (Keenleyside et al., 1990; Wisenden et al., 1995). Sex-related differences in parental behaviour are typical for biparental cichlids

(Smith-Grayton and Keenleyside, 1978; Nakano and Nagoshi, 1990; Schwanck and Rana, 1991). Males, usually patrol the brood-rearing territory and repulse predators, while females concentrate on promotion of growth and development of the young (see Keenleyside, 1991 for a review). Sex differences in parental behaviour and separation of roles, including brood provisioning, was also observed in other animals such as birds (Moreno et al., 1995; Nishiumi et al., 1996; Carere and Alleva, 1998; Krebs et al., 1999; Woodard and Murphy, 1999).

The frequency of parental fin digs by both sexes increases with the age of the brood in the convict cichlid (Williams, 1972; Krischik and Weber, 1974; Wisenden et al., 1995; Zworykin et al., 2000) as well as in Jack Dempsey (Zworykin, 1998). The same trend was found in leaf lifting in the convict cichlid (Keenleyside et al., 1990; Wisenden et al., 1995). Wisenden et al. (1995) also found an interaction between sex of the parent and brood age in the case of leaf lifting but not fin digging. In other words, the pattern of fin digging frequency with the brood development in males and females were similar while those of leaf lifting were different. At the same time, in other investigations significant interaction in the case of fin digging was revealed both in the convict cichlid (Zworykin et al., 2000) and Jack Dempsey (Zworykin, 1998). This interaction might point to a more rapid increase of fin digging frequency with the brood age in females than in males.

Many other behavioural components of parental care in *"Cichlasoma"* species also change with the offspring age (Keenleyside et al., 1990; Keenleyside, 1991; Zworykin, 1993, 1995). If SUBS does have a food provisioning function, the increase of its frequency with brood age can be easily understood on the basis of parental investment theory (Clutton-Brock, 1991). Obviously, this trend is affected by increasing demands of the growing progeny. Furthermore, it has been documented in many other animals providing their offspring. For example, feeding of nestlings increased with their age in the bachman sparrow, *Aimophila aestivalis* (Haggerty, 1992), eastern phoebes, *Sayornis phoebe* (Conrad and

Table 1. Summary of behavioural and ecological features of cichlid fishes performing parental food provisioning by means of stirring up the bottom substrate

Species	Forms of SUBS	Conditions of Observation	Distribution
Aequidens coeruleopunctatus (Kner et Steindachner, 1863)	FD (A. Stalsberg, pers. comm.)	In the field	South and Central America
Archocentrus nanoluteus (Allgayer, 1994	FD (A. Stalsberg, pers. comm.)	In the field	Central America
Archocentrus nigrofasciatus (Günther, 1869)	LL (Meral, 1973; Barlow, 1974; Keenleyside et al., 1990; Bussing, 1993; Wisenden et al., 1995) FD (Williams, 1972; Keenleyside et al., 1990; Lavery & Keenleyside, 1990; Wisenden et al., 1995; Zworykin et al., 2000) HD (D.D. Zworykin, pers. observ.)	In the field, outdoor ponds and under aquarium conditions	Central America
Astatheros alfari (Meek, 1907)	FD (Konings, 1989; A. Stalsberg, pers. comm.; B.D. Wisenden, pers. comm.)	In the field	Central America
"*Cichlasoma*" *octofasciatum* (Regan, 1908)	FD (Zworykin, 1998)	Under aquarium conditions	Central America and Florida
Guianacara owroewefi (Kullander et Nijsen, 1989)	FD (A. Stalsberg, pers. comm.)	Under aquarium conditions	South America
Herichthys carpinte (Jordan et Snyder, 1900)	FD (Konings, 1991b)	In the field. In this species fin digging is reported as a form of adults' foraging only.	Central America
Herichthys labridens (Pellegrin, 1903)	FD (Konings, 1989, 1991b; Artigas Azas, 1992, 1996)	In the field	Central America
Theraps panamense (Meek et Hildebrand, 1913)	LL (Townshend & Wootton, 1985)	In the field	Central America

FD - fin digging, LL - leaf lifting, HD - head digging

Habitat	Main natural food
This eurytropic species prefers rather small, shallow reservoirs with soft bottom containing detritus and silt. At the same time, it can also be found in biotopes with hard substrate (Konings, 1989)	Diet of this cichlid mainly consists of aquatic insects and other benthic invertebrates. Sometimes, vegetable food amplifies its ration (Zaret & Rand, 1971; Angermeier & Karr, 1983; Konings, 1989)
The data on this species, which have been described by R. Allgayer just in 1994, are very scanty and do not contain the reliable information on its ecology and feeding at nature. It is a close relative of the convict cichlid and *A. septemfasciatus*.	
This is an eurytropic species preferring clear streams and small rivers with hard bottom. In Lake Jilóa it is found in a habitat of thick vegetation. Finally, it lives in large polluted lakes, and in various biotopes with soft substrate containing silt and detritus (McKaye, 1977; Konings, 1989; Bussing, 1993, R.M. Coleman, pers. comm.)	Omnivorous species. It mainly feeds on benthic insects larva and other aquatic invertebrates as well as on vegetable food and detritus. The percentage of vegetation and detritus in its diet is quite fickle (Konings, 1989; Bussing, 1993; Winemiller et al., 1995; Trujillojimenez, 1998)
This fish is found in the Rio Puerto Viejo which would be classified as a moderately rapidly flowing river. It is common along shorelines and in silty backwaters of this river. (Konings, 1989; Bussing, 1993, R.M. Coleman, pers. comm.)	This mainly insectivorous fish eats aquatic insects but also takes other, primarily benthic invertebrates. Additionally, it ingests detritus and vegetation (Konings, 1989; Bussing, 1993, 1994; Winemiller et a., 1995)
Generalist, can be found both in clear small rivers and poorly lotic and swamp reservoirs with soft bottom containing a lot of silt and mud (Konings, 1989; Artigas Azas, pers. comm.)`	This carnivorous cichlid basically eats aquatic insect larvae and imagines. It also consumes terrestrial insects falling on the water surface. Large adults hunt for small fishes. (Jennings, 1986; Konings, 1989)
This fish inhabits clear rivers. Water has a slight yellow tint, but is transparent. Piles of detritus and silt are situated above the sand bottom (De Greef, 1995)	Zoobenthos is the basic food of this cichlid (De Greef, 1995)
This species mainly inhabits small rivers and streams with the clear water and rapid current. However, it is also found in more eutrophic reservoirs like ponds and even irrigation canals (Werner, 1995)	This cichlid feeds on insects, crustaceans, gastropods and other, primarily benthic invertebrates. Its diet also includes vegetable food (Konings, 1989, 1991b; Werner, 1995)
Inhabitant of clear streams and small rivers with sand bottom, occasionally covered by silt and detritus (Artigas Azas, 1992, 1996)	Gastropodophagous species which also takes crustaceans and benthic invertebrates (Konings, 1989, 1991b; Artigas Azas, 1992, 1996)
Inhabitant of clear small rivers and streams with the sand or other hard bottom (Townshend & Wootton, 1985; Konings, 1989)	This species usually considered as a grazer that picks up algae from rocks and other substrate. However, the appreciable part of its diet consists of zoobenthos (Angermeier & Karr, 1983; Konings, 1989)
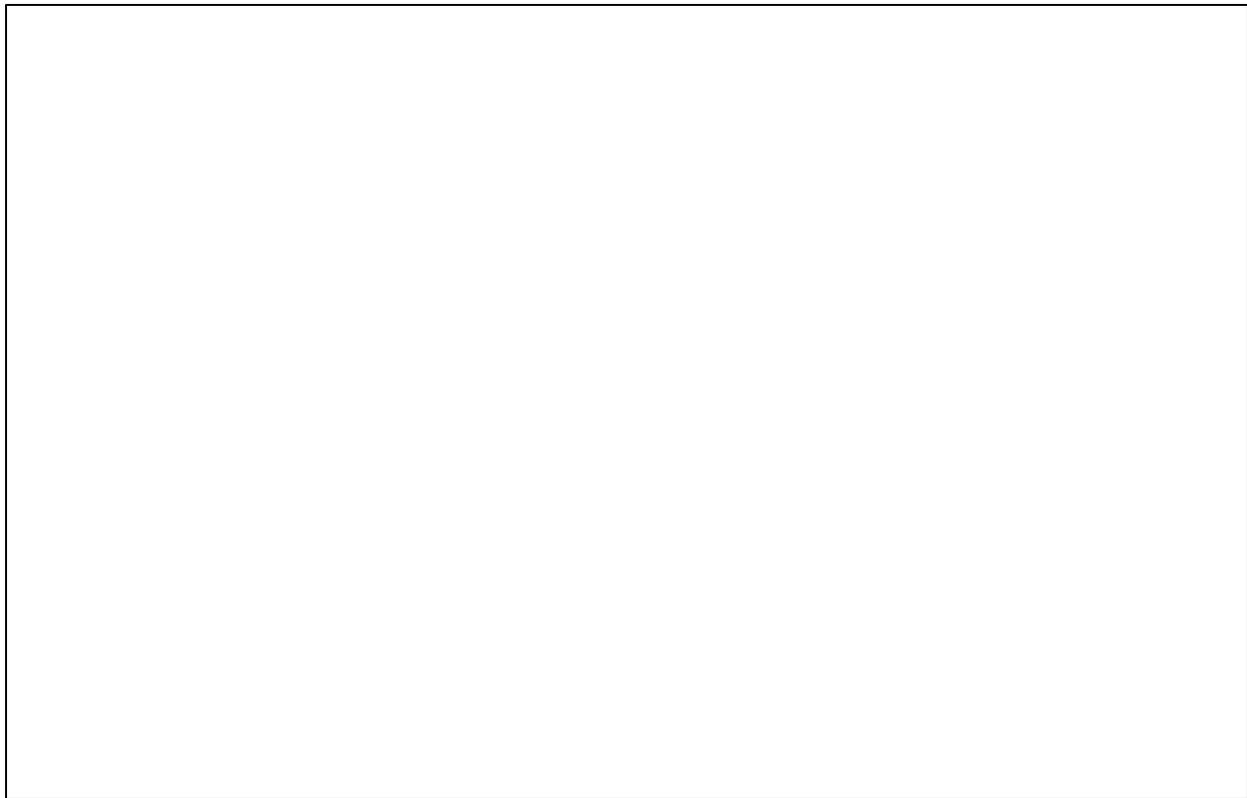
Figure 1. Fin digging frequency per 15 min by parental males and females of Jack Dempsey at five stages of brood development. The box polts give the median (point), 25, and 75% interquartiles (upper and lower ends of box), and a minimum and maximum values (whisker). Data before and after parents were fed are combined.

Robertson, 1993) and in the red-winged blackbird, *Agelaius phoeniceus* (Yasukawa et al., 1990; Westneat, 1995). However, the daily energetic expenditure of parents may be independent of brood age (Green and Ydenberg, 1994; Moreno et al., 1995) or increase of provisioning rate with the offspring age may depend on brood size (Lozano and Lemon, 1998).

It is also worth noting that parental cichlids start to fin dig before the beginning of exogenous feeding of the fry, as early as at the cave stage (Wisenden et al., 1995; Zworykin, 1998; Zworykin et al., 2000). This counterintuitive pattern may be a component of the "forestalling" activity described in a recent study (Zworykin, 1993). The hatching of wrigglers in Jack Dempsey is often accompanied by a sharp increase of female locomotion and appearance

in her behavioural repertoire of the elements coincident to care for fry but not wrigglers (see Zworykin, 1993, 1995 for more details).

The most sudden change in the frequency of SUBS occurs from 3 to 10 days after the onset of free-swimming (Wisenden et al., 1995; Zworykin, 1998). This could be partly determined by the fact that in cichlids (Ishibashi, 1974; Balon, 1991) as well as in many other bony fishes (Iwai, 1972; Makeeva, 1992) at first-feeding the yolk is not fully resorbed nor is the gut fully developed. Thus, during the initial period of free-swimming the food demands of the fry could be low, but subsequently they increase rapidly.

PROVISIONING FUNCTION OF SUBS
For more than 20 years SUBS was a priori considered as a form of food provisioning. This assumption was mainly based on observations that the fry immediately rush in and begin feeding in response to parental SUBS (Krischik and Weber, 1974; Keenleyside, 1978; Loiselle, 1985; Konings, 1989, 1991a; Keenleyside et

al., 1990; Lavery and Keenleyside, 1990; Keenleyside, 1991; Artigas Azas, 1992). The data given above allow us to consider SUBS as a component of parental care in cichlid fishes. However, they do not provide conclusive evidence for the food provisioning function of this behaviour, because the same trends would be expected if stirring up of the substrate had some other parental function. For example, even if SUBS is related to the feeding of fry, it may have a sole signal function, stimulating feeding activity of the young or indicating more profitable feeding areas, but not increasing food availability itself. No data stated so far allow us to rejects these alternatives.

The function of SUBS was assessed by Zworykin et al. (2000) for fin digging in the convict cichlid and perhaps might be extrapolated to other cichlids performing various types of SUBS. In this investigation, two kinds of Diptera larvae, largely differing in size, were found in the substrate of experimental aquaria. Parental cichlids do not fin dig with the same intensity, and examination of the fry gastrointestinal tract evidenced that higher frequency of parental fin digging was associated with a significantly higher consumption of large and presumably more profitable prey, which inhabited deep horizons of the substrate and were almost inaccessible for the young without parents. This led to a significant increase of the offspring growth rate. Thus, the adaptive function of fin digging behaviour, as increasing food availability for the offspring, was established.

It was also shown that at later brood stages, when parental care ceased, the fry of the high-digging parents were characterised by a significantly poorer ability to consume small larvae, which were predominantly accessible for them without parental aid. Offspring of the low-digging parents, however, presumably as a result of their individual experience, showed a considerably better ability to find these small larvae, increasing their growth rate. There may be, thus, an interesting trade-off between parental food provisioning and the offspring individual experience.

This trade-off would create a variety of presumably equally adaptive, alternative tactics, ranging from pronounced food provisioning to relative neglect. Alternative tactics are related to stable individual behavioural differences. The consistent individual differences in the frequency of fin digging were analysed in the convict cichlid (Budaev et al.,

1999). It was found that individual behavioural differences of parents in situations involving novelty, risk and aggression translate to individual differences in patterns of parental care, including fin digging. This significant correlation between temperaments and patterns of parental provisioning turned out to be sex specific, and bold, active and exploratory but less aggressive males tended to exhibit a significantly higher level of parental brood provisioning.

Since the provisioning function of SUBS seems apparent now, some results of the study of Lavery and Keenleyside (1990) would seem confusing at the first sight. Had this behaviour a sole signal function, its frequency would be independent of brood size. However, as long as SUBS is really a form of provisioning, its intensity could depend on the offspring number. Indeed, larger brood requires more food and parents usually provide more to larger broods (Yasukawa et al., 1990; Haggerty, 1992; Conrad and Robertson, 1993; Markman et al., 1995; Lozano and Lemon, 1998). Yet, according to Lavery and Keenleyside (1990), the frequency of fin digging in the convict cichlid was not affected by the brood size.

Because their study employed artificial brood size manipulations, the results may be difficult to interpret. The relationship between brood size and parental provisioning rates is not simple and depends on various factors. In birds these factors are studied much more than in fishes. Among birds performing brood provisioning, some species such as the great reed warbler, *Acrocephalus arundinaceus*, do not increase the intensity of brood feeding with number of offspring (Nishiumi et al., 1996). In the pied flycatcher, *Ficedula hypoleuca*, brood size has a significant positive effect on the daily energy expenditure of males and their number of feeding visits to the nest. However, no relationship was found between brood size and the energy expenditure or visiting rate of females (Moreno et al., 1995). Furthermore, according to Green and Ydenberg (1994), male ospreys, *Pandion haliaetus*, increase the daily energetic expenditure with brood size. However, they did not respond to brood size manipulations by altering their energetic expenditure, even though the growth rate of enlarged brood was

consequently reduced. Thus, parental energy expenditure and provisioning rates are not always directly determined by brood size, though the close relationship between them is likely.

NUTRITIVE STATUS OF ADULTS AS A MECHANISM REGULATING SUBS

Data on SUBS reveal that both in the field and under laboratory conditions cichlids perform this behaviour not only during parental care but also while foraging for themselves (Williams, 1972; Konings, 1991a, 1991b; Artigas Azas, 1992, 1996; Wisenden et al., 1995). According to field observations of Artigas Azas (1992), young *Herichthys labridens*, start to fin-dig as early as when they reach 2-3 cm in length. The author supposes that fry could copy the behaviour of parents, thereby learning to acquire food. This hypothesis, however, has not been experimentally tested. Some other fishes such as juvenile bluegill sunfish (*Lepomis macrochirus*) also perform SUBS to feed themselves (R.M. Coleman, pers. comm.). Because SUBS is associated with an adult feeding itself and provisioning offspring, Wisenden et al. (1995) suggested that parents may use their own nutritive status to assess the food availability for their young. This reasonable hypothesis, however, had rather weak experimental support. The authors found that fin digging was influenced by the substrate quality (poor versus rich) with only a marginal significance and was not influenced at all by the level of adult ration.

Even if SUBS is not influenced by the substrate quality and food availability, it may nevertheless be associated with the nutritive status of parents. There are at least two reasons to suppose that the current satiation state of parents may be the key factor determining SUBS intensity. First, so long as SUBS is a form of adults foraging (Williams, 1972; Artigas Azas, 1992; Wisenden et al., 1995), it should depend upon satiation. Second, feeding of both adults and young in many Central American "*Cichlasoma*" species is associated with benthos and drift (Konings, 1989; Wisenden et al., 1995; W.A. Bussing, pers. comm.). Therefore, stirring up of substrate by adults should increase food availability for both themselves and fry, in which case correlation between satiation levels of parents and offspring is expected.

My recent study of fin digging in Jack Dempsey (Zworykin, 1998) confirmed this hypothesis. I have shown that the fin digging frequency was influenced by the parents' own current satiation state during performance of fin digging. Specifically, it was higher in hungry than in satiated parents, both in males (Figure 2a) and females (Figure 2b). Probably, it was the current physiological state of parents rather than assessment of food availability, which determined their behaviour. So long as substrate digging improves feeding opportunities of both adults and fry, changes in parents and offspring satiation would correlate. Therefore, adult cichlids could be able to infer the food demands of the fry through the adult's own satiety. Furthermore, a single proximate mechanism regulating fin digging both in adult foraging and in fry provisioning can be expected. Natural selection would be more likely to maintain such an economical mechanism than to create an independent one, specifically dedicated to estimation of fry satiety. It would be more beneficial for the parent to use an already existing behavioural mechanism than to invest into a specialised one, such as visual assessment of the fry appearance or behavior. Furthermore, a possible mechanism based on assessment of the offspring body condition does not allow to estimate their immediate motivational state. In addition, a mechanism involving assessment of the offspring behaviour (e.g. their feeding pattern) requires a reasonably sophisticated cognitive machinery, which would be relatively costly. Alternatively, there might be a generalised short-term effect of satiation, however, my previous study (Zworykin, 1993) showed that both overall activity and certain types of parental behaviour in females of Jack Dempsey did not decrease with satiation.

FACTORS PROBABLY ASSOCIATED WITH EVOLUTION OF SUBS

First, note that all behavioural units exhibiting by cichlids during SUBS are multifunctional and can be performed for purposes other than provisioning of offspring. For example, the digging of caves for eggs and wrigglers, and maintenance of caves are performed using the mouth and fins, and are known to be typical components of nest-building and parental behaviour in cichlid fishes. Beats by pectoral fins are also used by

Table 2. Average percent of detritus and insects in the diets of *Astatheros alfari* and the convict cichlid at two rivers of Costa Rica.

Species	Rio Tortguguero (Winemiller et al., 1995)		Rio Puerto Viejo (Bussing, 1993)	
	detritus (%)	insects (%)	detritus (%)	insects (%)
A. alfari	26	38	15	>55
A. nigrofasciatus	53	4	15	>55

cichlids for fanning of eggs (see Baerends and Baerends van Roon, 1950; Keenleyside, 1978; Keenleyside, 1991 for reviews). Fishes from other families also dig caves for their eggs using the pectoral fins (Morris, 1954; Tavolga, 1954) or combinations of fins, mouth and body movements (Keenleyside, 1972; 1979). Even the management of the leaf during leaf lifting is not a peculiar skill. For example, *Bujurquina vittata* spawn on loose leaves resting on the substrate. The parents, when disturbed, move their eggs by grasping the edge of the leaf in the mouth and swimming away with it (Timms and Keenleyside, 1975; Keenleyside and Bietz, 1981). Spawning onto movable substrate and similar parental behaviour have been also reported in *Aequidens coeruleopunctatus* (Barlow, 1974) and some *Satanoperca* species (Cichocki, 1976; Newman, 1995, 1998).

Thus, if SUBS is a multifunctional behaviour, which function should be considered primary? Based on literature and my own data, one possible evolutionary scenario can be suggested. Initially, stirring up the substrate may have been primarily a pattern of adult foraging in the ancestors of the contemporary "*Cichlasoma*" species. It may be expected that natural selection favoured individuals which used this behaviour more actively during the breeding period, because this would increase the offspring survival. As such, selection could preserve the mechanism regulating the frequency of fin digging associated with adults' feeding behaviour. In addition, it should create an adjustment for parental fin digging performance for optimisation of parental investment. Such process seems to be a typical case of the evolutionary expansion and/or shift of function of behaviour (Severtsov, 1987).

Of course, it is impossible to restore the exact evolutionary course of events, but the above scenario appears to be the most likely for several reasons. First, there are species in which SUBS is associated with both own feeding and brood provisioning and species which stir up the substrate only during their own foraging. However, species in which SUBS is associated with only brood provisioning are unknown. Second, SUBS is widespread among various fishes, besides cichlids, just as a form of foraging. It seems to be a base for the evolution of not only parental provisioning but also other behaviours, for example interspecific feeding commensalism in surmullets with ocellated wrasses (Mochek, 1987) and in *H. labridens* with *H. bartoni* (Konings, 1991a).

On the whole, the origin of parental brood provision on the basis of adults foraging activity is relatively common in various animals. For example, in leech *Helobdella triserialis* the cocoons are attached to the belly of the parent (Kutschera, 1992). Larvae and young are both carried around attached to the belly of the leech. The parent attacks water snails by inserting its proboscis into the soft parts of the snail and sucking the body fluid of this prey. The attached juvenile leeches participate in the meal by sucking on those parts of the snail that were pierced by the proboscis of the parent.

It is worth noting that parental brood provisioning through SUBS is mainly widespread among closely related species of the monophyletic subfamily Cichlasomatinae (Table 1). The only known

exception is relatively more distant toward this group *Guianacara owroewefi*. However, the occurrence of SUBS in this species is not confirmed. Anyway, all nine cichlid species performing SUBS belong to the two most distal subfamilies of the family Cichlidae (Kullander, 1998). This can provide indirect evidence that SUBS has a short evolutionary history, perhaps shorter than the deviation of the Cichlasomatinae and Geophaginae branches from the monophyletic tree of the family Cichlidae.

One could suppose that the evolution of parental SUBS may occur through an expansion and translation of foraging behaviour of adults to their parental care. At first sight, this hypothesis is consistent with the assumption of Wisenden et al. (1995), who suggested that both adults and fry of such species as the convict cichlid feed in nature primarily on the same food: algae and microfauna in the benthos, so that the available food is suitable for both adults and fry. This is why Wisenden et al. (1995) assumed that parents may use their own nutritive status to estimate the food availability for their fry. Indeed, parental provisioning with the adult diet is widely distributed among various animals (Clutton-Brock, 1991). Yanagisawa and Sato (1990) also supposed that in the Tanganyikan mouthbrooding cichlid *Tropheus duboisi* the essential condition for parental food provisioning by means of buccal feeding is the same diet of both adults and young.

Nonetheless, while this assumption may be true for buccal feeding, it is not necessarily the case for fin digging. In all cichlids displaying SUBS feeding of both adult and young is certainly associated with substrate (Table 1). However, most of these species, including the convict cichlid, are primarily zoobenthophagous and none is a detritovory specialist. Moreover, detritophagy is generally not typical for the New World cichlids (Bowen, 1979, 1983; Mérigoux and Ponton, 1998), even though the diet of many insectivore and zoobenthovore cichlids does occasionally include detritus and algae (Bowen, 1983; Konings, 1989; Bussing, 1993). In general, there are different extents of omnivory in various cichlid fishes showing SUBS. For example, *H. labridens* is a very

specialised gastropodovore, whereas the convict cichlid is a typical generalist whose diet may differ between habitats.

Some data on feeding of the convict cichlid and *Astatheros alfari* from two rivers of Costa-Rica are given in Table 2. The trophic spectrum of *A. alfari* is obviously more stable than that of the convict cichlid. It is possible that the fish considered by W.A. Bussing as the convict cichlid was in reality *Archocentrus septemfasciatus*, which had not yet been described at the time of his study and is more widespread in the Rio Puerto Viejo than the convict cichlid (R.M. Coleman, pers. comm.). However, the comparison of the convict cichlid with other similar species also points out the more broad trophic niche of this cichlid. For example, as stated by P. Trujillojimenez (1998), the diet of the convict cichlid is more manifold than that of "*Cichlasoma*" *istlanum* (26 prey categories versus 13 ones). This data on feeding accords with certain morphological features indicating that the convict cichlid is more adapted for consumption of zoobenthos than related species (Winemiller et al., 1995).

The dietary opportunism of the omnivorous convict cichlid allows us to suppose the significant effect of food abundance and rate of feeding competition on its diet composition. This species may be expelled by more specialised species to other feeding habitat. Note that Wisenden et al. (1995) carried out all observations on the convict cichlid in nature during the reproductive period (December to June). In Central America, this period partly overlaps with the dry season. However, it is the season, when the least abundance of food, the greatest feeding competition among fishes and consequently the least overlap of trophic spectrums are found in this region (Zaret and Rand, 1971; Trujillojimenez, 1998). Consequently, there is no wonder that under such conditions the convict cichlid is compelled to feed on detritus.

In my opinion, the origin of foraging activity by means of SUBS was possible just because the main food of adult fish is represented by zoobenthos but not by detritus. For relatively large fish it is senseless to stir up and consequently crumble up the loose material before taking its fragments. This behaviour is more likely to reveal benthic organisms, especially discrete macro-zoo-objects. The data on natural feeding habits of "*Cichlasoma*" species support this hypothesis (Table 1). Following Zaret and Rand (1971), *Aequidens*

coeruleopunctatus also mainly feeds in nature on discrete and moving benthic animals.

Concerning feeding of young cichlids, it is also unlikely that both adults and fry of macro-zoo-benthovore fishes consume the same food, at least because of the obvious difference in size-related accessibility of this food. For example, adult *H. labridens* primarily feed on gastropods, whereas this diet is inaccessible for its fry. Indeed, ontogenetic changes in diet composition have been reported in many cichlids (Lowe-McConnell, 1991; Noakes, 1991; Mérigoux and Ponton, 1998; Piet, 1998). According to Angermeier and Karr (1983), aquatic invertebrates constitute about 95 % of trophic spectrum in young *A. coeruleopunctatus*. However, in adults the share of this food is reduced on average up to 45 %. Correspondingly, the share of other foods in the diet of adults increases. Furthermore, vegetable food is only eaten by large adults of this species (Angermeier and Karr, 1983). Finally, it is known that if there is a sufficient supply of plankton and drift, irrespective of species-specific food preferences of adults, during the first weeks of exogenous feeding juveniles of most Central American cichlids will feed on this rather than detritus or even benthos (Konings, 1989; Lowe-McConnell, 1991; W.A. Bussing, pers. comm.).

Thus, though the assumption of Wisenden et al. (1995) appears to be erroneous, feeding of both adult and young cichlids is associated with substrate and, regardless of the differences between adult and juvenile diets, stirring up of the substrate is likely to increase the food availability for adults and, perhaps to a greater extent, for fry.

It is interesting that SUBS in cichlids is also associated with inter-specific commensalism. *H. bartoni* do not stir up the substrate but its juvenile may profit from non-parental SUBS of *H. labridens* with which it lives sympatrically. While adults of the latter species forage for themselves digging the sand, fry of the former one rush in and pick their choice from the mulch (Konings, 1991a, 1991b). It is worth noting, that diets of these two species are quite similar and this similarity is more pronounced in fry than in adults. If adults and fry feed on the same diet, the food, discovered during SUBS, should be of interest to both adult *H. labridens* and young *H. bartoni*, because the juvenile diets of these two species are identical. However, if the diet of these cichlids does change with age, there would be no conflict between adult *H. labridens* and young

H. bartoni. Most probably, this explains why the fry of *H. bartoni* are not expelled from feeding sites of *H. labridens*. Presumably, the fry is attracted by small feeding objects that are not attractive to large *H. labridens*. In the case of non-overlapping feeding interests, additional expenditure of energy for expelling of commensals are certainly meaningless.

Obviously, stirring up the substrate increases availability of several types of food differing in their composition and size. Thus, SUBS primary used by adults for their own foraging, could also be helpful for providing the fry with fine food. Consequently, selection could favour this behaviour within the framework of parental care. It is known that even among cichlids with highly specialised feeding morphology, there is a paradoxically high degree of plasticity in feeding behaviour (McKaye and Marsh, 1983; Greenwood, 1984; Liem, 1991; Yamaoka, 1991; Dempster et al., 1995). One could suppose that evolution of this form of parental provisioning occurred among fishes breeding in habitats that are poor with respect to plankton, where the similarity of adult and young trophic spectrums is most pronounced. On the other hand, such evolutionary process could accompany colonisation of new habitats. Indeed, according to Dempster et al. (1995), high plasticity in feeding behaviour of cichlids allowed a high degree of dietary opportunism which was a key factor determining their success during colonisation of new habitats. This is even more expressed in less specialised species.

There is no wonder that many cichlids displaying SUBS are generalists which avoid competition switching between many available habitats. One of the most striking example is Jack Dempsey, widely distributed throughout in Central America and even reached Florida (Jennings, 1986). Such broad and relatively swift expansion was probably possible due to eurytropy of this species, inhabiting almost any habitat, including poorly lotic and swamp reservoirs with soft bottom containing a lot of silt and mud (Jennings, 1986; Konings, 1989; Artigas Azas, pers. comm.). A similar case is *Aequidens coeruleopunctatus*, which initially inhabited only South America, but later rapidly occupied Central America
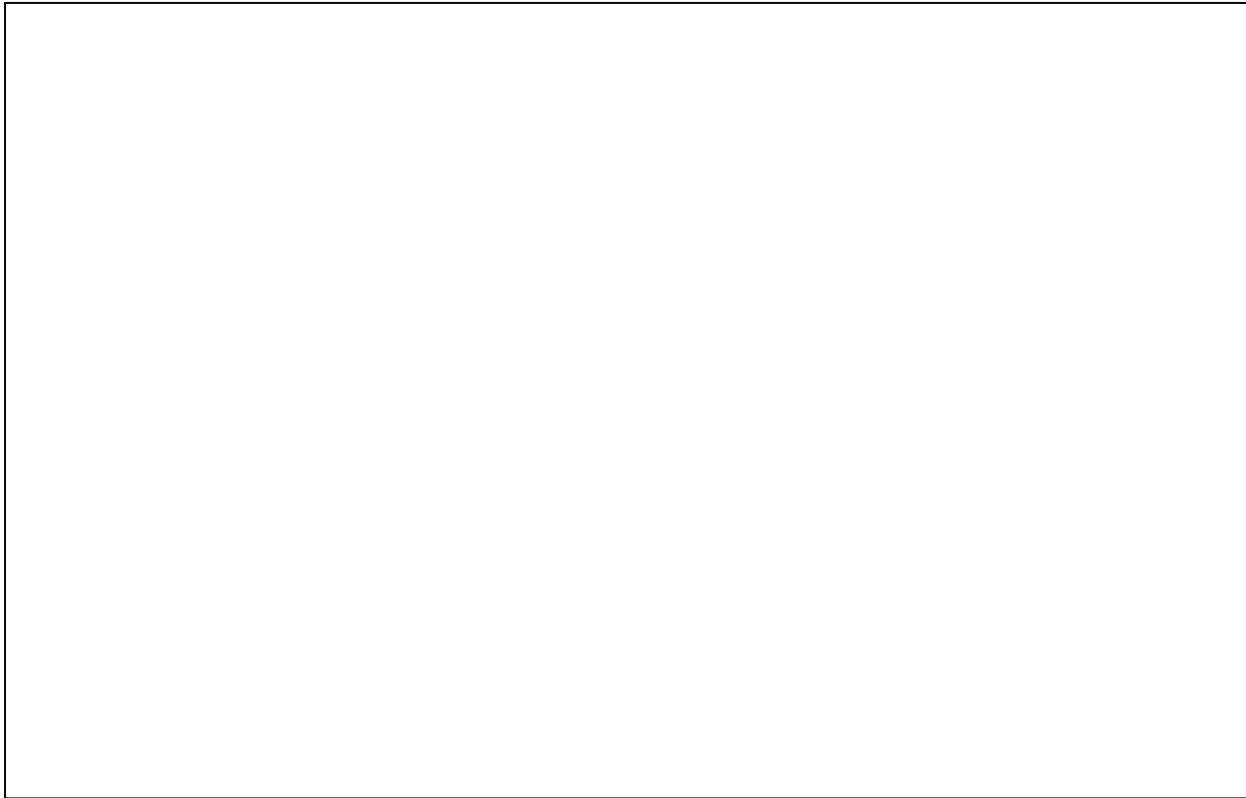
Figure 2a. Effect of satiety on frequency of fin digs per 15 min by parental males of Jack Dempsey at five stages of brood development. Conventions are as in Figure 1.

(Konings, 1989). The distribution of SUBS mainly among Central American cichlids (Table 1) is certainly not unexpected. The patterns of ecomorphological divergence, in relation to cladogenesis of the family Cichlidae, indicate a faster rate of evolutionary diversification of ecological (particularly, feeding) niches in Central American cichlids compared with South American and African faunas (Winemiller et al., 1995).

It is less clear, however, why cichlids performing SUBS mainly inhabit small lakes, rivers and streams but not large reservoirs (Table 1). R.M. Coleman (pers. comm.) supposes that the reason for a lack of SUBS in large reservoirs is that in general there are very few large bodies of water in Central America and those that there are, namely Lakes Managua and Lake Nicaragua have such low visibility as to make observations impossible. However, the

habitat-related difference remains even within forms and populations of the same species. For example, two forms of *H. labridens* inhabiting different biotopes can be distinguished in north central Mexico. One is found in the springs of the Rioverde valley and the other is restricted to Verde and Santa Maria rivers. Only the former form exhibits SUBS (Artigas Azas, 1996). Probably, this remarkable difference is associated with ecological conditions that differ markedly between these habitats. The influence (not always obvious) of ecological factors and, in particular, their seasonal stability on evolution of cichlid fishes have been noted by many authors (Zaret and Rand, 1972; Lowe-McConnell, 1975, 1991; Mina, 1991). Evidently, special field studies are needed to investigate how evolution of SUBS is affected by various ecological factors, including water and bottom conditions, food abundance and composition, predation etc. In this respect, a comparative study of two forms of *H. labridens* seems very promising.

At the same time, it is possible that the factors mentioned are associated with only one of many

Figure 2b. Effect of satiety on frequency of fin digs per 15 min by parental females of Jack Dempsey at five stages of brood development. Conventions are as in Figure 1.

possible evolutionary scenarios. For example, SUBS could evolve simultaneously among several groups. The behaviour like SUBS have been reported in an Asian cichlid *Etroplus suratensis* (Barlow, 1974) and African species *Pelmatochromis guentheri* (Myrberg, 1965). They occupy distant phylogenetic positions in relation to American Cichlasomatinae and live on other continents.

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