Comment on 'Biparental mucus feeding: a unique example of parental care in an Amazonian cichlid'

Buckley and colleagues (Buckley et al., 2010) describe parental care in discus cichlids of the genus *Symphysodon*, demonstrate that immunoglobulin is present in the mucus secreted by breeding discus, and propose that discus might be an interesting novel model system for studies of mammal-like parental care.

Hildemann (Hildemann, 1959) appears to have been the first to describe parental care in discus, providing detailed analyses of the behaviours re-visited by Buckley and colleagues (Buckley et al., 2010). Parental investment is provided after fertilization of the eggs not just in discus but in all cichlids (*ca*. 1600 species), and many other families of fish (for reviews, see Blumer, 1979; Breder and Rosen, 1966; Gross and Sargent, 1985). In fact, parental care is exhibited in around 22% of teleost fish, and in 72% of non-teleost fish (Sargent and Gross, 1993). Sargent and Gross also review the literature and the proposed models that investigate the cost of reproduction and the parent–offspring conflict within fish (Sargent and Gross, 1993), citing early examples, just after the publication of Robert Trivers' theory (Carlisle, 1982; Presley, 1976; Trivers, 1974).

In most fish parental care involves fry guarding or provisioning; for example, breeding convict cichlids (species name) actively disturb the substrate using their pectoral fins to release micro-organisms for their fry to feed on, even though the parents themselves do not feed on such small prey items (Keenleyside, 1981; Krischik and Weber, 1975; Williams, 1972).

The highly developed bi-parental care and fry mucus-feeding behaviour observed in *Symphysodon* spp. is also widespread – at least 28 species have been reported to exhibit fry mucus-feeding behaviour in four families (Noakes, 1979), and this behaviour has evolved many times, in species separated on distant branches of the fish phylogeny, including the Osteoglossiforme *Arapaima gigas* (Liiling, 1964; Menezes, 1951).

Fry feeding on the mucus secreted onto the skin of their parents is called 'contacting' and has been studied in detail in Midas cichlids (*Amphilophus citrinellus*), orange chromides (*Etroplus maculatus*) and discus (*Symphysodon* spp.), in both the laboratory and the wild (Noakes, 1973; Noakes and Barlow, 1973; Ward and Barlow, 1967). The results of Buckley and colleagues (Buckley et al., 2010) on the role of the parents in this behaviour confirm earlier work on the Midas cichlid (*A. citrinellus*) (Schütz and Barlow, 1997).

Whilst it has been well documented that the fry of *Symphysodon* spp. are feeding on the mucus secreted by their parents (Chong et al., 2005; Noakes, 1979; Perrone and Zaret, 1979) [see also Hildemann (Hildemann, 1959) and references therein], it has also been shown that, in contrast to mammals, mucus is not the only meal they are getting. Critically, Bremer and Walter (Bremer and Walter, 1986) found that there are more secretocytes undergoing mitosis in breeding individuals of *S. discus* than in non-breeders and analysis of the faeces of the contacting fry showed that they were consuming these cells and other micro-organisms that are present on the skin of the adults.

However, one area in which the analogy may break down is in Buckley and colleagues' description of weaning (Buckley et al., 2010). The time at which the 'weaning' behaviour is proposed to occur coincides with the time when juvenile fish in the wild would naturally disperse from their parents. At this point in the breeding cycle, parental care has finished in the wild for most cichlids, including those that exhibit contacting behaviour (Noakes and Barlow, 1973). In fact, under aquarium conditions, if Midas cichlid (*A. citrinellus*) fry are left with their parents they eat from them so vigorously in the fourth week that they create wounds on the parental skin (Barlow, 2000). In the wild, such a situation would never occur, as dispersal would have already separated the young fish from their parents (Barlow, 2000).

The most interesting result reported by Buckley and colleagues (Buckley et al., 2010) is that immunoglobulin concentrations are higher in breeding discus than non-breeding discus, and are highest in wild breeding individuals. This result is fascinating and opens up opportunities for future research. What we need to know now is whether this immunoglobulin is passed on to the contacting fry in the same concentrations as it is found in the mucus. If it is, how does the increased amount of immunoglobulin affect the growth and survival of these fry? Away from the immunoglobulin result, there remain other interesting questions for contacting behaviour. The secretocytes found on discus by Bremer and Walter (Bremer and Walter, 1986) appear to be specialized cells; are these types of cell present in other fish that are known to have contacting fry?

The case of parental care in fish is indeed a fascinating model system for answering a variety of questions about the cost of reproduction, and the parent–offspring conflict, and many investigations have already been conducted. It is my hope that modern technologies and techniques can help us to better understand these systems and their problems.

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Response to "Comment on 'Biparental mucus feeding: a unique example of parental care in an Amazonian cichlid'"

Many models of parental investment consider offspring as passive participants where parents decide upon appropriate levels of investment. However, in 1974, Trivers introduced the theory of parent–offspring conflict, which views offspring as active participants soliciting investment from parents (Trivers, 1974). Although parent–offspring conflict in its broadest sense may apply to any sexually reproducing species showing parental investment (Trivers, 1974), in oviparous species, those that lay eggs, pre-parturition conflict between future offspring and parents is unlikely (Crespi and Semenuik, 2004). Post-parturition conflict is often difficult to determine if parental care is confined to parental defence of offspring. The stickleback, *Gasterosteus aculeatus*, is an example of an oviparous species where females lay eggs and then males guard and fan the developing embryos. To our knowledge there is no concrete evidence in oviparous fish species that developing offspring are able to directly manipulate parental investment. There is clear potential for chemical communication between parents and offspring to occur post-parturition in oviparous fish species (e.g. Mourabit et al., 2010) but a role in parent–offspring conflict remains speculative. Certainly, many previous models of parental investment motivated by teleost fishes focus on factors that influence a parent's decision to invest in offspring only from the perspective of the parent (reviewed by Sargent and Gross, 1993) without active influence by offspring.

In *Symphysodon* (and some other species of cichlids) parents provide offspring with an opportunity to gain nutrition from parental mucus and offspring perform behaviours (known as contacting, micronipping, parent-touching) to maximise attainment of this food. While not all contacting behaviours in fish are trophic in function (Noakes, 1979), where nutrition is obtained through this behaviour, offspring have the potential to demand more investment than the parent is selected to give (Trivers, 1974). Mucus-feeding behaviour stands out as a situation where measurable parent–offspring conflict post-parturition occurs. Ongoing, unpublished experiments in our laboratory allow us to manipulate both parental investment and offspring demand during this period of conflict in *Symphysodon* spp. Only a few species of fish (<0.2%) perform such parental care behaviours where parent–offspring conflict can be studied post-parturition.

In the context of mucus feeding, 'mucus' is a term used to describe a secretion containing a variety of substances [e.g. Buckley et al. (Buckley et al., 2010) measured immunoglobulin, protein, hormones and ions] in the same way that mammalian 'milk' refers to a liquid containing fats, proteins, sugars, immunoglobulins and micro-organisms. Therefore, provision of fish 'mucus' as a form of parental care could be considered analogous to mammalian 'milk'. In lactating species, postnatal parental care can be divided into three periods according to the age of the offspring (Trivers, 1974). The last of these periods is the weaning period where most contact between parent and offspring is initiated by the offspring, with parents showing open avoidance and even aggression towards offspring (Trivers, 1974). Only by studying the behaviour of both parent and offspring is it possible to determine whether a weaning conflict exists. Our study (Buckley et al., 2010) documents changes in parental care during the breeding period of *Symphysodon* and highlights that in week three, open avoidance by the parents can be observed in this species and offspring actively seek out their parents during this period. These observations of both parental and offspring behaviour are directly in line with Trivers' description of the third period of parental care in mammals (Trivers, 1974).

This fascinating behaviour seen in *Symphysodon* spp. certainly raises many questions. Currently we are investigating, among other things, whether parental immunoglobulins found in this mucus meal are measurable in discus fry. We have recently demonstrated that mucus of adult fish inhabiting metal-contaminated waters or eating a metal-contaminated diet contains measurable levels of contaminants that can be passed on to offspring through mucus feeding (R. J. Maunder, J.B., A.L.V. and K.A.S., unpublished results).

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