



Parental investment in relation to offspring quality in the biparental cichlid fish *Pelvicachromis taeniatus*

Timo Thünken^{a,*}, Denis Meuthen^a, Theo C.M. Bakker^a, Harald Kullmann^{b,1}

^aInstitute for Evolutionary Biology and Ecology, University of Bonn

^bZentrum für Didaktik der Biologie, University of Münster

ARTICLE INFO

Article history:

Received 8 December 2009

Initial acceptance 8 February 2010

Final acceptance 31 March 2010

Available online 8 May 2010

MS. number: 09-00776R

Keywords:

body size

brood care

brood size

cichlid

Pelvicachromis taeniatus

Theory predicts that parents should adjust their parental investment to the reproductive value of the brood. Previous studies have mainly investigated the relationship between brood size, brood age and the intensity of care. However, the impact of brood quality traits such as the offspring's average body size on parental investment has received relatively little attention. We examined the parental response to brood quality in the biparentally brood-caring cichlid fish *Pelvicachromis taeniatus*. We manipulated offspring quality by manipulating the food availability for the free-swimming fry and measured the parental response over 4 weeks. Generally, care decreased over the 4 weeks suggesting that parents adjust care to decreasing offspring vulnerability. However, parents of relatively low-quality broods, that is, of broods with relatively small average individual body size, showed a greater reduction in care than parents of high-quality broods resulting in a significant difference in care provided in the fourth week. The result suggests that parents adjust their care to brood quality and supports the predictions of the parental investment theory. Furthermore, mothers of high-quality fry were significantly more aggressive towards their partner than mothers of low-quality fry. This result is discussed in the context of parental response to brood value. Generally, females invested more in brood care than males.

© 2010 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.

By providing brood care, animals improve the survival and reproduction chances of their offspring and thereby increase their inclusive fitness (Hamilton 1964). However, parental brood care involves costs, caused by, for example, greater predation risks and energy loss (Clutton-Brock & Vincent 1991; Smith & Wootton 1995). Individuals should care for their offspring according to their reproductive value and should be able to increase their reproductive success by trading off present and future parental investment (parental investment theory: Trivers 1972; Dawkins & Carlisle 1976; Sargent & Gross 1985; Clutton-Brock & Vincent 1991). According to this theory, maximum care should only be provided to broods of high reproductive value whereas parents should reduce care for broods of lower reproductive value to save energy for future reproductive events.

The reproductive value of offspring is assumed to be determined by variables such as brood size, offspring age and offspring quality (reviewed in Montgomerie & Weatherhead 1988). Parents should invest more in larger broods because there is a higher probability that more offspring will reach independence and reproduce.

Several studies in various taxa showed greater parental investment in larger broods than in smaller ones (e.g. mammals: Koskela et al. 2000; birds: Wallin 1987; Rytönen 2002; Tilgar & Kikas 2009; fish: Coleman et al. 1985; Lavery & Keenleyside 1990). When a brood is too small, it might even be deserted or cannibalized (Schwanck 1986; Mrowka 1987; Beissinger 1990; Sargent 1992; Jennions & Polakow 2001; Manica 2002), which is assumed to be adaptive (e.g. Mehliis et al. 2009).

The probability of reproduction is higher in older offspring than in younger ones (Dawkins & Carlisle 1976; Boucher 1977). Therefore, it is sometimes assumed that parental investment should generally increase with offspring age (see Montgomerie & Weatherhead 1988). However, the results of studies examining the relationship between parental care and offspring age are ambiguous. Several studies showed an increase in care with increasing age (Montgomerie & Weatherhead 1988; Rytönen et al. 1990; Clutton-Brock & Vincent 1991; Lavery & Colgan 1991; Lavery 1995b; Rytönen et al. 1995; Wisenden & Keenleyside 1995), whereas others are indicative of decreasing care (St John & Corning 1973; Svare & Gandelman 1976; Dale et al. 1996; Koskela et al. 1997, 2000).

To our knowledge, parental adjustment to brood quality has received relatively little attention (but see Lyon et al. 1994; Bize et al. 2006; Griggio et al. 2009 as examples of parental individual favouritism within broods). Brood quality can be manifested, for example, by the offspring's average body size, which may be

* Correspondence: T. Thünken, Institute for Evolutionary Biology and Ecology, University of Bonn, An der Immenburg 1, 53121 Bonn, Germany.

E-mail address: tthuenken@evolution.uni-bonn.de (T. Thünken).

¹ H. Kullmann is at the Zentrum für Didaktik der Biologie, University of Münster, Hindenburgplatz 34, 48143 Münster, Germany.

affected by harsh environmental conditions such as low food availability. A study by Rytkönen (2002) on great tits, *Parus major*, suggested that parents adjust their brood-caring behaviour to offspring quality. However, other studies failed to find a significant effect (Curio & Regelmann 1987; Koskela et al. 2000).

Cichlids in general are characterized by intense brood care (Barlow 2000) and thus are especially suited to test the prediction of the parental investment theory. Under natural conditions the value of a brood might rapidly change, for example when a brood is dramatically reduced by predation (e.g. Keenleyside & Mackereth 1992; Wisenden et al. 2008). Previous studies in cichlids showed a decline in parental care when the brood size, that is the offspring number, was experimentally reduced in the convict cichlid, *Cichlasoma nigrofasciatum* (Lavery & Keenleyside 1990) and the blue acara cichlid, *Aequidens coeruleopunctatus* (Carlisle 1985; Jennions & Polakow 2001; Vélez et al. 2002), supporting the parental investment theory. Brood value might also be influenced by continuously varying environmental variables such as food availability. Parents might be confronted with fry of low quality in harsh environments and thus should adjust investment accordingly.

The aim of the present study was to investigate parental investment in relation to offspring quality in the biparentally brood-caring cichlid fish *Pelvicachromis taeniatus*. This is a socially monogamous, stream-dwelling cichlid from soft-water rivers in Western Africa (Thünken et al. 2007a). Males establish nest sites (usually a cave) and guard them until a female arrives (T. Thünken, personal observation). Both sexes show courtship behaviour and are highly selective during mate choice (Thünken et al. 2007a, c; Baldauf et al. 2009a, b). The female spawns 20–150 eggs into the nest cavity. While the male guards the area in front of the nest cavity, the female stays inside and cares for the eggs and wrigglers (larvae that still have a yolk sac). After about a week the fry have absorbed their yolk sacs and leave the cave. The free-swimming fry are guarded by both parents until they reach independence.

In our experiment, we manipulated brood quality by manipulating the food availability for the free-swimming fry but keeping that of parents unaffected, and examining parental care for offspring differing in nutritional state over 4 weeks. This long observation period additionally allowed us to investigate the relationship between offspring age and parental care.

METHODS

Experimental Animals

Experimental animals were either wild-caught or second-generation laboratory-bred fish. Wild-caught fish were collected as juveniles or subadults with hand nets from the Moliwe river near Limbe, Cameroon (04°04'N, 09°16'E) in June 2007. Fish were transported in fish bags filled with river water to the institute in Germany. All fish survived the flight and were in good condition on arrival at the institute. Laboratory-bred fish originated from individuals caught in 2003 from the Moliwe River. Prior to the experiment, fish were kept in large tanks (50 × 50 cm and 30 cm deep) in groups of approximately 30 individuals. To prevent reproduction, no caves were available. The water temperature was kept constantly at 25 °C, which is the mean temperature in the Moliwe river. Experiments were conducted between February and October 2008.

Experimental Set-up

The experiments were conducted in 24 test tanks (16 tanks: 40 × 45 cm and 30 cm deep; eight tanks: 50 × 40 cm and 30 cm deep). Each tank was filled with 40 litres of water. Tank water consisted of 20 litres of distilled water (pH 7.0; electrical

conductivity about 0 mS/m) and 20 litres of tap water (pH 8.0 ± 0.1; electrical conductivity 330 ± 20 mS/m). Visual contact between tanks was prevented using tar paper. Each tank contained gravel sand, a gully filter, an aquarium heater and a ceramic cave as well as approximately 4 g of Java moss, *Vesicularia dubyana*. The light was provided in a 12:12 h light:dark cycle (from 0900 to 2100 hours) by an automatic dimmer; water temperature was kept constant at 25 °C during the experimental period.

After assigning the male fish to the tanks (one male per tank), we allowed them to settle down for 2 days and to occupy the caves. Afterwards, one brightly coloured, haphazardly chosen, reproductively active female was introduced into each of the males' tanks. Altogether, 47 pairs were arranged, 10 of them comprising wild-caught individuals. Fish were fed with a mix of frozen *Artemia* and *Chironomus* larvae. The caves were checked for eggs when the pairs showed the following typical breeding behaviours: the female stayed inside the cave nearly the whole time and/or the male stayed in front of the cave, together with a lack of courting behaviour. To check the caves for eggs, they were carefully and slowly raised and turned in the direction of the observer.

In total, 39 pairs spawned and 29 pairs reared the fry until the free-swimming stage. As soon as the fry swam around freely the number of larvae was estimated (mean of three counts) and they were assigned to a feeding regime. We assigned the first offspring group to a feeding regime haphazardly (the first group was poorly fed) and alternated the assignment of the subsequent offspring groups between the two feeding regimes. In total, 15 offspring groups were assigned to the well-fed and 14 groups to the poorly fed feeding regime. Seven times the experiment had to be stopped because of illness or death of one or both parents (in total four times, three times parents of well-fed offspring) or filial cannibalism (three times, see below). In these cases we assigned new offspring groups according to the feeding regime of the discarded experiments to maintain the balance between the treatments. Eventually, 12 offspring groups were well-fed (six of them descended from wild-caught fish) and 10 groups poorly fed (three of them descended from wild-caught fish).

The poorly fed groups (pf) were fed with living *Artemia* nauplii only in the morning, whereas the well-fed groups (wf) received the same amount of additional nauplii in the afternoon. The amount of food for the offspring was adjusted to the estimated number of larvae. In the first and second week of free swimming, fry were fed with 10 µl of concentrated living *Artemia* nauplii per larva using an Eppendorf micropipette. From the third week on, the food ration was increased to 15 µl of *Artemia* nauplii per larva. Normally, parents did not consume the living *Artemia*. During the experimental phase each parent was fed daily with four red *Chironomus* larvae (ca. 2.5 cm long), which the fry could not consume. The first feeding of the fry was conducted in the morning before the daily observation. Parental as well as the second fry feeding of the well-fed groups took place in the afternoon. The order of feeding among tanks was randomized each day.

On the 10th day of filial free swimming we carefully replaced 20 litres of the water with 10 litres of fresh tap water and 10 litres of osmotic water. Algae were removed from the panes with cotton at the same time to facilitate further observation. After the 4-week observation period, the body size of the young was measured on the 29th day approximately 4 h after the initial feeding in the morning. We used a digital calliper to measure the small fish to the nearest 10 µm. We also counted the young of each pair.

Before and after the experiment, parental body masses and standard lengths (SL, snout to the beginning of the tail fin) were measured to an accuracy of 0.001 g and 1 mm, respectively. Within pairs, the male was always the larger parent. Generally, wild-caught fish were larger than laboratory-bred fish in standard length and

Download English Version:

<https://daneshyari.com/en/article/2417272>

Download Persian Version:

<https://daneshyari.com/article/2417272>

[Daneshyari.com](https://daneshyari.com)