



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

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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.

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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

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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

body mass (Mann–Whitney U tests: all $P < 0.05$). However, size differences between the sexes within pairs did not differ significantly between wild-caught and laboratory-bred pairs (Mann–Whitney U test: $U = 42$, $N_{\text{wild}} = 9$, $N_{\text{lab}} = 13$, $P = 0.292$). By chance, fathers of poorly fed young (median, interquartile ranges: SL: 5.90 cm, 5.81–6.36 cm; mass: 4.80 g, 4.75–4.40 g) were significantly larger than fathers of well-fed young (median, interquartile ranges: SL: 5.52 cm, 5.21–5.7 cm; mass: 4.04 g, 3.48–4.40 g; Mann–Whitney U tests: SL: $U = 8$, $N_{\text{pf}} = 10$, $N_{\text{wf}} = 12$, $P < 0.001$; mass: $U = 10$, $N_{\text{pf}} = 10$, $N_{\text{wf}} = 12$, $P < 0.001$; see [data analysis](#)). Mothers of poorly fed young did not differ significantly in mass (2.34 g, 2.14–2.44 g) and standard length (4.27 cm, 4.25–4.37 cm) from mothers of well-fed young (mass: 1.98 g, 1.65–2.39 g; SL: 4.12 cm, 4.01–4.46 cm; Mann–Whitney U tests: both $P > 0.05$). Consequently, the size differences within pairs were also greater between parents of poorly fed fry than between parents of well-fed fry (Mann–Whitney U tests: $U = 18.5$, $N_{\text{pf}} = 10$, $N_{\text{wf}} = 12$, $P = 0.006$). The absolute increase in size of the parents during the experimental period did not differ significantly between the two treatment groups (Mann–Whitney U tests: all $P > 0.05$).

Quantification of Brood Care Behaviour

The parental brood care behaviour was observed daily over 4 weeks by a person naïve to the treatment groups. To ensure the undisturbed intake of food by the young, daily observation started approximately 30 min after the morning feeding. The observation order of the tanks was randomized by lot each day. Each tank was observed for 5 min. The observer was positioned approximately 1.5 m from the front pane of the tanks. To let the fish become accustomed to the presence of the observer, observation started after approximately 30 s. Every 30 s, we scored whether the male, the female, both or neither cared for the fry. Behaviour was defined as brood care when an individual was one body length or less from the fry. Additionally, we scored the number of jolts from both parents within the 5 min observation period. Jolting is defined as quick, lateral jerking or twitching movements of the head and body, which is interpreted as a calling behaviour in the presence of danger to make the offspring settle on the substrate (Keenleyside 1991). Furthermore, we scored the number of attacks between parents. Attacking was defined by a fish ramming its snout into the body of its partner.

Data Analysis

Twenty-five pairs spawned and reared the fry successfully until the free-swimming stage. Three pairs that cannibalized their free-swimming young during the experiment were excluded from the main analysis. Eventually, 12 pairs rearing well-fed young and 10 pairs rearing poorly fed young were analysed for brood care behaviour using R 2.6.1 (R Development Core Team, Austria, Vienna) and SPSS 12 (SPSS Inc., Chicago, IL, U.S.A.). We used generalized linear mixed models (GLMMs, R function `lmer` in library `lme4`) with a logit link function and a binomial error distribution to estimate the fixed effect of filial feeding (poorly fed/well-fed) and observation day (1–28) and their interaction on brood care ('presence': one or both parents cared; 'absence': neither parent cared). To account for repeated observations of the same pairs, we included 'pair identity' as a random factor. We included standard length of males, size difference between the sexes, brood size and origin of the parents (wild-caught or F1) as a covariate in the GLMM. Additionally, we conducted a further analysis in which we excluded two pairs with the greatest size differences between parents from the poorly fed treatment and two pairs with the smallest size differences from the well-fed treatment. After the exclusion of the four pairs the size

difference between sexes was no longer significantly different between treatment groups (Mann–Whitney U test: $P > 0.05$). In the [Results](#), we refer to this analysis as the 'reduced sample'.

To examine differences between the sexes we analysed the cases when only one parent provided care using a GLMM (with female providing care 'present' or 'absent' as the response variable). To investigate the relationship between filial feeding and parental aggression and warning behaviour, respectively, we conducted a GLMM (R function `lmer` in library `lme4`), with a log link function and Poisson error distribution. Number of attacks or joltings, respectively, were entered as the response variable and sex and food treatment as fixed factors. Pair identity and individual identity nested within pair identity were entered as random factors.

Likelihood-ratio tests assessed whether the removal of a variable caused a significant decrease in model fit. Hence, degrees of freedom always differed by one. Nonsignificant ($P > 0.05$) factors and interactions were removed from the analysis (Engqvist 2005). P values refer to the increase in deviance when the respective variable was removed. Given test probabilities are two tailed throughout.

Offspring of the two treatment groups showed no signs of illness or abnormal behaviour. Fry of both feeding regimes showed significant growth (when the fry start to swim free, at the beginning of the feeding regimes in this study, they are approximately 5–7 mm long, unpublished data); fry of the two feeding regimes differed only in the growth rate, which was higher in the additionally fed group. After the experiments all fish were fed ad libitum. Adult fish of both treatment groups were in good condition and showed no obvious differences. The study conformed to the legal requirements of Germany and no licences were required for the collection or import of fish or for the study.

RESULTS

After the experimental phase, fry of the two feeding treatments showed a significant difference in body size: well-fed fry were significantly larger than poorly fed fry (Mann–Whitney U test: $U = 6$, $N_{\text{pf}} = 10$, $N_{\text{wf}} = 12$, $P < 0.001$; [Fig. 1](#)). The average brood size (number of individuals per brood) did not differ significantly between well- and poorly fed young (median, interquartile range: pf: 34.5, 22–47; wf: 46.5, 35.5–58.75; Mann–Whitney U test:

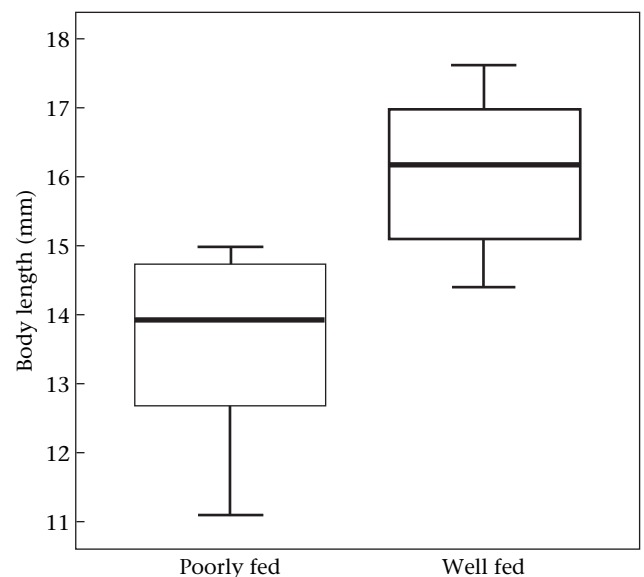


Figure 1. Body length (median \pm quartiles, ranges) of 10 poorly fed and 12 well-fed full-sibling groups of juveniles after the feeding treatment of 4 weeks.

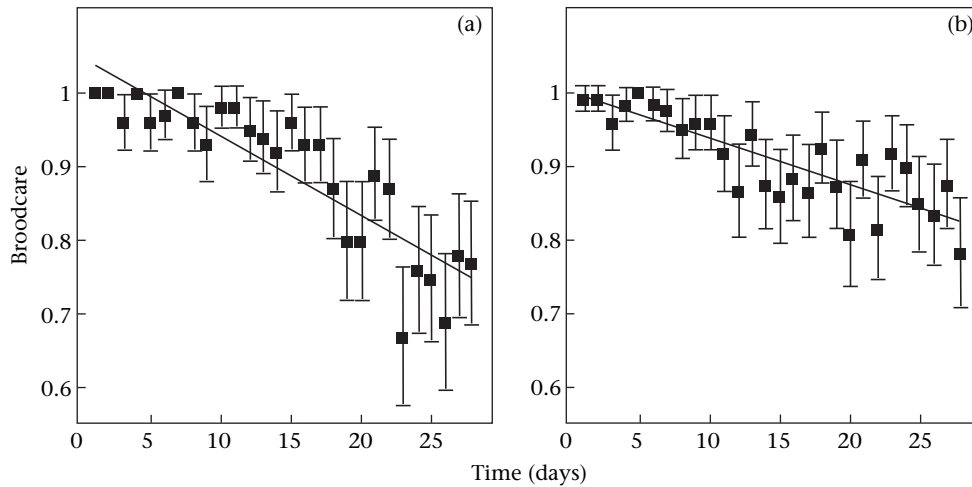


Figure 2. Average proportion of time \pm SE that (a) 10 groups of poorly fed and (b) 12 groups of well-fed offspring were cared for by one or both parents during daily 5 min observations over the experimental period of 4 weeks. The lines are the least-square regression lines.

$U = 6$, $N_{pf} = 10$, $N_{wf} = 12$, $P = 0.14$). Generally, the amount of care decreased with time (GLMM: $\chi^2 = 173.46$, $P < 0.001$; Fig. 2). There was a significant interaction between treatment and time (GLMM: $\chi^2 = 13.289$, $P < 0.001$, Fig. 2), that is, the reduction in care was greater in the poorly fed treatment than in the well-fed treatment. This effect was also found in the reduced sample (see Methods; GLMM: $P < 0.001$). We therefore analysed the single weeks separately. Parental care did not differ significantly between the treatment groups during the first 3 weeks (GLMMs: 1st week: $\chi^2 = 0.107$, $P = 0.742$; 2nd week: $\chi^2 = 1.122$, $P = 0.289$; 3rd week: $\chi^2 = 0.171$, $P = 0.679$). In the fourth week, however, well-fed fry received significantly more care than poorly fed fry (GLMM: $\chi^2 = 6.390$, $P = 0.011$; reduced sample: $P < 0.01$). Neither male standard length, origin of the parents (wild-caught or F1), brood size or size difference between the sexes within pairs significantly explained variation in brood care behaviour (GLMMs: all $\chi^2 < 3.15$, all $P > 0.05$; reduced sample: all $P > 0.270$). Generally, females spent significantly more time caring than males (GLMM: intercept: $z = 5.457$, $P < 0.001$).

The interaction between treatment and sex of the parent significantly explained variation in attacks (GLMM: $\chi^2 = 5.433$, $P = 0.019$; Fig. 3). In the well-fed treatment, females were significantly more aggressive than males (GLMM: $\chi^2 = 13.417$, $P < 0.001$) but not in the poorly fed treatment (GLMM: $\chi^2 = 0.785$, $P = 0.375$; Fig. 3). Females of the well-fed treatment attacked significantly more than females of the poorly fed treatment (GLMM: $\chi^2 = 10.383$, $P = 0.001$). The different treatments had no significant effect on aggression of the males (GLMM: $\chi^2 = 3.029$, $P = 0.081$; Fig. 3). Neither treatment nor the interaction between treatment and sex significantly predicted variation in joltings (GLMMs: treatment: $\chi^2 = 0.066$, $P = 0.796$; interaction: $\chi^2 = 2.293$, $P = 0.130$). Females, however, generally jolted significantly more often than males (GLMM: $\chi^2 = 17.543$, $P < 0.001$).

The three cannibalized broods, which were excluded from the main analysis, were significantly smaller than noncannibalized broods (median brood size, interquartile ranges of cannibalized broods: 10, 8–16; noncannibalized broods: 30.5, 24.25–40; Mann–Whitney U test: $U = 2$, $N_1 = 3$, $N_2 = 22$, $P = 0.003$).

DISCUSSION

In the present study we investigated the impact of offspring quality on parental investment in the biparentally brood-caring

cichlid *P. taeniatus*. We manipulated offspring quality by providing the free-swimming fry with low or high food rations and examined the parental response over 4 weeks. Food availability had a significant effect on offspring body size. After 4 weeks of food ration manipulation, well-fed offspring were larger than poorly fed offspring. Offspring body size is known to be closely related to fitness in many species (Sogard 1997). For example, larger offspring are better competitors for resources (e.g. Bashey 2008).

Generally, parental brood care decreased with time, that is, older offspring received less care than younger ones. Parents of poorly fed offspring showed a greater reduction in care than parents of well-fed offspring. Differential parental care was especially pronounced between treatment groups in the fourth observational week when poorly fed fry received significantly less parental care than well-fed fry. To our knowledge the present study is one of the first providing experimental evidence for parental adjustment to brood quality. By adjusting care to low-quality broods parents are able to save energy for subsequent breeding cycles (e.g.

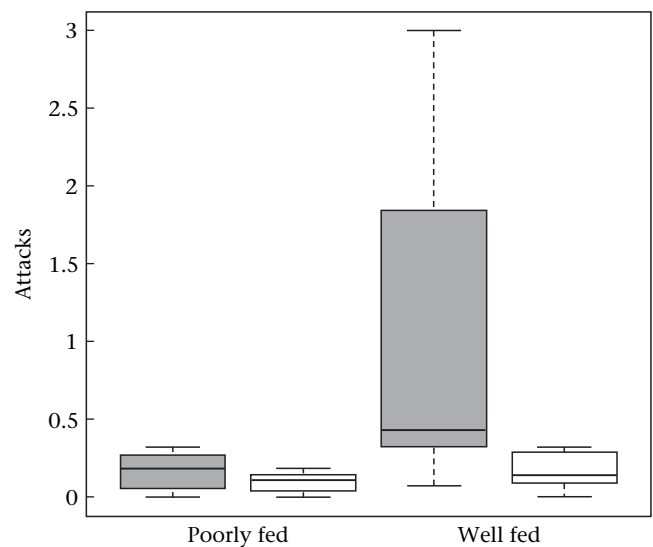


Figure 3. Number of attacks (median \pm quartiles, ranges) against their partner by mothers (grey bars) and fathers (white bars) of 10 groups of poorly fed and 12 groups of well-fed fry during daily 5 min observations over the experimental period of 4 weeks.

Montgomerie & Weatherhead 1988). The results are thus consistent with the parental investment theory suggesting that the optimal level of present investment should maximize the sum of present and future reproductive success (Sargent & Gross 1985). By chance, fathers of the poorly fed offspring were larger than fathers of the well-fed young resulting in a difference in parental size ratio between treatments. Male/female size ratio has been suggested to influence the parental roles and thus brood care in convict cichlids (Iitzkowitz et al. 2005). However, neither male size nor parental size ratio significantly explained parental effort. Furthermore, when we removed pairs with the most extreme size ratio from both treatments the size ratio differences between treatments were no longer significant. The treatment effects, however, remained significant. In addition to that, the main result of the present study was a different temporal trend in the two treatments rather than a general difference in care which might have been expected if the size differences within pairs had influenced care.

We found significant sex differences between treatments in attacks against the partner: mothers of well-fed fry showed more aggression than their male partners whereas parents of poorly fed fry did not differ significantly in aggression. This result is surprising because one might expect that the sexual conflict over care (e.g. Houston et al. 2005) should be smaller in parents with offspring of relatively higher quality. On the other hand, female aggression level could be taken as an indicator of their defence behaviour and consequently aggressiveness might be interpreted as maternal investment. In this case, increased female aggressiveness might be an adjustment to the higher brood quality. For example, in the bank vole, *Clethrionomys glareolus*, female aggression was also positively correlated with the reproductive value of the brood (Koskela et al. 2000). Alternatively, the female aggression might be a response to male behaviour or might be caused by the observed differences in parental size ratio.

Smaller broods had a higher probability of being cannibalized than larger broods. This result is consistent with earlier studies in different cichlid species (Schwanck 1986; Mrowka 1987) and confirms previous studies showing that parents adjust their investment to brood size (Carlisle 1985; Jennions & Polakow 2001; Vélez et al. 2002).

Parental adjustment to brood care raises the question, on which cues is parental assessment based? Visual cues have been shown to be important in parent–offspring recognition in cichlids (Myrberg 1975). Body size of the fry (the trait we measured) might be used by the parents as an indicator of brood quality. Besides body size, body coloration and odour might also function as proxies for quality because they have been shown to be affected by the nutritional state (Lyon et al. 1994; Bize et al. 2006; Griggio et al. 2009; Mas et al. 2009). Visual as well as olfactory cues play a role in social interactions in *P. taeniatus* (Baldauf et al. 2009a, b; Thünken et al. 2009). Their importance in parental offspring assessment would be an interesting question for future experiments.

In our experiment, parental care clearly decreased with increasing offspring age and thus contradicts the assumption that the intensity of care is generally positively associated with offspring age (see Montgomerie & Weatherhead 1988). However, the result is not surprising and similar results are found in other animals (St John & Corning 1973; Svare & Gandelman 1976; Lavery 1995a; Dale et al. 1996; Koskela et al. 1997, 2000). As Montgomerie & Weatherhead (1988) pointed out, brood defence, for instance, should decline when the offspring become increasingly independent and less vulnerable to predation. This statement is in accordance with findings in convict cichlids, which show a parental behaviour similar to *P. taeniatus*: in convict cichlids, parental care first increases from the egg stage to the wriggler stage when the fry are particularly prone to predation (e.g. Lavery & Colgan 1991;

Lavery 1995a). Then, with increasing age (and size) the fry become less vulnerable to predators because they are more difficult to consume, at least by conspecific predators, and are able to avoid predation by themselves more actively. Consequently, parental care then declines with increasing age although the reproductive value of the young increases (e.g. Wisenden 1994; Wisenden et al. 2008). A similar pattern was found in bank voles (Koskela et al. 2000). This suggests that the intensity of care depends, on the one hand, on the necessity of care which is, for example, influenced by offspring vulnerability and, on the other hand, by offspring value. Clearly, care should be stopped when it has no influence on offspring fitness. Thus, in *P. taeniatus*, the trade-off between current and future reproductive success appears to lead to a parental adjustment to brood quality as well as to brood vulnerability.

Compared to males, females spent more time protecting the young, gave more warning signals and, at least mothers of high-quality broods, were more aggressive indicating that females generally invest more in brood care than males. This result is in accordance with findings in convict cichlids with a similar mating system (Lavery & Keenleyside 1990; Lavery & Kieffer 1994; Wisenden et al. 2008). Generally, uncertain paternities as well as higher variance in male than female mating success are suggested to lead to female-biased parental investment (Kokko & Jennions 2008). The genetic mating system of *P. taeniatus* is unknown. The very long sperm observed in *P. taeniatus* (Thünken et al. 2007b), however, might be an adaptation to sneaking, that is, to sperm competition (see also Fitzpatrick et al. 2009 for the relationship between sperm length and sperm competition in cichlids). Sneaking could lead to considerable uncertainty in paternity and thus could drive the evolution to female-biased investment.

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