Females produce larger eggs for large males in a paternal mouthbrooding fish

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When individuals receive different returns from their reproductive investment dependent on mate quality, they are expected to invest more when breeding with higher quality mates. A number of studies over the past decade have shown that females may alter their reproductive effort depending on the quality/attractiveness of their mate. However, to date, despite extensive work on parental investment, such a differential allocation has not been demonstrated in fish. Indeed, so far only two studies from any taxon have suggested that females alter the quality of individual offspring according to the quality/attractiveness of their mate. The banggai cardinal fish is an obligate paternal mouth brooder where females lay few large eggs. It has previously been shown that male size determines clutch weight irrespective of female size in this species. In this study, I investigated whether females perform more courtship displays towards larger males and whether females allocate their reproductive effort depending on the size of their mate by experimentally assigning females to either large or small males. I found that females displayed more towards larger males, thereby suggesting a female preference for larger males. Further, females produced heavier eggs and heavier clutches but not more eggs when paired with large males. My experiments show that females in this species adjust their offspring weight and, thus, presumably offspring quality according to the size of their mate.

Keywords: differential allocation; paternal mouthbrooding fish; male size; attractiveness; parental quality; egg size adjustment

1. INTRODUCTION

When an individual invests in a reproductive event according to the expected pay-off from that event and the pay-off is dependent on the quality or attractiveness of the partner, this behavioural plasticity is referred to as differential allocation. Originally described by Burley (1986), the differential allocation hypothesis assumes a trade-off between successive reproductive events (Stearns 1992) and that individuals allocate differently according to the quality of their current mate and the likelihood of finding a better mate in the future (Sheldon 2000). Balzer & Williams (1998) suggested that female reproductive effort can be divided into 'primary' reproductive effort (egg size, clutch size and laying date (in birds)) and 'secondary' reproductive effort (parental care). To date, females have been shown to allocate their primary reproductive effort as well as secondary reproductive effort differentially in several taxa, for example birds (e.g. Burley 1986, 1988; De Lope & Møller 1993; Petrie & Williams 1993) amphibians (Reyer *et al.* 1999) and insects (Wedell 1996; reviewed by Sheldon 2000). However, in fish, although there are correlational studies consistent with differential allocation, there is no experimental evidence that fish control investment in this fashion. Since size and fecundity typically correlate strongly in fish (e.g. Perrone 1978; Berglund *et al.* 1986) and most fish show indeterminate growth, there is generally a particularly steep trade-off between female reproduction and growth in this taxon (e.g. Warner 1984). Therefore, allocating extra resources to current reproduction is likely to be at the cost of future fecundity, so the existence of differential allocation is by no means self-evident in fish.

Interestingly, although many studies have shown that the number of offspring may be changed when differential allocation occurs, only two recent studies of zebra finches (*Taeniopygia guttata*) (Gil *et al.* 1999) and mallards (*Anas platyrhynchos*) (Cunningham & Russell 2000) have suggested that the quality of individual offspring can also be controlled by females according to the attractiveness of their mate. Thus, in addition to exploring whether differential allocation occurs in a wider range of taxa, more experimental studies are needed in order to determine whether females commonly influence offspring quality according to the attractiveness of their mate.

(a) *Study species and rationale*

A particularly promising candidate species for the study of reproductive investment in fish as well as differential allocation of offspring quality is the sexually monomorphic banggai cardinal fish (*Pterapogon kauderni*), which is a small (standard length maximum 55 mm) obligate paternal mouthbrooding fish (Allen & Steene 1995). Pairs are formed *ca.* 2 weeks before spawning in this sex role-reversed marine species and a female gives all her eggs to a single male (author's own observations). Prior to pair formation and during the time between pair formation and spawning the female courts the male using quite elaborate display behaviours (Vagelli 1999; author's own observations). The most obvious of these behaviours, at least to a human eye, is the 'rush' behaviour that females perform by folding their pelvic, dorsal and anal fins and swimming quickly past a male for a distance of 10–40 cm. This behaviour is common both in the field and in aquaria prior to spawning (author's own observations) and is likely to be highly important in attracting a male. Egg clutches in this species consist of remarkably few

(maximum *ca.* 70) large (2–3 mm in diameter) eggs (Allen & Steene 1995; Vagelli 1999; author's own observations). The larvae of this fish have no pelagic phase. Further, even though female size is positively correlated with both egg size and the number of eggs within naturally formed pairs, male size is the chief determinant of the weight of the clutch on the day after spawning, that is larger males brood heavier egg clutches independent of the size of the female with which they have spawned (Kolm 2001). The size of their male partner therefore has a significant effect on a female's reproductive output. Thus, differential allocation by females depending on the size of the male, i.e. greater investment when breeding with larger males, may be an adaptive strategy in this species. In that previous study (Kolm 2001), a trend was also found suggesting that male size affected egg size. However, those preliminary results need further clarification in order to determine to what extent female investment depends on the size of the male.

In this study, female rush courtship behaviour was quantified as a way of potentially determining whether females really prefer and, thus, perform more courtship towards larger males. Further, I investigated whether female banggai cardinal fish allocate their primary reproductive effort (here quantified as the number of eggs, total clutch weight and mean egg weight) differentially according to the size of the male. This was done by experimentally assigning either large or small males to medium-sized females and thereafter quantifying the females' primary reproductive effort as the dry weight of eggs. This is the most reliable estimate of female reproductive effort in this fish as females provide no care for their offspring.

2. EXPERIMENTAL METHODS

(a) *Stocking and experimental system*

All fish were wild caught and obtained from a Swedish fish dealer and held in eight 400 l marine aquaria prior to the experiments. The aquaria were connected in parallel with water being filtered through a central filtering unit consisting of a 400 l plastic tank, a mechanical filter, a protein skimmer and a 100 l biofilter. A pump provided circulation through the aquaria. Each individual aquarium was supplied with four separate inlets and outlets, thereby forming 32 separate 100 l compartments in total (divided by opaque PVC sheets). The temperature of the aquaria was held constant at 27 °C and the salinity ranged between 32 and 34‰. The photoperiod was a 10 L : 14 D cycle. The fish were fed frozen brine shrimp and mysids *ad libitum* once per day.

(b) *Experimental design*

Twenty-four males and 24 females of varying size (mean $\pm$ s.d.) (males = 46.9 ± 3.44 mm and females = 47.2 ± 2.25 mm) were used in this study. Prior to the experiment, both males and females were measured to the nearest 0.5 mm and individually isolated for 3 weeks in order to decrease any effects of previous experiences. In order to investigate whether females increased their primary reproductive effort when paired with a large male, a two-group design was carried out in which 12 females were individually paired with a large male and 12 females were individually paired with a small male. In order to control for potential maternal effects resulting from female size, females of similar size were assigned to both groups. Each female was

paired with her pre-assigned mate at the start of the experiment and the pair were placed in a 100 l compartment containing four plastic plants with a green mesh at the bottom of the aquarium. The mesh enabled detection of any eggs falling to the bottom of the aquarium during spawning. Clutches were measured soon after the spawning event (see Vagelli (1999) for details on spawning behaviour in this species). Spawning was detected by observing the pairs once per hour between 11.00 and 18.00 (the spawning peak in this species is usually early in the afternoon) (author's own observations). The male was caught directly after spawning and the entire egg clutch removed from his mouth with a pair of forceps. Any eggs that had fallen to the bottom of the aquarium were removed with a hand net. All eggs were counted and their dry weight measured to the nearest 0.1 mg (oven at 60 °C for 40–48 h until no further weight loss was observed). The dry weight of the entire clutch was simply divided by the number of eggs as a measure of individual egg weight (here referred to as the mean dry weight per egg).

The time of spawning was not observed to within an hour of spawning in five of the 19 pairs that spawned. In these pairs several eggs were found at the bottom of the tank and in some cases only a few eggs were found. Since I could not rule out the possibility that some eggs had been eaten or lost through filtration, these pairs were only included in the mean egg weight analysis. Therefore, the sample sizes of the pairs included in the analysis for the number of eggs and total clutch weight and mean egg weight differed (table 1). However, there were no significant differences between treatment groups in female size or variance in female size regardless of these restrictions (table 1). As intended, there were highly significant differences between the treatment groups for male size (table 1).

(c) *Behavioural observations*

After pairing, each experimental pair was observed every afternoon at 16.00 for 5 min and the number of female rush displays was counted. Observations were made each day until spawning occurred.

(d) *Statistical analysis*

Since I had previously (Kolm 2001) experimentally shown that larger males had heavier clutches in their mouths on the day after spawning, a clear *a priori* prediction could be made about the direction of the results, namely that the number of eggs, clutch weight and mean egg weight should be higher in the group where females were paired with large males. Thus, the probabilities reported here are one-tailed. After having tested for normality, all tests were performed using parametric statistics involving a *t*-test allowing for unequal variances between groups (Gans 1991) and a directional ANCOVA using female size as the covariate. Analyses of the females' display behaviours were performed on log-transformed data. Power analyses were conducted using the G-POWER statistical power test (Faul & Erdfelder 1992).

3. RESULTS

The observations of female courtship behaviour showed that females performed more rush displays towards larger males than towards smaller males when controlling for the total time of observation. Females paired with large males performed a mean ($\pm$ s.d.) number of 0.26 ± 0.17 rushes per minute of observation

Table 1. Differences and variances in the average size (mm) of the males and females in a two-group design (pairs consisting of female plus large male or female plus small male) for individuals included in the mean egg weight analysis and the total clutch weight and clutch size analysis.

(See the text for details. The significance levels are from two-sample *t*-tests testing for differences between the groups.)

	♂ size (mm)	variance	<i>t</i>	<i>p</i>	♀ size (mm)	variance	<i>t</i>	<i>p</i>
mean egg weight analysis								
large ♂♂ (<i>n</i> = 11)	49.8	6.62	6.09	< 0.001	47.1	3.74	0.46	0.65
small ♂♂ (<i>n</i> = 8)	43.9	2.53			46.7	3.35		
total clutch weight and clutch size analysis								
large ♂♂ (<i>n</i> = 8)	50.0	9.07	4.82	< 0.001	47.4	4.10	0.26	0.80
small ♂♂ (<i>n</i> = 6)	43.8	3.28			47.2	3.57		

time and females paired with small males performed a mean ($\pm$ s.d.) number of 0.14 ± 0.07 rushes per minute of observation time (two-tailed *t*-test allowing for different variances performed on log-transformed data, $t_{17} = 2.25$ and $p = 0.04$) (figure 1). There was no significant correlation between female size and the number of rush displays performed ($F_{1,17} = 1.41$, $r = 0.27$ and $p = 0.25$).

Nineteen of the original 24 pairs spawned. In the remaining five pairs, one individual died in four cases and one pair did not spawn before termination of the experiment (6 weeks after pair formation). There was no significant effect of male size on the likelihood of spawning (Fisher's exact test (one-tailed), females plus large males 11 out of 12 pairs and females plus small males eight out of 12 pairs) ($p = 0.16$). Latency to spawn was also unaffected by male size when controlling for female size: females paired with large males had a mean ($\pm$ s.d.) latency period of 22.4 ± 6.34 days, whereas females paired with small males had a mean latency period of 22.6 ± 3.50 days (ANCOVA with female size as the covariate, $F_{1,16} < 0.0001$ and $p = 0.995$).

A multiple regression analysis revealed that the mean egg weight and number of eggs together explained virtually all of the variation in the total clutch weight ($F_{2,11} = 1093$, $r = 0.99$ and $p < 0.0001$). However, the mean egg weight was a stronger determinant of the total clutch weight (standardized regression coefficient $\pm$ standard error, mean egg weight = $0.810.02$, $t_{11} = 37.6$ and $p < 0.0001$ and number of eggs = $0.660.02$, $t_{11} = 30.7$ and $p < 0.0001$). In order to compare the slopes of the two regressions the standardized 95% confidence intervals for the two independent variables were compared (standardized regression coefficient $\pm$ 95% confidence interval, mean egg weight = 0.81 ± 0.05 and number of eggs = 0.66 ± 0.05) and did not overlap. In addition, the mean egg weight had a higher coefficient of variation (CV = 11.7) than the number of eggs (CV = 8.9). Therefore, changes in the mean egg weight will have more effect on the total clutch mass than will changes in the number of eggs. Furthermore, no negative correlation was found between egg size and the number of eggs ($F_{1,12} = 0.08$, $r = 0.08$ and $p = 0.79$).

There was a significant effect of treatment (male size) when comparing the mean dry weight per egg between females paired with large and small males. Females

Figure 1. Mean ($\pm$ s.d.) number of rush displays performed per minute of observation for females paired with large males (filled bars) (*n* = 11) and females paired with small males (open bars) (*n* = 8). * $p < 0.05$.

paired with large males spawned eggs with a mean ($\pm$ s.d.) dry weight per egg of 3.7 ± 0.5 mg, whereas females paired with small males produced lighter eggs with a mean ($\pm$ s.d.) dry weight per egg of 3.2 ± 0.2 mg (one-tailed *t*-test allowing for different variances, $t_{17} = 2.44$ and $p = 0.014$ and one-tailed ANCOVA with female size as the covariate, $F_{1,16} = 5.05$ and $p = 0.02$) (see figure 2a). There was also an effect of treatment (male size) on the total clutch weight. Females paired with large males had a mean total clutch dry weight of 0.192 ± 0.02 g, whereas females paired with small males had a mean total clutch dry weight of 0.167 ± 0.02 g (one-tailed *t*-test allowing for different variances, $t_{12} = 2.02$ and $p = 0.034$) (see figure 2b). A one-tailed ANCOVA with female size as the covariate also produced a significant effect of treatment ($F_{1,11} = 3.69$ and $p = 0.04$). However, there was no difference in the number of eggs laid by females in the two treatments. Females paired with large males laid 52.1 ± 4.82 eggs and females paired with small males laid 50.5 ± 4.46 eggs (one-tailed *t*-test allowing for different variances, $t_{12} = 0.65$ and $p = 0.26$ and one-tailed ANCOVA with female size as the covariate, $F_{1,11} = 0.35$ and $p = 0.28$) (see figure 2c). The statistical power of the latter tests was 0.48.

Figure 2. (a) Mean (+s.d.) dry weight per egg for females paired with large males (filled bars) ($n = 11$) and females paired with small males (open bars) ($n = 8$). * $p < 0.05$. (b) Mean (+s.d.) dry weight of a total egg clutch for females paired with large males (filled bars) ($n = 8$) and females paired with small males (open bars) ($n = 6$). (c) Total number (+s.d.) of eggs in a clutch for females paired with large males (filled bars) ($n = 8$) and females paired with small males (open bars) ($n = 6$).

4. DISCUSSION

Female banggai cardinal fish displayed the rush behaviour more often towards larger males. Furthermore, females produced heavier eggs and, as a consequence, a

heavier clutch when experimentally paired with larger preferred males.

That females performed more display behaviour towards larger males suggests that females find larger males more attractive than smaller males and, therefore, spend more time and effort courting larger males. Similar results have been shown in the pipefish (*Syngnathus typhle*), another species with female courtship and paternal care, where females court larger males more intensely and exert a strong preference for larger males (Berglund *et al.* 1986). As I have previously shown that male size limits the reproductive output of a pair in the banggai cardinal fish (Kolm 2001) this preference is likely to be caused by direct effects resulting from potential differences in parental abilities between males of different size.

Females of this species adjusted their investment in their eggs during the time-interval between pair formation and spawning according to the size/attractiveness of their current mate. This adjustment was not costly in terms of the time taken to spawn since there was no significant difference in the latency to spawn between treatments. The potential benefit of larger eggs is that larger eggs are likely to produce larger offspring with higher chances of survival and higher growth, for which there is evidence from many species of fish (reviewed by Heath & Blouw 1998; Einum & Fleming 1999). The effect of an increase in egg size on offspring quality in this species, which lays a very small clutch (Vagelli 1999) and in which there is no pelagic larval phase, may be particularly important. The effect of partner size on egg size carried over to the total clutch weight, which was higher in females paired with large males. This means that, when a female is spawning with a large male, she invests more of her resources into eggs than when spawning with a smaller male, thereby suggesting that a female sacrifices some of her future growth (and thereby future reproductive success) when spawning with a large male. To the author's knowledge, only one study has actually quantified the impact of differential allocation on future reproduction. Reyer *et al.* (1999) found that female waterfrogs of the *Rana lessonae*–*Rana esculenta* complex laid smaller clutches when amplexed by undesired males and responded to this reduced primary reproductive effort by laying either an extra clutch the same year or a larger clutch the following year. Although this specific effect on future reproduction was not addressed in the present study, the increase in clutch weight when spawning with a large male certainly also suggests a similar trade-off between current and future reproduction in the banggai cardinal fish.

Surprisingly, egg number did not differ significantly between treatments, which may imply that egg size is more important for female fitness in this species than egg number. However, the power of this test was rather low. The mean egg weight had a higher coefficient of variation than did egg number and explained more of the variation in the total clutch weight than did egg number, suggesting that egg number is a less plastic variable than egg size and that change in the size of individual eggs will have larger effects on the total clutch investment than will changes in egg number. Furthermore, no negative correlation between egg size and the number of eggs was found as normally expected (e.g. Svärdsön 1949). This suggests that differential allocation might cancel out the trade-off

between egg size and egg number in this fish, at least within a single reproductive event.

Why should females vary their egg size rather than egg number according to the size of their current mate? One possible explanation is that only large males are capable of oxygenating large eggs sufficiently because they have a larger buccal cavity. Large fish eggs have higher metabolic rates and thicker boundary layers than small eggs (Rombough 1988). Furthermore, since oxygen exchange in fish eggs mostly consists of passive diffusion that depends on the surface to volume ratio of the egg (E. Pettersson, personal communication), it is probable that a large egg (with a smaller surface to volume ratio as compared to a small egg) needs relatively more oxygen than a small egg in order to survive and mature. Van den Berghe & Gross (1989) found that, in coho salmon (*Oncorhynchus kisutch*), larger eggs had lower survival compared to smaller eggs in gravel containing less oxygen. It is therefore highly likely that small males are less able to oxygenate larger eggs in a mouthbrooding fish where males provide oxygen to the eggs by actively rotating the egg mass. This explanation is consistent with Sargent *et al.*'s (1987) model, which predicted that, in species where parental care influences egg mortality and the quality of parental care varies, females who are able to decrease egg mortality through improved parental care should increase their egg size.

A second more general explanation as to why females should invest more overall when paired with larger males is that larger males may be less likely to cannibalize the brood. Age-specific filial cannibalism by males is known to occur in other species of cardinal fish (Okuda *et al.* 1997). These authors suggested that small, i.e. younger, males face a steeper trade-off between reproduction and growth than do large males (Roff 1992; Stearns 1992). If so, small males may be more prone to eat the brood, thus saving energy for later breeding attempts. As females in this species spawn all their eggs at once to a single male and eggs are dumped if a male is not encountered (author's own observations), females appear to be unable to retain eggs. Hence, fecundity is likely to be determined before females encounter males and varying the size rather than the number of eggs may hence be a female's only option for allocating differentially.

This is the third study to report that females may alter the quality of individual offspring according to the attractiveness/quality of their mate. Cunningham & Russell (2000) found that female mallards produced larger eggs for more attractive males, while Gil *et al.* (1999) found that female zebra finches laid eggs with higher testosterone levels when paired with more attractive males. The benefits from this female behavioural plasticity in the banggai cardinal fish are likely to be direct, as the quality of male parental care most probably varies with male size. Thus, I suggest that females respond adaptively to the quality of their current mate by adjusting their primary reproductive effort (egg size) in order to maximize the outcome of each reproductive event. Together with other recent studies, this finding suggests that it is vital that such differential allocation is taken into account when investigating the effects that parents have on the quality of their offspring (e.g.

Mousseau & Fox 1998; Gil *et al.* 1999; Cunningham & Russell 2000; Sheldon 2000).

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