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# Influence of Mate Quality on Reproductive Decisions in a Fish with Paternal Care

BY

NICLAS KOLM



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**Abstract**

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Female reproductive decisions have been suggested to be highly influenced by mate quality. I have studied whether offspring quality may be adjusted by females to match the attractiveness of males and how strong control females have over their reproductive investment focusing on egg size. This was done in the Banggai cardinalfish (*Pterapogon kauderni*), a sex-role reversed obligate paternal mouthbrooder where males invest heavily into reproduction. As this species is suitable for both laboratory experiments and field studies it is an ideal candidate for the study of reproductive investment.

Mating was size-assortative and both males and females benefited from pairing with large partners. However, male size determined the reproductive output of a pair. Females courted large males more intensively and produced larger, but not fewer eggs when mated to large males as compared to small males. Further, this matching of egg size to mate attractiveness may be fast. Female courtship behaviours contained honest information regarding both clutch weight and egg maturity, traits that may be highly important for male mate choice. Surprisingly, males played an important part in territory defence suggesting relatively equal sex-roles in this species. Also, this species showed stable group structures which may be important for the evolution of female plasticity in reproductive investment due to high variance in quality of available mates.

This thesis suggest that females have a remarkable control over their reproductive investments and that male quality may be highly influential on reproductive decisions regarding offspring quality. Furthermore, it suggest that sexual selection may have strong effects on the evolution of egg size and parental care on a whole.

*Keywords:* sexual selection, differential allocation, evolution of egg size and parental care

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## PAPERS INCLUDED IN THE THESIS

This thesis is based on the following papers, which are referred to in the text by their Roman numerals:

- I Kolm Nicolas . (2002). Male size determines reproductive output in a paternal mouthbrooding fish. *Animal Behaviour* 63: 727-733.
- II Kolm Nicolas. (2001). Females produce larger eggs for large males in a paternal mouthbrooding fish. *Proceedings of the Royal Society of London Series B* 268: 2229-2234.
- III Kolm Nicolas, Olsson Jens. (2003). Differential investment in the Banggai cardinalfish: can females adjust egg size close to egg maturation to match the attractiveness of a new partner?. *Journal of Fish Biology* (In press).
- IV Kolm Nicolas. Female courtship in the Banggai cardinalfish: honest signals of egg maturity and reproductive output?. (Manuscript).
- V Kolm Nicolas, Berglund Anders. Sex-specific territorial behaviour in the Banggai cardinalfish (*Pterapogon kauderni*). *Environmental Biology of Fishes* (In press).
- VI Kolm Nicolas, Berglund Anders. (2003). Wild populations of a reef fish suffer from the "nondestructive" aquarium trade fishery. *Conservation Biology* 17(3): 910-914.
- VII Kolm Nicolas, Ahnesjö Ingrid. Evolution of egg size and parental care in fishes. (Manuscript).

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Article I, II, III, V and VI were printed with permission from the publisher

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## Introduction

Mating in nature is rarely random (Andersson 1994). Instead, individuals go to great lengths to find a mate with particular assets that meet rather specific criteria. Such criteria, or phenotypic traits such as for instance a male's forehead patch in the collared flycatcher, may be linked with direct benefits for choosy individuals, such as, a good territory, rich in food for potential offspring according to indicator models (e.g. Pomiankowski 1988, Andersson 1994). Such traits may, however, also be linked to indirect benefits such as the providing of genes of good quality that will enhance the survival of a choosy individual's offspring (again in line with indicator models). Choosing a partner with traits that are likely to be beneficial for individual fitness is thus usually done based on fitness related phenotypic characters (e.g. Andersson 1994). Examples of such characters are, for instance, the clicking sound of a courting male damsel fish, where the frequency of clickings is positively correlated to how capable a male is in taking care of eggs (Knapp & Kovach 1991), or the size of a male's forehead patch in the collared flycatcher where offspring sired by males with large forehead patches are genetically superior, with higher survival (Sheldon et al. 1997).

## **Sex roles and mutual mate choice**

Traditionally we have viewed females as highly choosy when it comes to mating, whereas males have often been regarded to mate with any willing female (e.g. Clutton-Brock & Vincent 1991). This is often the case as males tend to invest much less into reproduction (i.e. cheap sperm and little or no parental care) while females produce highly costly eggs and provide most of the care of offspring. This difference in reproductive investment usually results in that males are limited only by the number of copulations they can perform with different mates, whereas females are limited by the need to provide the best possible conditions (e. g. egg yolk, shelter, parental care, good genes) for their offspring to maximise their reproductive success. Hence, males usually have higher potential reproductive rates (PRR) than females, which lead to males competing over females and choosy females (e.g. Clutton-Brock & Vincent 1991). In some species, however, and particularly so in fishes (e.g. Sargent 1997), males play an important role in parental care and this has lead to that both sexes may invest relatively equal resources into reproduction (e.g. Sargent 1997). In some species, this has gone so far as males investing more into reproduction than females, resulting in females having a higher PRR than males and thus to sex-role reversal, with females competing for access to males. One example of such a sex-role reversed species is the deep snouted pipefish (*Syngnatus typhle*) (Berglund & Rosenqvist 1990). In this species, males brood the eggs in a pouch that supplies the eggs with both oxygen and nutrients, and the PRR are higher for females than for males. The higher PRR in females results

in a higher availability of females willing to mate in the natural populations as compared to the number of males willing to mate, and hence females compete over access to males (e.g. Kvarnemo & Ahnesjö 1996). In such sex-role reversed species, however, females are always burdened by the cost of producing eggs. Therefore, the differences in PRR's between the sexes in sex-role reversed species are relatively small as compared to the differences in PRR:s in species with conventional sex roles. Mutual mate choice is therefore common in sex-role reversed species such as in the pipefish (Sandvik-Widemo 2003). Mutual mate choice is expected when both sexes benefit from being choosy and even though that may be the case for many species, empirical studies on the subject are still scarce.

### **Differential allocation**

Individuals' reproductive success may not only be affected by their precopulatory mate choice, however. Burley (1986) hypothesised that individuals may also affect their reproductive success by investing into a reproductive event according to the attractiveness of the mate (i.e. its expected pay-off). Under the trade-off between current and future reproduction (Roff 1992, Stearns 1992), individuals may thus invest more resources into reproductive events with a high fitness pay-off, and consequently be forced to invest less in future reproductive events (Sheldon 2000). Reproductive events yielding high pay-off may be those with more attractive partners providing, for instance, particularly good care and/or good genes for the offspring. There are a number of mechanisms through which individuals may increase their

reproductive investment in a specific reproductive event, and such examples exist for virtually all taxa (Sheldon 2000, Kolm 2001). For instance, females mated to attractive males have been shown to increase the level of care (Burley 1986, 1988), increase clutch size (Balzer & Williams) or even offspring quality (Cunningham & Russel 1999, 2002, Gil et al. 2000, Kolm 2001). Of particular interest are examples suggesting that also offspring quality may be controlled by females, under influence by the attractiveness of the male. Such examples suggest that paternal effects may be mediated through the female. There is of course no reason why males may not invest differentially according to the attractiveness of their mate. This would be expected particularly in species where there is a large variation in female quality and hence an expected pay-off from mating with females of different attractiveness.

The mating game between males and females is clearly extremely complex (e.g. Badyev & Qvarnström 2002). Each reproductive event involves both collaboration and manipulation requiring extensive communication by both sexes to reach the decisions regarding their reproductive investment (Badyev & Qvarnström 2002). According to Burley (1986), differential allocation may be a way for individuals to obtain or retain attractive mates. This important feature of the differential allocation hypothesis states that not only do males need to display their attractiveness, but females may also display their potential reproductive investment in a particular male. Hence, we expect differentially allocating females to signal their reproductive

investment using plastic traits, such as, display behaviours that are correlated to their reproductive investment.

Clearly, substantially more research is required for us to fully understand how parents may affect offspring quality. In order to do that, however, we need to identify model species with which we can perform experiments in order to disentangle the causes behind these decisions. One such model organism may be the Banggai cardinalfish (*Pterapogon kauderni*).

### **Evolution of egg size and parental care in fishes**

There is a strong link between egg size and parental care in fishes. Both within and between species this manifests itself as a positive correlation between egg size and the amount of parental care invested in those eggs. Several hypotheses exist attempting to uncover the causality behind this correlation (e.g. summarised by Shine 1989), however, no real empirical support exists suggesting that one is better than the others. To date, the influence of sexual selection on the positive correlation between egg size and parental care has not been properly addressed. Furthermore, new studies have shown that the oxygen demands of differently sized eggs may not be as straightforward as previously thought and this has implication for the evolution of egg size and care (Einum et al. 2002). Clearly, there is a need for a synthesis of the implications of sexual selection on the evolution of egg size and parental care and also the effect of different oxygen demands for differently sized eggs on the existing hypotheses.

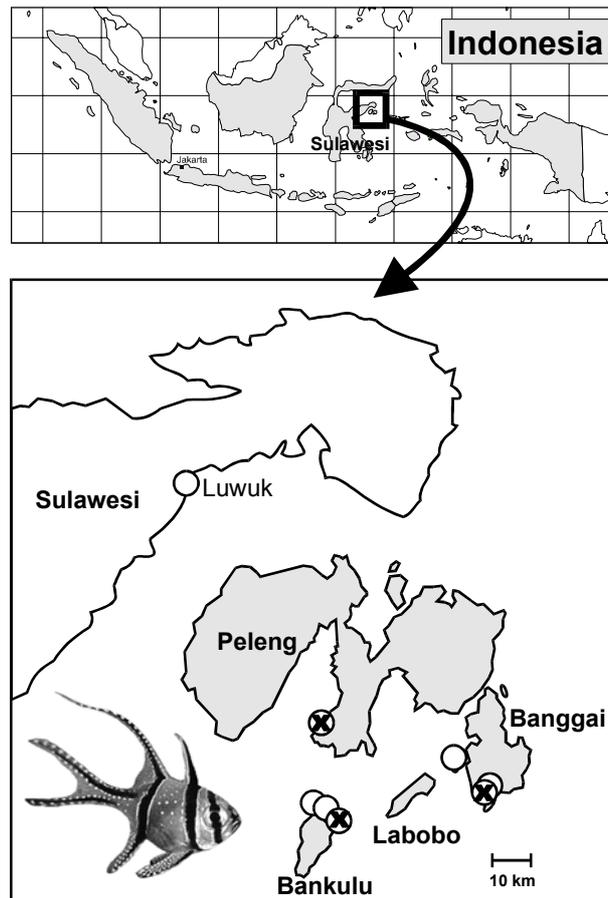
As egg size and parental care are fundamental traits for individual fitness, it is vital that we increase our understanding of the evolution of these traits and how they are associated. Given the extreme variation in reproductive strategies and egg size in fishes, this group is ideal to study in order to gain understanding into these processes.

## **Model species and methods**

The Banggai cardinalfish (*Pterapogon kauderni*) is a small (max 55 mm) paternal mouthbrooder with an extremely small clutch size (maximum 90 eggs) and large eggs (c. 3 mm). It is virtually unique among reef fish as it has no juvenile pelagic larval phase (Allen & Steene 1995; Vagelli 1999). Because a pelagic larval phase is the main dispersal method in most reef fish (e.g., Leis 1991), the Banggai cardinalfish has a limited distribution and has only been naturally found in the Banggai archipelago off the east coast of Sulawesi, Indonesia (Fig. 1).

The Banggai cardinalfish lives in groups of 2- 500 individuals hovering in shallow waters (c. 1-2 m depth) within and above groups of long-spined sea urchins (*Diadema setosum*), where they seek shelter when threatened (Allen & Steene 1995; own observations). It is also encountered in the vicinity of sea anemones and branching stone corals (Allen 2000; Vagelli & Erdmann 2002; N. K. & A. B., personal observations). Originally described in 1933 (Koumans 1933) the species was rediscovered in 1995 (Allen & Steene 1995) and

subsequently has become a popular aquarium fish (Allen 2000; Vagelli & Erdmann 2002).



**Figure 1.** Map of the Banggai archipelago in east-central Sulawesi, Indonesia. White spots indicate the locations that were sampled for the study of the effects from the aquarium trade. White spots marked by **X** indicates the three locations where the experiment on sex-specific territorial defence was made. In the lower left corner is a picture of the Banggai cardinalfish.

In this sex-role reversed marine species, pairs are formed up to two weeks before spawning and a female gives all her eggs to a single male (own observations). Prior to pair formation and during the time between pair formation and spawning the female courts the male using quite elaborate courtship behaviours (Vagelli 1999, Kolm 2001). The female courtship mainly consists of two distinct behaviours: the "twitch" and the "rush". The twitch consists of the female folding her pelvic, anal and dorsal fins together while twitching her body close to the male. Females perform the rush by folding the pelvic, dorsal and anal fins and quickly swimming past the male for a distance of 10-40 cm (Kolm 2001). The most obvious, at least to a human eye, of these behaviours is the "rush" behaviour that females perform by folding their pelvic, dorsal and anal fins and quickly swimming past the male for a distance of 10-40 cm. This behaviour is common both in the field and in aquaria prior to spawning (own observations) and is likely to be highly important in attracting a male.

#### *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 experiments. The aquaria were connected in parallel with water being filtered through a central filtering unit consisting of a 400 l plastic tank, a mechanic filter, a protein skimmer and a 100 l biofilter. A pump provided circulation through the aquaria. Each individual aquarium was supplied with 4 separate in- and outlets, forming in total 32 separate 100 l compartments (divided by opaque PVC sheets) in which all

experimental pairings took place. Temperature was held constant at 27°C and salinity ranged between 32-34 ‰. The photoperiod was 10 h light 14 h dark. Animals were fed frozen brine shrimp and mysids ad libitum once per day. Prior to all experiment, both males and females were measured to the nearest 0.5 mm and individually isolated for three weeks in order to minimise any effects of prior experiences. Females were individually isolated in the aquarium system used for stocking and experiments (see above) and males were individually isolated in 27 l aquaria filtered with an air-pump-driven sponge filter and 30 % water changes every three days.

#### *Field studies*

All field studies were performed in shallow lagoons in the Banggai archipelago (Fig. 1). For the study of the effect of aquarium trade fisheries on the Banggai cardinalfish (Kolm & Berglund 2003), 8 locations were sampled (Fig. 1). For the field experiment on sex-specific territorial behaviour (Kolm & Berglund, in press), three of these locations were used (Fig. 1).

## **Aim of the thesis**

This thesis aims to study the importance of mutual mate choice in the Banggai cardinalfish and the control that females have over their reproductive investment and to what extent it is affected by the attractiveness of the partner. Furthermore, the behaviours in territory defence and female courtship are investigated to verify the sex roles of the Banggai cardinalfish, and more importantly, the information context of female courtship behaviours in a species where females differentially allocate resources into reproduction according to mate attractiveness. As there is a strong link in fishes between egg size and parental care, I have also reviewed the evolution of egg size and parental care coevolution, focusing on the influence of sexual selection, together with Ingrid Ahnesjö in order to assess current trends and future prospects in this research area.

## **Results and discussion**

### *The influence of male and female size*

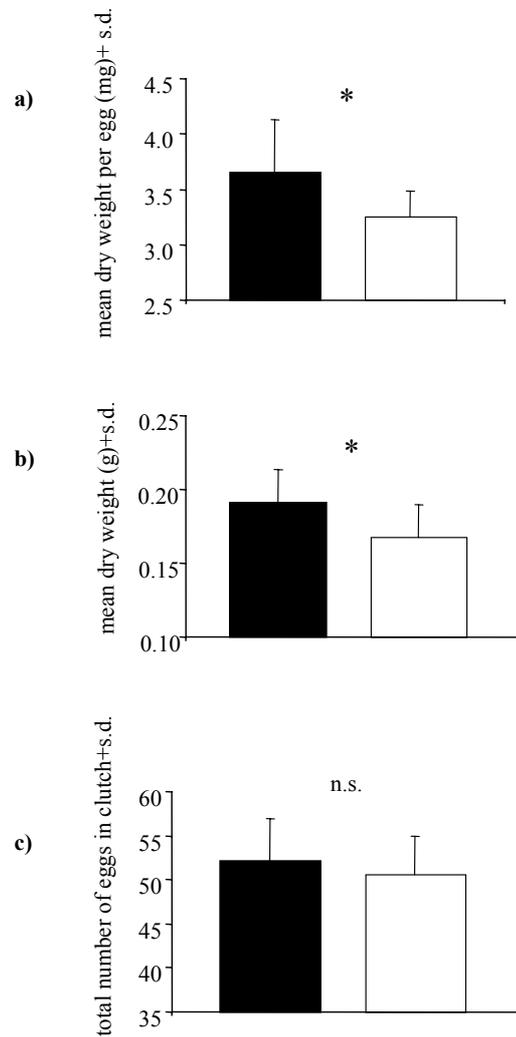
Body size can have strong effects on reproductive success in both males and females, and in many species large individuals are preferred as mates (e.g. Andersson 1994). In **paper I** (Kolm 2002), I show that mate choice for size is important for both sexes in the Banggai cardinalfish, but that male size determines the reproductive output of a

pair. When pairs were allowed to form freely, a size-assortative mating pattern was observed ( $r=0.77$ ,  $N=24$ ,  $p<0.001$ ) and the size of pair members was positively correlated to reproductive output as determined by total clutch weight and egg size (clutch weight:  $F_{1,18}=73.9$ ,  $r=0.90$ ,  $p<0.0001$ , egg size:  $F_{1,18}=4.6$ ,  $r=0.46$ ,  $p<0.05$ ). To separate the potential benefits from mate choice for size for each sex, these pairs were subsequently used to form reversed size-assortative pairs, i.e. the largest male paired to the smallest female and vice versa. Here, clutch weight was positively correlated with male size ( $F_{1,17}=5.3$ ,  $r=0.49$ ,  $p<0.05$ ) but non-significantly negatively correlated to female size ( $F_{1,17}=3.7$ ,  $r=-0.42$ ,  $p=0.07$ ). This suggests that the size of the male influences clutch weight. For egg size on the other hand, the size of both sexes seemed important as neither male size ( $F_{1,17}=0.014$ ,  $r=-0.03$ ,  $p=0.91$ ) nor female size ( $F_{1,17}=0.134$ ,  $r=0.09$ ,  $p=0.72$ ) was significantly correlated to egg size. The study reveals benefits for mutual mate choice on size in this species: larger females give larger eggs and larger males can brood heavier clutches. Furthermore, these results suggest the possibility for females to differentially allocate resources into the eggs according to the size of her mate.

#### *Differential allocation of egg size*

When individuals receive different returns from reproductive investment dependent on mate quality, they are expected to invest more when breeding with higher quality mates (Burley 1986, Sheldon 2000). In **paper II** (Kolm 2001), I investigated whether females

allocate their reproductive effort depending on the size of their mate by experimentally assigning females to either large or small males. The results show that female Banggai cardinalfish prefer larger males which they court more intensively. Further, females paired to large males spawned eggs with a mean dry weight/egg  $\pm$  s.d. of  $3.7 \text{ mg} \pm 0.5$ , whereas females paired to small males produced lighter eggs: mean dry weight/egg was  $3.2 \text{ mg} \pm 0.2$  (one-tailed t-test allowing for different variances,  $t_{17}=2.44$ ,  $p=0.014$ ; Fig. 2a). There was also an effect of male size on the total clutch weight. Females paired to large males had a mean total clutch dry weight of  $0.192 \text{ g} \pm 0.02$ , whereas females paired to small males had a mean total clutch dry weight of  $0.167 \text{ g} \pm 0.02$  (one-tailed t-test allowing for different variances,  $t_{12}=2.02$ ,  $p=0.034$ ; Fig. 2b). There was, however, no difference in the number of eggs laid by females in the two treatments. Females paired to large males laid  $52.1 \pm 4.82$  eggs and females paired to small males  $50.5 \pm 4.46$  eggs (one-tailed t-test allowing for different variances,  $t_{12}=0.65$ ,  $p=0.26$ ; Fig 2c).



**Figure 2.** a) Mean dry weight per egg + standard deviation 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 dry weight total egg clutch + standard deviation for females paired with large males (filled bars, n=8) and females paired with small males (open bars, n=6). c) Total number of eggs in clutch + standard deviation females paired with large males (filled bars, n=8) and females paired with small males (open bars, n=6).

My results show that females in this species adjust offspring weight, and thus presumably, offspring quality, according to the size of their mate. One possible explanation for this is that only large males are capable of oxygenating large eggs sufficiently, because they have a larger buccal cavity. This explanation is consistent with Sargent et al.'s model (1987), 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. Females may pay for this in terms of future reproduction, however, as they invest more of their resources and hence probably sacrifices future growth. Further, the more intense courting towards larger males may also carry a cost in increased predation.

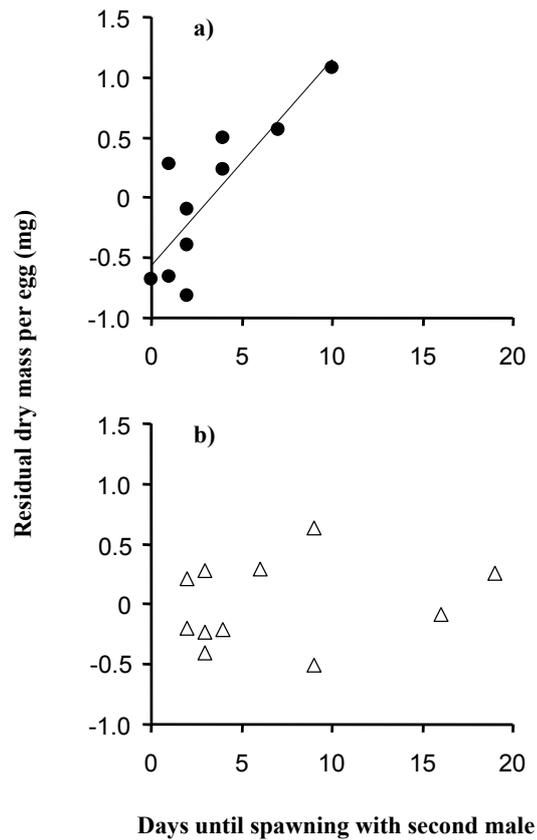
*How rapid is this matching of egg size to mate attractiveness?*

It has now been shown in both birds (Cunningham & Russel 1999) and fish (Kolm 2001) that females may put more resources into eggs when mated to attractive mates. However, the degree of control that females exert over such changes in egg size is unknown. This may have strong implications in species which we are likely to find differential allocation. In **paper III** (Kolm & Olsson 2003), we show that such changes in egg size to match the attractiveness of the mate may be quite rapid. We investigated whether females can change their egg investment according to the different attractiveness of a new mate after eggs have already matured in response to an earlier mate, female Banggai cardinalfish were first allowed to produce eggs for small

(unattractive) or large (attractive) males. Then, when spawning was initiated, but prior to actual spawning, their partner was switched to either a significantly larger or a significantly smaller partner, respectively. A strong positive correlation was revealed between egg size and days until spawning with the second male for the females initially paired to a small and then a large male (Fig 3a). Within a few days, these females apparently increased their egg size to match the attractiveness of their new male. However, no correlation between days until spawning and egg size in females initially paired to a large and then a small male was found (Fig 3b). This suggests that females were unable to adjust egg size in response to a decrease in mate attractiveness.

Females in this species were apparently able to increase their egg investment long after the onset of egg maturation in response to a change in the attractiveness of the current mate. This suggests that differential investment in egg size may not only be limited to species with extended pair bonds but that this phenomenon may be much more common than previously supposed. This highlights the need for this phenomenon to be taken into consideration when addressing parental influence on offspring quality using multiple male experimental designs. However, there may be complex interactions between female size, male size, egg size and latency that could not be addressed properly in this study due to small sample sizes. Further experiments with ample sample sizes allowing control over these potential interactions are needed before definite conclusions can be

drawn over the options that females face regarding allocation of their resources into reproduction.



**Figure 3.** a) Correlation between days until spawning with second male and residual (residuals from the regression on female length vs. egg size) mean dry mass per egg for females in the small-large treatment (Linear regression:  $n=10$ ,  $r^2=0.66$ ,  $P=0.004$ ). b) The same correlation for females in the large-small treatment (Linear regression:  $n=11$ ,  $r^2=0.05$ ,  $P=0.53$ ).

*Female courtship displays and their information content*

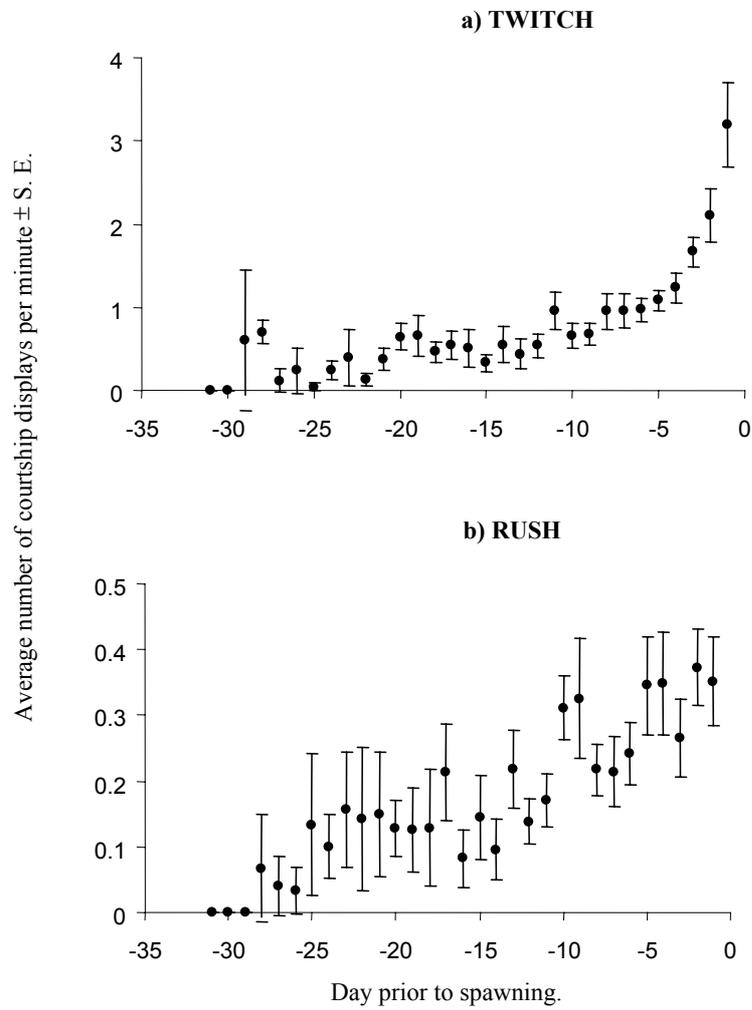
Despite the vast literature on male courtship behaviours, little is known about the function and information content of female courtship behaviours. Female courtship behaviours may be important in many species, particularly where both sexes invest heavily in the offspring, and if such behaviours contain honest information regarding a female's potential reproductive investment they may be particularly important in male mate choice. In **paper IV**, I show that different female courtship behaviours contain different information regarding potential reproductive effort and egg maturity (proximity to spawning). Using observations of two female courtship behaviours (the "rush" and the "twitch") from experimental pairings, I addressed whether these courtship behaviours contained information on female reproductive output (clutch weight) and egg maturity (proximity to spawning), traits commonly associated with male mate choice. I especially focused on the importance of these courtship behaviours in relation to other female characters such as size and condition using multiple regression. I found that one of these behaviours, the rush, was a strong predictor of fecundity, whereas size, condition and the twitch behaviour were not (table 1).

**Table 1.** Results from multiple regression with clutch weight as the dependent variable. Included as independent variables are female size, female condition, rush behaviour and twitch behaviour. All independent variables were log-transformed prior to analysis.  $\beta$  is the standardised regression coefficient.

Independent variables	$\beta$	S. E.	$t_{(14)}$	$p$
Female size	0.01	0.21	0.02	0.98
Female condition	0.35	0.23	1.53	0.15
Rush	0.59	0.21	2.74	0.02
Twitch	0.40	0.22	1.82	0.09

Multiple  $r^2=0.49$ ,  $F_{(4, 14)}=3.3$ ,  $p=0.04$

The number of twitches increased closer to spawning and showed an exponential relationship with day prior to spawning (average  $r$  for all correlations between number of twitches (log-transformed) and day prior to spawning  $\pm$  S. D. =  $-0.61 \pm 0.24$ ,  $t_{28}=13.4$ ,  $p<0.0001$ , Figure 4a). Also the number of rush behaviours increased closer to the day of spawning, but linearly so (average  $r$  for all correlations between number of rushes and day prior to spawning  $\pm$  S. D. =  $-0.31 \pm 0.24$ ,  $t_{28}=6.8$ ,  $p<0.001$ , Figure 4b). The slope of the curves differed significantly (dependent t-test:  $t_{28}=4.6$ ,  $p<0.0001$ ) indicating that the twitch is a stronger predictor of how close to spawning a female is as compared to the rush.



**Figure 4.** a) Correlation between twitch intensity (mean  $\pm$  s. e. for each day) and proximity to actual spawning. b) Correlation between rush intensity (mean  $\pm$  s. e. for each day) and proximity to actual spawning. See text for details.

The results suggest that female courtship behaviours may convey highly important information in a mate choice context. I suggest that

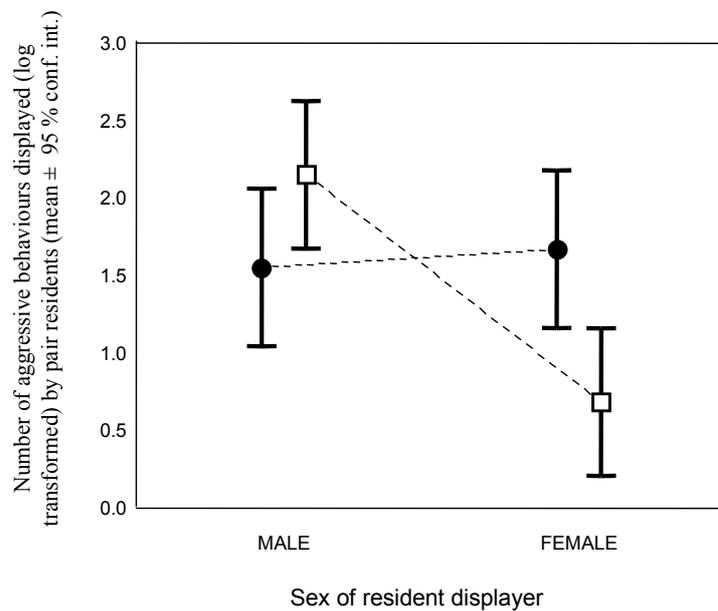
this is an example of how the mating game consisting of both conflict and common fitness interests between the sexes may select for complex sexual communication through displays between mating partners (Badyaev & Qvarnström 2002).

*Male importance in territory defence*

In **paper V** (Kolm & Berglund, in press), we performed a field experiment where we introduced individuals larger and more attractive than its resident counterpart to formed pairs. We show that contrary to previous studies on other cardinalfish species, and contrary to expectations in a sex role reversed species, the male was the main aggressor towards an intruder regardless of the sex of the intruder (males (mean  $\pm$  SD):  $6.9 \pm 5.8$ ; females:  $3.3 \pm 3.3$ ; factorial ANOVA with sex of intruder and sex of displayer as factors (performed on log transformed data):  $F_{1,26}=7.9$ ,  $p=0.009$ ). Moreover, residents were more aggressive towards intruders of their own sex, as there was a significant interaction for number of aggressive displays between sex of intruder and sex of displayer (factorial ANOVA on log transformed data:  $F_{1,26}=10.9$ ,  $p=0.003$ ; Figure 5).

A post hoc analysis showed that this interaction was primarily due to females displaying less aggressively towards male intruders than towards females (Tukey test:  $p=0.03$ ; Figure 5). For males, the difference in number of displays towards males and females was not significantly different (Tukey test:  $p=0.31$ ; Figure 5), although it was in the hypothesised direction. Further, even though females often

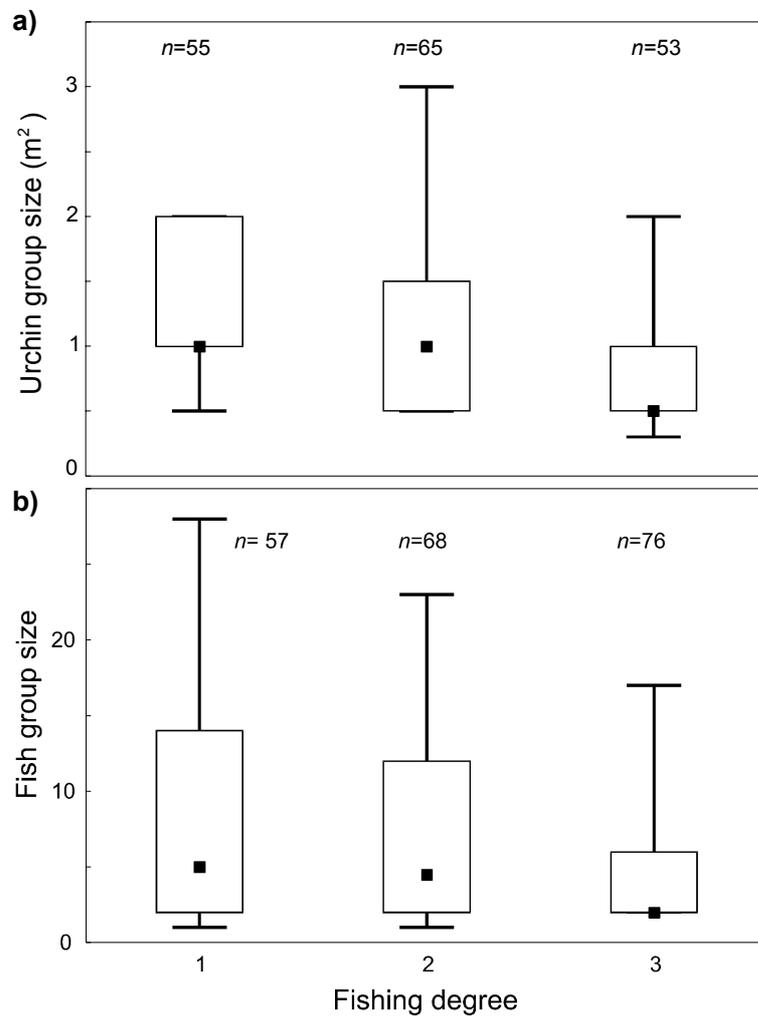
courted introduced, larger males, no intruder managed to overtake the partnership of any resident. Our results implies that sex roles in the Banggai cardinalfish are more complex than just simply being reversed, a notion recently suggested also in other species of cardinalfish (Okuda 2001; Okuda 1999).



**Figure 5.** Number of aggressive behaviours (sum of lateral displays and bites) displayed by resident males and females towards an introduced male (□) or female (●). There was a significant interaction between sex of displayer and sex of intruder. Females displayed aggressively less towards a male than towards a female intruder (see text for details).

*Stable group structures and their implications*

In **paper VI** (Kolm & Berglund 2003), we surveyed eight sites in the Banggai archipelago to quantify population density (total population size and group size), age distribution (quantified as the quota of numbers of juveniles/adults) and habitat quality (i.e., sea urchin density). Through interviews with local fishers we estimated the fishing pressure at each site and related this to data on fish density. We found a marginally significant negative effect of fishing pressure on density of fish ( $r_s = -0.69$ ,  $n=8$ ,  $p=0.057$ ) and significant negative effects on group size in both sea urchins and fish (urchins: mean area of urchins per group  $\pm$  SD, fishing degree 1:  $1.3 \pm 0.9$ ; fishing degree 2:  $1.4 \pm 1.5$ ; fishing degree 3:  $1.1 \pm 1.1$ , ANOVA on log-transformed data:  $F_{2, 168} = 5.0$ ,  $p < 0.01$ , Fig. 6a, fish: mean number of fish per group  $\pm$  SD, fishing degree 1:  $11.5 \pm 15.5$ ; fishing degree 2:  $9.5 \pm 12.1$ ; fishing degree 3:  $5.7 \pm 6.5$ , ANOVA on log-transformed data:  $F_{2, 195} = 3.2$ ,  $p = 0.04$ , Fig. 6b). We did not find any effect of fishing on fish size structure.



Kolm & Berglund Fig. 4

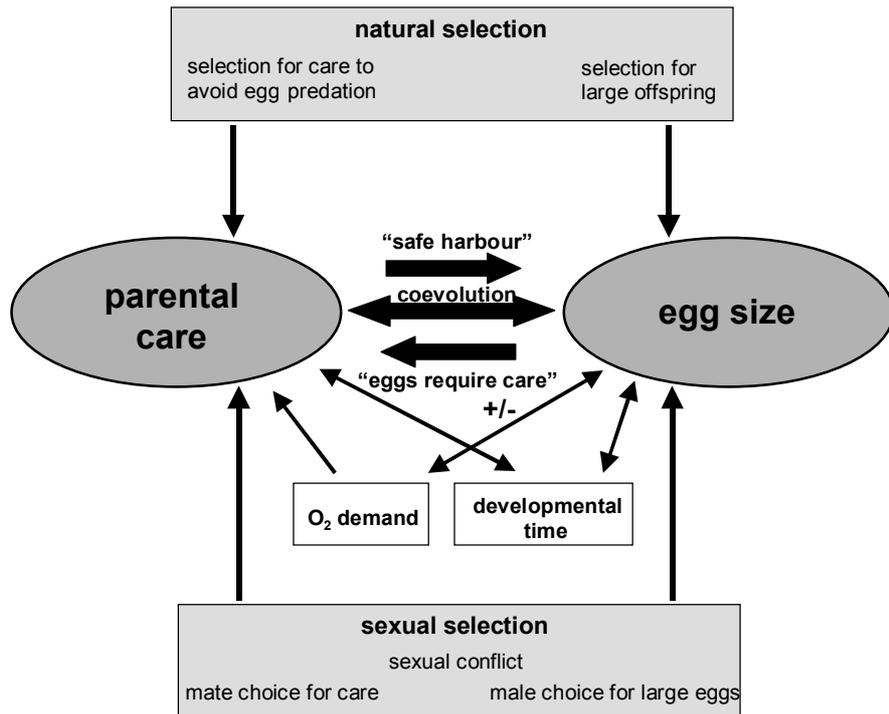
**Figure 6.** a) Effect of fishing degree (1: low, 3: intense) on group size of sea urchins: black square, median; box, 25-75th percentile; whisker, 10-90th percentile (ANOVA on log-transformed data:  $F_{2, 168} = 5.0, p < 0.01$ ). b) Effect of fishing degree on group size of cardinalfish: symbols as for a. (ANOVA on log-transformed data:  $F_{2, 195} = 3.2, p = 0.04$ ).

Our results suggest that the Banggai cardinalfish is under severe threat from the aquarium trade fisheries. Furthermore, our results suggest that groups are highly stable in this species as group size decreased with increased fishing. This may have strong implications for the evolution of differential allocation in this species. If groups are highly stable it means that the number of potential mates may be highly limited for females, especially since males have such long brooding cycles. Hence, if there is high variance in male quality and the supply of high quality males that are not already brooding is highly unpredictable, it may be adaptive for females to have a high plasticity in their reproductive investment. I suggest that such stable group structures may have influenced the evolution of differential allocation in this species.

#### *Evolution of egg size and parental care in fishes*

Understanding the evolution of progeny size is a key goal in life-history biology. Particular attention has been directed to this question in fishes, where substantial variation in egg size exists both between and within species. There is a common covariation in fishes between egg size and the extent of parental care, which suggests that a strong link exists between propagule size and the reproductive expenditure of parents (Shine 1978, Sargent et al. 1987). However, the causality behind this positive correlation between egg size and the extent of care in fishes remains largely unsolved. According to Shine (1989) there are four, not mutually exclusive, explanations for the general and positive correlation between care and egg size (Fig. 7): i) parental care

*per se* favours an increase in egg size, ii) increased egg size favours the evolution of care, iii) coevolution between these two previous variables, and iv) other independent factors may simultaneously select for more care and larger egg size (Shine 1989).



**Figure 7.** Diagram of how different selective pressures may affect egg size and parental care in fishes.

Finding the answer to this “chicken or the egg” problem could provide us with vital keys for the understanding of the evolution of parental care and egg size. In **paper VII** (Kolm & Ahnesjö) we review models and literature on the positive correlation between egg size and parental

care with particular focus on how sexual selection may affect the positive correlation between egg size and care. We show that sexual selection may be highly important for the evolution of egg size and care both through mate choice and sexual conflict (Fig. 7).

## **Conclusions**

This thesis shows that females have remarkable control over their reproductive investment, and that reproductive decisions to a large degree may be affected by mate attractiveness. In the Banggai cardinalfish, the size of both males and females have important consequences for the reproductive output of a pair and females produced larger eggs for larger, more attractive males. This means that females are investing more of their resources when mating with large males and may thus sacrifice future growth and future reproduction through such differential allocation. The likely value of producing larger eggs for larger males may lie in that only large males can successfully brood large eggs, which produce larger offspring with higher fitness. This matching of egg size to the attractiveness may also be quite rapid, suggesting that differential allocation may not only be limited to species with prolonged pair bonds. Furthermore, I show that both male and female choice may be highly important to consider when addressing the outcome of a particular reproductive event. In the Banggai cardinalfish, females play the active role in courting and court larger more attractive males more intensively. These female

courting behaviours contain honest, important information regarding both reproductive investment (clutch weight) and proximity to spawning. Therefore, females may use courtship signals to attract high quality males by displaying how much resources they are willing to invest in a reproductive event with a specific male. This highlights the need to also focus on females when addressing potential information content in sexual displays. Males in this sex-role reversed species did, however, play an important part in territory defence, suggesting that our view of sex roles may deserve reconsideration and prior to labelling a species as sex-role reversed, one needs to consider the roles that both sexes play with caution. The apparent stable group structure in the Banggai cardinalfish may have had implications for the evolution of female plasticity in reproductive investment as the relatively small group sizes in this species may lead to high variance in the quality of available mates. Finally, it is evident that sexual selection may have a strong influence on the evolution of egg size and parental care and may therefore be a strong factor behind the incredible variation and species richness among fishes.

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