

# Mothers adjust egg size to helper number in a cooperatively breeding cichlid

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Mothers should adjust the size of propagules to the selective forces to which these offspring will be exposed. Usually, a larger propagule size is favored when young are exposed to high mortality risk or conspecific competition. Here we test 2 predictions on how egg size should vary with these selective agents. When offspring are cared for by parents and/or alloparents, protection may reduce the predation risk to young, which may allow mothers to invest less per single offspring. In the cooperatively breeding cichlid *Neolamprologus pulcher*, brood care helpers protect group offspring and reduce the latter's mortality rate. Therefore, females are expected to reduce their investment per egg when more helpers are present. In a first experiment, we tested this prediction by manipulating the helper number. In *N. pulcher*, helpers compete for dispersal opportunities with similar-sized individuals of neighboring groups. If the expected future competition pressure on young is high, females should increase their investment per offspring to give them a head start. In a second experiment, we tested whether females produce larger eggs when perceived neighbor density is high. Females indeed reduced egg size with increasing helper number. However, we did not detect an effect of local density on egg size, although females took longer to produce the next clutch when local density was high. We argue that females can use the energy saved by adjusting egg size to reduced predation risk to enhance future reproductive output. Adaptive adjustment of offspring size to helper number may be an important, as yet unrecognized, strategy of cooperative breeders. **Key words:** cichlids, cooperative breeding, intraspecific competition, maternal effects, maternal investment, offspring size. [*Behav Ecol* 18:652–657 (2007)]

Life-history theory predicts that females should increase their investment in offspring quality if young run a high risk of encountering adverse environmental conditions (Bernardo 1996; Mousseau and Fox 1998). In several species of fishes, insects, and amphibians, larger offspring do better under adverse environmental conditions than small young, whereas under benign conditions the latter survive equally well or even better (e.g., Mousseau and Fox 1998; Eium and Fleming 1999). Propagule size is often highly plastic, and it has been proposed that females tailor egg size adaptively to the environment their offspring will encounter after birth (Bernardo 1996; Mousseau and Fox 1998; Taborsky 2006a, 2006b). The production of larger, more energy-rich eggs has to be traded off against current brood size or against future reproductive potential if current clutch size is kept constant (Roff 1992).

Apart from investment in propagule size, parents can raise the survival probabilities of offspring also after birth by provisioning them and by providing protection. Females may trade off their energy investment in eggs against investment in brood care as both are costly (reviewed in Clutton-Brock and Godfray 1991). Energetic constraints may be relaxed when caring females receive help from a mate or from alloparents. Brood care helpers can have positive short-term (Brouwer et al. 2005; Woxvold and Magrath 2005) and long-term effects on offspring survival (Hatchwell et al. 2004), and they can reduce the workload of breeders (Hatchwell and Russell 1996; Cockburn 1998; Balshine et al. 2001; Russell et al. 2003), which may increase the breeders' current (Taborsky 1984; Stacey and Koenig 1990; Peer and Taborsky

2007) or future reproductive success (Mumme et al. 1989). In most cases, more helpers provide more brood care in total (reviewed in Legge 2000), although the amount of care each helper contributes may be reduced with increasing group size (Stacey and Koenig 1990; Woxvold and Magrath 2005). Only in a few cases group members fully compensate for the presence of additional helpers by decreasing their efforts so that the total brood care in a group remains constant (Hatchwell 1999, Legge 2000).

Although an effect of helpers on brood size has been demonstrated in fish (Taborsky 1984) and birds (e.g., Woxvold and Magrath 2005), nothing is known about how the presence of helpers affects female investment decisions about initial offspring size. Here we test 2 predictions on female adjustment of egg size to 2 major selective agents to which their offspring will be exposed, mortality risk and intraspecific competition. Our model system is the cooperatively breeding Lake Tanganyika cichlid *Neolamprologus pulcher*, which has been studied intensively regarding the ecological and social determinants of cooperative breeding (Taborsky and Limberger 1981; Taborsky 1984, 1985; Balshine et al. 2001; Heg et al. 2004, 2005; Stiver et al. 2004; Bergmüller et al. 2005; Bergmüller and Taborsky 2005; Dierkes et al. 2005). *Neolamprologus pulcher* lives in social groups consisting of a breeding pair and up to 36 subordinates, including typically 1–9 brood care helpers (see Figure 1 in Balshine et al. 2001) which participate in all parental duties including the defense of young from predators (Taborsky and Limberger 1981; Taborsky 1984).

In aquatic environments, predation risk usually decreases with increasing body size of prey (e.g., Sogard 1997; McCormick and Hoey 2004). In *N. pulcher*, offspring survival chances increase with the number of helpers present in a group (Brouwer et al. 2005). Therefore, we predicted that *N. pulcher* females may reduce their propagule size, when more helpers are present, and consequently, each offspring has a reduced mortality risk. This would allow females to save energy by reducing the per capita investment in reproduction

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without lowering the survival chances of offspring. The saved investment may be spent for raising the reproductive rate either by increasing current brood size or future reproductive output.

Females' decisions about egg size should also account for expected levels of competition among young. As offspring of cooperative breeders usually delay dispersal and stay in their natal territories as helpers, direct interactions during early life occur with members of the natal group or with neighboring groups. In *N. pulcher*, local intraspecific competition for food is of minor importance, as this species feeds mainly on ephemeral resources outside their territories (Taborsky and Limberger 1981). However, helpers intensively defend the family territory against similarly sized conspecifics from neighboring groups (Taborsky et al. 1986). Juvenile dispersal occurs between neighboring groups (Stiver et al. 2004; Bergmüller et al. 2005) and may generate competition for shelters. Helpers are less likely to disperse successfully when neighboring groups are large (Bergmüller et al. 2005). If a larger egg size results in a long-term size advantage in competitive interactions and for dispersal opportunities (e.g., in lizards, Svensson and Sinervo 2000, and marine invertebrates, Marshall et al. 2006), *N. pulcher* females should produce bigger eggs when neighboring groups are large. As bigger eggs need longer to become mature than small eggs (e.g., Campos-Mendoza et al. 2004), females are expected to take longer to produce a clutch when local density is high.

## METHODS

### Study species

Social groups of *N. pulcher* (referred to as *N. pulcher* and *Neolamprologus brichardi*, see Grantner and Taborsky 1998) typically consist of a breeding pair, immature and mature helpers of both sexes, and offspring of the most recent clutch produced by the breeders (Taborsky and Limberger 1981; Taborsky 1984). In the laboratory, breeder females usually produce clutches of 100–300 eggs (Taborsky 1984). Freshly hatched larvae are cared for in a central breeding shelter by young produced in previous clutches, which clean the eggs from fungi and remove sand and other obstacles from the breeding shelter. In addition, fish above 2 cm standard length (SL) and the breeding pair guard and defend the territory against predators and competitors for space. Helpers mature at a size of  $\geq 3.5$  cm SL (Taborsky 1984) corresponding to an age of  $\geq 220$  days (Skubic et al. 2004), and they may stay in their natal territory long after maturation (Dierkes et al. 2005; Stiver et al. 2004; Taborsky and Limberger 1981). Large helpers are often unrelated to the breeding pair (Taborsky and Limberger 1981; Dierkes et al. 2005) but accrue direct benefits through received protection (Taborsky 1984; Heg et al. 2004), reproductive parasitism (mainly male helpers; Dierkes et al. 1999), and territory inheritance (Balshine-Earn et al. 1998, Dierkes et al. 2005). By joining in brood care, they pay rent for being allowed to stay in the territory (Taborsky 1984, 1985; Balshine-Earn et al. 1998, Bergmüller et al. 2005; Bergmüller and Taborsky 2005). In contrast to larger helpers, small helpers and young are related to the breeder pair with a relatively high probability (Taborsky and Limberger 1981; Dierkes et al. 2005), accruing also indirect benefits by caring for younger siblings or half-sibs (Brouwer et al. 2005).

We use the term “helpers” for all group members (except the breeding pair) that are larger than 2 cm SL (see Balshine et al. 2001) as only those fish participate in defense of the brood chamber and the territory (e.g., Taborsky 1984). Smaller group members ( $\leq 2$  cm SL) are referred to as “young.”

### Husbandry of experimental fish

The experiments were conducted at the Ethologische Station Hasli of the Institute of Zoology, University of Bern, Switzerland, under license 40/05 of the Veterinary Office of Kanton Bern. We used laboratory-reared offspring of fish originating from a population near Mpulungu, Zambia, at the southern end of Lake Tanganyika. Social groups were kept in 100-l tanks or in 100-l compartments of 200-l tanks, in both cases having visual contact to other *N. pulcher* groups. Each tank was equipped with a 3-cm layer of fine-grained river sand, an internal biological filter, and clay flower pot halves (12 cm diameter) serving as shelters and breeding substrate. Water temperature was held at  $27 \pm 1$  °C and water quality was kept constant, close to the values found in Lake Tanganyika (Taborsky B, unpublished data). The light:dark cycle was set to 13:11 h with 10 min dimmed light periods in the morning and evening to simulate natural light conditions at Lake Tanganyika. The fish were fed 6 days a week with either commercial flake food (4 days/week) or a mixture of frozen zooplankton (2 days/week).

### Experiment 1: variation of helper number

Sixteen social groups of *N. pulcher* kept in 100-l aquaria were used for the first experiment. Twelve groups had existed and reproduced regularly already for about 1 year without being manipulated. The sizes of these groups may have been influenced by the quality of the breeder pair, for example, better breeders may have been able to produce more young and to sustain larger family sizes. As we aimed to investigate the effect of helper number on egg size independently of breeder quality, we manipulated the group sizes of these 12 families by removing 1–19 group members of different sizes, among them 1–9 helpers. Numbers of removed helpers were uncorrelated to helper numbers that remained in the groups ( $r = -0.29$ ,  $P = 0.34$ ,  $n = 12$ , Pearson correlation analysis). In addition, we removed all young present at the time of manipulation (0–15 individuals), as they would have grown larger than 2 cm SL during the  $\leq 3$ -month period between the manipulation and egg collection. This was done to prevent a bias toward very small helpers in the size-structures of groups. Also the number of removed young did not correlate with helper number left in the groups after manipulation ( $r = -0.14$ ,  $P = 0.66$ ,  $n = 12$ ). In addition, we created 4 new groups from adult and juvenile individuals living in stock tanks (for procedure, see Taborsky 1984). After the manipulations, all groups were left undisturbed for at least 3 months 1) to allow helpers to consolidate their position in the manipulated groups, 2) to remove a helper if consolidation failed (i.e., if expulsion occurred), and 3) to allow females to adjust their reproductive investment strategy to the new conditions. Expulsions of helpers by other group members caused a bias toward small group sizes in final group compositions. At the time of egg collection, the 16 experimental groups contained between 0 and 9 helpers (i.e.,  $> 2$  cm SL). At this time, 12 groups contained between 6 and 60 young ( $\leq 2.0$  cm SL) of broods produced after our manipulations of group size, 3 groups had no young, and in 1 group the number of young was unknown. We also tested for a potential effect of the number of young on female investment.

### Experiment 2: variation of local density

We divided ten 200-l tanks in a central 100-l compartment and 2 lateral 50-l compartments on either side by 2 transparent Plexiglas separations. In each central compartment, we established a social group consisting of an adult male and female,

a large- (mean: 5.1 cm SL, range 4.8–5.2 cm SL) and a medium-sized helper (mean: 4.2 cm SL, range 3.8–4.4 cm SL) using fish that had been kept in large aggregations in stock tanks. Each set of 2 helpers consisted of a male and a female with sexes being balanced equally among large- and medium-sized helpers. If the 2 helpers did not tolerate each other within a week, they were exchanged for a new set of helpers. Otherwise, a male and a female of breeder size ( $>6.0$  cm SL) were added that had been haphazardly chosen from stock tanks containing a large school of fish. During the following 2 days, groups were carefully checked to find out whether the helpers were accepted by the breeders (i.e., helpers were not overtly attacked by breeders and had access to shelters). If helpers were not accepted within 5 days, the breeder pair was exchanged against another adult male and female. All 4 group members were unrelated to each other.

After another 3–6 days, we placed mixed-sex groups of either  $2 \times 8$  (high density) or  $2 \times 2$  (low density) conspecifics in the 2 lateral compartments of each experimental tank. We collected the first clutches produced after the onset of the treatments. Further, we recorded the period between transferring the adult pair to the experimental tank and first spawning. This period reflects the time breeders took to produce a clutch because in the stock tanks, where the adults had lived for several months prior to the experiment, no eggs were laid. After collecting the first clutch, those 5 groups that had been exposed to high neighbor densities during the first trial were switched to the low-density treatment, whereas the 5 low-density groups of the first trial were switched to the high-density treatment. After the switch of treatments, the next clutch was collected for analysis. Two of 10 families did not produce a clutch in the second trial (one in each treatment).

### Morphological measurements

We checked for the presence of eggs every 1–2 days in the morning (at 27 °C *N. pulcher* eggs take about 3 days until hatching). We collected clutches in the afternoon after spawning was completed by gently removing them from the flower pot and transferring them to a petri dish with a pair of soft, flexible forceps. Despite utmost care, on average, 6.9% of the eggs were ruptured during this procedure. We counted all the eggs of a clutch to determine total clutch size, but only intact eggs were dried (70 °C, 36 h). After drying, each clutch was weighed twice to the nearest 0.0001 g. Between the 2 measurements, eggs were transferred to a fresh petri dish. Between-measurement error was very small ( $\pm 0.0086\%$ ). This excludes the possibility that debris present in the tank water that might potentially have been transferred with the eggs to the first dish biased our results. We used the mean of the 2 measurements for further analysis. Mean egg dry weight was used as a measure of mean egg size. It was calculated as clutch dry weight divided by total clutch size. After collecting the clutch, we measured SL of all group members  $>2$  cm SL with a measuring board with 1-mm grid and estimated lengths to the nearest 0.5 mm by eye. Weights were taken to the nearest 0.01 g on an electronic balance, and female condition was measured as weight relative to structural size by calculating Fulton's condition factor  $K = (\text{weight}/\text{SL}^3) \times 100$  (see Bolger and Connolly 1989).

### Data analysis

The resources a female invests in a given clutch may be influenced by her body size (measured as SL) and her energetic state (estimated by the condition factor  $K$ ). In order to reduce the variance caused by these confounding variables, we used the residuals of a multiple regression of mean egg size on

female SL and  $K$  (standardized coefficients,  $\beta_{\text{SL}} = 0.23$ ,  $P = 0.39$ ;  $\beta_K = 0.25$ ,  $P = 0.36$ ; entire model:  $R^2 = 0.11$ ,  $F_{2,13} = 0.79$ ,  $P = 0.48$ ) and clutch size on SL and  $K$  (standardized coefficients,  $\beta_{\text{SL}} = -0.033$ ,  $P = 0.90$ ;  $\beta_K = -0.26$ ,  $P = 0.35$ ; entire model:  $R^2 = 0.07$ ,  $F_{2,13} = 0.47$ ,  $P = 0.64$ ) for the statistical analyses of experiment 1. SL and  $K$  were not correlated (Pearson correlation,  $r = -0.084$ ,  $P = 0.77$ ,  $n = 16$ ). Female body weight was highly correlated with SL ( $r = 0.96$ ,  $P < 0.001$ ,  $n = 16$ ) and was therefore not included in the analysis. In addition to the analysis using residuals, we also analyzed the effect of helper number on egg size with the original, unadjusted data.

The sizes of helpers in a group might confound the predicted effect of helper number on mean egg size, as large helpers defend the breeding territory more effectively than small ones (Taborsky and Limberger 1981; Taborsky et al. 1986). However, mean helper size (range: 2.8–6.6 cm) was not related to helper number (Pearson correlations,  $r = -0.33$ ,  $P = 0.24$ ) or mean egg size ( $r = -0.071$ ,  $P = 0.81$ ;  $n = 14$  for these correlation, as 2 groups did not have helpers).

In experiment 2, we did not adjust for female SL and  $K$  when analyzing repeated measures data of females.

We considered the possibility that clutch weight, that is, the product of egg weight and clutch size, may be influenced by helper number or local density of competitors. In both experiments, clutch weight was highly correlated with clutch size (experiment 1:  $r = 0.98$ ,  $P < 0.001$ ,  $n = 16$ ; experiment 2:  $r = 0.97$ ,  $P < 0.001$ ,  $n = 16$ ), whereas there was no significant relationship between clutch weight and egg weight (experiment 1:  $r = 0.26$ ,  $P = 0.34$ ,  $n = 16$ ; experiment 2:  $r = 0.35$ ,  $P = 0.18$ ,  $n = 16$ ). Apparently, in *N. pulcher*, the variation in clutch weight is almost entirely caused by variation in clutch size. To avoid redundancies, we did not include clutch weight in our analyses.

As general linear models, including regression models, require normality of error (see Grafen and Hails 2002, p. 136), we tested the distribution of residuals of all regression models for normality. The distribution of residuals never deviated from normal (Kolmogorov–Smirnov tests, all  $P$  values  $\gg 0.1$ ). When sample sizes were below 10, we used nonparametric statistics as it is not possible to test reliably for a deviation from a normal distribution for such small sample sizes.

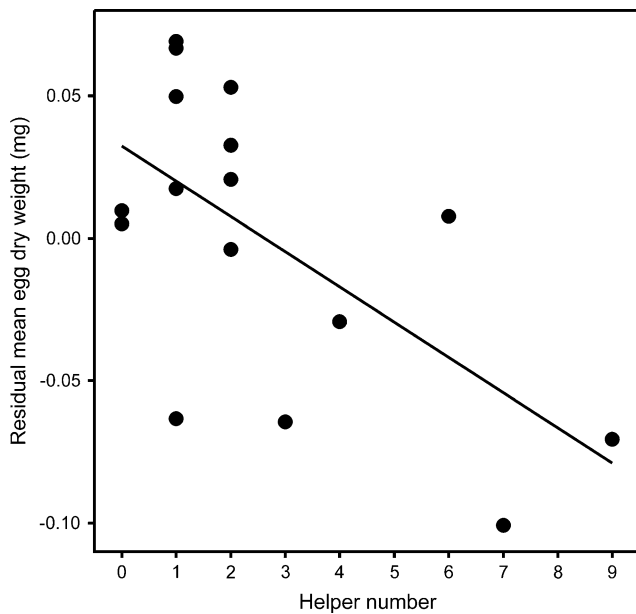
All statistical analyses for experiments 1 and 2 were done with SPSS 13.0, SPSS Inc., Chicago, IL.

## RESULTS

### Experiment 1: helper number

Residual mean egg size (after adjusting for female SL and  $K$ ) decreased with increasing helper number, whereas it was not related to residual clutch size (standardized coefficients,  $\beta_{\text{helpers}} = -0.60$ ,  $P = 0.017$ ;  $\beta_{\text{clutch size}} = 0.10$ ,  $P = 0.64$ ; entire model:  $R^2 = 0.39$ ,  $F_{2,13} = 4.22$ ,  $P = 0.039$ ). We then simplified the model by removing the nonsignificant effect of clutch size, and calculated the univariate regression of residual egg weight on helper number ( $\beta = -0.62$ ,  $R^2 = 0.38$ ,  $F_{1,14} = 8.69$ ,  $P = 0.011$ ; Figure 1). The effect of helper number on mean egg size was also significant when using the raw data without adjusting for female size and condition ( $\beta = -0.59$ ,  $R^2 = 0.35$ ,  $F_{1,14} = 7.58$ ,  $P = 0.016$ ). Neither residual clutch size ( $R^2 = 0.026$ ,  $F_{1,14} = 0.38$ ,  $P = 0.55$ ) nor the unadjusted values of clutch size ( $R^2 = 0.035$ ,  $F_{1,14} = 0.50$ ,  $P = 0.49$ ) were affected by helper number.

In a separate regression analysis, we tested if the number of young ( $\leq 2$  cm SL) present in groups may have influenced egg size. There is no evidence that this was the case (standardized coefficients,  $\beta_{\text{young}} = 0.37$ ,  $P = 0.18$ ;  $\beta_{\text{clutch size}} = 0.17$ ,  $P = 0.53$ ; entire model:  $R^2 = 0.19$ ,  $F_{2,12} = 1.45$ ,  $P = 0.27$ ).



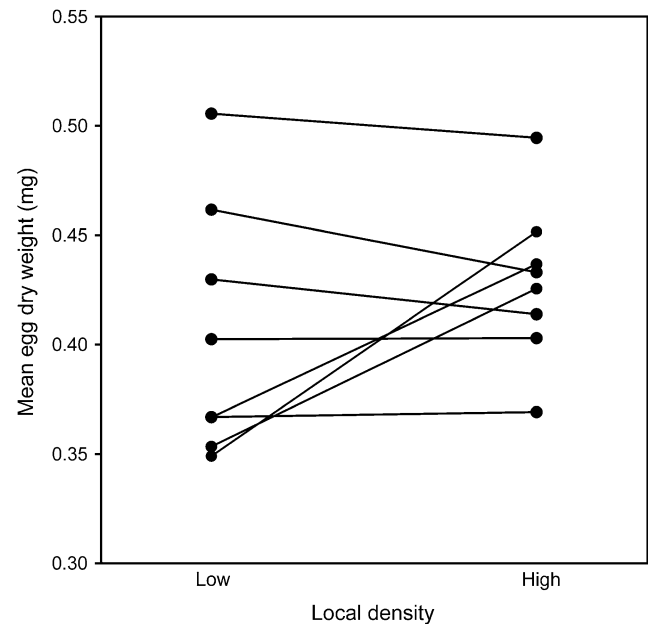
**Figure 1**  
Effect of helper number on residual mean egg size after adjusting for the influence of female size and body condition on egg size ( $n = 16$ ).

### Experiment 2: density

The manipulation of local density had no effect on egg size ( $T = 12$ ,  $P = 0.40$ ,  $n = 8$ ; Figure 2) or clutch size ( $T = 17$ ,  $P = 0.89$ ,  $n = 8$ ; Wilcoxon matched-pairs signed-rank tests). However, females took longer to produce their first clutch when the simulated neighbor density was high (Mann–Whitney  $U$  test,  $U = 2$ ,  $P = 0.023$ ,  $n_1 = 5$ ,  $n_2 = 5$ ), and the time to produce a clutch increased with the produced egg size as predicted (Pearson correlation,  $r = 0.60$ ,  $P = 0.008$ ,  $n = 18$  clutches; correlations are also significant if durations to spawning of first and second clutch of a female were analyzed separately). Also in this experiment, clutch size did not correlate with egg size, and opposite to expectation, the correlation coefficient was positive (first clutch of each female tested, Spearman rank correlation:  $r_s = 0.26$ ,  $P = 0.33$ ,  $n = 10$ ; residual egg size vs. residual clutch size after adjusting for female SL and K:  $r_s = 0.24$ ,  $P = 0.36$ ).

### DISCUSSION

Female *N. pulcher* produced smaller eggs when more helpers were present, whereas egg size was unaffected by the number of young present in the group. To our knowledge, this is the first experimental evidence that females adjust their investment in individual offspring to the number of helpers. We argue that *N. pulcher* females can reduce their egg size in the presence of many helpers without losing reproductive success because the survival chances of young increase with helper number in this species (Brouwer et al. 2005). An observational study of the cooperatively breeding meerkats, *Suricata suricatta*, suggests that helper number can also positively correlate with breeder investment. In the presence of more helpers, breeder females were heavier, and females that were heavier at conception weaned heavier pups (Russell et al. 2003). Saving energy by fine-tuning the investment in offspring quality to helper number may be a general but hitherto neglected mechanism allowing cooperative breeders to benefit from the presence of helpers. So far, the relationship be-



**Figure 2**  
Density effect on egg size; lines connect values of individual females in 2 treatments.

tween egg size and brood care has been predominantly addressed at the across-species level, and the relationships detected between the 2 traits were positive, negative, or absent (e.g., Sargent et al. 1987; Nussbaum and Schultz 1989; Kolm et al. 2006).

Surprisingly, the decrease in egg size with helper number was not accompanied by an increase in clutch size, and there was no significant relationship between egg size and clutch size. Similarly, in experimental studies with fish and birds where females adjusted egg size to the quality of their current partners, clutch size remained unaffected (*Pterapogon kauderni*, Kolm 2001; *Anas platyrhynchos*, Cunningham and Russell 2000; *Coturnix chinensis*, Uller et al. 2005; and *Serinus canaria*, Leitner et al. 2006). This suggests that egg size can readily be adjusted to current environmental conditions without necessarily affecting the clutch size. None of these studies obtained data on long-term effects of egg-size adjustment on clutch size or other reproductive parameters. However, a long-term study on our study species showed that in the presence of helpers, females laid significantly more eggs than when helpers were absent (Taborsky 1984). This suggests that females may benefit from an increased future reproductive rate when more help is provided and that the adjustment of egg size found in this study is one possible mechanism underlying this increase in fecundity. The reduction of egg size may save energy, which then increases female residual reproductive value. Other positive long-term effects of helpers on female reproduction include a reduced workload (e.g., Legge 2000), which may reduce the energy expenditure of breeder females and/or may increase their opportunities for feeding (Taborsky 1984; Cockburn 1998; Balshine et al. 2001; Russell et al. 2003).

Alternatively, the expected negative correlation between egg size and clutch size might have been confounded by quality differences of individuals, which makes it difficult to detect trade-offs (van Noorwijk and de Jong 1986). In our analyses, we adjusted for female size and body condition, but these are not the only possible parameters determining the quality of a breeder female. Moreover, trade-offs may only be visible

when energy is limited (for an example in another cichlid species, see Taborsky 2006b), whereas in our study, food rations were not restricted. Finally, we cannot exclude the possibility that some eggs were cannibalized by helpers (von Siemens 1990) and that changes in clutch size resulting from this egg loss may have blurred the expected relationship between egg size and clutch size because when more helpers are present, the chances of egg cannibalism might be greater.

Often, cooperative breeding evolves when habitats are saturated (e.g., Komdeur 1992), which may require special adaptations to intense resource competition. In order to test whether females adjust egg size to the expected level of intraspecific competition of offspring, we manipulated the number of fish in the direct vicinity of the focal family. The 2 simulated competition levels were well distinguished by the family fish, as helpers showed more defense behavior against neighbors in the high-density treatment than in the low-density treatment (Bruitjes R and Taborsky M, in preparation). In contrast to our expectation, eggs were not significantly larger when local density was high, although females took longer to produce a clutch in high local densities as we had predicted, and the time to produce a clutch increased with egg size. It is possible that the relationship between local density and egg size is more subtle than we expected, and a much larger sample size would be required to demonstrate it. Mean egg sizes were indeed larger in the high-density treatment (0.43 mg) than in the low-density treatment (0.40 mg), and in the 3 females that produced highly dissimilar egg sizes between treatments, the difference was in the expected direction (see Figure 2).

Long-term consequences of maternal effects on egg size were observed in some animals (juvenile *Uta stansburiana*, Svensson and Sinervo 2000, and postmetamorphic colonial marine invertebrates, *Botrylloides violaceus*, Marshall et al. 2006) but not in others (*Oncorhynchus tshawytscha*, Heath et al. 1999). Hence, a relationship between competition levels and egg size might not exist in *N. pulcher*, if egg-size effects on competitive performance are rather short term. By the time young become helpers, *N. pulcher* may have already compensated for small initial larval size, for example, by catch-up growth (Metcalf and Monaghan 2001). In this case, adjusting egg size to the density of neighboring groups should not be expected. Finally, females may be able to adjust egg size only when exposed to density differences for longer periods. However, this seems unlikely as fish are able to adjust egg size to environmental triggers even closely before spawning (Kolm 2001) and because females in our experiments did respond to the experimental manipulations by taking longer to produce a clutch when the simulated local density was high.

Our results have implications for future research both on reproductive strategies of cooperative breeders and on environmentally induced maternal effects. Egg-size adjustments to helper number and the amount of help received may be an important component of female resource allocation in highly social species. If helpers are related to breeder females, the reduction of egg size when helpers contribute to offspring survival may yield also indirect fitness benefits to helpers through an increase of the female breeder's fecundity and residual reproductive value (Cockburn 1998). More generally, experimental studies of environmentally induced maternal effects on offspring size focused largely on resource availability and density-related stress (Mousseau and Fox 1998). Our results suggest that when producing eggs, mothers may directly respond to the expected level of protection of young. This should be considered as a factor that may be of similar importance as resource availability in determining maternal investment strategies.

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