



## Effects of maternal stress on egg characteristics in a cooperatively breeding fish

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### ABSTRACT

Elevated stress experienced by a mother can compromise both her own reproductive success and that of her offspring. In this study, we investigated whether chronically stressed mothers experienced such effects in cooperatively breeding species, in which helpers at the nest potentially compound the negative effects of maternal stress. Using *Neolamprologus pulcher*, a group-living cichlid fish from Lake Tanganyika, we observed the effects of experimentally increased stress on female reproductive success (measured as inter-spawn interval, and number of eggs) as well as egg characteristics including egg size and cortisol concentrations. Stress levels were manipulated by repeated exposure to the acute stresses of chasing and netting. Stressed females had longer inter-spawn intervals and laid fewer, smaller eggs. Although no significant differences in egg cortisol concentrations were detected between control and stressed females, egg cortisol concentration fell between spawns in control but not in stressed fish. No effect of helper number was detected for any parameter examined, except there appeared to be less change in egg cortisol content in groups with helpers present. Our results suggest that stress imposes fitness costs on breeding females, and social regulation of a dominance hierarchy does not appear to exacerbate or alleviate the negative effects of maternal stress.

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### 1. Introduction

Stress, resulting from sudden perturbations (acute) or from constant challenges (chronic) in the environment, induces a suite of important physiological and behavioural responses. Natural selection has shaped stress responses to enhance an organism's ability to cope with the stressor and to eventually regain homeostasis (Chrousos 1998; Charmandari et al. 2005). A key component of the physiological stress response is the mobilization of glucocorticoid (GC) stress hormones (cortisol or corticosterone) via activation of the hypothalamic-pituitary-adrenal (HPA, in tetrapods; in fish the HPI or hypothalamic-pituitary-interrenal) axis. The ability to mount an appropriate stress response is generally considered beneficial. However, a prolonged elevation of GCs in response to long-term exposure to stressors can have detrimental effects on an individual, including reductions in growth and immune function, and the suppression of reproduction (Chrousos, 1998; Wendelaar Bonga 1997; Charmandari et al. 2005; Schreck 2010). Stressful conditions experienced early in life (or in utero) may have profound impacts later in life (Contreras-Sánchez et al. 1998; Rondó et al. 2003; Hayward and Wingfield 2004; Ostrand et al. 2004; Sloman 2010). In this study, we used a cooperatively breeding fish species to explore whether stress experienced by breeding females projects onto the

next generation. We examined the effects of chronic maternal stress (induced by repeated exposure to an acute stressor) on female reproductive rates, fecundity, and egg characteristics.

To our knowledge, the potential fitness costs of maternal stress have not yet been experimentally manipulated in cooperatively breeding species. Cooperative breeders are group-living species, in which subordinate group-members forgo reproduction to help raise the offspring of dominant individuals. We predicted that the effects of maternal stress on offspring number and quality would be exaggerated in social cooperative breeders due to the energy requirements and challenge of maintaining dominance over subordinates in the social group (see Goymann and Wingfield 2004). To date, the impact on reproductive success of maternal stress during gestation has been studied in several species that are not cooperative breeders. For example, maternal stress results in lowered birth-weight in human, *Homo sapiens*, infants (Rondó et al. 2003), slower juvenile growth rates in Japanese quail (*Coturnix coturnix japonica*, Hayward and Wingfield 2004), smaller egg clutches in moor frogs (*Rana arvalis*, Räsänen et al., 2005), and smaller eggs and young in rainbow trout (*Oncorhynchus mykiss*, Campbell et al. 1992; Contreras-Sánchez et al. 1998).

To address the impact of maternal stress on reproductive fitness in a cooperative breeder, we used the cichlid fish, *Neolamprologus pulcher*, endemic to Lake Tanganyika, Zambia. *N. pulcher* live in highly social groups organized into linear dominance hierarchies based on size, with a breeding male and female pair at the top of the hierarchy and 1–20 subordinate helpers (Taborsky and Limberger, 1981;

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Balshine et al. 2001; Heg et al. 2005). The dominant breeders remain in their position for 3–12 months (Stiver et al. 2004) and subordinates rarely breed in the wild but can eventually gain dominance and breeding status, via inheritance or take-over (Fitzpatrick et al. 2008, Stiver et al. 2009). *N. pulcher* groups live in communally defended rocky territories clustered together into subpopulations at 3–45 metres depth (Stiver et al. 2008). In these territories, female breeders may be exposed to a number of potential environmental and social stressors. First, breeders often experience elevated predation pressure and frequently defend their young against predators (Balshine et al. 2001). Second, individuals constantly need to vigorously defend their territories against encroaching, neighbouring conspecifics as well as heterospecific space competitors (Desjardins et al. 2008). Third, dominant breeders must police subordinates to control their reproduction (Goymann and Wingfield, 2004; Fitzpatrick et al. 2008). Exposure to such stressors has the potential to repeatedly raise GC levels and therefore could have fitness implications for both breeding females and their offspring.

We made a series of predictions for the effects of maternal repeated stress on reproductive fitness in *N. pulcher* based on findings in the literature. One, we predicted that stressed breeder females would take longer to reproduce. In rainbow trout, both chronic and acute stress caused delays in ovulation and spawning (Campbell et al. 1992; Contreras-Sánchez et al. 1998). Two, we predicted that stressed fish would lay fewer, smaller eggs, as chronic stress was found to reduce egg mass in rainbow trout (Campbell et al. 1992; reviewed in Schreck et al. 2001). Three, we predicted that cortisol levels would be higher in the eggs of stressed compared to those of unstressed (control) females. Similar findings of maternal transfer of GCs have been observed in egg yolk of Japanese quail (Hayward and Wingfield 2004) and in the eggs of coho salmon, *Oncorhynchus kisutch* (Stratholt et al. 1997). A final prediction stems from the novel aspect of our study. We predicted that the presence of helpers would increase the stress experienced by breeder females and therefore that females with more helpers would exhibit a heightened response to an experimental stressor. This notion is supported by work in which female damselfish (*Pomacentrus amboinensis*, a coral-dwelling social fish), in environments with multiple conspecifics exhibited higher cortisol levels and consequently hatched smaller juveniles than those that were allowed to breed in isolation (McCormick 2006). Goymann and Wingfield (2004) predicted that there would be greater physiological stress (termed allostatic load) for dominant individuals in species where acquiring and maintaining dominance is difficult. In *N. pulcher*, few individuals manage to attain a breeding position and individuals that do so must regularly assert their dominance to maintain their position (see Mileva et al. 2009 for a full allostatic load calculation for *N. pulcher*). Thus we predicted that under normal control conditions, breeding females with helpers or with many helpers would lay eggs containing higher cortisol levels than females without helpers or with few helpers. We also aimed to investigate the effects of helper presence on egg size in stressed females.

## 2. Methods

### 2.1. Fish husbandry and housing

All fish (*Neolamprologus pulcher*, Cichlidae) used in this experiment were held at McMaster University, Hamilton, Ontario, Canada. They were either descendants of wild-caught breeding pairs captured in 2002, or were wild-caught breeding pairs from early 2008, captured at the southern tip of Lake Tanganyika. Twenty stable social groups, ones in which spawning had occurred prior to the beginning of the experiment, were chosen for use in this experiment. Each social group was housed in a 189 L tank and groups consisted of a dominant breeding male and female with 0–4 subordinates of either sex (7 groups had no helpers; 2 groups had 1 helper; 5 groups had 2 helpers;

1 group had 3 helpers; and 2 groups had 4 helpers). Social groups had well-established dominance hierarchies. In addition to the social group, the 20 tanks contained a ~2 cm layer of sand, a water heater, a thermometer, two mirrors, and two flowerpot halves (to deposit eggs on), and was aerated using two foam filters. Water temperature was held at  $26 \pm 2$  °C and the light: dark cycle was maintained at 13:11 h throughout the experiment. Each group was fed *ad libitum*, Nutrafin basix Large Flake commercial cichlid food once daily in the morning. To ensure that sufficient food was provided, an excess of flakes was left on the tank bottom for at least 1 hour before removal.

All fish husbandry protocols, as well as experimental procedures used for chasing and netting fish and egg sampling (see below), were reviewed and approved by the Animal Research Ethics Board of McMaster University (Animal Utilization Protocol # 06-10-59) and adhere to the animal handling guidelines specified by the Canadian Council for Animal Care.

### 2.2. Experimental setup and egg collection

In each tank, the two flowerpot halves on which the fish could spawn were lined with a sheet of roughened flexible transparent plastic; note that roughened acetate was provided after smooth acetate proved to be an inappropriate spawning substrate (see Discussion). Tanks were monitored daily for spawning and once spawning was noted, tanks were assigned to either the “stressed” or “control” treatment in an alternating fashion. This first spawning day was considered Day 1 of the experiment. On this day, the plastic sheet was removed, and eggs were dried carefully with kimwipes and photographed together with a ruler, using a digital SLR camera (Canon EOS Rebel 300D). The eggs were then gently scraped off the plastic surface, weighed to the nearest 0.001 g, and stored at  $-80$  °C for later analysis of egg cortisol concentrations (note that the small size of *N. pulcher* precludes collection of non-terminal blood samples for cortisol analysis – hence the emphasis on egg cortisol concentrations as a proxy for plasma cortisol concentrations in females). The breeding female and male were also caught on Day 1, and measured for standard length and body mass (Table 1).

The ten breeding females assigned to the control treatment were not subjected to any stressor other than the regular weekly tank cleanings, and were simply fed daily. The ten breeding females assigned to the “stressed” treatment were subjected to a daily stressor for up to 80 days in addition to their weekly cleaning and daily feeding regimes. These “stressed” females were chased with a net for 2–5 min twice per day for 50 days (once in the morning before 12 pm, and once in the afternoon, allowing more than 3 h between chasing events). By the end of 50 days no spawning had occurred, and so the stressor was therefore changed to netting for 10 min, once daily for

**Table 1**

Morphological characteristics, body condition and specific growth rate of control and stressed females at 1<sup>st</sup> and 2<sup>nd</sup> spawn.

Variable	Control females (mean $\pm$ se)	Stressed females (mean $\pm$ se)
Body mass at 1 <sup>st</sup> spawn (g)	8.95 $\pm$ 0.55	8.35 $\pm$ 0.54
Body mass at 2 <sup>nd</sup> spawn (g)	9.48 $\pm$ 0.66	8.07 $\pm$ 0.59*
SL at 1 <sup>st</sup> spawn (cm)	6.64 $\pm$ 0.14	6.39 $\pm$ 0.10
SL at 2 <sup>nd</sup> spawn (cm)	6.83 $\pm$ 0.15	6.52 $\pm$ 0.14
Fulton's K at 1 <sup>st</sup> spawn	3.04 $\pm$ 0.08	3.17 $\pm$ 0.08
Fulton's K at 2 <sup>nd</sup> spawn	2.95 $\pm$ 0.092	2.89 $\pm$ 0.11
Specific growth rate (% $\Delta$ mass per day)	0.10 $\pm$ 0.07	-0.06 $\pm$ 0.03*

SL refers to the standard length and is a commonly used length metric in fisheries research in which body length minus the tail is determined. Fulton's K refers to an index of body condition; the calculation of this variable and specific growth rate is detailed in the text. Asterisks denote a significant difference between control and stressed females ( $p < 0.05$ , see text for details of statistical tests used).

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