

**MATERNAL STEROIDS IN BROWN TROUT EGGS INFLUENCE
JUVENILE BEHAVIOUR AND PHYSIOLOGY**

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Introduction

Populations of juvenile salmonids are characterised by a large degree of individual variation in several behavioural and physiological traits that influence life history strategies (see Metcalfe et al., 1995). Factors influencing the development of such variation around first feeding are not well understood.

Large quantities of maternal hormones are found in newly fertilised teleost eggs, and may play a role in the endocrine control of early development (Brooks et al., 1997). Our study investigated whether variation in cortisol (F) and testosterone (T) levels in brown trout eggs could result in individual variation in juvenile physiology and behaviour.

Methods

Eggs were stripped from five mature female brown trout and fertilised with milt pooled from three mature males. Each family was divided into three equal-sized groups, and one group from each family immersed for 2 h in a water bath containing 200 µg/l F, 200 µg/l T, or no steroid. All groups were reared in separate baskets in hatchery troughs until first feeding, when they were transferred to hatchery tanks and reared under identical conditions.

Eggs were sampled from each group pre-fertilisation, immediately after the 2-hour immersion period, and two and seven days after treatment. Egg T and F

concentrations (ng/egg; not corrected for recovery efficiency) were measured using radioimmunoassay.

Ten individuals from each group were sampled at hatching, and an estimate of yolk-sac utilisation (ratio of yolk-sac larva:larva weight; YSL:L) was calculated for each individual.

At 3-4 months beyond first feeding, the weight-corrected standard metabolic rates (rSMR) of 20 fish from each treatment group were measured following the methods of Cutts et al. (1998). At the same time, triads comprising size-matched siblings, one from each treatment group, were introduced into sections of an artificial stream, and behaviours, body colour, and position were scored for 24 hours. Dominance ranks within each triad were assigned on the basis of the observation scores. Twenty-four triads were observed within each family.

At 5 months after the onset of exogenous feeding, the remaining fish ($n > 60$ /group) were killed, measured and sexed. A condition factor ($100 \times \text{weight}/\text{length}^3$) was calculated for each individual.

Data were examined for treatment effects using ANOVA, GLM with binary error structure (sex ratios), and polytomous logistic regression (dominance relationships). Correlation was used to examine associations between variables and egg steroid concentrations. A p -value less than 0.05 was considered significant.

Results

Hormone levels in eggs before and after treatment are shown in Table 1. Control T levels varied significantly between families. Levels of T and F in control eggs were negatively correlated. Treatment significantly elevated egg steroid levels above controls for at least 7 days post-treatment. Testosterone levels remained constant over this time, while 57-84% of F in F-treated eggs had cleared within 2 days. Steroid uptake varied between families (Table 1), but was not related to egg size, hydration or initial steroid levels. Elevated levels of T were approximately physiological, as were F levels by 2 days post-treatment. Treatment did not affect mortality rates, which were very low in all groups.

Table 1. Egg parameters for each family. Hormone concentrations (ng/egg) are from eggs immediately post-treatment, except where indicated (n=6).

	Family				
	1	2	3	4	5
Control F	0.19	0.17	0.10	0.25	0.12
Treated F	0.63	0.47	0.59	0.82	1.10
Uptake (ng)	0.44	0.30	0.49	0.57	0.98
% Increase	232	176	490	228	817
2 d post-treated F	0.21	0.20	0.11	0.30	0.18
Control T	0.07	0.16	0.12	0.02	0.13
Treated T	0.30	0.34	0.59	0.20	0.21
Uptake (ng)	0.23	0.18	0.47	0.18	0.08
% Increase	329	113	392	900	62

There were significant inter-family differences in control levels of some physiological variables measured. Cortisol or T treatment could affect yolk-sac absorption at hatching, and metabolic rate, size and dominance relationships of juveniles. Treatment had no effect on sex ratios. The effects of treatment were not consistent between families; family-specific treatment effects are shown in Table 2.

Groups with lower mean T concentrations had higher juvenile metabolic rates and relatively less yolk at hatching. Although not significant, higher egg F concentrations appeared to have the same effect on yolk-sac absorption, and may also be associated with higher female:male ratios and juvenile condition factors.

Conclusion

We suggest that naturally occurring variation in levels of maternal F and T in brown trout eggs can lead to variation in offspring physiology and behaviour, but that the effect of hormone concentration is dependent on interaction with other genetic or non-genetic parental contributions to the offspring. The degree of inter-family variation found here has implications for experimental design.

Table 2. Results of within-family comparisons by treatment group. C: control, F: cortisol-treated, T: testosterone-treated, N/S: non-significant.

	Family				
	1	2	3	4	5
YSL weight (mg)	N/S	C>T	N/S	N/S	N/S
L weight (mg)	N/S	N/S	C>T	T>F	C>T
YSL:L	N/S	N/S	T>F,C	F>C>T	T>F,C
rSMR (ml O ₂ .h ⁻¹ x10 ⁻³)	N/S	N/S	N/S	C>F,T	N/S
Final weight (g)	N/S	N/S	T>C	F>C,T	F>C,T
Final length (cm)	N/S	N/S	T>C	F>C	F>C,T
Condition factor	N/S	N/S	T>C	F>T	F>C,T
Sex ratio	N/S	N/S	N/S	N/S	N/S
Dominance	T>C	N/S	N/S	N/S	N/S

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