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**Highly fecund mothers sacrifice offspring survival to maximize fitness**

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Why do highly fecund organisms apparently sacrifice offspring size for increased numbers when offspring survival generally increases with size<sup>1–3</sup>? The theoretical tools for understanding this evolutionary trade-off between number and size of offspring have developed over the past 25 years<sup>1,4–10</sup>; however, the absence of data on the relation between offspring size and fitness in highly fecund species, which would control for potentially confounding variables, has caused such models to remain largely

hypothetical<sup>11,12</sup>. Here we manipulate egg size, controlling for maternal trait interactions, and determine the causal consequences of offspring size in a wild population of Atlantic salmon. The joint effect of egg size on egg number and offspring survival resulted in stabilizing phenotypic selection for an optimal size. The optimal egg size differed only marginally from the mean value observed in the population, suggesting that it had evolved mainly in response to selection on maternal rather than offspring fitness. We conclude that maximization of maternal fitness by sacrificing offspring survival may well be a general phenomenon among highly fecund organisms.

One of the most intensely studied maternal traits is egg size, owing to its direct consequences for offspring fitness<sup>1,3</sup>. Individual mothers are forced to trade off offspring quantity against quality during reproduction<sup>13,14</sup>. Much of the theoretical work on this question of reproductive allocation has focused around the seminal paper of Smith and Fretwell<sup>4</sup>. Because of the trade-off between egg size and number, their model predicts the evolution of an optimal egg size that maximizes maternal fitness (product of number of offspring and their fitness), with mothers having the upper hand in this parent-offspring conflict. This potentially explains the existence of species experiencing massive mortality during juvenile stages, because offspring survival rates that maximize maternal fitness may be low compared with those maximizing offspring fitness. When considering the impact that the Smith-Fretwell model has had on aspects of life-history theory<sup>1,5–10</sup>, it is worrying that empirical support from highly fecund species is lacking. The general validity of the Smith-Fretwell model has previously been questioned on the basis of data from organisms producing few offspring<sup>12</sup>, and it has been criticized for being too simplistic<sup>11</sup>.

We therefore undertook an experimental field study using Atlantic salmon to test empirically whether maternal or offspring fitness is maximized in highly fecund species (egg numbers range from 1,791 to 18,847)<sup>15</sup>. Egg size was manipulated by rearing females to adulthood in captivity. This procedure resulted in some females producing highly variable egg sizes (mean coefficient of variation = 18.5%) relative to that found in the wild (4.0%; S.E. and I.A.F., unpublished data). A sample of small and large eggs from each of eight females was fertilized by one male, producing a total of eight pairs of full-sib groups. At the eyed stage, equal numbers of small and large eggs within a pair were buried in separate artificial gravel nests<sup>3</sup>, producing a total of 16 such nests. Small eggs were on average 31.4% lighter than their large siblings ((mean ± s.d.) small: 85.4 ± 15.1 mg; large: 125.4 ± 13.4 mg;  $t_7 = 6.06$ ,  $P = 0.001$ , paired samples  $t$ -test). The size separation within family groups was responsible for 69.2% of the total variation in egg size within the population, randomizing the effects of other maternal or genetic traits potentially correlated with egg size. Thus, this design allowed us to test for a causal relationship between egg size and offspring fitness<sup>16,17</sup>. It excluded the possible effects of interactions with other maternal traits that may cause the optimum egg size to vary among females within natural populations<sup>1,6,18</sup>. Juveniles emerging from the nests were released in a natural stream, and were sampled 28 and 107 d after median emergence to assess their success.

**Table 1 Selection on egg size for Atlantic salmon**

	$\beta$	$\beta'$	$P$	$\gamma$	$\gamma'$	$P$
Offspring survival	19.65 (5.05)	0.488 (0.126)	0.001	-573.8 (343.5)	-14.30 (8.54)	0.069
Maternal RS	14.43 (5.85)	0.358 (0.145)	0.009	-723.7 (305.5)	-18.02 (7.59)	0.023

Selection gradients relate relative offspring survival and maternal reproductive success (RS, proportion offspring survival × potential maternal fecundity) to egg size. Directional selection gradients (unstandardized,  $\beta$ ; standardized,  $\beta'$ ) are estimated from linear regression coefficients, and nonlinear (stabilizing) selection gradients (unstandardized,  $\gamma$ ; standardized,  $\gamma'$ ) are estimated from regression coefficients of squared deviations from the mean<sup>21</sup>. Standard errors are indicated in parentheses. Residuals from regressions between the traits and log-transformed fitness measures proved to be normally distributed, allowing parametric tests of significance<sup>21</sup>.

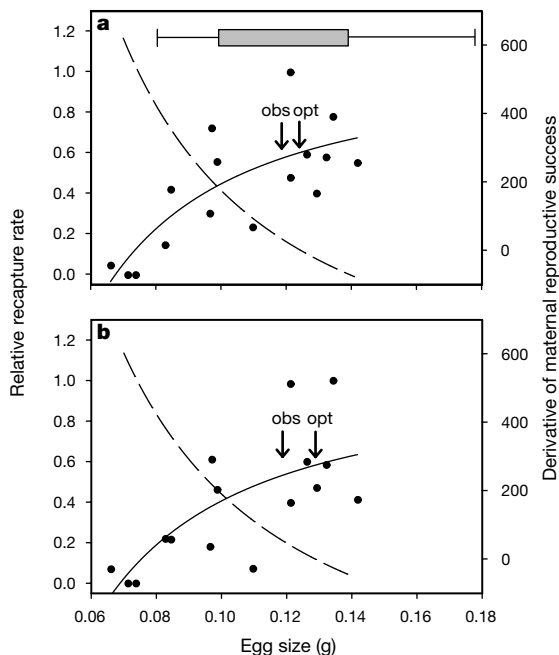
Egg size affected both timing of, and size at emergence from, gravel nests. Juveniles from small eggs emerged from the nests on average 3 d earlier than their siblings from large eggs ( $t_7 = 7.32$ ,  $P < 0.001$ , paired  $t$ -test). At this point, juveniles from small eggs weighed 33.1% less than their siblings from large eggs ((mean  $\pm$  s.d.) small:  $115.9 \pm 21.3$  mg; large:  $174.6 \pm 19.1$  mg;  $t_7 = 6.18$ ,  $P < 0.001$ ). At recapture, 28 and 107 d after median date of emergence from nests, there was still a strong positive effect of egg size on body size (first recapture: body weight =  $-0.02 g + 4.16 \times$  egg weight,  $r^2 = 0.81$ ,  $P < 0.001$ ; second recapture: body weight =  $0.82 g + 8.02 \times$  egg weight,  $r^2 = 0.43$ ,  $P = 0.011$ ). Thus, egg size had strong effects on traits closely linked with fitness<sup>2,3</sup>.

During the first period (0–28 d after median emergence) juveniles from large eggs experienced significantly higher survival, measured as proportion recaptured, than their siblings from small eggs ((mean proportion recaptured  $\pm$  s.d.); small:  $0.048 \pm 0.046$ ; large:  $0.145 \pm 0.043$ ;  $t_7 = 5.46$ ,  $P = 0.001$ , paired test). The same pattern also appeared when considering the effect of mortality within the stream alone, that is, removing those caught in the drift samples from the release numbers (small:  $0.059 \pm 0.054$ ; large:  $0.184 \pm 0.036$ ;  $t_7 = 5.39$ ,  $P = 0.001$ ), and when considering fish caught in drift samples as survivors (small:  $0.252 \pm 0.074$ ; large:  $0.363 \pm 0.105$ ;  $t_7 = 3.22$ ,  $P = 0.015$ ). Consistent with other results<sup>2</sup>, there was no additional effect of egg size on survival during the second period (28–107 d after median emergence,  $n = 14$ ,  $r = -0.12$ ,

$P = 0.690$ ). Thus, maternal traits appear to be most intensely shaped during early juvenile stages, and less so later on when expression of offspring genes may become more important for their success. The overall relation between egg size and proportion recaptured was best described by asymptotic regressions (Fig. 1).

Estimated selection gradients demonstrate strong directional selection towards larger egg size (Table 1). Furthermore, a significant negative quadratic term for maternal reproductive success suggests that selection acted directly to reduce the variance in egg size through stabilizing selection. We regard these results as a confirmation of the Smith–Fretwell model, legitimizing the use of its assumptions and predictions in development of other life-history models<sup>5–10</sup>. Moreover, there was a close fit between optimal and observed egg size (Fig. 1). This indicates that mean egg size in Atlantic salmon has evolved as a response to selection on maternal fitness.

When considering the strong phenotypic selection on egg size, one might expect this trait to be relatively invariable. Thus, large intrapopulation variation in egg size, commonly observed in a wide range of organisms<sup>1</sup> as well as in the study population (Fig. 1), raises an interesting evolutionary problem. Functional constraints on egg size caused by morphological features in certain taxa (for example reptiles) have been suggested to cause such variation<sup>12,14</sup>. Furthermore, several hypotheses explain intrapopulation variation in egg size as adaptive phenotypic plasticity caused by interactions between egg size and correlated maternal traits on offspring fitness<sup>1,6,18</sup>. Although the problem of intrapopulation variation can not be solved by traditional optimality models<sup>11</sup>, this does not imply that these models are incomplete as a means of predicting mean optimal egg size, as successfully shown here. Rather, further development of models and empirical work on evolution of reproductive traits will probably benefit from applying and extending the basic assumptions and predictions of these models. □



**Figure 1** Relation between egg size and relative recapture rate (scaled to a maximum of 1) of juvenile Atlantic salmon 28 (a) and 107 (b) days after median emergence from nests. Each data point represents mean values for one nest. The asymptotic functions (solid curves) relating offspring recapture rates to egg size ( $m$ ) are of the form  $F(m) = 1 - (m_{\min}/m)^a$ , where  $m_{\min}$  is the minimum viable egg size and  $a$  is a constant<sup>8</sup>. Dashed lines represent the derivative of the function relating maternal reproductive success to egg size (reproductive success =  $F(m)M/m$ ) given a total egg mass ( $M$ ) of 450 g (mean of the native population<sup>18</sup>). The derivative equals zero for the egg size that maximizes maternal reproductive success<sup>6</sup> (opt), assuming variation in total egg mass among females does not affect offspring survival (for example, the intensity of offspring sibling competition is unrelated to female fecundity<sup>9</sup>). Observed mean (obs), and standard deviation and range (box plot) of egg size of the native population<sup>18</sup> (adjusted for increase in size owing to absorption of water,  $16.4 \pm 3.4\%$ ,  $n = 23$  females; S.E. and I.A.F., unpublished data) are indicated.  $m_{\min} = 0.0676$  g,  $a = 1.5066$ ,  $r^2 = 0.59$ ,  $P < 0.001$  (a);  $m_{\min} = 0.0688$  g,  $a = 1.3950$ ,  $r^2 = 0.50$ ,  $P = 0.002$  (b).

Methods

The adults used originated from gametes obtained from wild fish of the study population. The resulting embryos were incubated in the hatchery and from the onset of exogenous feeding, the juveniles were reared in 2-m<sup>2</sup> indoor, flow tanks for three months. Thereafter, they were reared in 8-m<sup>2</sup> freshwater, outdoor tanks (density during maturation 350 fish (1 kg) per tank) under a natural light regime and fed commercial food *ad lib*. The resulting egg size variation was within the range observed in females in nature<sup>15</sup>. Such variability is probably related to the position of the egg relative to blood vessels in the female ovary during development<sup>19</sup>. The relative chemical composition (that is, percentage of water, protein and lipids) and weight-specific energy content of different sized eggs from females reared in this way has previously been found not to differ<sup>3</sup>. Furthermore, under favourable hatchery conditions offspring from small eggs performed as well as siblings from large eggs<sup>3</sup>. Thus, the obtained variability in egg size appears to be independent of genetic, or other characteristics of the oocytes themselves.

Juveniles emerging from the nests were anaesthetized, weighed ( $\pm 0.1$  mg), and group marked using alcian blue dye and adipose fin clips. They were then held for 24 h in an enclosure submerged in the stream Ålabekk (see ref. 20) to ensure recovery before being released. A total of 1,401 emerging juveniles were released, all at the same location. Losses from the population through migration were controlled by an inaccessible waterfall above and drift nets below the 140-m long experimental area. Body size and survival was assessed by sampling 28 d after median emergence, during which Ålabekk was electrofished five times. Juveniles were then re-marked and re-released, before being sampled again using the same procedure 107 d after median emergence. There were no indications that larger fish within the size range studied were easier to catch, as there were no significant differences in the size of fish captured on different days ((mean weight  $\pm$  s.d.) first period: day 1,  $0.42 \pm 0.14$ , day 2,  $0.48 \pm 0.10$ , day 3,  $0.47 \pm 0.07$ , day 4,  $0.46 \pm 0.08$ ,  $F_{3,132} = 1.55$ ,  $P = 0.204$ ; second period: day 1,  $1.80 \pm 0.55$ , day 2,  $1.64 \pm 0.47$ , day 3,  $2.09 \pm 0.00$ ,  $F_{2,82} = 0.86$ ,  $P = 0.427$ ; see also ref. 2).

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**Cortical ensemble activity increasingly predicts behaviour outcomes during learning of a motor task**

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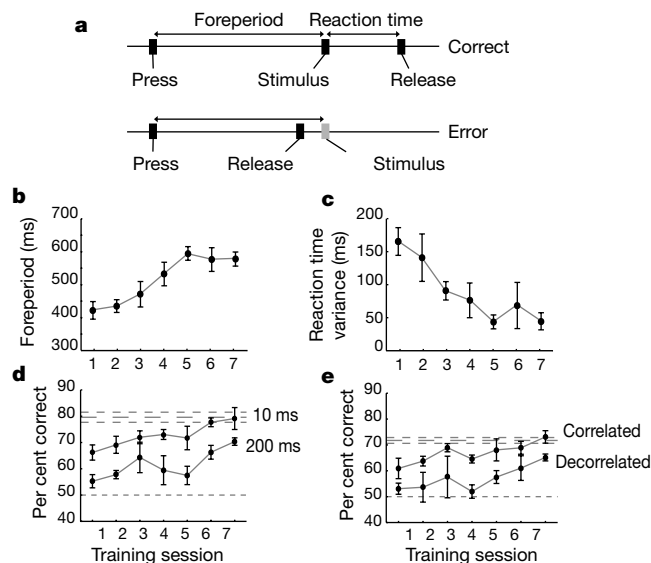
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When an animal learns to make movements in response to different stimuli, changes in activity in the motor cortex seem to accompany and underlie this learning<sup>1–6</sup>. The precise nature of modifications in cortical motor areas during the initial stages of motor learning, however, is largely unknown. Here we address this issue by chronically recording from neuronal ensembles located in the rat motor cortex, throughout the period required for rats to learn a reaction-time task. Motor learning was demonstrated by a decrease in the variance of the rats' reaction times and an increase in the time the animals were able to wait for a trigger stimulus. These behavioural changes were correlated with a significant increase in our ability to predict the correct or incorrect outcome of single trials based on three measures of neuronal ensemble activity: average firing rate, temporal patterns of firing, and correlated firing. This increase in prediction indicates that an association between sensory cues and movement

emerged in the motor cortex as the task was learned. Such modifications in cortical ensemble activity may be critical for the initial learning of motor tasks.

Traditional theories of cortical function propose that information in the central nervous system is represented primarily by the firing rate of single neurons<sup>7,8</sup>. Learning new motor contingencies should therefore primarily involve changes in the average firing of neurons located in sensorimotor cortical areas. Behaviourally relevant information can also be represented in temporal patterns of neuronal firing (on a ms scale) and correlated neuronal activity<sup>9–15</sup>. It is not known whether these other schemes of neuronal representation are significant in the physiological modifications associated with the initial learning of a motor task. To address this issue, we compared the potential contribution of three neuronal coding schemes (average firing rate, temporal patterns of firing, and correlated activity) for predicting the behavioural outcome of single trials throughout the period required for rats to learn a reaction-time task. We also compared concurrent neural ensemble and electromyography (EMG) recordings to establish that any increase in single trial prediction by ensemble activity was not due to differences in movements on the correct and error trials.

Rats were trained to perform a reaction-time task in which they were required to hold down a response lever throughout a variable interval (the foreperiod, 400–800 ms) and to release the lever in response to vibrotactile or auditory trigger stimuli with a short (< 1 s) reaction time (Fig. 1a). Correct trials occurred when the rats sustained the lever press until the presentation of the trigger stimuli and released the lever with a short reaction time. Error trials occurred when the rats released the lever before the trigger stimulus. During the first of week of training, the rats exhibited significant increases in the time they were able to wait for the trigger stimulus, from 422.3 ± 30.9 ms (day 1) to 577.8 ± 24.8 ms (day 7; repeated-measures analysis of variants (ANOVA): *P* < 10<sup>-4</sup>; Fig. 1b). Although the rats' reaction times during these sessions did not change (day 1: 320.8 ± 41.5 ms; day 7: 271.6 ± 32.9 ms;



**Figure 1** Improvements in behavioural performance paralleled increases in the neuronal predictions of trial outcomes. **a–c**, As the rats learned the task (**a**), they sustained lever presses over longer foreperiods (**b**) and exhibited decreased variance in their reaction times (**c**). **d**, Predictions of trial outcomes based on neuronal activity increased with training and, by day 6–7, achieved levels equal to those in fully trained rats (upper lines, mean ± s.e.m.). Chance discrimination was 50% (lower dashed line). Temporal patterns of firing (from smoothing over 10-ms intervals) predicted trial outcomes better than average firing rates (combined over 200 ms). Likewise, predictions based on correlated firing were significantly better than those based on decorrelated ensemble activity.