Commentary
Maternal stress, glucocorticoids, and the maternal/fetal match hypothesis
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Could maternal stress enhance offspring phenotype? Elevated blood glucocorticoids (GCs) are thought to redirect a parent towards self-maintenance, presumably enhancing survival over current reproductive success. But could elevated GCs increase survival rates for both mothers and offspring?

We’ve known for a decade or more that elevated maternal GCs can alter offspring phenotype. This in itself is exciting (in a mechanistic sense), as it represents a non-genetic maternal factor programming offspring phenotype, with changes lasting over the offspring’s lifetime (Seckl, 2004). Over the last decade, data from the biomedical literature overwhelmingly supports relationships between prenatal stress and long-term health disorders (for review see Viltart and Vanbesien-Mailliot, 2007). Across the other vertebrate classes, elevation of glucocorticoids in the mother during egg production reduces offspring growth, condition, and body size (Eriksen et al., 2006; Hayward and Wingfield, 2004; Meylan and Clobert, 2005; Saino et al., 2005).

However, evidence is mounting for an adaptive function of maternal stress. In 2004, Gluckman and Hanson proposed that maternal stress is a developmental cue to offspring, programming their future phenotype to better survive in harsh environmental conditions (assessed from the biomedical literature; Gluckman and Hanson, 2004). Hayward and Wingfield (2004) suggested an alternative view: maternal stress during development matches offspring need to maternal ability, ‘lessening the burden of parental care’ (from the comparative literature; Hayward and Wingfield, 2004). Gluckman and Hanson wrote of ‘matching’ between prenatal and postnatal environments to benefit the offspring, while Hayward and Wingfield indicated ‘matching’ between mother and offspring to benefit the mother.

For his PhD dissertation, Dr. Oliver Love examined both maternal and offspring aspects of the match hypothesis. Love focused on embryonic GC exposure as the mechanistic link between environmental factors and fetal growth/development. To test this hypothesis, Love and Williams elevated maternal GC levels during lay to create offspring that may expect to be raised in poor conditions (Figs. 1A,B; Love et al., 2005). Male offspring from ‘poor condition’ (GC elevated) mothers had lower hatch mass, slower growth rate, and lower mass at day 5 after hatch as compared to the males from ‘good condition’ mothers (Fig. 1C; Love et al., 2005); female offspring showed no differences between groups. The reduction in male offspring mass and growth rate should make feeding young less challenging; the data therefore suggest a link between chick need and maternal ability.

To directly test the maternal match hypothesis, Love clipped the wings of mothers to reduce their maternal ability, and looked at return rates of those mothers the next year (Love and Williams, in press). When clipped mothers raised broods programmed for good quality mothers, return rates were only ~12%. However, when similarly clipped mothers raised broods programmed for low quality environments, the maternal return rate was indistinguishable from control mothers raising control broods (~35%, Fig. 1D). Hence, matching offspring need to maternal ability benefits the mother through increased survival.

In this issue, Love and Williams examine the match hypothesis from the chick perspective (Love and Williams, 2008). Does prenatal stress alter chick physiology in a direction beneficial for the chick? Here, newly laid eggs were treated with GCs to create a yolk environment representative of a ‘poor condition’ mother; the authors then measured baseline and handling-induced GC levels during the nestling phase. Chicks hatched from GC treated eggs had significantly lower GC reactivity (the elevation in GCs measured in response to
handling and restraint stress, Fig. 1C). This reduction led to 30% less GC secreted over the 30 min restraint period. Is this reduction in stress reactivity adaptive for the chick? Love points out that chicks raised under conditions of unpredictable food delivery suppress their reactivity (from Kitaysky et al., 2005). He argues that low reactivity will benefit the chick, reducing the use of GCs and therefore reserving glucose levels when payoff is unpredictable. Here, low GC secretion is a ‘predictive adaptive response’ (Gluckman and Hanson, 2004), where poor maternal condition is a predictive cue of the severity of the postnatal environment, and low GC secretion is an adaptive response to that cue. Love uses these arguments to suggest that matching chick physiology to environmental/maternal quality will increase chick survival.

Results examining prenatal stress effects on offspring GC reactivity are mixed. In guinea pigs, maternal stress also reduces GC reactivity, but the effects are highly sex- (males) and stage- (early maternal treatment) specific (Lingas and Matthews, 2006). However, in quail, monkeys, female guinea pigs and the majority of rat studies, prenatal stress increases offspring GC reactivity (Hayward and Wingfield, 2004; reviewed in Kapoor et al., 2006; Weaver et al., 2004). Both Hayward and Wingfield, 2004 (quail) and Kapoor et al., 2006 (review) argue for an adaptive benefit to increased GC reactivity: they suggest that the increase is adaptive in that it may enhance fear or vigilance behaviors in offspring expecting a hostile environment. Hence, there are arguments for both decreased and increased GC reactivity representing predictive adaptive responses.

Do I buy Love’s argument that reduced GC reactivity increases offspring survival in unpredictable environments (Fig. 1D)? Not quite yet. In stress physiology work, there is a large gap in knowledge between GC secretion and expected fitness benefits (Breuner et al., in press). Low GC reactivity may very well increase survival in unpredictable environments, but the predicted fitness benefits have not yet been tested.

Love and Williams continue to publish impressive work. This paper maintains the same strong experimental approach of their previous work. Field physiology work commonly tests only 16 to 20 animals. For this study, Love monitored 68 nests, checking each often enough to inject eggs within 3 h of lay. Through this exceptional field work, Love has taken an evolutionary approach to stress physiology, answering questions that previously were limited to lab studies. The incorporation of the ecological relevance to these questions is invaluable.

In summary, most evidence remain firmly on the side of glucocorticoids promoting survival at cost to current reproduction. However, it would behoove those of us in this field to remember that glucocorticoids may match offspring phenotype to environmental limitations, benefiting the current reproductive effort as well as parental survival.
References


