THE ADAPTIVE ROLE OF MATERNAL STRESS

Dr Michael J Sheriff of Pennsylvania State University outlines how maternal stress may adaptively prepare offspring, increasing their future performance and fitness

Medical practitioners and evolutionary biologists are investing great effort into determining the role of maternal stress as a significant inducer of transgenerational phenotypic plasticity in offspring. Given the significant influence of the biomedical literature, many of the phenotypic responses in offspring to maternal stress have been viewed as unavoidable negative outcomes (e.g. small birth weight or high anxiety) that are assumed to reduce fitness. However, since these studies are not designed to recognise, or experimentally test, the evolutionary history and ecological relevance of the maternal stress-offspring phenotype relationship, they offer a biased underestimate of the potential advantages of maternal stress-induced phenotypic plasticity. Recently, integrative ecologists have proposed that maternal stress may play adaptive roles across a wide variety of taxa if stress-induced phenotypes better prepare offspring for a stressful postnatal environment. This 'adaptive hypothesis' challenges the traditional negative-outcome perspective, and evidence to support this hypothesis is accumulating.

The mechanisms of maternal stress effects

Maternal stress can alter the morphology, physiology, and behaviour of the offspring, i.e. the offspring's phenotype. The mechanisms by which offspring phenotype is shaped by maternal stress can act both pre- and postnatally, depending on whether the animal is egg-laying or placental, and the amount of subsequent parental care. In egg-laying species, discrete and finite levels of maternally derived stress hormones (glucocorticoids) are deposited into eggs as a function of the relative stressfulness of the mother during egg production. In placental species, offspring exposure to maternal stress can fluctuate throughout pregnancy, producing a dynamic exposure over time. Laboratory studies have shown that this exposure to maternal stress during embryonic development causes changes in methylation patterns (i.e. epigenetic changes that increase or decrease gene transcription) throughout the offspring genome. In addition to direct exposure to maternal stress hormones, offspring phenotype may be indirectly influenced by stress-induced changes to maternal behaviour, condition, and physiology (beyond just GC levels). Ultimately, the mechanisms driving maternal stress effects are likely a combination of direct and indirect offspring exposure to maternal stress.

Dr Michael J Sheriff

Evaluating the role of maternal stress

Determining whether maternal stress is adaptive or maladaptive requires the consideration of a number of critical points. First, we must appreciate that the value of the offspring's phenotype, whether stress-induced or not, can be understood only by examining performance or fitness in an ecologically relevant context (and not simply assuming the quality based on the phenotype alone). Thus, the past, present, and future environments that mothers and their offspring are likely to experience must be considered, given the fitness of offspring will depend upon the future environments they are likely to interact with. Second, we must consider the evolutionary and life history context of the organism before experiments can be designed to test phenotype-performance relationships, given that their life history will influence how maternal stress-induced signals shape offspring phenotypic change. Third, we must appreciate that testing phenotypic performance in a singular postnatal environment (most often a benign non-stressful environment) is invalid for determining the role of maternal stress. This is of particular importance given that there are likely very different costs/benefits associated with offspring phenotypic performance and fitness depending upon whether or not the future environment matches that of the one the mother experienced.

To test the adaptive potential of maternal stress and tackle the complex relationship between maternal stress and offspring phenotype Sheriff's research group uses an interdisciplinary approach that combines the fields of physiology, ecology, neurobiology, and evolution. They use both standard and state-of-the-art techniques, including radioimmunoassays and respirometry, to measure physiological changes, electron microscopy to measure changes in the neurophysiology of the brain, behavioural analyses to test maternal behaviour and offspring performance, and survival estimates to test offspring fitness. Sheriff's research group examines each stage across the maternal stress-offspring phenotype relationship. As such, their research focuses on: 1) how ecological stressors alter maternal stress and how this in turn affects

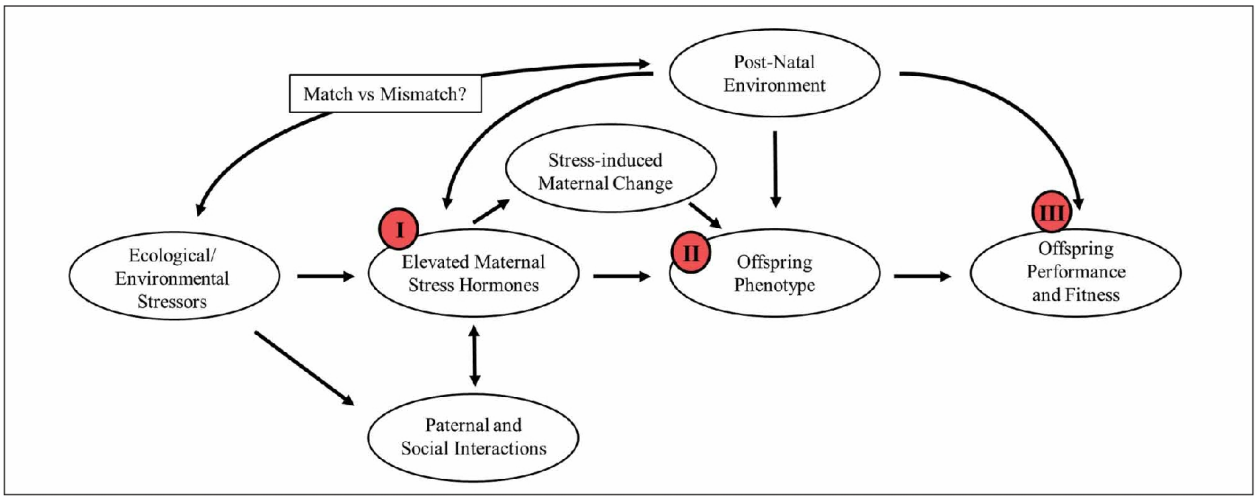

Fig. 1 The complex pathway of how an ecological/environmental stressor experienced by the mother can alter her offspring's phenotype via changes in her stress hormone levels, with implications for offspring performance and fitness. To better understand the maternal stress-offspring phenotype relationship it is important to appreciate 1) the interaction between the mother and her environment, and what salient stressor may she be responding to; 2) the mechanisms, in addition to maternal stress hormones, that may alter offspring phenotype and the specificity of the phenotypic response; and 3) the performance and fitness value of a given phenotype across both stressful and non-stressful future environments (i.e. environments that match and are mismatched with those the mother experienced during pregnancy). (Figure adapted from Sheriff et al. *2017,* Integrative and Comparative Biology: *doi:org.10.1093/icb/icx105)*

maternal behaviour and care, as well as maternal physiology (other than stress hormones), including metabolic rate, and nutrient and hormone (e.g. testosterone) allocation to the developing offspring; 2) how this in turn affects offspring phenotype, including morphology (e.g. size, weight, growth rate), physiology (e.g. stress and sex hormones, metabolic rate), and behaviour (e.g. foraging, vigilance, etc.) at birth and at different time points in the offspring's life; and 3) the relative performance and fitness of offspring with stress-induced phenotypes and non-stress phenotypes across both stressful and non-stressful natural environments. They combine both field observations and laboratory experiments using wild or wild-caught animals, across a range of taxa from snowshoe hares to eastern fence lizards, which, importantly, maintain their evolutionary history and relationship with their natural environment.

Future directions

The study of how maternal stress shapes offspring phenotype has intensified over the past decade, and a shift from viewing maternal stress as a unanimous cost to mothers and offspring is beginning to give way to an appreciation that altered offspring phenotypes have the potential to perform better under certain future environmental circumstances. Nevertheless, this new perspective is still in its infancy with much to be developed theoretically and tested empirically. Sheriff's research group will continue to broadly test the adaptive potential of maternal stress to better understand its role in natural systems with a focus on:

1) Understanding the gamut of mechanisms of how maternal stress may alter offspring phenotype, from maternal stress hormones to postnatal maternal care;

2) Understanding the specificity of the maternal stress-offspring phenotype relationship, i.e. can offspring modulate their phenotypic response to maternal stress specific to a particular stressor that the mother experiences? For example, do offspring have a different phenotype if the mother experiences predation risk from an owl as opposed to from a snake?;

3) Understanding offspring performance and fitness outcomes under real-life, natural conditions to adequately assess the adaptive potential of stress-induced phenotypes immediately upon birth but also at adulthood; and

4) Understanding how evolved maternal stress-offspring phenotype relationships may either limit or enhance an animal's ability to cope with and respond to novel, human-induced ecological or environmental stressors (e.g. tourism, invasive species, changes in seasonality, noise pollution, etc.).

Sheriff argues that critical in understanding the maternal stress-offspring phenotype relationship is that we integrate across biological disciplines from physiology to ecology and evolution, to investigate and test the adaptive potential of maternal stress in naturally occurring systems.

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