Born to cope with stress

When a mother experiences stress, the prevailing view is that this is detrimental to the life chances of her offspring. But **Dr Michael Sheriff**, of Penn State University, challenges this paradigm. His research on wild animals suggests that mothers experiencing natural stress may be preparing their offspring to survive and thrive under those conditions.

There is a growing body of research suggesting that animals are influenced not just by their genes and environment (nature and nurture) but also by the circumstances their mother experienced before they were even born. Studies on a wide diversity of vertebrates (from fish to mammals) and even insects have shown that exposure to maternal stress hormones can permanently alter a youngster's size, growth, physiology, and behaviour. But how can stress be transferred from mother to young? Is the impact positive or negative? And how are human activities impacting on the process?

RESPONDING TO STRESS

Animals respond to stressful experiences by releasing hormones known as 'glucocorticoids', which stimulate a behavioural response to maximise their chances of survival, such as spending more time scanning for predators. The pathway of glucocorticoid release, which involves the hypothalamus, pituitary, and adrenal glands, is found in all vertebrates, indicating its importance to survival.

Studies have shown that stressors such as predation and lack of food both increase glucocorticoid production in mammals, birds, and fish. Even more subtle stressors, such as position in a social hierarchy, can impact upon hormone levels, as documented in animals from lizards to starlings. Recent studies have also shown that human impacts, such as destruction or degradation of a species' habitat, and the effects of climate change, can increase glucocorticoid levels in wild animals.

However, for breeding mothers, the behaviours induced by stress hormones may impact her young, to a positive or negative effect. For instance, they might cause her to spend less time on crucial activities such as incubating eggs or feeding her young. However, it is now becoming increasingly apparent that glucocorticoids themselves may also cause physiological changes in a mother's offspring: in snowshoe hares, the young of stressed mothers tend to be smaller, have higher levels of stress hormones themselves, and display naturally anti-predator behaviours even in the absence of predators.

So, can glucocorticoids – either directly or through altering a mother's behaviour – actually impact the survival of offspring, and is this for better or worse? Dr Sheriff notes that 'we still lack a testable quantitative framework to assess these costs and

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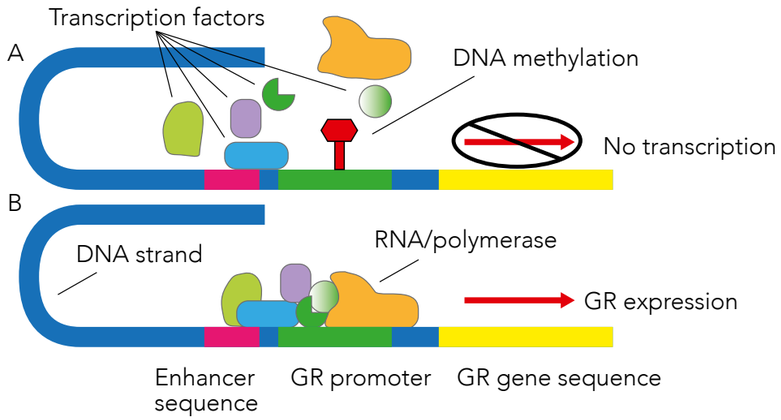

Maternal stress may prime offspring for their future environment through epigenetic changes in their DNA. (A) offspring from a stressed mother may have greater DNA methylation, reducing glucocorticoid receptor (GR) expression, (B) while offspring from unstressed mothers may have lower DNA methylation and greater GR expression (figure adapted from Love et al. 2013, Functional Ecology)

benefits'. His research aims to explore the question in a holistic way: from the environmental context through to changes in offspring physiology and behaviour and how these individual changes affect the dynamics of the whole population.

BE PREPARED

Young vertebrates entering the world for the first time are at their most vulnerable. But Dr Sheriff believes that glucocorticoids produced by the mother may shift the odds in favour of their survival and success, preparing them physically, physiologically, and behaviourally for stress they may encounter in their immediate or distant future.

So how exactly can stress hormones in adult animals affect their offspring? Normal levels of glucocorticoids are essential for brain development, and altered levels can have permanent effects on the structure and function of the developing brain, including the hippocampus, amygdala, hypothalamus, pituitary, and adrenal glands responsible for stress hormone production. Thus, exposure to elevated glucocorticoid levels during early development can cause animals to produce more glucocorticoids of their own. Laboratory studies have even shown that prenatal stress can affect the way genes are activated and deactivated in the brain and throughout the body, with effects lasting long into adulthood.

In this way, maternal stress primes a mother's offspring physiologically for the environment they are to experience as adults – as long as that environment remains unchanged. Dr Sheriff calls this the 'environmental-match hypothesis'. The effect can be beneficial in a stable environment, where the stress experienced by offspring matches that experienced by their mother. However, it could be counterproductive where the stresses change markedly from generation to generation, for instance in a rapidly-changing environment – such as one subject to high levels of human impact. This can lead to what Sheriff terms 'evolutionary traps', where mothers effectively misjudge the stresses to which their offspring will be subjected.

This has also been observed in animals that experience cyclical population expansion and contraction, such as snowshoe hares. Dr Sheriff is now working to develop a quantitative framework – based in Error Management Theory – that allows field-testing of the relative fitness of animals depending on whether their environment is matched or mismatched to their mother's in terms of stress.

Glucocorticoids produced by a mother may shift the odds in favour of her offspring's survival and success

Q&A

How did you come up with the idea that maternal stress might be a good thing in terms of pre-programming offspring to survive in a stressful environment?

This idea builds on a great deal of previous work, but ultimately the consistent finding across vertebrate taxa that maternal stress alters offspring phenotype, means that this effect has been conserved over evolutionary time. This means that this ability had to be adaptive. Critical in our assessment of the adaptive potential of this effect is an understanding of the particular life history and salient selection pressures that have shaped the evolution of an organism's stress (hypothalamic-pituitary-adrenal) axis.

How much do we know about the molecular-genetic mechanisms underpinning this pre-programming? How much have we got left to learn?

We know extremely little, and the study of the underpinning mechanisms is in its infancy.

Why did you choose lizards as a species to test your hypothesis?

The eastern fence lizard – fire ant system has been studied by Dr Tracy Langkilde for over a decade – I came very late to this system. She has shown some fascinating aspects of how fence lizards have responded to the relatively recent invasion by fire ants through their stress physiology and behavioural responses. She has shown that fire ants increase maternal stress levels and that offspring from invaded sites have different behaviours than those from uninvaded sites. Building on these findings Dr Langkilde and I thought that it would be an ideal system in which to test the adaptive potential of maternal stress. Here, we had a very well-studied system in which we could manipulate maternal stress hormone levels in an ecologically relevant manner, measure offspring phenotypic responses (changes in offspring morphology, physiology, and behaviour), and then test if these altered phenotypes survived better in fire ant-invaded sites.

What have you found so far in your project on the eastern fence lizards?

We are only two years into this project, but have some very exciting results we hope to publish shortly. Kirsty MacLeod, a post-doctoral fellow, has shown that in a mother repeatedly stressed by hormone exposure in the lab had lower survival and reproduction. Thus, although elevated stress hormone levels may greatly increase immediate survival when facing a predator-stressor, over time this reduces individual fitness. David Ensminger, a PhD student, has found that elevated maternal stress hormones altered the hormonal and nutrient allocation to eggs, which in turn, resulted in altered offspring morphology, physiology, and behaviour. Interestingly, this phenotype seems to provide a baseline-type antipredator defence best suited for birds (the lizard's other major predator), but a response-type antipredator defence best suited for fire ants. Lastly, Dustin Owen, a PhD student, has found that maternal stress elevates embryonic heart rate and potentially metabolic rate. This may lead to faster hatching, allowing offspring to spend less time in the egg (a very vulnerable time when exposed to fire ant predation). During this summer we will test for maternal stress effects on offspring neurobiology, metabolic rate, and ultimately their survival.

How can maternal stress effects alter the ability of animals to cope with and respond to human-induced changes to their environment?

I think two different scenarios may play out. The first is that maternal stress effects will lead to evolutionary traps – when an animal's normally adaptive response becomes maladaptive, and this leads to their decline. This could occur in two ways: first, mothers could fail to respond to novel stressors, thus resulting in an unaltered offspring phenotype when necessary, or, second, mothers may perceive unstressful factors (e.g., tourism) as stressful, responding inappropriately and unnecessarily altering offspring phenotypes. Both maternal responses are likely to reduce maternal and offspring fitness.

Alternatively, if the humans increase the magnitude or direction of a maternal stress response that is already there, it may allow a rapid and adaptive response. For example, if humans introduce a novel predator that greatly increases predation pressure, maternal stress effects may allow prey in the area to respond and cope with the novel predator if it has a similar hunting style to their current predators.

VIEW FROM THE FENCE

While most studies of maternal stress effects are lab-based, Dr Sheriff's research focuses on wild animal populations. His current project, with Dr Tracy Langkilde (also of Penn State University) involves the US eastern fence lizard. Funded by the National Science Foundation, the project aims to test the hypothesis that maternal stress effects predispose offspring to survive future stressful conditions.

The eastern fence lizard provides a unique opportunity to compare mothers and their young in stressful and stress-free conditions. Some populations of the lizards are regularly threatened by the predatory fire ant – an invasive species that threatens the survival of many vertebrates in the US – and others are not. Partnering with local schools and youth groups, Drs Sheriff and Langkilde will measure and manipulate glucocorticoids in lizard mothers and their eggs. They will then release young that have experienced high or low levels of hormones into stressful and stress-free environments (i.e., sites with and without fire ants), and measure levels of survival. Thus, they will test whether prenatal stress prepares the lizards to survive in a stressful environment.

This is one of the few studies to examine the effects of maternal stress on offspring in a wild animal. Dr Sheriff hopes his research will bring these effects to the attention of ecologists and evolutionary biologists, to encourage further testing of the concept in a wide range of animal species, and he insists, 'to emphasise the importance of the ecological and evolutionary context'. If he is proved right, the prevailing view of maternal stress as harmful may just be turned on its head.

Detail

RESEARCH OBJECTIVES

Dr Sheriff's research interests fall broadly on how ecological stressors (too many predators or competitors, not enough food, etc.,) can influence the physiology and behaviour of free-living animals, how this affects their survival and reproductive success, and ultimately scales from the individual to impact population and community dynamics. He addresses one of the fundamental questions in biology: what limits and regulates animals in their natural world?

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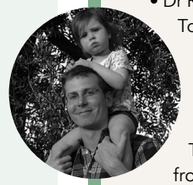
COLLABORATORS

- Dr Oliver Love (University of Windsor)
- Dr Tracy Langkilde (Pennsylvania State University)
- Dr Rudy Boonstra (University of Toronto)



BIO

Dr Michael Sheriff received his BSc from the University of Toronto (2005), and his PhD from the University of British Columbia (2010). He held an NSERC post-doctoral fellowship at the University of Alaska Fairbanks. He is an assistant professor at the Pennsylvania State University. His research focuses on the mechanisms that limit and regulate animal populations in the natural world.

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