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Special Issue

The comparative biology of environmental stress: behavioural endocrinology and variation in ability to cope with novel, changing environments

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Coping with perturbations of the environment such as severe storms and other climatic extremes, habitat degradation, changes in predator numbers, invasive species and social disruption is one of the most essential physiological and behavioural processes. The palaeontological record shows that organisms have had to cope with environmental perturbations throughout the history of life on Earth. These ancient processes show highly conserved mechanisms, but also great flexibility in responses to social and physical environment challenges. Adrenocortical responses to perturbations can trigger a coping response called the emergency life history stage (EHLS). However, if the adaptive value of the ELHS declines because of trade-offs with other life history stages such as breeding, then the adrenocortical response to acute perturbations (stress) can be modulated. Mechanisms involve allostasis and reactive scope with three foci of regulation: hormone secretion, transport and response. It is now well known that modulation of the adrenocortical responses to perturbations occur through gene–environment interactions during development and throughout the life cycle. These modulations involve individual differences in gender, age, experience and condition as well as latitudinal, altitudinal and hemispheric variations. Dramatic consequences of human-induced rapid environmental change such as increasing frequency and intensity of environmental perturbations will likely have implications for continued adaptation to extreme events. Note that modulation of the stress response also involves three major processes: modulation of robustness (i.e. become more resistant to acute stress); modulation of responsiveness (i.e. modulate the actual response to stress for more flexibility); and modulation of resilience (i.e. how quickly and completely the recovery is after the perturbation has passed). Mechanisms underlying these modulations remain largely unexplored.

How organisms respond to a changing environment is an emerging problem that is becoming a greater focus of basic research, especially in the light of global change (reviewed in Visser 2008; reviewed in this issue: Sih 2013; Slabbekoorn 2013; Sol et al. 2013). In recent years the occurrence of natural disasters and extreme weather events has increased. In North America, in 2012 alone, we have seen severe tornadoes, floods, drought, extreme heat and cold, dust storms and hurricanes. Although planet Earth has undergone dramatic changes in climatic, biological and geophysical conditions repeatedly in the past, these have occurred over time spans of millions, not tens, of years, allowing evolution of mechanisms by which organisms respond to environmental change such as seasons, day night cycles, high tide/low tide, and so forth (e.g. Wingfield 2008a, b). Geological strata and fossil evidence indicate that seasonality is ancient, and unpredictable events, perturbations of environment were probably frequent. In the early Cambrian, evidence indicates minor local and short-lived perturbations in fossils revealed by sediment movements of organisms probably affected the life cycles of these organisms (Babcock et al. 2001).

To address the issues of how organisms respond to and cope with environmental change at all levels, key questions include: how do organisms organize their life cycles, the time components of those cycles and synchronize them with other individuals in a predictable environment (e.g. seasons)? It is well known that organisms respond to internal cues (classical homeostasis) and external cues from both the physical and the social environments. These interact to regulate changes in morphology, physiology and behaviour in complex ways, which affect the evolution of mechanisms that allow individuals to cope with a changing world (e.g. Huey et al. 2003; Duckworth 2009). Superimposed on these systems are facultative responses to unpredictable events in the environment (i.e. perturbations).

The frequency of severe climatic events such as floods, droughts, storms, heat waves and cold spells has increased dramatically in the

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past 50 years, and to a lesser extent, the intensity of these events has also been enhanced (Easterling et al. 2000; Benison & Stephenson 2004). At least 725 000 humans died and economic losses of more than $700 billion have accrued during this period (Benison & Stephenson 2004). In north temperate regions such as England, average temperature shifts as small as 1–2 °C can result in an increase in the frequency of summer heat events from once every 75 years to once every 3 years (1.3–33%, Munich Re Group 2003; also see Francis & Hengeveld 1998). In France, lower temperatures overnight for many years have been accompanied by increased frequency of hail storms and severe thunderstorms (Dessens 1995; Francis & Hengeveld 1998). Moreover, warmer temperatures in the U.S.A. can bring heavier precipitation in many areas (Gordon et al. 1992; Francis & Hengeveld 1998). In other words, what we have called the '100-year storm' is occurring more and more frequently. What toll of animal losses and destruction of environment also occurs during these events is not well known, but climate-induced extinctions of plants and animals are increasing (Easterling et al. 2000; Meehl et al. 2000), including losses following extreme perturbations of the environment (Wingfield et al. 2011a, b). How populations cope with increasing frequency and intensity of perturbations of the environment, and how some then rebound from these events is only just beginning to be explored (Wingfield et al. 2011a, b).

To understand why and how organisms cope with a capricious environment requires an analysis of what is happening in the field and how the physical and social environments might exert their effects. For example, there is no single definition of what an extreme event is. Therefore, a review of what is known about the characteristics of environmental perturbations will be useful. Benison & Stephenson (2004) suggested criteria for evaluation of extreme events and their occurrences as follows.

(1) How rare are they? This requires some way to document their frequency.

(2) How intense are they? What is the threshold for this?

(3) What impacts do they exert on environments and organisms in them that might influence recovery and subsequent life histories?

Problems can arise when comparing extreme conditions in different locations (Francis & Hengeveld 1998; Benison & Stephenson 2004). For example, wind extremes on the open ocean generally do not have as severe an impact on pelagic organisms as do wind extremes on plants and animals in a tropical forest. Similarly, cold extremes in a dry tropical forest may be more destructive to life than those in a high-latitude boreal forest. Furthermore, we cannot assume that each individual in a given locality experiences extreme conditions in the same way because of differences in territory quality, food supply, social dominance, infection, and so forth (Wingfield et al. 2011a, b). This raises a critical issue at a mechanistic level that has not been fully appreciated until recently. The concept of the 'exposome' is potentially very useful to assess not only what the perturbations might be, but how they also might interact through the life cycle of an individual. The exposome is the spectrum and cumulative effects of all environmental exposures from conception to death (Wild 2005). It is a highly variable and dynamic entity that evolves throughout life and is completely unique to an individual. One can also imagine both good and bad components of the exposome that interact (Wild 2005; Smith & Rappaport 2010). The external exposome involves the physical environment, abiotic and biotic, whereas the social exposome includes agonistic and affiliative interactions, and social status. The internal exposome addresses issues such as homeostatic damage and responses of heat shock proteins, DNA repair, mitigation of oxidative damage, pollutants, infection, ageing, injury, et cetera, that are important components of overall coping systems. Because the exposome is different for each individual, it will be important to be able to estimate it during the life cycle of that individual. To do this, or even obtain a vague estimate, it is critical to analyse what the components of the exposome might be. The potential spectrum of environmental factors affecting life cycles have been reviewed many times (e.g. for examples from many different perspectives, see Wingfield 2008a, b), including both the predictable life cycle (daily, tidal, seasonal routines, etc.) and the unpredictable environment and perturbations. All of these are part of the exposome, but how to measure it empirically is a major challenge for the future. None the less, some estimate of the exposome at the individual level, along with assessment of habitat quality in which the individual finds itself, will provide essential insight into how and why organisms vary in their responses to the environment. Hereon the focus will be on the unpredictable components of the exposome.

LABILE PERTURBATION FACTORS (LPFS), OR 'MODIFYING FACTORS'

Perturbations of the environment happen in many ways that are important to understand because of the implications for response mechanisms. Some are transient (labile) and others may be longer term (more permanent such as climatic events, human disturbance), but all require varying degrees of acclimation in the short term. From the perspective of the exposome there are two major types of labile perturbations (from Wingfield et al. 2011a, b).

Indirect (Reactive Responses)

The individual responds immediately to a sudden threat including the rapid fight-or-flight response in which the adrenal medulla cells release epinephrine within seconds, followed by an increase in glucocorticoid secretion from the adrenal cortical cells (e.g. Wingfield et al. 1998; Sapolsky et al. 2000). These secretions constitute the classic stress response and trigger immediate behavioural traits to avoid the perturbation as well as to mobilize energy to fuel coping strategies. The perturbation may be over in seconds and probably does not contribute significantly to longer-term energy costs (assuming the individual survives). Examples are: loss of mate or offspring to a predator; brief chase by a predator; psycho-social stress (dominant attack, bullying, etc.); sudden severe storm (e.g. tornado, thunderstorm); fire; flood from rain that fell many kilometres away (e.g. Okavango Delta, desert stream beds (arroyos or wadis)); earthquakes; tsunamis; volcanic eruption; accident (e.g. running from a falling rock or tree). Because the perturbation is brief, an individual that survives does not incur any detriment such as loss of body condition. The normal life history stage can continue within minutes to hours, and for this reason, the labile perturbation factor can be termed indirect.

Direct (Allostatic Responses)

Longer-term perturbations of the environment that are still labile, but may be prevalent over hours or even a few days, force an individual to abandon its normal life history stage (e.g. interrupt breeding or migration) because of reduced or restricted access to resources such as food or shelter. Examples of these factors are: prolonged storms or temporary climate change (e.g. El Niño Southern Oscillation Event); infection; injury; change in social status; predator density (i.e. longer-term risk); hypoxia; and repeated acute stressors. A more detailed analysis of these factors can be found in Wingfield (2012a). Note that, unlike indirect factors, direct factors are not immediately life threatening. However, deteriorating conditions mean reduced food intake and/or greater