

Review



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How birds cope physiologically and behaviourally with extreme climatic events

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As global climate change progresses, the occurrence of potentially disruptive climatic events such as storms are increasing in frequency, duration and intensity resulting in higher mortality and reduced reproductive success. What constitutes an extreme climatic event? First we point out that extreme climatic events in biological contexts can occur in any environment. Focusing on field and laboratory data on wild birds we propose a mechanistic approach to defining and investigating what extreme climatic events are and how animals cope with them at physiological and behavioural levels. The life cycle of birds is made up of life-history stages such as migration, breeding and moult that evolved to match a range of environmental conditions an individual might expect during the year. When environmental conditions deteriorate and deviate from the expected range then the individual must trigger coping mechanisms (emergency life-history stage) that will disrupt the temporal progression of life-history stages, but enhance survival. Using the framework of allostasis, we argue that an extreme climatic event in biological contexts can be defined as when the cumulative resources available to an individual are exceeded by the sum of its energetic costs—a state called allostatic overload. This allostatic overload triggers the emergency life-history stage that temporarily allows the individual to cease regular activities in an attempt to survive extreme conditions. We propose that glucocorticoid hormones play a major role in orchestrating coping mechanisms and are critical for enduring extreme climatic events.

This article is part of the themed issue 'Behavioural, ecological and evolutionary responses to extreme climatic events'.

1. Introduction

Organisms have evolved to match behaviour and physiology to the predictable environmental variation in their particular habitats. In order to maximize fitness, most organisms express different life-history stages (e.g. breeding, migration, moult) that modify morphology, physiology and behaviour across time to optimize performance. To time the expression of each life-history stage appropriately, organisms rely on environmental cues that signal predictable changes in conditions such as seasons, day/night, low tide/high tide, etc. (e.g. [1–5]). Thus, animals avoid the overlapping of life-history stages that are energetically expensive and could affect fitness negatively.

Even though many organisms have evolved adaptations for predictable environmental variation, unexpected events creating an unanticipated environment can have negative impacts on the organism (environmental perturbations). Such changes may include deterioration in habitat quality, increased incidence of injury/disease, shifts in predation pressure, anthropogenic changes and disruptive weather events. Here we focus primarily on climatic perturbations of the environment that are especially relevant given that the incidence of catastrophic weather events such as floods, droughts, storms, heatwaves and cold spells have

risen in frequency almost 10-fold in the past 50 years [6]. Furthermore, there has also been an increase in duration and intensity of such events in recent decades attributed to climate change (e.g. [7], see also [8,9] in this issue for a broad discussion of definitions and terminology).

2. Definition of an extreme climatic event

Efforts to study 'extreme climatic events' have been stymied by lack of a consistent and broadly applicable definition [8,9]. One reason for this difficulty is that concepts of 'extreme' must be appropriate for the organism or biological systems under study and unbiased by the perspective of the scientists developing them [10–13]. At present two major definitions have been used. First, the climatological definition uses a frequency distribution of climatic events and designates conditions falling within an arbitrary percentage region (often 5%) at either end of the distribution as extreme [10–12]. The second, but far less frequently used type, addresses environmental conditions that become sufficiently harsh to elicit population- and individual-based biological responses. These types of reactions have included changes in mortality rates, reproductive success, morphology and physiology, though no consistent set of criteria has emerged [10–14]. Caution is needed, however, because biological definitions of extreme climatic events cannot distinguish other negative climatic events that may not fall within the extreme 5% margins defined by climatologists [10]. This means that biological definitions may identify more events as extreme than climatological or, alternatively, that extreme events under a biological definition may not appear to be so if they do not conform to the climatological definition.

Extreme climatic events vary in frequency, intensity and duration. For instance, long-term extreme climatic events (termed compound events [9]) can last from weeks to months such as the extreme cold spell in the spring of 2013 in North America and Europe, and a strong El Niño Southern Oscillation event, or they can be short-term such as a hurricane or tornado (termed simple events [9]). What constitutes an extreme climatic event is highly variable across environments. For example, an accumulation of 20 cm of snow in western Washington State, USA, would represent an extreme event whereas the same snowfall would merely be an inconvenience in Montreal, Canada. Similarly, a 20 m per second wind over the open ocean would be a routine event, but would likely be extreme in a forest [14,15]. Extreme climatic events impact both plants and animals which may result in population declines as well as changes in distribution and phenology. This ultimately leads to the evolution of regulatory mechanisms as individuals adjust to a changing climate and the occurrence of extreme climatic events. While biological definitions of extreme climatic events can emphasize population level and individual responses that are very important [14–17], until recent years there have been very few studies that have addressed the underlying physiological and behavioural mechanisms down to cell and molecular levels.

3. Variation in what constitutes an extreme climatic event for an individual

While a climatological definition is intuitively appealing and a useful categorization in many respects, we wish to make the

case for a biological definition of extreme climatic events because some individuals in a population may perceive an event as extreme and others may not. A climatological definition does not account for variation in how an event is experienced by the individual organism that may experience such events differently from another. Combinations of factors, biotic and abiotic, predictable and unpredictable will determine how extreme the event may be [18,19]. These factors, in turn, have variable effects on organisms depending on body condition, history of disease, social status, life-history stage (e.g. breeding versus wintering), or even 'carry-over' effects from prior events [20,21]. Furthermore, climatological definitions of extreme events that are limited to a percentage window may fail to capture the full range of extreme climatic events on biological processes. As the climate changes, events that fall within a window of extremes will shift, representing a greater percentage of observed weather. However, organisms may not have changed in their ability to cope with such conditions and thus the window may no longer adequately describe the full range of conditions that constitute an extreme event. We argue that organism responses to extreme climatic events, including susceptibility and resilience, cannot be predicted solely by climatic definitions. To illustrate this point, we present a series of case studies below that highlight the diversity of responses to extreme climatic events across environments.

4. Case studies: Arctic-breeding songbirds, species level variation in responses to extreme spring weather

The Arctic is undergoing rapid changes in temperature and snow-melt dates [22,23]. Here we examine responses of two Arctic-breeding migratory songbirds the Lapland longspur, *Calcarius lapponicus*, and Gambel's white-crowned sparrow, *Zonotrichia leucophrys gambelii* to 'extreme' conditions in spring of 2013 on the North Slope of Alaska. This period featured record low temperatures and persistent snow cover throughout the Northern Hemisphere extending into the late spring during the migration and breeding periods [24,25]. Arrival dates for white-crowned sparrows and Lapland longspurs were markedly delayed, which is likely the case for most migrants in that year [24]. These extreme conditions resulted in reduced body condition in both Lapland longspurs and white-crowned sparrows as they arrived on the breeding grounds [24].

In addition to cold springs, shifts in climate are resulting in greater occurrence of snowfall during the critical period of egg laying and incubation [22,24]. Although these events might not always be classified as extreme according to the climatological definition, they do present challenges that may be perceived as extreme by the birds that are enduring them. Snowstorms reduce access to resources necessary for breeding and will eventually cause both Lapland longspurs and white-crowned sparrows to abandon territories and form mixed flocks, resulting in reproductive failure for the current brood [24,26].

5. Case studies: Adélie penguins, combined events with extreme consequences

Turning to the other Pole, we examine the case of breeding Adélie penguins, *Pygoscelis adeliae*, in the Terre Adélie sector

of Antarctica. This anecdote illustrates how multiple events that individually may or may not fit the climatological definition of extreme may prove catastrophic in combination. During the austral summer, Adélie penguins typically breed in subzero temperatures and strong katabatic winds blowing north from the continental icecap [27–29]. As in the Arctic, such conditions would be considered extreme by a subjective observer, but reflect the climatological norm for Adélie penguins (see also [18,30]). During the 2013/2014 breeding season, the colony at Pétrels Island (66°40' S, 140°01' E) experienced unprecedented complete reproductive failure with loss of all chicks on the island prior to fledging. This was the first such record for the site [28]. From a biological perspective the complete reproductive failure of a colony is certainly indicative of an extreme event, but in this case the cause has been attributed to two simultaneous weather events during the 2013/2014 breeding season. First, the summer was unusually warm leading to periods of rain that, combined with subsequent snow-melt, posed significant thermal challenges to drenched young chicks adapted to the typically cold and dry conditions of the region. Compounding these increased thermal challenges, uncharacteristically low wind speeds at the colony failed to disperse sea-ice cover, which increased the distance parents had to travel to forage at sea dramatically. This decrease in resource availability ultimately led to less chick provisioning. The combined result of these two events was complete reproductive failure of the colony—which may have significant future consequences for the population as well as the local ecosystem [28]. This case highlights the fact that to us, seemingly positive environmental changes such as increased temperature and decreased wind speed may in combination constitute an extreme event for a species adapted to a polar environment. Further, it illustrates the need to integrate climatic and biological definitions when assessing whether an extreme event has occurred.

6. Case studies: snow petrels, extremes that matter, extremes that do not

Snow petrels, *Pagodroma nivea*, spend their entire life cycle in Antarctica, usually in pack ice [18,31]. In general, high winds and snow may not constitute severe conditions for snow petrels unless food availability is also affected. In January 2010 at the French Polar Institute in Dumont D'Urville (66°40' S, 140°01' E), east Antarctica, several days of high winds and snow had only a negligible effect on nesting snow petrels. However, on the fourth day, temperatures soared to record highs (7.7°C on 23 January) and snow turned to rain. Drifted snow in nest cavities melted rapidly resulting in flooding and abandonment of nests, loss of eggs and newly hatched young [18,19]. Whereas snow and ice would be considered more extreme for the investigators, at least in this instance it was not a problem for this species [31]. Some petrels hatched chicks while inundated with snow. On the other hand, we see that warmer temperatures and effects of flowing water (not extreme for investigators) appeared to constitute an extreme climatic event for snow petrels resulting in 90% reproductive failure. Choosing nest sites sheltered from snow or ice positively alters the petrel's selective environment, but that same decision may create an environment that is detrimental in a different context such as flooding.

7. Case studies: extreme heat

Many animals and plants are adapted to seasonal heat especially by using micro-habitats (for reviews see [15,32,33], see also Gardner *et al.* [34], for longer term responses). This tolerance of what to us are extreme conditions can be exacerbated by further extreme events of even higher environmental temperatures. Animals may already be near the upper edge of their thermal tolerance range due to limited mechanisms of cooling, as opposed to the wide variety of mechanisms by which physiology may be adapted to low temperatures [33]. Furthermore, behavioural mechanisms such as facultative migrations may be useless when temperature extremes are widespread forcing birds to endure the event. As with humans [35], fatalities during extreme heat events have been recorded in birds both in Australia and North America (reviewed in [15,33,36]). The single largest high temperature event on record occurred in 1932 when a heatwave struck much of southern Australia, with air temperatures reaching 49°C. This extreme event led to the deaths of tens of thousands of birds despite the availability of water sources nearby [37]. More recently, a multiday heatwave with temperatures in excess of 45°C led to the deaths of thousands of small birds in Western Australia (approx. 500 km north of Perth; reviewed in [33]). These heat-related mass mortality events highlight the example of climatological extremes and biological extremes matching. Such matching examples and others that do not necessarily match underscore the importance of understanding physiological responses of organisms to extreme events in order to predict the scope and degree by which populations will be able to resist future extremes.

8. A new take on the biological-based approach to extreme climatological events: physiological mechanisms using allostasis as a concept to define extreme events at population and individual levels

We propose an organism-based biological approach to define extreme climatic events rooted in physiological and behavioural mechanisms of responses to harshening/deteriorating environmental conditions as a means of detecting, exploring and predicting how organisms respond. Using the concepts of allostasis and the emergency life-history stage as a framework allows identification of when an organism is experiencing an extreme climatic event based on quantifiable physiological and behavioural changes in response to altered environmental conditions. It also allows researchers to predict when changed environmental conditions may negatively affect organisms in different physiological and behavioural states according to sex, reproductive status, prior condition, etc. [14,16,38,39]. The framework may provide a reliable and consistent way to define an extreme climatic event across contexts, populations and individuals.

Allostasis, stability through change, attempts to extend the concepts of homeostasis in a world that is changing predictably (e.g. seasons) and unpredictably (e.g. weather events, human disturbance). It depends on energetic considerations beginning with the energy in the environment (food), that is designated as *Egained* (*Eg*) and is dynamic, quantitatively

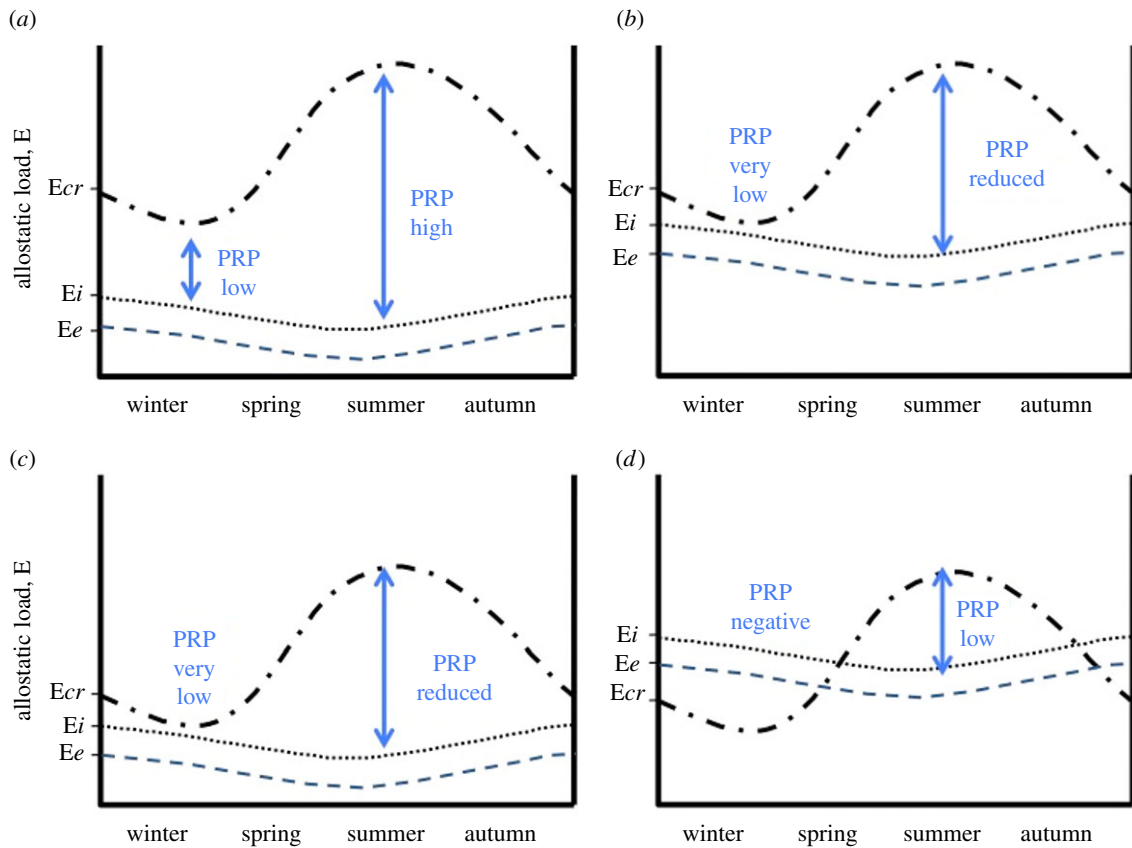


Figure 1. Perturbation resistance potential (PRP) in different seasons. E_{cr} is the cumulative energetic resources available to an individual. E_e represents the existence energy and E_i is the additional energy required to go about daily routines (see [14,38–40]). $PRP = E_{cr} - E_e + E_i$ (vertical blue arrows). (a) PRP is higher in summer allowing more energetically demanding life-history stages such as breeding, moult and migrations to occur. (b) $E_e + E_i$ are higher and because E_{cr} remains unchanged then PRP is very low in winter and reduced in spring and summer. (c) $E_e + E_i$ remain the same as in (a) but E_{cr} is greatly reduced resulting in very low PRP. The worst case scenario is shown in (d) where $E_e + E_i$ are increased and E_{cr} is reduced. Now PRP is negative in winter and greatly reduced in spring and summer. When PRP is low then extreme climatic events could result in allostatic overload type 1.

and qualitatively, and also generally predictable (figure 1, [39]). E_{gained} is a function of day length as well because longer days allow more primary productivity (figure 1). Specific individual characteristics such as social status, body condition and territory quality can also influence E_{gained} in terms of access to food and variation of quality with habitat. Given these diverse contributions to energy available to the individual we consider the cumulative resources available (E_{cr}) that ultimately affect an individual and are critical for the allostasis concept but are largely ignored in other discussions of allostasis and reactive scope [14,16,41–43]. In the absence of considering E_{cr} , then the assumption must be that food and access to it is ad libitum. In captive studies this may be true but in the natural world ad libitum is rare. Furthermore, as pointed out by Walsberg [42], energy balance is not always a good index of allostatic load (stress). However, if one considers E_{cr} in the framework of allostasis and resources available then many processes regarded as having trivial costs (such as social status) actually carry large costs, but in terms of access to food and shelter (E_{cr}). Thus although social status in some contexts may have little effect on allostatic load, reduced access to E_{cr} could have profound potential impacts on vulnerability to further environmental changes [44,45]. Below we explore the implications of E_{cr} and allostatic load and the potential regulation and modulation of hormonal responses for coping with environmental perturbations [14,43,46].

Hypothetical variations in E_{cr} with different seasons indicate that resources tend to be low in winter when primary

productivity is least, and much higher in spring and summer when primary productivity is greater (figure 1, [32,39]). E_e represents the existence energy for an individual across seasons and E_i is the additional energy required to go about daily routines such as foraging, assimilating food, territory maintenance etc. (figure 1, [32,39]). Both E_e and E_i tend to be higher in winter when temperatures are lower and food is harder to find compared with spring and summer [32,39].

9. Allostatic overload and the emergency life-history stage

When costs of daily and seasonal routines, the current life-history stage and additional unpredictable events such as perturbations exceed E_{cr} , then allostatic overload type I occurs. It is at this point that the emergency life-history stage, or survival stage, is triggered and the life-history stage for that time of year is abandoned so that all available energetic resources can be devoted to self-preservation [14,32,38,39]. The activation of the emergency life-history stage comes with trade-offs such as abandonment of reproduction or delayed arrival on breeding grounds depending on the time of year (e.g. [14,15]). Importantly, an individual must ideally trigger the emergency life-history stage before E_{cr} is exceeded by current energetic costs so that some reserves are available to maintain homeostasis in a shelter, or fuel movement away to a refuge or habitat where survival is possible. It should be noted that this emergency

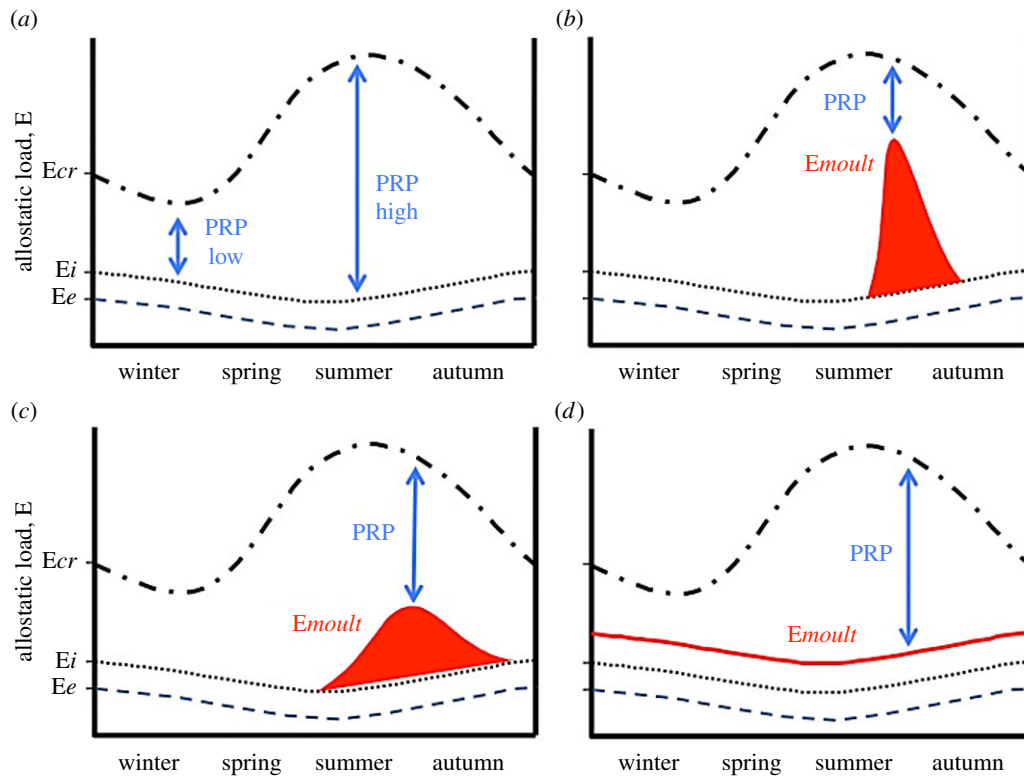


Figure 2. Life-history stage and perturbation resistance potential (PRP). (a) Identical to (a) in figure 1. (b) Costs of a life-history stage (e.g. *Emoult*) occur in summer, then E_{cr} is sufficient to cover energetic costs but PRP is reduced. (c) If the moult life-history stage progresses more slowly, then costs will be lower but extended in time resulting in greater PRP. (d) If moulting occurs slowly over the entire year then energetic costs would be much lower but constant (red line in (d)). In this scenario, PRP would be only slightly lower than in (a).

life-history stage is not always successful and some events can result in high mortality (for review and examples see [15,46]).

10. Perturbation resistance potential

A key concept of vulnerability to extreme climatic events or environmental stress in general is the 'perturbation resistance potential' (PRP, [18,19]). It is a function of the difference between resources available (E_{cr}) and the sum of costs of daily and seasonal routines (E_e and E_i). Thus perturbation resistance potential = $E_{cr} - E_e + E_i$ (see vertical blue arrows in figure 1) and ideally should be kept as large as possible to provide ample resources to cope with perturbations of the environment without having to trigger the emergency life-history stage [18,19]. In figure 1a, perturbation resistance potential is low in winter but much higher in summer allowing more energetically demanding life-history stages such as breeding, moult and migration to occur without exceeding available resources. It can also be seen how low perturbation resistance potential in winter might mean that the individual is more susceptible to an extreme climatic event increasing energetic costs compared to in summer. In figure 1b, $E_e + E_i$ could be higher because of, for example, an injury to an individual that has increased costs of daily routines and/or parasite load. Elevated costs may also occur because of competition with conspecifics or avoidance of predators reducing perturbation resistance potential compared with figure 1a. In figure 1c, $E_e + E_i$ remains the same as in figure 1a but E_{cr} is greatly reduced owing to, for example, a climatic event, poor quality territory, etc. This latter example shows perturbation resistance

potential is again lowered but for different reasons. The worst-case scenario is shown in figure 1d where $E_e + E_i$ are increased as in figure 1b and E_{cr} is reduced as in figure 1c. Now perturbation resistance potential is negative in winter requiring migration to a location where resources are more abundant (or hibernation). In spring and summer perturbation resistance potential is greatly reduced in figure 1c resulting in very little energy margin for breeding or moulting. These individuals would also be very vulnerable to energetic costs of further extreme events. When perturbation resistance potential is low then extreme climatic events will result in rapid allostasis overload type 1. If an environmental perturbation such as an extreme climatic event results in perturbation resistance potential declining to zero, or becoming negative (allostasis overload type 1), then the event fits our definition of extreme and the individual expressing a life-history stage appropriate for that time of year cannot cope with current conditions. Allostasis overload type 1 then represents a biological example of the effect of an extreme climatic event as experienced by an individual.

The variation in perturbation resistance potential shown in figure 1 does not take into account life-history stages such as migrations, breeding and moulting that are also energetically demanding and must be timed to occur when E_{cr} can support such efforts [14,39]. However, adjustments of expression of life-history stages through timing, duration and intensity can maximize perturbation resistance potential so that unpredictable perturbations such as extreme climatic events may potentially be endured (figure 2). This example shows the moult life-history stage. Figure 2a is identical to figure 1a and is presented for easy reference. Here cumulative food resources and reserves (E_{cr}) are much higher in spring

and summer (see also figure 1) and daily costs of maintenance and routines ($E_e + E_i$) tend to be lower at these times maximizing perturbation resistance potential. If we then include costs of the moult life-history stage in figure 2*b* then E_{cr} is sufficient to cover energetic costs of that life-history stage but perturbation resistance potential is reduced (vertical blue arrows). This means that susceptibility to further extreme climatic events is greater, but animals usually counter this risk by scheduling moulting to a time of year when E_{cr} is very high and weather is more stable (e.g. summer, [14,15]).

If the moult life-history stage progresses more slowly, then costs will be lower but extended in time resulting in greater perturbation resistance potential during moult in figure 2*c* versus figure 2*b*. Another option is to eliminate a separate moult life-history stage altogether and spread moulting over the entire year but at a very slow rate (e.g. as in the zebra finch, *Taenopygia guttata*; see [47]). As a result, energetic costs of moulting would be much lower but constant (red line in figure 2*d*). In this scenario perturbation resistance potential would be only slightly lower than in figure 2*a*. Adjustments of the intensity and duration of other life-history stages could also be made in diverse ways to maximize perturbation resistance potential over the entire year. In this way, the individual may be able to maintain internal and external resources to cope with further perturbations of the environment except for those most extreme climatic events that could still result in energetic costs exceeding E_{cr} .

11. Glucocorticoids and the emergency life-history stage: mechanisms for coping with extreme climatic events

The classic adrenocortical response to environmental stress is one hormone regulatory system that has been investigated most broadly in relation to extreme environmental events in general. The hypothalamo-pituitary-adrenal (HPA) axis responds to perturbations of the environment by triggering a cascade of hormonal secretions beginning in the hypothalamus and ending with increased synthesis of glucocorticoids (corticosterone in birds) that orchestrate a suite of physiological and behavioural coping responses (see [15,46,48,49]). There is also extensive experimental evidence that corticosteroids orchestrate changes in foraging behaviour, facultative migratory behaviour, inhibition of unnecessary processes such as reproductive behaviour and territorial aggression in birds, as well as energy mobilization in general and immune system function (see [14,16,48,49] for extensive discussions). It should be pointed out that in relation to glucocorticoid effects on energy mobilization, analysis of the literature indicates that the long assumed relationship with glucose levels in blood do not always exist [41,50] although permissive actions at the level of the liver may be in operation including mobilization of free fatty acids and triglycerides—important sources of energy in birds [14,50]. Other hormone systems are also involved in regulation of the emergency life-history stage such as epinephrine, cytokines and others but these are beyond the scope of this paper.

There is now very extensive evidence from free-living species responding to natural environmental perturbations as well as standardized stressors applied in the field and laboratory that the HPA axis is activated resulting in elevations

of circulating corticosteroids (see [14] for broad review of vertebrates, also [15] for responses to weather events). Elevation of glucocorticoids is a response to deleterious environmental variation and is often accompanied by activation of the emergency life-history stage. Corticosterone in the blood of birds at baseline levels (called A to B, see [14,32,50]) regulate daily and seasonal changes in metabolism and osmoregulation in relation to homeostasis (see [14,49]). As corticosterone levels rise with elevated energetic costs (level B) then mobilization of energy through gluconeogenesis is triggered (but see [41]) and at highest titres (level C) enable increased foraging, escape activity consistent with leaving the immediate area and increased night restfulness saving energy to be used for survival the next day (see [14,17,30,32,50] for extensive reviews). These actions cover the reactive scope [14,41] of corticosterone and are consistent with activities triggered in the emergency life-history stage during an extreme climatic event.

12. Mechanisms of glucocorticoid action and their role in coping with extreme climatic events

How the reactive scope of glucocorticoids may direct responses to extreme climatic events has important components at cell and molecular levels. Actions of glucocorticoids have distinct mechanisms at baseline levels, (A to B, [51], see also the reactive scope model of Romero *et al.* [41]) probably mediated through an intra-cellular, high affinity receptor (mineralocorticoid receptor or MR), generally associated with maintenance of day-to-day functions and predictable events. At 'stress' induced levels (level C) glucocorticoids are associated with coping mechanisms to deal with perturbations of the environment [50]. These actions of glucocorticoids likely involve binding to another intra-cellular receptor, the glucocorticoid receptor (GR), that has lower affinity for corticosterone than the mineralocorticoid receptor and is only bound at high circulating levels of glucocorticoids (e.g. [16,50,51]). There is also strong evidence for a third type of receptor associated with target cell membranes that can mediate very rapid actions (seconds to minutes, [52]) of glucocorticoids compared with the other intra-cellular receptors that affect gene transcription directly but much more slowly (hours). The fast acting membrane receptor [51] appears to have specific actions on locomotor activity but only in the breeding season in white-crowned sparrows [52]. Again, it is important to note that actions of glucocorticoids can be very different at basal levels (level A) versus changes of baseline levels of glucocorticoids during the day or annual cycles (level B) [14,50,51]. Changes of glucocorticoid levels within levels A and B allows expression of behavioural and physiological phenotypes within the normal range of environmental variation. Level C is the highest category of circulating glucocorticoids (e.g. induced by allostatic overload type 1) that triggers coping mechanisms outside the normal range of environmental variation (see figure 1).

13. Adrenocortical responses to environmental variation and extreme climatic events

Many field studies repeatedly show that weather events which trigger the emergency life-history stage have elevated plasma

corticosterone levels above baseline (i.e. levels A and B to C [14,15,17,24]). This appears to be true whether the focal species is living at low or mid-latitudes in mesic environments, or in more extreme environments such as polar regions or high altitude. These populations may already be coping with cold, snow, rain, etc. as part of their daily and seasonal routines before exposure to an extreme climatic event. There are numerous examples for each of these scenarios that have now been reported and have been reviewed extensively in relation to weather events [14,15]. However, there are some exceptions such as in Lapland longspurs and white-crowned sparrows breeding in Arctic environments where they differ in some physiological indicators of exposure to extreme climatic events. Lapland longspurs responding to an extreme weather event had elevated levels of corticosterone when tested with a standardized stressor (capture, handling and restraint) whereas baseline levels were not different [24,26]. Similar results were obtained for white-crowned sparrows breeding at the northern edge of their range in Alaska and in a more harsh environment (see [53]). There may be numerous reasons to explain these apparent anomalies given that corticosterone receptors can change, as can blood levels of a binding protein, corticosterone-binding globulin [14]. Because corticosterone bound to corticosteroid-binding globulin is generally thought not to be able to enter target cells, then levels of this protein in blood will be an important consideration for future studies (but see [54]). Other components of the secretion-transport-target cell cascade, such as corticosteroid metabolizing enzymes that can deactivate corticosterone or promote its action, will also be important for future investigations to fully understand the hormonal control of responses to extreme climatic events (see [14,16] for extensive discussion).

Given the widespread demonstration that weather events resulting in altered life-history stages are accompanied by elevated circulating levels of corticosteroids, it is now appropriate to depict the hypothetical relationships of circulating corticosterone to the range of environmental variation expected when a specific life-history stage is expressed (figure 3). Environmental conditions can be expected to be good, poor or bad for each life-history stage (figure 3) but perturbation resistance potential and baseline levels of corticosterone allow the individual to cope with this range of conditions. Baseline corticosteroid levels in blood tend to rise as conditions deteriorate and increase allostatic load. These concentrations increase through level A (homeostatic level, lightest shade of grey, see also [41]) and level B (reactive scope for that reaction norm, middle shade of grey). When conditions become extreme (right hand vertical line) then corticosterone levels rapidly increase to level C as a result of allostatic overload that then triggers facultative responses such as the emergency life-history stage (darkest shade of grey). The slope of the lines for circulating glucocorticoids will vary among life-history stages. For example, baseline levels of corticosterone in Gambel's white-crowned sparrow tend to be lowest in the year during moult and show the least increase in response to a standardized stressor of capture, handling and restraint [14]. In contrast, during spring migration and arrival on Arctic breeding grounds, baseline levels are high and stress titres are the greatest of the year ([14,53] for review and discussion).

It is possible that rising corticosteroid levels within levels A and B and as environmental conditions vary from good to bad and extreme (figure 3), might be involved in determining phenotypes that are expressed under such conditions [55,56].

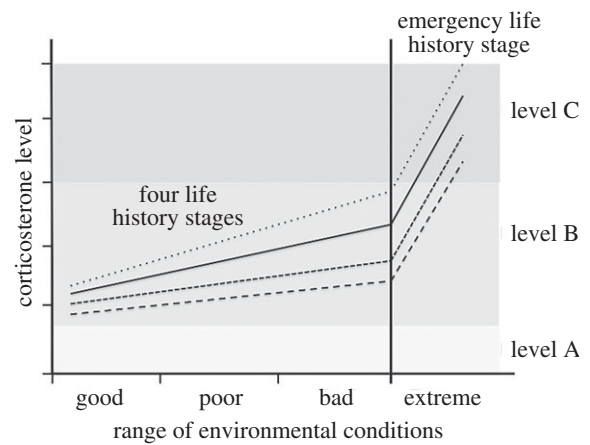


Figure 3. The hypothetical relationships of circulating glucocorticoids and the range of environmental conditions expected when a specific life-history stage is expressed. Environmental conditions can be expected to be good, poor or bad for each life-history stage. Baseline corticosteroid levels in blood tend to increase slowly as conditions deteriorate and increase allostatic load. These concentrations rise above level A (homeostatic level, lightest shade of grey) and within level B (reactive scope for that life-history stage, middle shade of grey). When conditions become extreme (right hand vertical line) then corticosterone levels increase rapidly to level C as a result of allostatic overload; that then triggers facultative responses such as the emergency life-history stage (darkest shade of grey). The slope of the lines for circulating corticosteroids will vary among life-history stages. Four are presented here with one showing low baseline and rate of increase as well as maximum level. Such variation in the dynamics of corticosteroid responses to deteriorating weather events and stress in general are common [14,32].

Examples could include changing morphological, physiological and behavioural traits within an individual as conditions deteriorate leading to differences among individuals and populations. Many other factors could then have an influence on how individuals respond to extreme climatic events. It should also be borne in mind that specific corticosterone reactive phenotypes can develop such as reactive/proactive individuals depending upon varying environments both biotic and abiotic (e.g. [55–57]). These in turn may add to the broad spectrum of ways by which individuals and populations respond to the same extreme climatic events. Note also that the scenarios in figure 3 no longer assume that plasma corticosterone levels increase in parallel with allostatic load (as suggested earlier in [32,39]), but may increase slowly at first and then rise rapidly when conditions become more extreme.

14. Conclusion and new directions

What constitutes an extreme climatic event? Firstly it is important to differentiate between climatological definitions of extreme events and the biological contexts that result in a response by an organism to that event. It is clear that many extreme climatic events do elicit a behavioural and physiological coping response but this can also occur in less extreme climatic conditions. Some individuals in a population may be experiencing extreme conditions in what otherwise would not be considered an extreme event climatologically because of other circumstances such as habitat quality, body condition, social status, etc. A mechanistic approach is suggested to define and investigate further what extreme climatic events are in biological contexts and how animals cope

with them at physiological and behavioural levels. An allostatic load approach allows us to assess the resources available to an individual in relation to costs incurred by daily routines and additional stress. This is called the perturbation resistance potential. When the perturbation resistance potential reaches critically low levels, or even becomes negative, this is a signal of an extreme event (including climatic) and the emergency life-history stage is triggered allowing the individual to cope. This disrupts the temporal progression of life-history stages, but enhances survival. Evidence is growing that glucocorticoid hormones play a major role in orchestrating coping mechanisms and are critical for enduring extreme climatic events.

Additionally, including the framework of phenotypic plasticity provides two levels of concepts that could be useful to define when an event should be considered 'extreme'. On one hand, predictable and unpredictable changing environmental conditions at short time scales promote the reversible expression of different phenotypes within individuals (i.e. phenotypic flexibility, [55,56,58–60]). These reversible transformations in morphological, behavioural and physiological traits might involve a positive outcome in terms of fitness (see [4,5]). In contrast, the concept of 'developmental plasticity', environmentally induced variations in the traits of individuals during development, are normally irreversible [4]. These variations can be described by empirical relationships such as reaction norms [61,62], but what this may mean at mechanistic levels remains to be clarified. In the particular case of reversible endocrine traits—mediators of many behavioural responses—the concept of phenotypic and endocrine flexibility has been recently introduced [1,5,30,56,58,59]. Endocrine responses are not necessarily best examined as positive or negative but may display important and informative patterns of variation within and between individuals. Taff & Vitousek [56] differentiated between the potential (i.e. maximum flexibility) and realized endocrine flexibility (the exhibited endocrine flexibility by one individual in different contexts), and between the magnitude of within-individual changes of endocrine traits (i.e. scope of flexibility) and the speed of flexibility or how fast the endocrine response takes to be expressed. Such approaches may be useful to integrate with the concepts of allostasis and perturbation resistance potential to predict hormonal mechanisms underlying coping with extreme climatic events.

As proposed by Piersma & Drent [59], the environmental components of the total phenotypic variance can be divided into separate factors, reversible (flexibility) and

non-reversible (plasticity). The interaction between these two components allows us to understand how much of the organismal response to environmental perturbations is a result of reversible variations shaped by developmental stages [57]. However, both phenotypic flexibility and plasticity have associated limits and costs, and cannot be expressed without energetic expenditures.

One of the most obvious costs is the potential expression of a phenotype that mismatches the environment and therefore has lower fitness [63]. Such mismatches in the endocrine system and environmental perturbations may increase with global change undermining coping mechanisms for extreme climatic events [6,64]. In addition, there are plasticity and flexibility costs *per se*, such as maintenance, which are related to sensory and regulatory mechanisms [40,63–65]. In terms of limits, the lag-time between the environmental change and the phenotypic response is pivotal and could have important fitness effects. Integration of these concepts and coping with environmental extremes will provide new insights and hypotheses for mechanistic investigations, especially as global climate change drives more extreme climatic events. Theoretical approaches that bring together allostasis, perturbation resistance potential, reactive scope and phenotypic flexibility along with data on responses to extreme weather events (see [66] for modelling approaches) will be particularly insightful for future research directions.

Ethics. No original investigations are presented here, but the published studies by these authors were all conducted with the University of California, Davis, Institutional Animal Care and Use Committee approval.

Data accessibility. No original data are presented.

Authors' contributions. J.C.W. wrote the original version after discussion with all authors. The other authors then contributed equally to subsequent discussions and drafts.

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References

- Ball GF, Bentley GE. 2000 Neuroendocrine mechanisms mediating the photoperiodic and social regulation of seasonal reproduction in birds. In *Reproduction in context* (eds K Wallen, J Schneider), pp. 129–158. Cambridge, MA: MIT Press.
- Murton RK, Westwood NJ. 1977 *Avian breeding cycles*. Oxford, UK: Clarendon Press.
- Lofts B, Murton RK. 1968 Photoperiodic and physiological adaptations regulating avian breeding cycles and their ecological significance. *J. Zool. (Lond.)*, **155**, 327–394. (doi:10.1111/j.1469-7998.1968.tb03056.x)
- Wingfield JC. 2008 Organization of vertebrate annual cycles: implications for control mechanisms. *Phil. Trans. R. Soc. B* **363**, 425–441. (doi:10.1098/rstb.2007.2149)
- Wingfield JC. 2008 Comparative endocrinology, environment and global change. *Gen. Comp. Endocrinol.* **157**, 207–216. (doi:10.1016/j.ygcen.2008.04.017)
- Beniston M, Stephenson DB. 2004 Extreme climatic events and their evolution under changing climatic conditions. *Glob. Planet. Change* **44**, 1–9. (doi:10.1016/j.gloplacha.2004.06.001)
- Rahmstorf S, Coumou D. 2011 Increase of extreme events in a warming world. *Proc. Natl Acad. Sci. USA* **108**, 17 905–17 909. (doi:10.1073/pnas.1101766108)
- Ummenhofer CC, Meehl GA. 2017 Extreme weather and climate events with ecological relevance: a review. *Phil. Trans. R. Soc. B* **372**, 20160135. (doi:10.1098/rstb.2016.0135)
- van de Pol M, Jenouvrier S, Cornelissen JHC, Visser ME. 2017 Behavioural, ecological and evolutionary responses to extreme climatic events: challenges and directions. *Phil. Trans. R. Soc. B* **372**, 20160134. (doi:10.1098/rstb.2016.0134)
- Bailey LD, van de Pol M. 2016 Tackling extremes: challenges for ecological and evolutionary research

- on extreme climatic events. *J. Anim. Ecol.* **85**, 85–96. (doi:10.1111/1365-2656.12451)
11. Meehl GA, Zwiers F, Evans J, Knutson T, Mearns L, Whetton P. 2000 Trends in extreme weather and climate events: issues related to modeling extremes in projections of future climate change. *Bull. Am. Meteorol. Soc.* **81**, 427–436. (doi:10.1175/1520-0477(2000)081<0427:TIEWAC>2.3.CO;2)
 12. Meehl G *et al.* 2000 An introduction to trends in extreme weather and climate events: observations, socioeconomic impacts, and model projection. *Bull. Am. Meteorol. Soc.* **81**, 413–416. (doi:10.1175/1520-0477(2000)081<0413:AITTIE>2.3.CO;2)
 13. Parmesan C. 2007 Influences of species, latitudes and methodologies on estimates of phenological response to global warming. *Glob. Change Biol.* **13**, 1860–1872. (doi:10.1111/j.1365-2486.2007.01404.x)
 14. Romero LM, Wingfield JC. 2016 *Tempests, poxes, predators and people: stress in wild animals and how they cope*. Oxford, UK: Oxford University Press.
 15. Wingfield JC, Ramenofsky M. 2011 Hormone-behavior interrelationships of birds in response to weather. In *Advances in the study of behavior*, vol. 43 (eds H Jane Brockmann, TJ Roper, M Naguib, JC Mitani, LW Simmons), pp. 93–188. Burlington, MA: Elsevier Inc. Academic Press.
 16. Romero LM, Platts SH, Schoech SJ, Wada H, Crespi E, Martin LB, and Buck CL. 2015 Understanding stress in the healthy animal—potential paths for progress. *Stress* **18**, 491–497. (doi:10.3109/10253890.2015.1073255)
 17. Wingfield JC, Silverin B. 2009 Ecophysiological studies of hormone-behavior relations in birds. In *Hormones, brain and behavior*, 2nd edn, vol. 2 (eds DW Pfaff, AP Arnold, AM Etgen, SE Fahrbach, RT Rubin), pp. 817–854. New York, NY: Academic Press.
 18. Wingfield JC, Kelley JP, Angelier F. 2011 What are extreme environmental conditions and how do organisms cope with them? *Curr. Zool.* **57**, 363–374. (doi:10.1093/czoolo/57.3.363)
 19. Wingfield JC *et al.* 2011 Organism-environment interactions in a changing world: a mechanistic approach. *J. Ornithol.* **152**, 279–288. (doi:10.1007/s10336-011-0668-3)
 20. Crossin GT, Trathan PN, Phillips RA, Dawson A, Le Bouard F, Williams TD. 2010 A carryover effect of migration underlies individual variation in reproductive readiness and extreme egg size dimorphism in macaroni penguins. *Am. Nat.* **176**, 357–366. (doi:10.1086/655223)
 21. Williams TD. 2012 Hormones, life history, and phenotypic variation: opportunities in evolutionary avian endocrinology. *Gen. Comp. Endocrinol.* **176**, 286–295. (doi:10.1016/j.ygcen.2011.11.028)
 22. Nelson FE *et al.* 1997 Estimating active-layer thickness over a large region: Kuparuk river basin, Alaska, U.S.A. *Arc. Alp. Res.* **29**, 367–378. (doi:10.2307/1551985)
 23. Xiaogang S, Philip M, Daqing Y. 2015 Warming spring air temperatures, but delayed spring stream flow in an Arctic headwater basin. *Environ. Res. Lett.* **10**, 064003. (doi:10.1088/1748-9326/10/6/064003)
 24. Krause JS, Pérez JH, Chmura HE, Meddle SL, Hunt KE, Sweet SK, Gough L, Boelman N, Wingfield JC. 2016 The effects of extreme spring weather on body condition and stress physiology in arctic-breeding songbirds. *Gen. Comp. Endocrinol.* **237**, 10–18. (doi:10.1016/j.ygcen.2016.07.015)
 25. Senner NR, Verhoeven MA, Abad-Gómez JM, Gutiérrez JS, Hooijmeijer JCEW, Kentie R, Maserio JA, Tibbitts TL, Piersma T. 2015 When Siberia came to the Netherlands: the response of continental black-tailed godwits to a rare spring weather event. *J. Anim. Ecol.* **84**, 1164–1176. (doi:10.1111/1365-2656.12381)
 26. Astheimer LB, Buttemer WA, Wingfield JC. 1995 Seasonal and acute changes in adrenocortical responsiveness in an arctic-breeding bird. *Horm. Behav.* **29**, 442–457. (doi:10.1006/hbeh.1995.1276)
 27. Adolphs U, Wendler G. 1995 A pilot study on the interactions between katabatic winds and polynyas at the Adélie Coast, eastern Antarctica. *Antarct. Sci.* **7**, 307–314. (doi:10.1017/S0954102095000423)
 28. Ropert-Coudert Y *et al.* 2014 A complete breeding failure in an Adélie penguin colony correlates with unusual and extreme environmental events. *Ecography* **37**, 1–3. (doi:10.1111/j.1600-0587.2013.00236.x)
 29. Turner J *et al.* 2005 Antarctic climate change during the last 50 years. *Int. J. Climatol.* **25**, 279–294. (doi:10.1002/joc.1130)
 30. Wingfield JC. 2016 Ecophysiological studies of hormone-behavior relations in birds: future challenges in a changing world. In *Hormones, brain, and behavior*, 3rd edn (eds D Pfaff, J Balthazart). New York, NY: Elsevier Press.
 31. Chastel O, Weimerskirch H, Jouventin P. 1993 High annual variability in reproductive success and survival of an Antarctic seabird, the snow petrel, *Pagodroma nivea*. *Oecologia* **94**, 278–285. (doi:10.1007/BF00341328)
 32. Wingfield JC. 2004 Allostatic load and life cycles: implications for neuroendocrine mechanisms. In *Allostasis, homeostasis and the costs of physiological adaptation* (ed. J Schulkin), pp. 302–342. Cambridge, UK: Cambridge University Press.
 33. McKechnie AE, Hockey PA, Wolf BO. 2012 Feeling the heat: Australian landbirds and climate change. *Emu* **112**, i–vii. (doi:10.1071/muv112n2_ed)
 34. Gardner JL, Rowley E, de Rebeira P, de Rebeira A, Brouwer L. 2017 Effects of extreme weather on two sympatric Australian passerine bird species. *Phil. Trans. R. Soc. B* **372**, 20160148. (doi:10.1098/rstb.2016.0148)
 35. Gershunov A, Cayan DR, Iacobellis SF. 2009 The great 2006 heat wave over California and Nevada: signal of an increasing trend. *J. Clim.* **22**, 6181–6203. (doi:10.1175/2009JCLI2465.1)
 36. Albright TP, Pidgeon AM, Rittenhouse CD, Clayton MK, Wardlow BD, Flather CH, Culbert PD, Radeloff VC. 2010 Combined effects of heat waves and droughts on avian communities across the conterminous United States. *Ecosphere* **1**, 1–22. (doi:10.1890/ES10-00057.1)
 37. Finlayson H. 1932 Heat in the interior of South Australia—holocaust of bird-life. *South Australian Ornithologist*. **11**, 158–160.
 38. Korte SM, Koolhaas JM, Wingfield JC, McEwen BS. 2005 The Darwinian concept of stress: benefits of allostasis and costs of allostatic load and the trade-offs in health and disease. *Neurosci. Biobehav. Rev.* **29**, 3–38. (doi:10.1016/j.neubiorev.2004.08.009)
 39. McEwen BS, Wingfield JC. 2003 The concept of allostasis in biology and biomedicine. *Horm. Behav.* **43**, 2–15. (doi:10.1016/S0018-506X(02)00024-7)
 40. Alud JR, Agrawal AA, Relyea RA. 2010 Re-evaluating the costs and limits of adaptive phenotypic plasticity. *Proc. R. Soc. B* **277**, 503–511. (doi:10.1098/rspb.2009.1355)
 41. Romero LM, Dickens MJ, Cyr NE. 2009 The reactive scope model—a new model integrating homeostasis, allostasis and stress. *Horm. Behav.* **55**, 375–389. (doi:10.1016/j.yhbeh.2008.12.009)
 42. Walsberg GE. 2003 How useful is energy balance as an overall index of stress in animals? *Horm. Behav.* **43**, 16–17. (doi:10.1016/S0018-506X(02)00033-8)
 43. Creel S, Dantzer B, Goymann W, Rubenstein DR. 2013 The ecology of stress: effects of the social environment. *Funct. Ecol.* **27**, 66–80. (doi:10.1111/j.1365-2435.2012.02029.x)
 44. Goymann W, Wingfield JC. 2004 Allostatic load, social status, and stress hormones—the costs of social status matter. *Anim. Behav.* **67**, 591–602. (doi:10.1016/j.anbehav.2003.08.007)
 45. McEwen BS, Wingfield JC. 2003 Response to commentaries on the concept of allostasis. *Horm. Behav.* **43**, 28–30. (doi:10.1016/S0018-506X(02)00039-9)
 46. Wingfield JC, Ramenofsky M. 1999 Hormones and the behavioral ecology of stress. In *Stress physiology in animals* (ed. PHM Balm), pp. 1–51. Sheffield, UK: Sheffield Academic Press.
 47. Zann RA. 1996 *The zebra finch: a synthesis of field and laboratory studies*. Oxford, UK: Oxford University Press.
 48. Crespi EJ, Williams TD, Jessop TS, Delehanty B. 2013 Life history and the ecology of stress: how do glucocorticoid hormones influence life-history variation in animals? *Funct. Ecol.* **27**, 93–106. (doi:10.1111/1365-2435.12009)
 49. Sapolsky RM, Romero LM, Munck AU. 2000 How do glucocorticosteroids influence stress responses? Integrating permissive, suppressive, stimulatory, and preparative actions. *Endocr. Rev.* **21**, 55–89.
 50. Landys M, Ramenofsky M, Wingfield JC. 2006 Actions of glucocorticoids at a seasonal baseline as compared to stress-related levels in the regulation of periodic life processes. *Gen. Comp. Endocrinol.* **148**, 132–149. (doi:10.1016/j.ygcen.2006.02.013)
 51. De Kloet ER, Karst H, Joëls M. 2008 Corticosteroid hormones in central stress response: quick-and-slow. *Front. Neuroendocrinol.* **29**, 268–272. (doi:10.1016/j.yfrne.2007.10.002)
 52. Breuner CW, Greenberg AL, Wingfield JC. 1998 Noninvasive corticosterone treatment rapidly

- increases activity in Gambel's white-crowned sparrows (*Zonotrichia leucophrys gambelii*). *Gen. Comp. Endocrinol.* **111**, 386–394. (doi:10.1006/gcen.1998.7128)
53. Krause JS *et al.* 2015 Breeding on the leading edge of a northward range expansion: differences in morphology and the stress response in the Arctic Gambel's white-crowned sparrow. *Oecologia* **180**, 33–44. (doi:10.1007/s00442-015-3447-7)
 54. Schoech SJ, Romero LM, Moore IT, Bonier F. 2013 Constraints, concerns and considerations about the necessity of estimating free glucocorticoid concentrations for field endocrine studies. *Funct. Ecol.* **27**, 1100–1106. (doi:10.1111/1365-2435.12142)
 55. Hau M, Casagrande S, Ouyang JQ, Baugh AT. 2016 Glucocorticoid-mediated phenotypes in vertebrates: multilevel variation and evolution. *Adv. Study Behav.* **577**, 287–318. (doi:10.1016/bs.asb2016.01.002)
 56. Taff CC, Vitousek MN. 2016 Endocrine flexibility optimizing phenotypes in a dynamic world. *Trends Ecol. Evol.* **31**, 476–488. (doi:10.1016/j.tree.2016.03.005)
 57. Monaghan P. 2008 Early growth conditions, phenotypic development and environmental change. *Phil. Trans. R. Soc. B* **363**, 1635–1645. (doi:10.1098/rstb.2007.0011)
 58. Piersma T, Lindstrom A. 1997 Rapid reversible changes in organ size as a component of adaptive behavior. *Trends Ecol. Evol.* **12**, 134–138. (doi:10.1016/S0169-5347(97)01003-3)
 59. Piersma T, Drent J. 2003 Phenotypic flexibility and the evolution of organismal design. *Trends Ecol. Evol.* **18**, 228–233. (doi:10.1016/S0169-5347(03)00036-3)
 60. Starck JM. 1999 Structural flexibility of the gastrointestinal tract of vertebrates—implications for evolutionary morphology. *Zool. Anz.* **238**, 87–101.
 61. Platt SA, Sanislow CA. 1988 Norm-of-reaction: definition and misinterpretation of animal research. *J. Comp. Psychol.* **102**, 254–261. (doi:10.1037/0735-7036.102.3.254)
 62. Schlichting C, Pigliucci M. 1998 *Phenotypic evolution: a reaction norm perspective*. Sunderland, MA: Philpapers, Sinauer.
 63. DeWitt TJ, Sih A, Wilson DS. 1998 Costs and limits of phenotypic plasticity. *Trends Ecol. Evol.* **13**, 77–81. (doi:10.1016/S0169-5347(97)01274-3)
 64. Angelier F, Wingfield JC. 2013 Importance of the glucocorticoid stress response in a changing world: theory, hypotheses and perspectives. *Gen. Comp. Endocrinol.* **190**, 118–128. (doi:10.1016/j.ygcen.2013.05.022)
 65. Liebl AL, Martin LB. 2012 Exploratory behavior and stressor hyper-responsiveness facilitate range expansion of an introduced songbird. *Proc. R. Soc. B* **279**, 20121606. (doi:10.1098/rspb.2012.1606)
 66. Chevin L-M, Hoffmann AA. 2017 Evolution of phenotypic plasticity in extreme environments. *Phil. Trans. R. Soc. B* **372**, 20160138. (doi:10.1098/rstb.2016.0138)