What are extreme environmental conditions and how do organisms cope with them?

John C. WINGFIELD[*], J. Patrick KELLEY, Frédéric ANGELIER

Department of Neurobiology, Physiology and Behavior, University of California, One Shields Avenue, Davis, CA 95616, U.S.A.

Abstract   Severe environmental conditions affect organisms in two major ways. The environment may be predictably severe such as in deserts, polar and alpine regions, or individuals may be exposed to temporarily extreme conditions through weather, presence of predators, lack of food, social status etc. Existence in an extreme environment may be possible, but then to breed or molt in addition can present major bottlenecks that have resulted in the evolution of hormone-behavior adaptations to cope with unpredictable events. Examples of hormone-behavior adaptations in extreme conditions include attenuated testosterone secretion because territoriality and excess courtship may be too costly when there is one opportunity to reproduce. The individual may even become insensitive to testosterone when target areas of the brain regulating reproductive behavior no longer respond to the hormone. A second example is reduced sensitivity to glucocorticoids following acute stress during the breeding season or molt that allows successful reproduction and/or a vital renewal of the integument to endure extreme conditions during the rest of the year. Reduced sensitivity could involve: (a) modulated response of the hypothalamo-pituitary-adrenal axis, (b) reduced sensitivity to high glucocorticoid levels, or (c) a combination of (a) and (b). Moreover, corticosteroid binding proteins (CBP) buffer responses to stress by reducing the movement of glucocorticoids into target cells. Finally, intracellular enzymes (11β-hydroxysteroid dehydrogenase and variants) can deactivate glucocorticoids entering cells thus reducing interaction with receptors. These mechanisms have important implications for climate change and increasing extremes of weather [*Current Zoology* 57 (3): 363–374, 2011].

Keywords   Extreme environment, Habitat configuration, Glucocorticoids, Stress response, Corticosteroid-binding proteins, Behavior

The phrase "extreme conditions" brings to mind severe weather (storms) and/or climates such as arctic-alpine habitats, deserts etc. However, we should be cautious in how extreme conditions are defined because many plants and animals that live in these environments are well adapted for day-to-day survival and are not "stressed" per se (e.g. Bartholomew, 1958, 1964, 1966; Martin and Wiebe, 2004). For example, a fish adapted to the hyperbaric conditions of the ocean abyss almost always die when brought to the surface. The latter is from our perspective a benign condition, but to the fish it is extreme. Nonetheless, although organisms living in such "extreme" environments are well adapted, the additional energetic costs of breeding or molting can be a major burden that may result in mobilization of stored resources and potential loss of fitness (e.g. Bartholomew, 1964).

An extreme environment to which an individual is adapted is predictably severe whereas there are also extreme events such as storms, temporary lack of food etc. that are frequently unpredictable. A combination of these two types can be particularly severe leading to stress and even death. Many other factors such as presence of predators, social status, infection and injury can contribute to "extreme conditions" even in mesic environments. Therefore a combination of factors, both predictable and unpredictable, will determine how extreme the environment may be, and may determine vulnerability to future perturbations (Wingfield, 2008) – i.e. a carry-over effect. The duality between extreme environment and extreme events underlies the development of a framework that can be used to determine physiological and behavioral mechanisms. We will focus primarily on hormonal mechanisms that regulate fairly rapid physiological and behavioral responses to those conditions.

1   Impact of Extreme Conditions: Implications for Humans and Biodiversity

There is growing evidence that climate change may result in more and greater extremes of weather and climate events. Mechanisms of how organisms will re-

spond to these events at a mechanistic level will provide a greater understanding of why some populations may thrive, some not change, and yet others decline (e.g. Pörtner and Farrell, 2008; Wingfield, 2008; Gaston et al., 2009). The incidence of catastrophic weather events such as floods, droughts, storms, heat waves and cold spells has risen almost 10-fold in the past 50 years (Easterling et al., 2000; Beniston and Stephenson, 2004). In the latter part of the 20th Century, such climatic events took over 725,000 human lives and resulted in economic losses of more than $700 billion during this period (Munich Rev., 2002; Beniston and Stephenson, 2004). Moreover, climate change events, and severe weather that goes with them, will have an impact on future productivity, incidence of crop diseases, the distribution of pests (Rosenzweig et al., 2001), and the harvesting of natural resources. Furthermore, climate change and severe weather is accompanied by increased human mortality (Greenhough et al., 2001) and have impacts on quality of human life including physical activity (Tucker and Gilliland, 2007).

In addition to effects of extreme conditions on human health and economics, animal losses and destruction of environments during these events are not well known. Climate-induced extinctions of plants and animals are increasing, as are changes in distribution and phenology (Deschenes and Moretti, 2009; Easterling et al., 2000; Meehl et al., 2000b). This in turn may lead to local adjustments of physiology, morphology and behavior patterns as individuals adjust to climate change (Parmesan et al., 2000; Root, 1988a, b, 1994). Combinations of traits may in turn either dampen or amplify the effects of natural selection acting within the population. Recent meta-analyses (Thackeray et al., 2010) indicate that changing phenologies are not uniform, and rates of change in primary producers versus consumers are different resulting in complex mismatches.

Severe weather events can result in catastrophic reproductive failure and population decline. For example, in king penguins *Aptenodytes patagonicus*, breeding on the Crozet Archipelago in the southern ocean, two tsunamis about two months apart inundated up 44% of the colony, killing chicks and eggs (Viera et al., 2006). How populations cope with, and then rebound, from these events at mechanistic levels is only just beginning to be explored.

2   Definitions of Extreme Conditions

There is no single definition of what extreme conditions are, and even less about how organisms might cope. What constitutes an "extreme environment" to us may not be so for an organism adapted to that environment, but it may be vulnerable to further perturbations especially when breeding or molting. Beniston and Stephenson (2004) suggest criteria for evaluation of extreme events and their occurrence:

a) How rare are they and how to document their frequency? How intense are they and what is the threshold for an extreme?

b) What impacts do they exert on environments and organisms in them and economic costs of damage?

Extreme weather can be considered an event outside the normal range of weather intensity (measured over decades) and therefore tends to be rare. But, such events appear to be increasing in recent decades (Francis and Hengeveld, 1998[1]). Meehl et al. (2000b) present a model where it is assumed that some weather or climatic variables are normally distributed and that changes in weather variance can be decoupled from changes in mean weather (Fig. 1). The black shaded areas (Fig. 1) represent extreme events such as, for example, unusual heat at the right end of the curve and intense cold at the left hand end. Where the vertical lines are placed delineating the boundary beyond which an event is considered extreme, is arbitrary in this figure, but is an important question to be resolved (Beniston and Stephenson, 2004). If global warming results in a slight change in the mean of the normal distribution of temperature to the right, then there will be an increase in extreme heat (Fig. 1). A shift in the mean to the left results in more extreme cold events. Changes in variance of weather/climate events could have even more dramatic effects on extreme conditions. The upper panel of Fig. 2 shows the effects of a change in variance of temperature with the mean decreasing and the curve expanding, resulting in more extreme temperature events. An even greater likelihood of extreme heat events results from combination of decreased variance and a shift to the right of the mean (Fig. 2). If the shift were to the left, then an increase in the likelihood of extreme cold events would occur. Changes in the intensity of events, in addition to frequency, are also likely (Katz and Brown, 1992; Meehl et al., 2000a,b; Munich Rev., 2002).

---

[1] Francis D, Hengeveld D, 1998. Extreme weather and climate change. Environment Canada, Minister of Supply and Services, Canada, cat. No. En57–27/1998–01E. 31 pp.
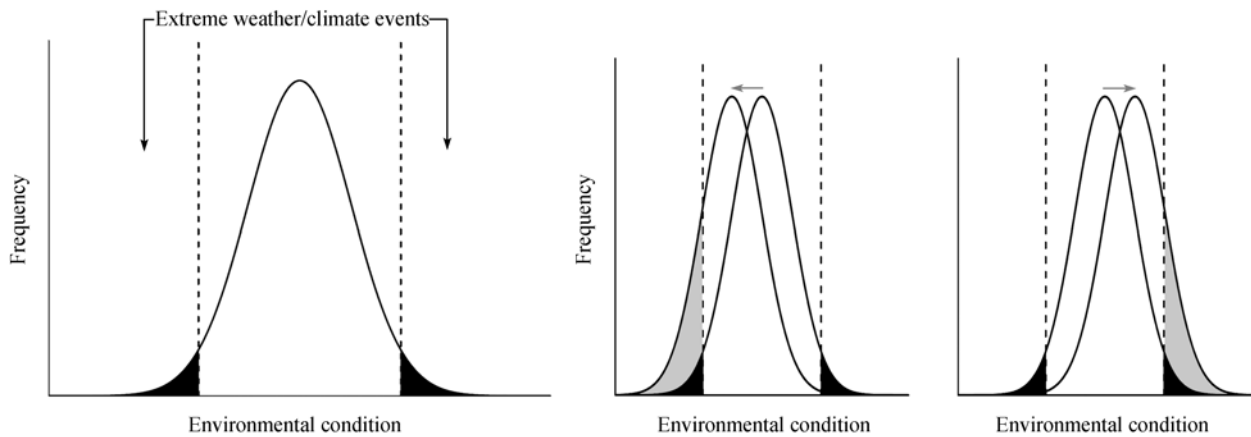
Fig. 1   Weather or climatic variables such as temperature, assuming a normal distribution
The black shaded areas represent extreme events such as extreme heat at the right end of the curve and extreme cold at the left hand end. The lower left hand panel shows a shift in the mean frequency to the left resulting in greater likelihood of more extreme cold events (gray shaded area). A shift in mean to the right (lower right hand panel) results in greater likelihood of extreme heat events. Modified and expanded from Meehl et al. (2000b). With permission of the author and the American Meteorological Society.
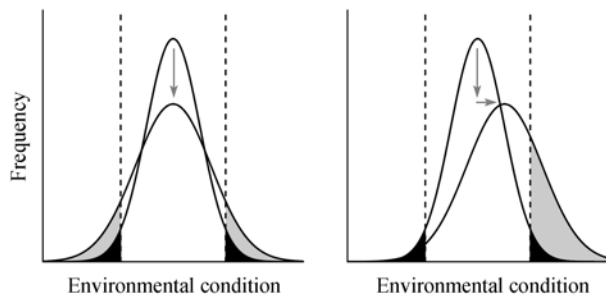

Fig. 2   Weather or climatic variables such as temperature, assuming a normal distribution as shown in Fig. 1
The black shaded areas represent extreme events such as, for example, extreme heat at the right end of the curve and extreme cold at the left hand end. Left panel shows effects of a change in variance of weather events with the mean decreasing and the curve expanding resulting in more extreme temperature events (gray shading). Right panel shows the effects of a combination of decreased variance and a shift to the right with the mean. An even greater likelihood of extreme heat events results (gray shaded area). If the shift were to the left, then an increase in the likelihood of extreme cold events would occur. Modified and expanded from Meehl et al. (2000b), with permission of the author and the American Meteorological Society.

Weather data from England show that small changes in average temperature, e.g. 1–2°C are accompanied by an increase in the frequency of extreme summer heat events from once every 75 years to once every 3 years (1.3% to 33%, Munich Rev., 2002; Francis and Hengeveld, 1998). In France, reduced overnight low temperatures over many years are accompanied by increased hail storms and severe thunderstorms (Dessens, 1995; Francis and Hengeveld, 1998). In the U.S.A. warmer temperatures tend to bring heavier precipitation in some areas (Gordon et al., 1992; Francis and

Hengeveld, 1998). All types of extreme weather have increased in frequency and intensity.

Beniston and Stephenson (2004) point out the difficulty of comparing extreme conditions in one area to another (see also Francis and Hengeveld, 1998). For example, wind extremes on the ocean may not have as severe an impact as in a tropical forest. Twenty centimeters of snow in Washington DC is perceived as an extreme condition, but not in Montreal (Francis and Hengeveld, 1998). Furthermore, it is probably not appropriate to assume that each individual in a population experiences extreme conditions in the same way. For example, one individual with a good territory with shelter and food will likely be less affected by severe weather than a neighboring individual with a poor quality territory with less food and shelter.

The considerable database on global climate change indicates that the predictable seasonal change in weather is shifting. This includes earlier springs, shorter winters, or changes in rainy and dry seasons. Organisms must shift their life cycles to match changing phenology, and those that are unable to adjust become "mismatched" with serious consequences for fitness (e.g. Visser et al., 2004). Superimpose on this the increased frequency and intensity of unpredictable weather events, then coping strategies such the emergency life history stage (Wingfield et al., 1998; Wingfield, 2003) are expressed more frequently and for longer (Wingfield, 2008) tending to disrupt the normal life cycle more. Next, it is important to consider types of perturbation factors that may contribute to extreme conditions.

3   How Can Extreme Events Affect Vertebrates? The Concept of Perturbation Factors

The dual issues of extreme conditions – predictable environments such as deserts, polar regions etc., and extreme events that are transitory and then return to normal are critical concepts. Events can be unpredictable in terms of timing, intensity and duration with many being brief (labile perturbations) and others more permanent (such as climate change, human disturbance). These kinds of unpredictable changes (perturbations of the environment) can contribute markedly to extreme conditions. There are three major types:

1) Permanent perturbation factors. Permanent changes in the environment result in death, chronic stress, or some form of acclimatization. Examples are injury resulting in permanent disability, infection (parasite load), global climate change, human disturbance (urbanization, habitat degradation), pollution (endocrine disruption) and invasive species that change the environment and compete for resources such as food and shelter.

2) Labile perturbation factors - indirect, i.e. reactive responses. These happen suddenly, usually with little warning, and the individual shows a behavioral and physiological response that is extremely fast (Wingfield et al., 1998). For example, an attack by a predator results in a brief chase with escape. Psycho-social stress fits this category such as an attack by a dominant. Examples from the physical environment include a brief severe storm (e.g. tornado, thunderstorm), fire, or a flood from rain that fell many kilometers away (e.g. desert streams), earthquakes, tsunamis, volcanic eruption, or running from a falling rock or tree. The individual must respond immediately to this sudden threat, usually with a fight or flight response. The event may be over in seconds and probably does not contribute significantly to longer term energy costs (assuming the individual survives).

3) Labile perturbation factors - direct (proactive). Longer term perturbations (hours to days and even weeks) can reduce resources such as food resulting in physiological and behavioral responses that allow an individual to take proactive action called the "emergency life history stage". This redirects the individual away from the normal life history stage (such as breeding, migrating) and promotes survival until the perturbation passes (e.g. Wingfield and Ramenofsky, 1999;

Wingfield et al., 1998). 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, hypoxia, and repeated acute stressors.

Together, the different types of perturbation factors combined with predictable environmental conditions can contribute to what is perceived by the individual as extreme conditions. If these conditions are short-lived, then an individual can probably cope without significant loss of fitness. But, if such conditions persist for weeks and months, or occur frequently as predicted for severe weather events, then the individual may be taxed beyond the scope of physiological and behavioral coping mechanisms.

4   Habitat Configuration: Vulnerability of Local Habitat to Extreme Events

4.1   Habitat configuration

An individual experiences its habitat in a unique way, sometimes very differently from its neighbor just meters away. This may be because of internal differences such as parasite load and injuries, social status, and to external differences such as microhabitat, presence of predators, etc. These may also interact to give complex individual experiences of the environment and therefore how it responds and regulates physiology, morphology and behavior. Because the conditions an individual experiences may lead to extremes for one but not another it is important to consider how the habitat is configured around particular individual.

Configuration is defined as the way parts or elements of something are arranged to fit together. Internal state (parasites, energy reserves, injury, age), integrated with external conditions in the habitat itself (e.g. territory/home range quality, weather and exposure, shelter, predators, population density) and social status determine how challenging environmental conditions may be. An individual must find a configuration of habitat that provides sufficient food so that it can fuel daily and annual routines, including breeding, and provides shelter against unpredictable perturbations etc. Available trophic resources must also cover costs of internal components such as parasites, injury, social status etc. Change in habitat configuration from perturbations such as human disturbance can also be a major upheaval and have potentially serious consequences for fitness.

4.2   Components of habitat configuration

The complex interactions of external and internal

factors are probably very extensive and some examples are listed in Table 1. This is by no means complete, and prior experience of extreme events can, through learning, also provide skills for dealing with perturbations in the future. Assessing such complex interactions will require a theoretical and biophysical approach that allows testable predictions about variation in biological processes under natural conditions, especially the interaction of abiotic and biotic factors. Porter et al. (2002) and Pörtner and Farrell (2008) use models for ecological predictions concerning distribution, energetic requirements and predator-prey interactions that have direct relevance to identifying extreme conditions, especially at the individual level. Although defining what constitutes extreme conditions should be tested widely, it is pertinent to ask how components of the external, internal and social environments might combine to become extreme conditions. Food and related resources are obvious potential factors in the following scenarios. Resources may be abundant for a limited but predictable period only or may be abundant for a limited but unpredictable period only. Alternately, resources may never be abundant, i.e. they are dispersed and difficult to obtain, or they may be highly abundant, whether seasonally or patchily concentrated. Some individuals with poor territories, or low social status and limited access to resources when available, experience extreme conditions whereas others with better territories and higher social status do not. Other variables of the physical environment that contribute to extreme conditions include the following. Temperature, wind speed and precipitation can all vary daily and seasonally in predictable or unpredictable ways, but must still allow some primary production unless the individual depends upon aeolian food resources. Additional examples are low partial pressure of oxygen, extremes of pH and osmotic pressure, trace element deficiency, high barometric pressure, and intense radiation. Extremes of social environment contribute in other ways such as position in hierarchy, especially at rare and patchy resources. Anthropogenic factors are important contributors to potentially extreme conditions including environmental pollutants, human disturbance, and habitat destruction/modification (Nisbet, 2000; Walker et al., 2005)

The next question is: do problems arise as the individual or population encounters more than one set of extreme conditions outlined above? Even in mesic habitats, extreme conditions could prevail if, for example, social extremes and human disturbance were combined. Recent work has shown that in cold climates such

as arctic and alpine regions, photoperiodic responses of plants regulate development at a time in spring when the likelihood of killing frosts is low (Keller and Körner, 2003). An early warm spell could result in premature development and vulnerability to subsequent sub-freezing conditions that would kill delicate spring growth (Heide et al., 1990). Plants become more responsive to local temperature as spring progresses (Prock and Körner, 1996). As global climate change results in earlier and earlier springs, plant development times have also advanced, but this may not be true for all arctic and alpine plants that are photoperiodic and resistant to temperature effects early in spring. These authors subjected 33 high alpine species of plants (from the east central Alps of Austria) to 12, 14.5, 15 and 16 hours of light per day and at two temperature regimes, 11/6℃ and 18/8℃ (day/night) temperature treatments. Shorter photoperiod tended to decrease flowering regardless of temperature treatment, whereas longer photoperiods resulted in flowering even at the colder temperatures. Overall, there appeared to be three response types: those insensitive to temperature flowering at both warm and cold temperatures; those that require warmer temperatures to flower; and those flowering at cold temperatures only (Prock and Körner, 1996).

Reproductive development and onset of breeding in birds also show population differences in responses to temperature. Those populations that breed at high latitude tend to regulate reproductive function primarily through photoperiod and temperature effects are minimal. In contrast, populations breeding at lower latitudes respond to photoperiod but low environmental temperature slows down gonadal development and retards

Table 1 Potential components of habitat configuration

External	Internal
Territory/home range	Body condition
Location (central/peripheral)	Age
Food availability	Parasite load
Weather	Injury
Exposure to weather	Proactive/reactive coping style
Shelter	Social status
Population density	Pollutant load
Predator density/variety	Developmental experience
Human disturbance	Maternal (paternal) effects
Presence of mate (social status)	Ability to access food resources
Group size (social status)	
Heterospecific competition (non-predator)	
Invasive species	

Table 2   Potential factors contributing to an "extreme environment"

Food and related resources are obvious potential factors in the following scenarios:
a) Resources may be abundant for a limited but predictable period only.
b) Resources may be abundant for a limited but unpredictable period only.
c) Resources are never abundant, they are dispersed and difficult to obtain.
d) Resources are abundant (may be seasonally), but patchy (i.e. highly concentrated).
There are variable extremes of physical environment that can contribute to extreme conditions as follows:
e) Temperature extremes (well beyond the individual's thermo-neutral zone, predictable or unpredictable) may occur seasonally/ daily.
f) Wind speed may vary in extremes seasonally/daily on a predictable schedule or are unpredictable.
g) Rainfall may show extreme variation seasonally/daily on a predictable schedule or are unpredictable.
h) Other factors that can contribute to an extreme environment include drought, fire, hypoxia, human disturbance, recreational etc. (see Nisbet, 2000; Walker et al., 2005).

onset of breeding whereas warmer temperatures speed it up (e.g. Wingfield et al., 1992, 1996, 1997, 2003; Silverin et al., 2008; Dawson, 2005).

Martin and Wiebe (2004) point out the variety of morphological, physiological and behavioral adaptations birds have evolved for coping with extreme conditions and large variation in arctic/alpine habitats (see also Richardson et al., 2003; Wingfield and Hunt, 2002; Wingfield et al., 2004). Clearly there has been selection for plastic phenotypes with the capability to buffer extreme conditions and maintain reproductive output, molt and survive the winter. Martin and Wiebe (2004) use the word resilience, the ability of individuals to experience disturbance and maintain normal processes, or what we call perturbation resistance potential (see below). As an example, in alpine ptarmigan (*Lagopus* sp), harsh spring weather and summer decreased clutch size but had no effect on egg size, hatchability, and mass of the chicks. There was no effect on adult survival through the breeding season or over winter. However, body condition, the number of hens producing clutches, success of the first nest and ability to renest were significantly reduced in the harsh year (Martin and Wiebe, 2004). These authors also describe many other possible adjustments alpine breeding birds have evolved to cope with extreme conditions.

5 How Can Animals Acclimatize/ Adapt? The Importance of Allostasis Mechanisms

Given the complex interplay of environmental conditions that are predictable (e.g. climatic) and the unpredictable perturbations that contribute to extreme conditions, what do we know about physiological and behavioral coping mechanisms that allow vertebrates to acclimatize in the short term and adapt in the longer term?

Allostasis, stability through change (Sterling and Eyer, 1988; Schulkin, 2003) is an emerging concept to link energetic demands and wear and tear of everyday life with the added effects of environmental perturbations (McEwen, 2000; McEwen and Wingfield, 2003, 2010). Important concepts are allostatic load and allostatic overload. The energetic costs of existence (Ee) and daily/annual routines (Ei) together constitute the allostatic load of every day life. This load can increase when breeding, migrating etc., but the costs are more than offset by food available in the environment (Eg, see McEwen and Wingfield, 2003; Korte et al., 2004, Wingfield, 2004). We expect allostatic load to be high in organisms living in extreme environments, especially when attempting to breed. Include unpredictable perturbations of the environment and allostatic load increases further (Eo). If the sum of Ee, Ei and Eo exceeds available trophic resources (Eg), then negative energy balance results in allostatic overload type 1 (McEwen and Wingfield, 2003, 2010; Romero et al., 2009). Hormonal mediators of allostasis such as glucocorticoids then trigger the emergency life history stage shifting the individual into a coping mode that reduces allostatic load to manageable levels (McEwen and Wingfield, 2003; 2010; Korte et al., 2004; Romero et al., 2009). Eo may be more permanently elevated because of a perturbation such as habitat destruction, injury etc., but the sum of Eo, Ee and Ei does not exceed Eg. This permanent rise in allostatic load is called allostatic overload type 2 (McEwen and Wingfield, 2003) and may be an important cause of extreme conditions for individuals in any habitat.

6 What Are the Predicted Hormone Responses to Extreme Conditions?

Referring back to the dual nature of extreme conditions, we can predict that hormone regulatory systems

associated with daily and annual routines would be modified for vertebrates adapted to extreme environments such as deserts, polar regions etc. Examples are hormones involved with daily metabolism, growth, migrations and reproduction. Additionally, the classical hormonal responses to unpredictable perturbations of the environment (endocrine stress responses) will also be modified and modulated over the year (e.g. Wingfield and Sapolsky, 2003). In extreme environments there are examples of very specialized hormone regulatory adaptations such as growth hormone control of antifreeze proteins in Antarctic fish (Idler et al., 1989; Fletcher et al., 1989) and hypoxia-induced proteins that regulate reproduction in fishes exposed to seasonal hypoxia in the Gulf Coast of North America (e.g. Thomas et al., 2007). There is an urgent need for more investigations of hormone regulatory mechanisms for physiology and behavior in extreme conditions, but here we will focus on one example that has been explored: birds breeding on the arctic tundra. For migrant birds arriving in the Arctic in spring, the potential for allostatic overload type 1 is very great and a variety of strategies, micro-habitats, varied diets etc. are used as well as hormone-behavior adaptations that allow them to cope so that breeding can begin as soon as conditions are favorable (Wingfield and Hunt, 2002; Wingfield et al., 2004). These hormone-behavior adaptations include:

1) Attenuated testosterone secretion because territoriality and excess courtship may be too costly in extreme environments. These birds are single brooded and then sensitivity to testosterone attenuated by reduced responsiveness of target areas in the brain.

2) During the breeding/molt events, sensitivity to acute stress is reduced enhancing reproductive success or development of a vital new integument to combat extreme conditions during the rest of the year. This reduced sensitivity could include a) modulated response of the adrenocortical response to stress, b) reduced sensitivity to high glucocorticosteroid levels, or c) a combination of a and b.

3) Increased corticosteroid binding protein (CBP) will buffer any acute responses to stress, etc. However, modulation of CBP levels may allow quick response if necessary.

4) The enzyme 11-beta-hydroxysteroid dehydrogenase (HSD) can convert glucocorticoids to an inactive form thus providing a deactivation shunt. Conversely, another form of this enzyme potentiates the active form ensuring activation glucocorticoid and mineralocorticoid receptors. Future studies of these enzyme systems

that determine access of glucocorticoids to receptors within the cell will likely be pivotal.

5) Changed sensitivity of hypothalamo-pituitary-adrenocortical axis as well as altered feedback sensitivity of glucocorticoids to hypothalamic and pituitary secretions.

Much more work remains to be done to determine mechanisms by which these changes occur, how they are regulated and how diverse these mechanisms may be across populations in different ecosystems and hemispheres. Are there constraints on the regulatory mechanisms with which vertebrates cope with extreme conditions, or have they evolved many different ways to endure?

7   Resilience: Perturbation Resistance Potential

As pointed out by Martin and Wiebe (2004) organisms that live in extreme environments and/or are exposed to unpredictable perturbations that result in extreme events have evolved physiological and behavioral strategies to cope. The allostasis model allows a framework to explain individual as well as population changes in allostatic load (McEwen and Wingfield, 2003). This includes resilience or the ability to resist environmental perturbations that would normally result in allostatic overload type 1. A potential mechanism is variation in the adrenocortical response to stress providing resistance potential to environmental perturbations. Modulation of the adrenocortical response to stress implies suppression to allow life history stages to be expressed and enhance fitness (Jacobs, 1996, Fig. 3). There is an adaptive value to expressing the emergency life history stage (ELHS) reflecting the extent to which the adrenocortical response to stress should be expressed. As the adaptive value of expressing the ELHS decreases it reaches a critical adaptive value when there is zero benefit (Fig. 3). At this point it is predicted that the adrenocortical response to stress would be partially or completely suppressed (Jacobs, 1996). In general, it is always adaptive to express the ELHS over a wide range of environmental predictability (Fig. 3). It is possible that in environments with very low predictability (chaotic) or very high predictability (constant) that the ELHS would not confer any fitness advantage (i.e. below the critical adaptive value) and the stress response would be absent (Fig. 3). However, there are times during the life cycle when the ELHS may also have lower adaptive value (Fig. 3).
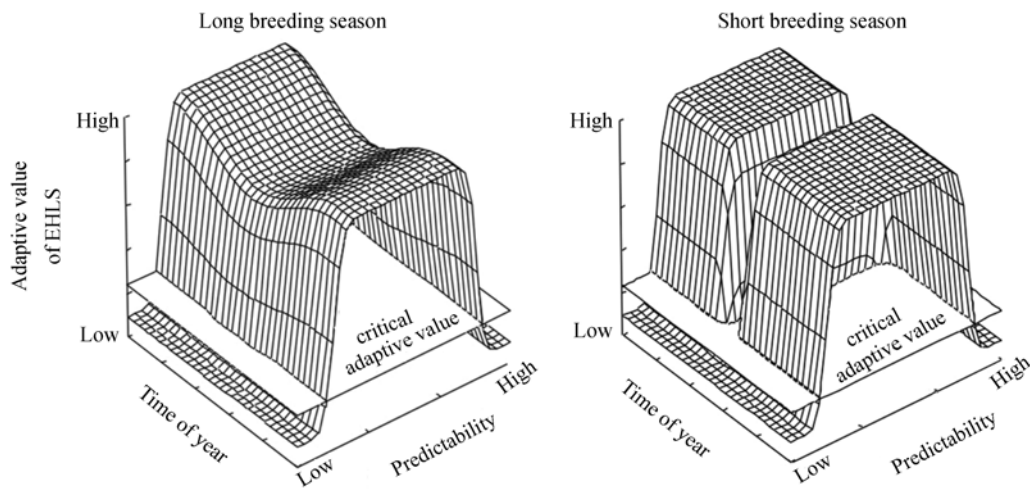
Fig. 3   Three dimensional figures showing the value of expressing an emergency life history stage (ELHS) as a function of time of year and predictability (stability) of environmental conditions

The vertical axes are the adaptive value of the ELHS that also reflects the extent to which the adrenocortical response to stress should be expressed. As the adaptive value of expressing the ELHS decreases it reaches a critical adaptive value when there is zero benefit. At this point, it is predicted that the adrenocortical response to stress would also be completely suppressed (Jacobs, 1996). In general, it is always adaptive to express the ELHS over a wide range of environmental predictability. It is possible that in environments with very low predictability (chaotic) or very high predictability (constant) that the ELHS would not confer any fitness advantage (i.e. below the critical adaptive value) and the stress response would be absent. However, there are times during the life cycle when the ELHS may also have lower adaptive value. An example (right hand panel) is a short breeding season when there is a trade-off of individual survival and reproductive success in the face of severe environmental conditions. Here the adaptive value of an ELHS falls below the critical level and the stress response should be suppressed. In the left hand panel, the trade-off of reproductive success and resistance to perturbations is weaker when the breeding season is longer allowing several potential nesting events. In this case the adaptive value of expressing an ELHS remains above the critical value and modulation of the stress response would be absent or slight (from Jacobs, 1996, with permission).

As the adaptive value of expressing an ELHS decreases, then the resistance potential (suppressed adrenocortical response to stress) increases (Fig. 4). This might be a linear response (solid line) or non linear (dashed line), or somewhere between those lines. The brood value hypothesis (Bokony et al., 2009) is a good explanation for why some individuals suppress the stress response and others do not. Furthermore, maximum corticosterone levels generated by acute stress reach higher levels in species that have higher annual survival rates (Hau et al., 2010). It should be borne in mind that the very act of suppressing the stress response to acute perturbations reduces the individual's ability to cope that may incur a cost in terms of allostatic load, "wear and tear", which could potentially reduce fitness in the long term. Conversely, suppressing the stress response may incur benefits in the short term by enhanced reproductive success and high quality molt that improves survival until the next breeding season.

Resource holding power of a resident of a territory or of high social status has an advantage to endure possible perturbations with potential for greater reproductive success, over winter survival etc. (e.g. Haley, 1994;

Hurd, 2006). Resource holding potential may result in even more benefits if the territory is high quality
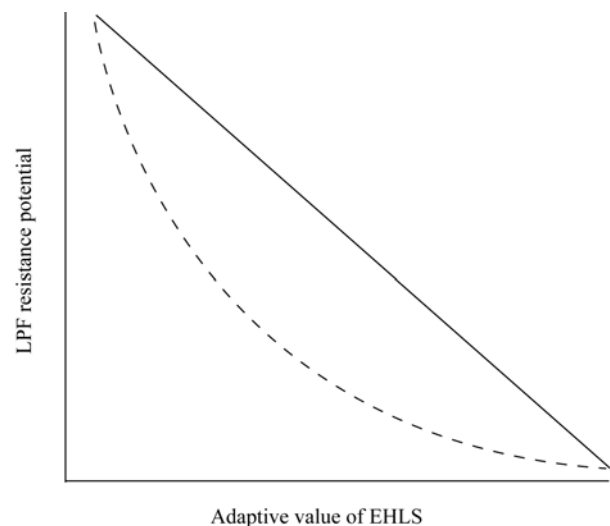

Fig. 4   As the adaptive value of expressing an emergency life history stage (ELHS) decreases, then the resistance potential [suppressed adrenocortical response to stress in relation to a Labile Perturbation Factor (LPF)] increases

This might be a linear response (solid line) or non linear (dashed line), or somewhere between those lines.

(Nijman and Heuts, 2000) and when social inertia is involved (Veiga et al., 2001). Resistance potential to labile perturbation factors (LPFs) varies with condition (Fig. 5) being decreased with low body condition but increased as body condition improves. Individuals in the best condition will be more resistant to LPFs and will show a blunted adrenocortical response to acute stress. Resistance potential will be less when LPFs are severe (dashed line) versus milder LPFs (solid line) and increases as basic energetic costs of daily and seasonal routines ($Ee+Ei$) decrease (Fig. 5). If the costs of daily/seasonal routines are low, extra resources can be dedicated to resisting effects of LPFs. Resistance potential to LPFs decreases as another function of body condition, degree of infection and disease (Fig. 5). Again, the slopes will be greater for severe LPFs and shallower for mild LPFs and will be higher in individuals with lower costs of daily/seasonal routines.

Building on Fig. 5, changes in resistance potential can be affected by costs of daily and seasonal routines ($Ee+Ei$) and resources available (Eg, Fig. 6). If resistance potential is decreased by disease, human disturbance, invasive species etc. then $Ee+Ei$ is effectively increased (Fig. 6). Any given perturbation, represented by Eo, beginning at the same time would trigger allostatic overload type 1 earlier. Higher $Ee+Ei$ is similar to allostatic overload type 2 and illustrates how it would interact with overload type 1. This effect can be exacerbated if Eg decreases and $Ee+Ei$ increases (Fig. 6). Conversely, lower $Ee+Ei$ will increase resistance poten-

tial and a perturbation will take longer to result in allostatic overload type 1 and trigger an ELHS (Fig. 6). If Eg also increases as $Ee+Ei$ is lowered then resistance potential becomes even greater (Fig. 6).

Another way of looking at LPF resistance potential is to consider the slope of Eo influenced by such factors as body condition (Fig. 7). For example, fat reserves will result in progressively shallower Eo lines with the steepest with no fat and the shallowest with most fat (Wingfield, 2004). Thus an ELHS will be triggered progressively later the more fat an individual has (Fig. 7) in relation to the same Eo. The same curves could be generated for social status with the steep curve for a subordinate and the shallowest for a dominant. Note that curves are different from those generated earlier (Wingfield, 2004; Goymann and Wingfield, 2004).

8   Conclusions

Extreme conditions can be found in severe environments such as polar regions, deserts and deep ocean. Although organisms may be highly adapted to live in such environments, they are vulnerable to further unpredictable perturbations that can tax an individual beyond the reaction norms for morphology, physiology and behavior. Even for populations in mesic environments, some individuals may have chronically elevated allostatic load because of low social status, poor territory quality and injury or infection. Taken together such high allostatic load represents extreme conditions compared with nearby neighbors that have a lower allostatic
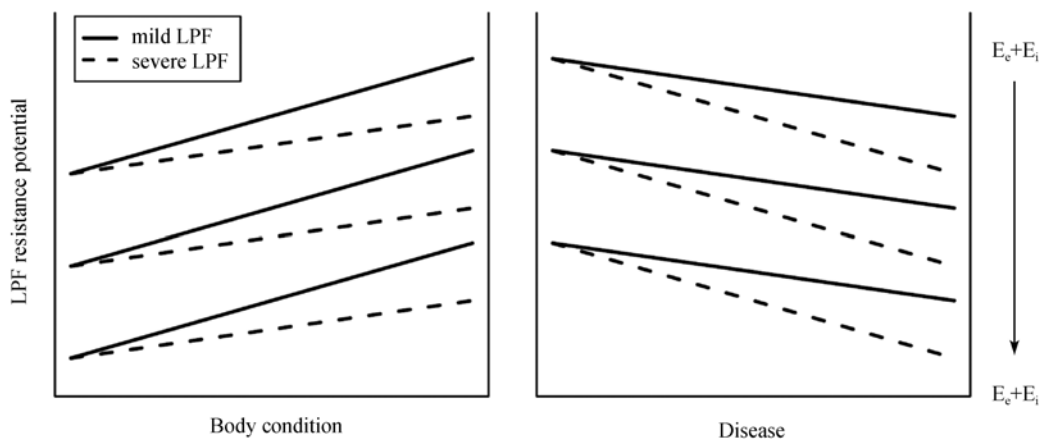

Fig. 5   Labile Perturbation Factor (LPF) resistance potential varies with condition
Resistance potential is decreased with low body condition but increases as body condition improves (left hand panel). Individuals in the best condition will be more resistant to LPFs and will show a blunted adrenocortical response to stress. Resistance potential will be less when LPFs are severe (dashed line) versus milder LPFs (solid line) and increases as basic energetic costs of daily and seasonal routines ($Ee+Ei$) decrease. If costs of daily/seasonal routines are low, extra resources can be dedicated to resisting effects of LPFs. Resistance potential to LPFs decreases as another function of body condition, degree of infection, and disease (right hand panel). The slopes will be greater for severe LPFs and shallower for mild LPFS. Additionally, beginning resistance potential will be higher in individuals with lower costs of daily/seasonal routines.
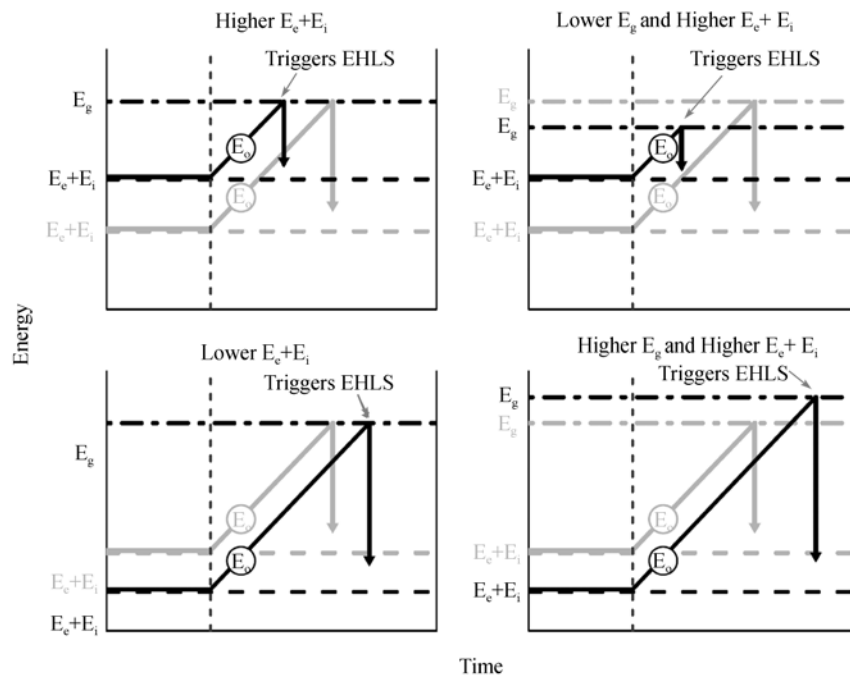
Fig. 6   The interaction of labile perturbation factor (LPF) resistance potential changes with costs of daily routines and resources available

Building on Fig. 5, this figure shows how changes in LPF resistance potential can be affected by costs of daily and seasonal routines ($Ee+Ei$) and resources available (Eg). If resistance potential is decreased by disease, human disturbance, invasive species etc. then $Ee+Ei$ is increased (top left panel). Any given perturbation represented by Eo and starting at the same time, would trigger allostatic overload type 1 earlier. Higher $Ee+Ei$ is similar to allostatic overload type 2 and shows how it could interact with overload type 1. This effect can be exacerbated if Eg decreases and $Ee+Ei$ increases (top right panel). Type 1 allostatic overload will trigger an emergency life history stage (ELHS) almost immediately. Conversely, a lower $Ee+Ei$ will increase resistance potential and a perturbation will take longer to result in allostatic overload type 1 and trigger an ELHS (lower left panel). If Eg also increases as $Ee+Ei$ is lowered then resistance potential becomes even greater (lower right panel).
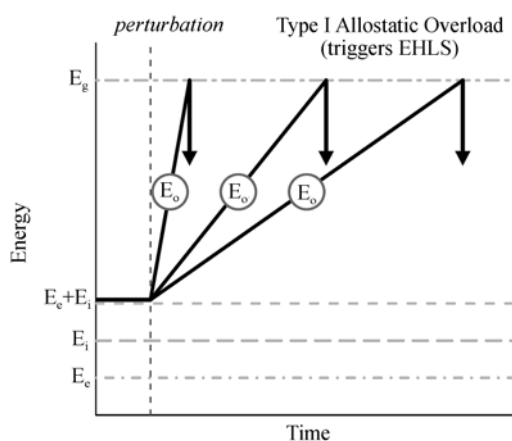

Fig. 7   The effects of labile perturbation factor (LPF) resistance potential on time to Type I allostatic overload

An additional way of looking at LPF resistance potential is to consider the nature of Eo. The slope of Eo can be influenced by such factors as body condition. For example, fat depot will result in progressively shallower Eo lines with the steepest with no fat and the shallowest with more fat. Thus an ELHS will be triggered progressively later the more fat an individual has. LPF resistance potential is thus increased with fat score in relation to the same Eo. The same curves can be generated for social status with the steep curve for a subordinate and the shallowest for a dominant. Note that curves are different from those generated earlier (Wingfield 2004; Goymann and Wingfield, 2004).

load. The physiological mechanisms by which organisms cope with extreme conditions have advanced over the past decades, but the hormonal mechanisms by which physiological and behavioral responses to extreme events are regulated have lagged behind. The concept of allostasis, and the related concepts of allostatic load and overload, have potential as a framework to determine if vertebrates in their environment are experiencing extreme conditions and to understand the hormonal control (reactive scope) mechanisms. Integrating hormonal, physiological and behavioral studies will be key to understanding why some populations and individuals are able to cope with extremes and others are not.

References

Bartholomew GA, 1958. The role of physiology in the distribution of terrestrial vertebrates. In: Hubbs CL ed. Zoogeography. Publ. 51, Washington D.C.: AAAS, 81–95.

Bartholomew GA, 1964. The roles of physiology and behavior in the maintenance of homeostasis in the desert environment. In: "Homeostasis and Feedback Mechanisms" Proc. XVIIIth. Symp. Soc. Exp. Biol. Pp. 7–29.

Bartholomew GA, 1966. Interaction of Physiology and Behavior under Natural Conditions. In: Bowman RJ ed. The Galapagos. Berkeley: Univ. Calif. Press, 39–45.

Beniston M, Stephenson DB, 2004. Extreme climatic events and their evolution under changing climatic conditions. Global Planetary Change 44: 1–9.

Bókony V, Lendvai AZ, Liker A, Angelier F, Wingfield JC et al., 2009. Stress response and the value of reproduction: Are birds prudent parents? Am. Nat. 173: 589–598.

Dawson A, 2005. The effect of temperature on photoperiodically regulated gonadal maturation, regression and molt in starlings: Potential consequences of climate change. Funct. Ecol. 19: 995–1000.

Deschenes O, Moretti E, 2009. Extreme weather events, mortality and migration. Rev. Econ. Stats. 91: 659–681.

Dessens J, 1995. Severe convection weather in the context of a nighttime global warming. Geophys. Res. Lett. 22: 1241–1244.

Easterling DR, Meehl GA, Parmesan C, Changon SA, Karl TR et al., 2000. Climate extremes: Observations, modeling and impacts. Science 289: 2068–2074.

Fletcher GL, Goddard SV, Davies PL, Gong Z, Ewart, KV, 1989. New insights into fish antifreeze proteins: Physiological significance and molecular regulation. In: Pörtner HO ed. Cold Ocean Physiology. Ottawa: Can. Soc. Zool., 239–265.

Gaston KJ, Chown SL, Calosi P, Bernardo J, Bilton DT et al., 2009. Macrophysiology: A conceptual reunification. Amer. Nat. 174: 595–612.

Gordon HB, Whetton PH, Pittock AB, Fowler AM, Haylock MR, 1992. Simulated changes in daily rainfall intensity due to the enhanced green-house effect: Implications for extreme rainfall events. Climate Dynam. 8: 83–102.

Goymann W, Wingfield JC, 2004. Allostatic load, social status, and stress hormones: The costs of social status matter. Anim. Behav. 67: 591–602.

Greenhough G, McGeehin M, Bernard SM, Trtanj J, Riad J et al., 2010. Extreme weather events in the United States. Environ. Health Perspect. 109: 191–198.

Haley MP, 1994. Resource holding power asymmetries, the prior residence effect, and reproductive payoffs in male northern elephant seal fights. Behav. Ecol. Sociobiol. 34: 427–434.

Hau E, Ricklefs RE, Wikelski M, Lee KA, Brawn JD, 2010. Corticosterone, testosterone and life-history strategies of birds. Proc. R. Soc. B 277: 3203–3212.

Heide O, Pederson K, Dahl E, 1990. Environmental control of flowering and morphology in the high-arctic *Cerastium regelii*, and the taxonomic status of *C. jenisejense*. Nordic J. Botany 10: 141–147.

Hurd PL, 2006. Resource holding potential, subjective value, and game theoretical models of aggressiveness signaling. J. Theor. Biol. 241: 639–648.

Idler DR, Fletcher GL, Belkhode S, King MJ, Hwang SJ, 1989. Regulation of antifreeze protein production in winter flounder: A unique function for growth hormone. Gen. Comp. Endocrinol. 74: 327–334.

Jacobs J, 1996. Regulation of Life History Strategies Within Individuals in Predictable and Unpredictable Environments. PhD Thesis, University of Washington.

Katz RW, Brown BG, 1992. Extreme events in a changing climate: Variability is more important than averages. Clim. Change 21: 289–302.

Keller F, Körner C, 2003. The role of photoperiodism in alpine plant development. Arctic, Antarctic Alpine Res. 35: 361–368.

Korte SM, Koolhaas JM, Wingfield JC, McEwen BS, 2004. 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.

Martin K, Wiebe KL, 2004. Coping mechanisms of alpine and arctic breeding birds: Extreme weather and limitations to reproductive resilience. Integr. Comp. Biol. 44: 177–185.

McEwen B, 2000. Allostasis and allostatic load: Implications for neuropsychopharmacology. Neuropsychopharmacol. 22: 108–124.

McEwen BS, Wingfield JC, 2003. The concept of allostasis in biology and biomedicine. Horm. Behav. 43: 2–15.

McEwen BS, Wingfield JC, 2010. Commentary: What is in a name? Integrating homeostasis, allostasis and stress. Horm. Behav. 57: 105–111.

Meehl GA, Zwiers F, Evans J, Knutson T, Mearns L et al., 2000a. 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.

Meehl GA, Karl T, Easterling DR, Changon S, Pielke Jr R et al., 2000b. An introduction to trends in extreme weather and climate events: Observations, socioeconomic impacts, and model projection. Bull. Am. Meteorolog. Soc. 81: 413–416.

Munich Rev, 2002. Topics, An Annual Review of Natural Catastrophes. Munich: Munich Reinsurance Company Publications, 49.

Nijman V, Heuts BA, 2000. Effect of environmental enrichment upon resource holding power in fish in prior residence situations. Behav. Proc. 49: 77–83.

Nisbet ICT, 2000. Disturbance, habituation, and management of waterbird colonies. Waterbirds 23: 312–332.

Parmesan C, Root TL, Willig MR, 2000. Impacts of extreme weather and climate on terrestrial biota. Bull. Am. Meteorolog. Soc. 81: 443–450.

Porter WP, Sabo JL, Tracy CR, Reichman OJ, Ramankutty N, 2002. Physiology on a landscape scale: Plant-animal interactions. Integ. Comp. Biol. 42: 431–453.

Pörtner HO, Farrell AP, 2008. Physiology and climate change. Science 322: 690–692.

Prock S, Körner C, 1996. A cross continental comparison of phenology, leaf dynamics and dry matter allocation in arctic and temperate zone herbaceous plants from contrasting altitudes. Ecol. Bull. 45: 93–103.

Richardson MI, Moore IT, Soma KK, Fu-Min L, Wingfield JC, 2003. How similar are high latitude and high altitude habitats? A review and a preliminary study of the adrenocortical response to stress in birds of the Qinghai-Tibetan plateau. Acta Zool. Sinica 49: 1–19.

Romero LM, Dickens MJ, Cyr NE, 2009. The reactive scope model: A new model integrating homeostasis, allostasis and stress. Horm. Behav. 55: 375–389.

Root TL, 1988a. Environmental factors associated with avian distributional limits. J. Biogeogr. 15: 489–505.

Root TL, 1988b. Energy constraints on avian distributions and abundances. Ecology 69: 330–339.

Root TL, 1994. Scientific/philosophical challenges of global change research: A case study of climatic changes on birds. Proc. Amer. Philos. Soc. 138: 377–384.

Rosenzweig C, Iglesias A, Yang XB, Epstein PR, Chivian E, 2001. Climate change and extreme weather events: Implications for food production, plant diseases and pests. Global Change Human Health 2: 90–104.

Schulkin J, 2003. Rethinking Homeostasis: Allostatic regulation in Physiology and Pathophysiology. Cambridge: MIT Press.

Silverin B, Wingfield JC, Stokkan K-A, Massa R, Järvinen A et al., 2008. Ambient temperature effects on photo-induced gonadal cycles and hormonal secretion patterns in great tits from three different breeding latitudes. Horm. Behav. 54: 60–68.

Sterling P, Eyer J, 1988. Allostasis: A New Paradigm to Explain Arousal Pathology. In: Fisher S, Reason J ed. Handbook of Life Stress, Cognition and Health. New York: John Wiley & Sons, 629–649.

Thackeray SJ, Sparks TH, Frederiksen M, Burthes S, Bacon P et al., 2010. Trophic level asynchrony in rates of phonological change for marine, freshwater and terrestrial environments. Global Change Biol. 16: 3304–3313.

Thomas P, Rahman MS, Khan IA, Kummer JA, 2007. Widespread endocrine disruption and reproductive impairment in an estuarine fish population exposed to seasonal hypoxia. Proc. R. Soc. B 274: 2692–2701.

Tucker P, Gilliland J, 2007. The effect of season and weather on physical activity: A systematic review. Public Health 121: 909–922.

Veiga JP, Moreno J, Cordero PJ, Minguez E, 2001. Territory size and polygyny in the spotless starling: Resource-holding potential or social inertia? Can. J. Zool. 79: 1951–1956.

Viera VM, Le Bohec C, Coté SD, Groscolas R, 2006. Massive breeding failure following a tsunami in a colonial seabird. Polar Biol. 29: 713–716.

Visser ME, Both C, Lambrechts MM, 2004. Global climate change leads to mistimed avian reproduction. Adv. Ecol. Res. 35: 89–110.

Walker BG, Boersma PD, Wingfield JC, 2005. Field endocrinology and conservation biology. Integr. Comp. Biol. 45: 12–18.

Wingfield JC, 2003. Control of behavioral strategies for capricious environments. Anim. Behav. 66: 807–816.

Wingfield JC, 2004. Allostatic load and life cycles: Implications for neuroendocrine mechanisms. In: Schulkin J ed. Allostasis, Homeostasis and the Costs of Physiological Adaptation. Cambridge: Cambridge University Press, 302–342.

Wingfield JC, 2008. Comparative endocrinology, environment and global change. Gen. Comp. Endocrinol. 157: 207–216.

Wingfield JC, Breuner C, Jacobs JD, Lynn S, Maney D et al., 1998. Ecological bases of hormone-behavior interactions: The "Emergency Life History Stage". Amer. Zool. 38: 191–206.

Wingfield JC, Hahn TP, Levin R, Honey P, 1992. Environmental predictability and control of gonadal cycles in birds. J. Exp. Zool. 261: 214–231.

Wingfield JC, Hahn TP, Wada M, Astheimer LB, Schoech S, 1996. Interrelationship of day length and temperature on the control of gonadal development, body mass and fat depots in white-crowned sparrows *Zonotrichia leucophrys gambelii*. Gen. Comp. Endocrinol. 101: 242–255.

Wingfield JC, Hahn TP, Wada M, Schoech S, 1997. Effects of day length and temperature on gonadal development, body mass and fat depots in white-crowned sparrows *Zonotrichia leucophrys pugetensis*. Gen. Comp. Endocrinol. 107: 44–62.

Wingfield JC, Hahn TP, Maney DL, Schoech SJ, Wada M et al., 2003. Effects of temperature on photoperiodically-induced reproductive development, circulating plasma luteinizing hormone and thyroid hormones, body mass, fat deposition and molt in mountain white-crowned sparrow *Zonotrichia leucophrys oriantha*. Gen. Comp, Endocrinol. 131:143–158.

Wingfield JC, Hunt K, 2002. Arctic spring: Hormone-behavior interactions in a severe environment. Comp. Biochem. Physiol. B 132: 275–286.

Wingfield JC, Owen-Ashley NT, Benowitz-Fredericks ZM, Lynn SE, Hahn TP et al., 2004. Arctic spring: The arrival biology of migrant birds. Acta Zool. Sinica 50: 948–960.

Wingfield JC, Ramenofsky M, 1999. Hormones and the behavioral ecology of stress. In:. Balm PHM ed. Stress Physiology in Animals. Sheffield, UK: Sheffield Academic Press, 1–51.

Wingfield JC, Sapolsky RM, 2003. Reproduction and resistance to stress: When and how. J. Neuroendocrinol. 15: 711–724.