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Forum

Harshness is not Stress

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ABSTRACT

We must differentiate between stressful and harsh environments to understand animals' resilience to global change. Harshness is not stress. Stressful environments activate the physiological stress response to increase energy availability, while harsh environments inhibit the physiological stress response to save energy.

GLOSSARY

Chronic stress: Long-term activation of the stress response (e.g. >4 weeks in mammals), leading to high energy expenditure that depletes endogenous energy reserves (glycogen, fat), without overcoming the stressor, which is non-adaptive.

Harsh environment: Environments characterized by persistent and long-lasting factors that threaten homeostasis and survival if the animal remains high energy expenditure.

Harshness: Long-lasting environmental conditions which decrease energy availability.

Harshness response: Behavioral and physiological responses to endure harshness. The harshness response of non-migrating animals is a decrease in energy expenditure, e.g. via reductions in metabolic rate and activity, including a down-regulation of the physiological stress response.

HPA-axis: Hypothalamic-pituitary-adrenal axis which releases glucocorticoids within minutes as a response to a stressful event, increasing energy availability to the animal. An adaptive system to overcome stress.

Long-term stress: Activation of the physiological stress response for extended periods of time (1 to 4 weeks in mammals).

Physiological stress response: Activation of the sympathoadrenal medullary axis and the HPA axis, which activates energy to quickly overcome the stress. Subsequently, baseline levels of stress hormones are restored via negative feedback. It is an evolved strategy to overcome stress.

Stress: Detrimental environmental events activating the physiological stress response.

Stressful environment: Environments characterized by events triggering the physiological stress response, leading to increased secretion of stress hormones causing energy mobilization.

Sympathoadrenal medullary axis: Activation of the sympathetic nervous system, which increases heartbeat and breathing and leads to an immediate release of catecholamines (adrenaline and noradrenaline). Part of the autonomic nervous system. Increases immediate energy expenditure to overcome stress.

(A) Moist spring season

Dry summer season



-2 °C - 27 °C
Most of annual rainfall
High food availability

5 °C - 42 °C
Rarely rain
Low food availability

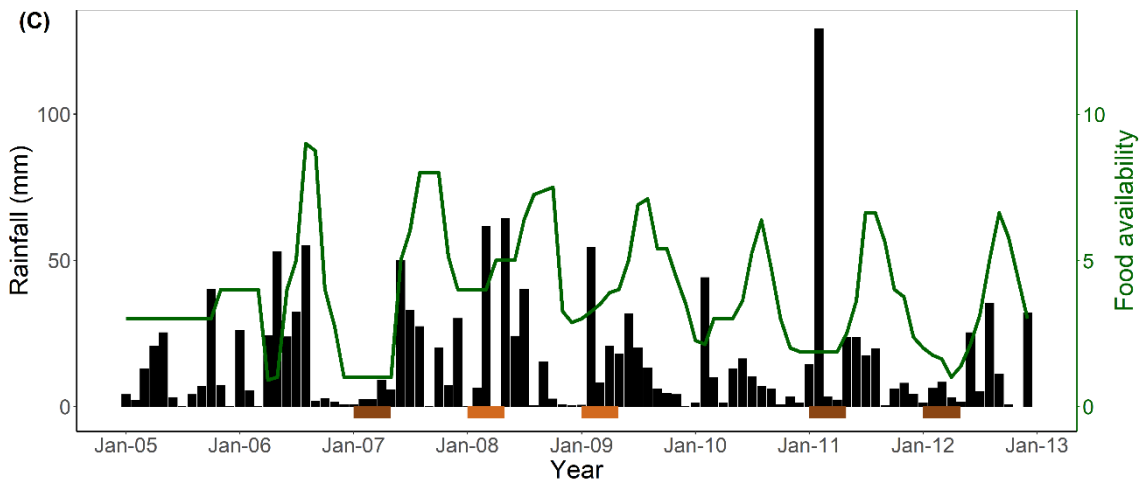
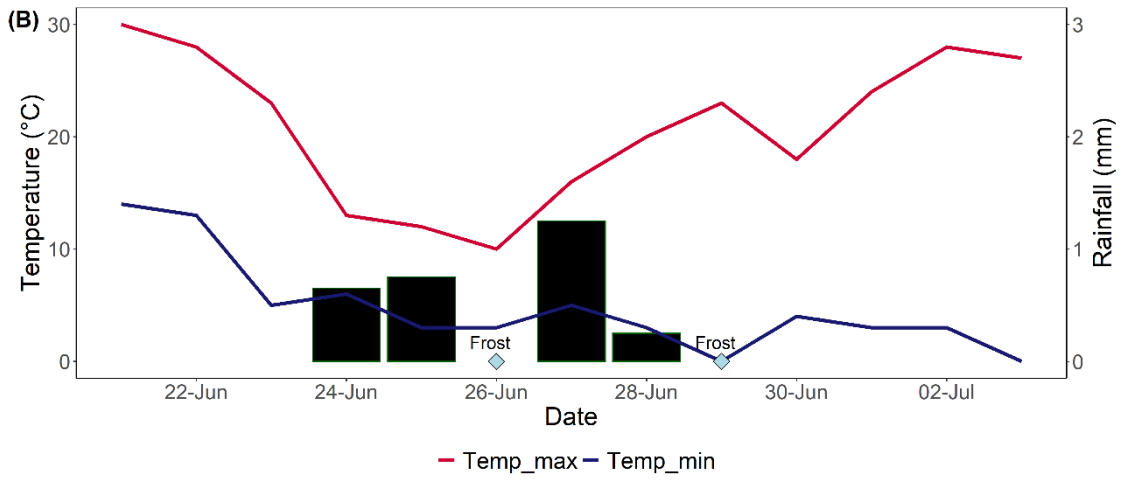


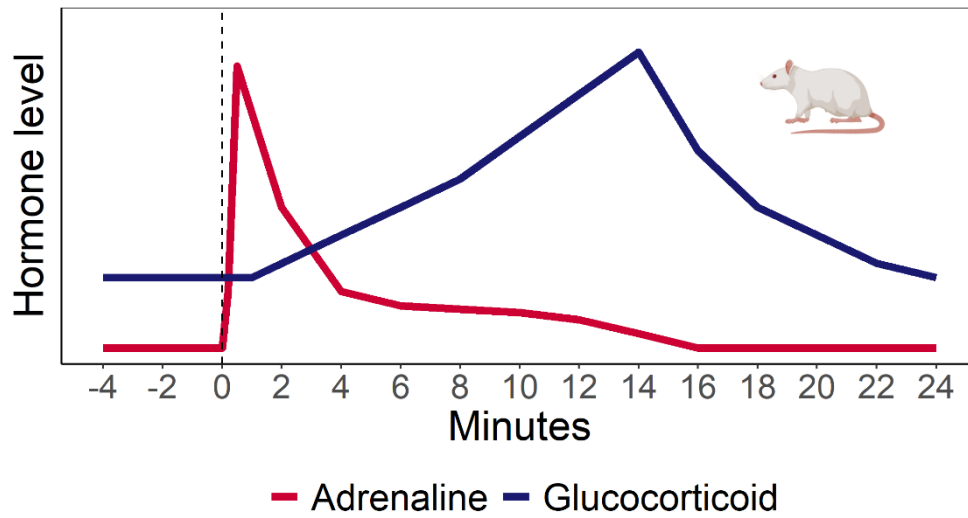
Figure 1: Weather, climate and its predictability in the Succulent Karoo semi-desert (data from the weather station at the Succulent Karoo Research Station): When is it stress, and when is it harshness?

(A) The Succulent Karoo in South Africa receives most rain in winter leading to high food availability in spring (left), The following hot dry summer is characterized by low food availability (right). Photos from R. Rimbach, Succulent Karoo Research Station.

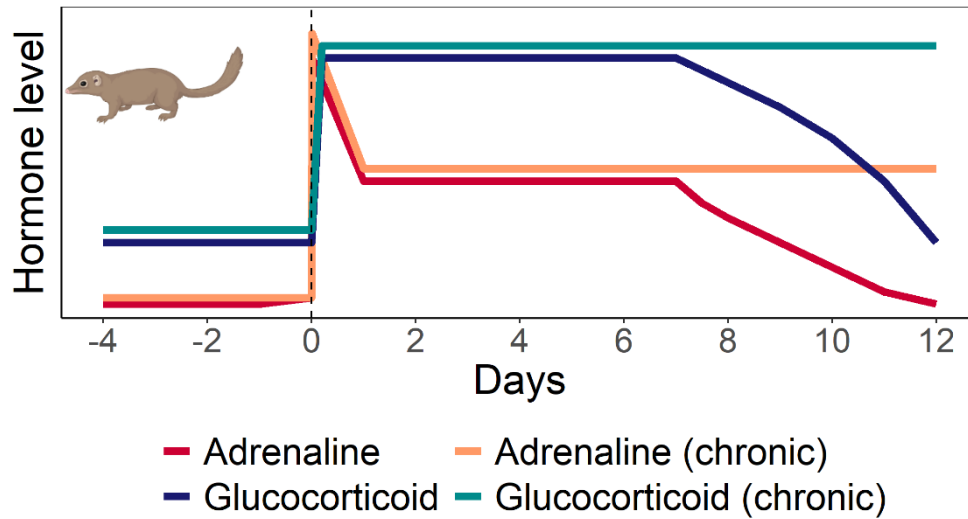
(B) Cold fronts (example from 2015) emanating from the Atlantic Ocean bring several days of rain and a sharp drop in temperatures including frost, affecting foraging and challenging thermoregulation of small mammals. This represents a stressful event requiring increased energy consumption to maintain thermoregulation in a period of reduced foraging.

(C) Rainfall and food availability (measured as food plant species / 4m²) over 8 years. The decline in food availability from the moist spring season (July-September) to the dry summer season (January-April) indicates the degree of harshness that varies from year to year. For example, a very harsh dry season in January to April 2007 (dark brown bar) was followed by dry seasons with 3-4 times higher food availability in 2008 and 2009 (light brown bars) and again very harsh dry seasons in 2011 and 2012 (dark brown bars). In each year, food was scarce for several months, harsh conditions that could not be overcome by increasing energy expenditure.

(A) Stress



(B) Long-term & chronic stress



(C) Harshness

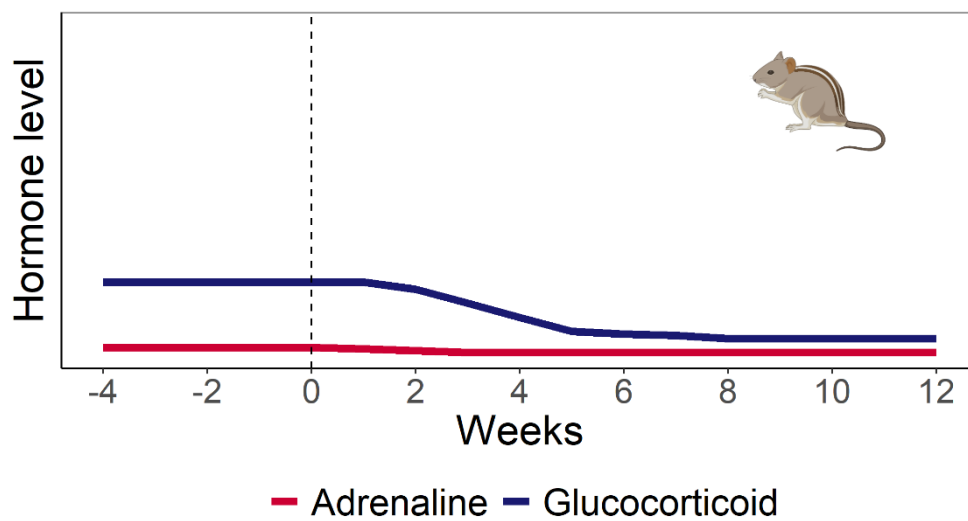


Figure 2. Physiological responses of mammals to stress, long-term and chronic stress, and harshness.

Response of the two stress systems (sympathoadrenal medullary axis secreting adrenaline and HPA-axis secreting glucocorticoids) to different environmental challenges leading either to stress (A), long-term or chronic stress (B), or creating harshness (C). The dashed line at 0 indicates the occurrence of stressful event or the onset of harsh conditions. Species drawing are from biorender.com.

(A): In laboratory rats (*Rattus norvegicus*; [1]) a short-term stressor (e.g. restraint) leads to an immediate increase in adrenaline and an increase in glucocorticoid levels within minutes that decrease again within half an hour.

(B): In tree shrews (*Tupaia belangeri*) [2], social stress within a group due to immigration or competition for dominance, increases glucocorticoid levels immediately (day 1). These levels remain high until the stressor is overcome (for example on day 8-10), e.g., when a new dominance hierarchy is established. If the stressor is not overcome, glucocorticoid levels remain chronically elevated. During the entire period, the sympathetic nervous system is activated (high sympathetic tone), leading to adrenaline levels above baseline.

(C): In striped mice (*Rhabdomys pumilio*) [3], harsh conditions, such as declining and subsequent low food availability over several weeks of the dry season (Fig. 1C), leads to a decrease in corticosterone levels, reducing energy expenditure in a period of energy restriction.

It is important to differentiate between stress and harshness

Individuals often face **stress** (see Glossary), such as extreme weather events, and **harshness**, such as long-lasting climatic extremes [4] (Fig. 1). Both stressful and **harsh environments** challenge homeostasis and survival, impacting fitness. Stress and harshness are often considered synonymous [4-9], but we maintain that the factors leading to stress differ from factors leading to harshness and that the resulting adaptive physiological responses are mutually exclusive.

Harsh environments affect social evolution and threaten biodiversity

Harsh environments with low rainfall and variable climate favor the evolution of complex animal societies with cooperative breeding [5, 8, 10]. Increasing harshness due to climate change, such as extended periods of heat and drought, has been identified as a major threat to biodiversity and ecosystem functioning [4, 7]. However, there is no clear definition of harshness, which is often wrongly assumed to be the same as stress or long-term stress [4-9]. To predict long-term consequences of harshness, we must identify which mechanisms evolved to cope with it, what their limits are, and when they might fail [11].

What is stress?

There is no consensus about the definition of **stress**, but two broad categories of definitions exist: (i) the response of an organism to any threatening or challenging environmental factor; or (ii) the activation of the **physiological stress response**. The first definition is problematic since it is subjective when factors become threatening. In contrast, the physiological stress response can be measured as an increase in stress hormone levels (Fig. 2). Thus, we define stress as the activation of the physiological stress response, which in mammals (which is the focus of our review) and other vertebrates consists of two axes [12, 13]: 1. The **sympathoadrenal medullary axis (SMA)**, in which the sympathetic nerve activates different organs (heart, lungs, blood vessels, digestive system, kidneys) within seconds and secretes catecholamines (adrenaline and noradrenaline), causing the fight or flight syndrome. 2. The **hypothalamic-pituitary-adrenal (HPA) axis**, leading to the secretion of glucocorticoids within minutes, stimulating gluconeogenesis in muscles and simultaneously inhibiting glucose utilization in nonessential tissues. Both SMA and HPA axis make energy available to overcome challenges that acutely threaten homeostasis and / or survival [12]. Stressful events are temporary, such as a predation attempt or a storm, leading to a short-term increase in energy expenditure via the SMA and HPA axis, enabling the animal to avoid (predation) or endure (storm) the stressful event. The stress response increases fitness because it enables the individual to overcome stressful events, at the cost of increased energy consumption [12]. Thus, stress is the activation of the physiological stress response to overcome the stressful event, after which the stress hormone levels decline (Fig. 2).

What is harshness?

In contrast to stress, harshness refers to long-lasting environmental challenges that cannot be overcome by increasing energy expenditure but instead necessitate energy saving. Examples of harsh conditions include drought, heat, and cold [5, 13], leading to food and/or water restriction. Harsh conditions challenge thermoregulation, metabolism and osmoregulation, and ultimately reproduction and survival. Harsh conditions cannot be overcome by increasing energy mobilization via activation of the physiological stress response unless it is harnessed for migration into less harsh environments.

One of the most common harsh conditions that animals experience is the seasonal reduction in food availability, due to cold, heat and / or drought. To endure low food availability, animals save energy by terminating reproduction, reducing physical activity and

metabolism, leading to a net decrease in daily energy expenditure [9]. For this, the **harshness response** leads to a decrease in the levels of metabolic hormones including those of the physiological stress response. Thus, while stress necessitates increased energy expenditure to overcome short-term challenges, harsh conditions necessitate energy savings to endure long-term challenges.

Harshness is neither long-term nor chronic stress

Stress, **long-term stress** and harshness do not only differ in the duration that the stressful event or the harsh conditions challenging the individual (Fig. 1), but also in the physiological response (Fig. 2). When the stress response lasts for several weeks until the stressful event is overcome, we call this long-term stress. Social stress due to immigration or changes in dominance hierarchy within a social group, can cause long-term stress, since it takes time to establish a new hierarchy. If the situation persists, it can sometimes be overcome by dispersal. In a classical experiment on social stress, von Holst [11] studied pair-living tree-shrews and introduced a second, subordinate male into the enclosure [2]. These subordinate males showed a strong physiological stress response, which under natural conditions would have led to dispersal. Not being able to disperse from the enclosure resulted in long-term and then **chronic stress**, causing body mass loss, detrimental health, and in some cases even death [2]. Thus, if the stressful condition is not overcome and the stress response remains activated, stress becomes chronic, leading to pathology. Humans (*Homo sapiens*) who cannot escape their stressful social or workplace environment suffer from chronic stress. Indeed, chronic stress mainly occurs in humans and in captive animals, but rarely under natural conditions [14].

The duration of the challenge is not the only difference between stress and harshness. Of greater importance is whether the challenge can be overcome by increasing energy expenditure (stress), or whether increasing energy expenditure would be detrimental (harshness). Long-term stress is characterized by delayed success in overcoming the stressful event and chronic stress is the failure in overcoming it. In contrast, harshness suppresses the stress response to enable endurance. Further, in contrast to stressful events (a predator, an immigrant male, a storm), harsh conditions do not occur suddenly. Instead, the harshness of the environment increases steadily over time, for example, climate becoming colder or hotter or dryer (Fig. 1C).

Unpredictability increases both stress and harshness

Unpredictability impacts both stress and harshness. Both become worse when they are unpredictable. For example, striped mice (*Rhabdomys pumilio*) from the Succulent Karoo [9], South Africa experience stressful events in the form of rainy cold fronts in winter when temperatures drop considerably (Fig. 1B), and these storms occur unpredictably. Striped mice live in a harsh environment characterized by summer dry seasons (Fig. 1A). There is large inter-annual variation in the decline of food availability during summer (Fig. 1C). Every generation lives for only one year, which means that every generation faces a dry season of unpredictable harshness.

Stress and harshness should be clearly defined for all taxa and all habitats

We can better predict consequences of global change on natural populations when we differentiate between stressful and harsh environments because they have opposing energetic and physiological consequences. The physiological stress response reduces an animal's ability to cope with harshness. However, as stressful events also occur in harsh environments (for example encounters with predators), future research should focus on understanding the trade-offs between coping with harshness *versus* reacting to stress, and how this trade-off changes with increasing harshness. While our review focused on terrestrial vertebrates and especially mammals, stress and harshness also need to be defined for marine habitats, invertebrates, and

plants. Ultimately, in harsh environments, any additional stress-induced energy expenditure, including human disturbance (e.g., hiking, harvesting vegetation), might be detrimental to already vulnerable species.

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