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Stress: Does it matter? A review of mechanisms and fitness consequences of stress in large herbivores

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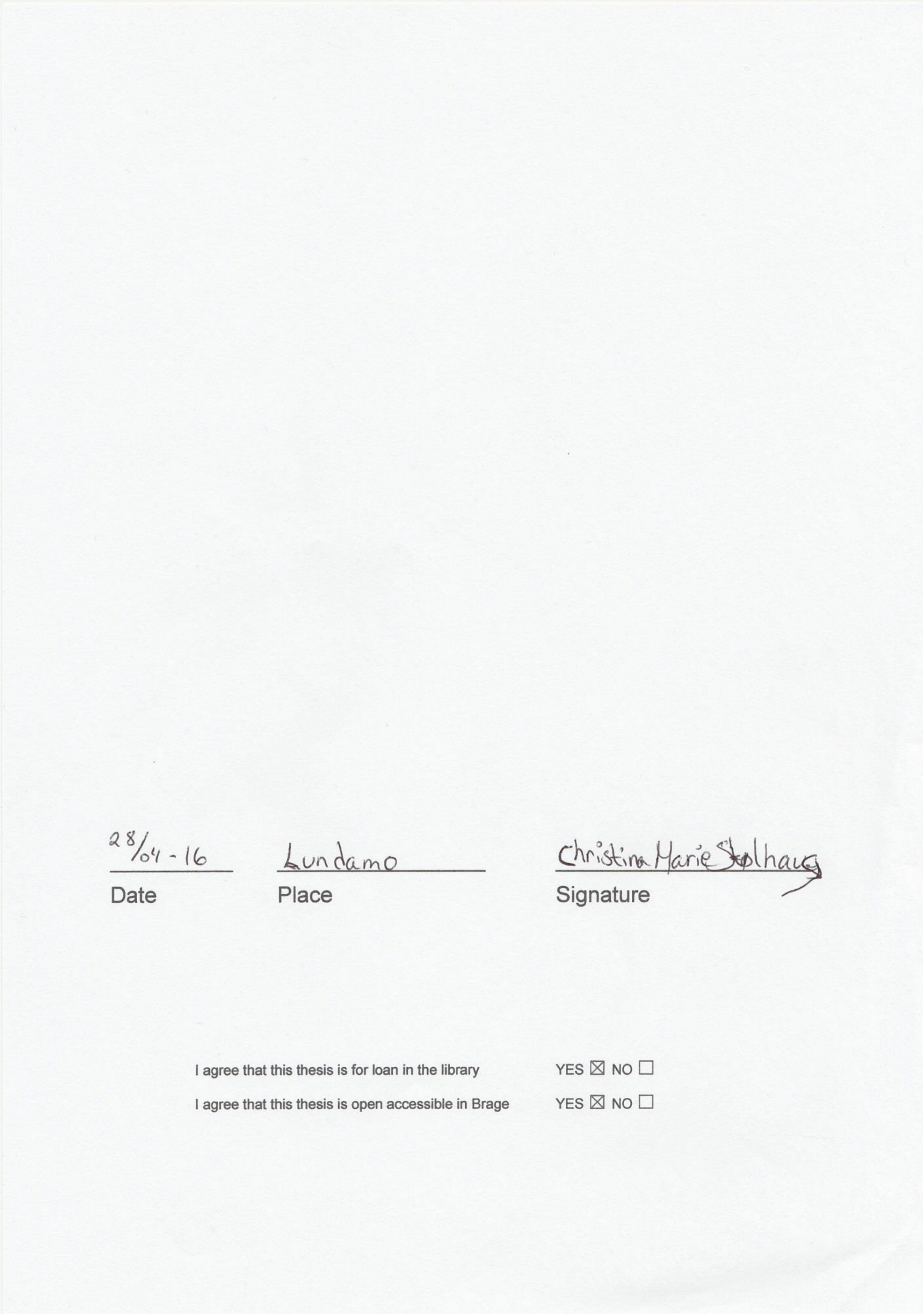

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Abstract

The recent discipline of ecophysiology investigates physiological adaptations of organisms to their environment. This opens for testing new research questions, such as more thorough investigations of the link between environmental stressors and physiological responses, or the role of stress as a biomarker of health and fitness. Many studies support the cort-fitness hypothesis, which predicts a negative relationship between stress and fitness, but they also show that this relationship is not linear. Animals need stress to keep themselves alert for hazards, but detrimental effects can occur at high release levels or in chronic situations. This review focuses on causes, mechanisms and consequences of stress on large herbivores, both for individual fitness and population dynamics.

Stress is a multidimensional physiological response that challenges internal stability, and can be measured through "stress hormones". These however fluctuate depending on a range of factors, and can be measured in different ways, depending on the research question. Therefore, caution should be taken when interpreting results. Stress can be described based on duration (acute or chronic) and type of stressor (physical or psychological). Chronic stress inhibits the body from returning to homeostasis, and can have a range of physiological consequences ultimately affecting fecundity, offspring survival and immunity. Although studies on the ecophysiology of wild animals, and especially large herbivores, are scarce, there is evidence that individual effects of stress can scale up to population dynamics.

Rangifer, due to its peculiar ecology, is particularly sensitive to the rapidly increasing human disturbance. Although so far only few studies provided physiological measures of stress hormones, these documented the occurrence of nutritional stress, and succeeded in establishing a causal link between human disturbance and physiological stress.

This review shows that there is reasons to believe that stress does matter, both at an individual and population level. There is an urgent need for more interdisciplinary studies to establish the link between different type of stressors and stress responses, and to better understand the relationship between stress, individual fitness and population dynamics. In particular, there is a need for studies on wild species that seem particularly sensitive to stress, such as *Rangifer*, in order to plan sound management and conservation strategies.

Keywords: Glucocorticoids, chronic stress, multiple- stressor context, HPA axis, population dynamics, large herbivores**,** *Rangifer*

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1. Introduction

Ecologists and physiologists have conducted studies on organisms for decades, both in laboratories and in the wild. However, only recently, by merging the two fields together, the study of ecophysiology has been developed. The relatively new discipline seeks to clarify the role and importance of physiological processes in the ecological relations of species in their natural habitat. The approach allows scientists to investigate important ecological questions, such as the role of a range of stressors on individual stress and, ultimately, population dynamics (e.g. Bradshaw 2003).

In recent years, both physiologists and ecologists have raised awareness of the role of stress as a biomarker for health and fitness (Fefferman & Romero 2013; Cattet *et al.* 2014). A milestone in stress studies is the cort-fitness hypothesis (Bonier *et al.* 2009b), which predicts that as the number of environmental challenges increases, the level of glucocorticoids - the primary stress hormones - increases, and negatively affects fitness (Bonier *et al.* 2009a). However, the relationship between stress and fitness is not linear, as first assumed (Bonier *et al.* 2009a; Busch & Hayward 2009). Stress responses are needed to keep animals alert and safe from predator attacks and other potential hazards (Wingfield *et al.* 1998; Arnemo & Caulkett 2007). Therefore, while short-term stress responses tend to be adaptive, a stress response activated for a prolonged period has the potential to be detrimental to the animal (McEwen & Wingfield 2003; McEwen & Wingfield 2010). An increasing amount of studies is therefore shifting focus from short-term effects of stress, to a long-term fitness perspective (Weinstock 2008; Sheriff 2015).

Studies investigating long-term consequences of stress at the individual level raise concern for potential impacts not only on individual level, but also on population dynamics and conservation. However, while there is relatively good understanding of stress effects on individual fitness in controlled conditions (lab animals; e.g. Saul *et al.* 2012), not much is known yet on fitness effects of stress on wild individuals, nor on whether individual effects scale up at the population level. Here I focus on the mechanisms of stress from an ecological perspective, and review available evidence of stress consequences for individual fitness and population viability in the wild. The review focusses on large herbivores and, in particular, on *Rangifer* which, due to its peculiar ecology, seem to be particularly sensitive to stress related to predation, hunting and increasing human disturbance across their circumpolar range (e.g. Whittington *et al.* 2011; Panzacchi *et al.* 2013).

2. What is stress?

2.1 Definitions

Stress is difficult to define (Romero 2004). Dantzer *et al.* (2014) define a “stressor” as a predictable or unpredictable environmental perturbation that causes “stress”, which is defined as a multidimensional physiological response that challenges internal stability. Animals can cope with stress through “stress responses”, which imply both physiological changes (such as secretion of glucocorticoids; e.g. Sapolsky, Romero & Munck 2000) and behavioral changes (such as fight- or flight response; e.g. Romero 2004; Wikelski & Cooke 2006; Stankowich 2008).

When a stressful event occurs, the body unconsciously activates physiological responses. As this response cannot last for long periods, the body brings back the physiological conditions to stability in a process called homeostasis (Davis 2006). Homeostasis keeps set-points that are essential for life, such as pH, body temperature, glucose levels and oxygen tension (Lupien *et al.* 2006). Homeostasis can be achieved through a process called allostasis, which is the process of achieving stability through physiological or behavioral change (McEwen & Wingfield 2003). Allostasis allows modification of the above-mentioned set-points through changes of intrinsic (such as age, body condition, reproductive status) and extrinsic (e.g. exposure to weather, predation risk) factors, in order to maintain the body in stable conditions during physical, psychological and environmental challenges (Sterling & Eyer 1988; Karlamangla *et al.* 2002; McEwen 2002; Dantzer *et al.* 2014). Further, the “allostatic load” is the daily or monthly amount of energy an individual need to have available to fulfill normal life history tasks, such as breeding. When the environment no longer provides the required energetic input, the individual goes into “allostatic overload”. Indeed, several authors (e.g. McEwen 2002; Arnemo & Caulkett 2007) distinguish between “good stress” (eustress), and “bad stress” (distress); while the former can be adaptive, the latter refers to the allostatic overload which serves no useful purpose and may trigger health consequences (McEwen & Wingfield 2003; McEwen 2005). This review focusses on distress, hereafter named “stress”.

2.2 Acute and chronic stress

Stressors and stress responses can be either short- or long- term or, in other words, acute or chronic. In case of acute stressors, such as a one-time predator attack (Boonstra 2013; Clinchy, Sheriff & Zanette 2013), GCs may increase temporarily (acute response) (Dantzer *et al.* 2014). However, when a stressor operates over longer periods, such as recurrent anthropogenic disturbance (Cabezas *et al.* 2007), the animal may manifest chronic stress responses (Dantzer *et al.* 2014), as the body may not be able to bring back the physiological conditions to homeostasis between recurring stressors.

2.3 Physical and psychological stress

In some cases, it is useful to characterize stress based on the types of stressor triggering it. However, as the number of stressors is virtually countless and varies across species, individuals, life-stages and conditions (see chapter 3), it is unrealistic to attempt compiling a clear-cut and comprehensive list across species. Broadly speaking, animals can show stress responses when they perceive risk for their well-being or that of related individuals (e.g. predation risk, hunting, capture, human disturbance), and when the environmental conditions are sub-optimal (e.g. poor trophic resources, inadequate temperatures). Literature provides an array of papers using the term “stress” to indicate different types of stressors triggering it. Here, following Wasser *et al.* (2011), we separate between *physical* and *psychological* stress. Physical stress refers to stress caused by “external” triggers, such as lack of food (nutritional stress; Bastille-Rousseau *et al.* 2015), direct disturbance (e.g. capture-related stress; Omsjoe *et al.* 2009) or temperature (e.g. thermal stress; Shrestha *et al.* 2014 - see chapter 4.1). On the contrary, psychological stress refers to stress triggered by the animals’ “inner” perception of the “landscape of fear” (Laundré, Hernández & Ripple 2010 - see chapter 4.2).

3. How to measure stress

Glucocorticoids (GCs) are a class of corticosteroids known as the “stress hormones”, as they are involved in the primary hormonal response during both acute and chronic stress (Möstl & Palme 2002; Romero 2004; Love *et al.* 2005; Arnemo & Caulkett 2007). However, only at high release levels are these associated with stress, as the primary role of the hormone is basic energy regulation (Busch & Hayward 2009). Still, GC concentrations are widely used in ecological studies as proxies of stress (e.g. Millspaugh *et al.* 2001; Millspaugh *et al.* 2002; Ashley *et al.* 2011), and have been suggested as “early warning sign” in conservation studies (Dantzer *et al.* 2014).

The GCs can be measured in different ways, and provide us with information at different time scales. A detailed description of methodological approaches for measuring GCs in wildlife is provided by a number of reviews (e.g. Keay *et al.* 2006; Sheriff *et al.* 2011; Dantzer *et al.* 2014), and falls outside the scope of this thesis. Most commonly, GCs are measured in the blood, saliva, excreta (feces and urine) and integumentary structures (hair and feathers). It is crucial to underline that while blood and saliva samples provide real-time levels of GC (Sheriff, Krebs & Boonstra 2010a), hair and feather samples are an increasingly used method to provide data on long-term GC release, during the entire hair growth period (Bortolotti *et al.* 2008; Russell *et al.* 2012; Macbeth 2013). Therefore, the choice of appropriate samples is crucial to answer different ecological questions, related to acute or chronic responses. It is also important to notice that not only different methodological approaches yield different results, but also the baseline glucocorticoids and stress response depends on a range of factors such as species, individuals, sex, age class, reproductive status, season and ecological context (Huber, Palme & Arnold 2003; Keay *et al.* 2006; Bonier *et al.* 2009a; Jaatinen *et al.* 2013). Therefore, an increasing amount of papers highlight the importance of planning carefully stress-studies based on specific methodological approaches targeted towards precise and testable hypotheses, and call for caution when interpreting study results and making generalizations (e.g. Millspaugh & Washburn 2004; Touma & Palme 2005; Madliger & Love 2014).

3.1 How to discriminate between different types of stress

A given individual can elicit similar GC releases in response to different types of stressors (such as fear, exercise, starvation, infection, anesthesia, pain, restraint, social interactions, mating; Colborn *et al.* 1991; Arnemo & Caulkett 2007; Koolhaas *et al.* 2011). Therefore, in wildlife populations it is challenging to trace back from the stress response to the stressor causing it, relying only on GC measurements. However, by adding ecophysiology data, multivariate analytical approaches can be conducted to answer questions in a multiple-stressor context (e.g. Wasser *et al.* 2011). The number of studies establishing a link between physiological responses and multiple stressors is however still very limited.

Broadly speaking, it is possible to investigate the link between physiological stress response and stressors by: 1) monitoring a range of physiological parameters (e.g. heart rate) in addition to GCs; 2) by performing interdisciplinary studies including physiological, environmental (e.g. temperature) and behavioral parameters (e.g. space use).

3.1.1 Combining physiological measurements

The choice of physiological parameters to monitor depends on the hypothesis to be tested, and on the choice/feasibility of the methodological approach (e.g. invasive vs. non-invasive techniques).

For example, during a capture event a range of physiological measurements allow monitoring capture-related stress to approach the complex series of hormonal events of stress responses (Arnemo & Caulkett 2007). In addition to the GC levels in the blood samples, temperature, heart rate and respiratory rates are frequently sampled to monitor vital signs and physiological responses to stress (Lian *et al.* 2017).

Nutritional stress can be measured by the modified amino acid triiodothyronine (T3) and thyroxine (T4) from the thyroid gland in the feces; T3 appears to be the more informative hormone to measure (Greco 2006; Wasser *et al.* 2010). Studies done on mammals, birds and teleost fish show that the thyroid hormones can be affected by both acute and chronic changes in nutrient intake (Eales 1988). As both GCs and T3 can be measured in the feces (Wasser *et al.* 2000; Wasser *et al.* 2010), multiple information can be extracted from the same sample, and allow to test for hypotheses related to both psychological and nutritional stress (Wasser *et al.* 2011; Ayres *et al.* 2012). In particular, several authors found that levels of T3 decrease when an animal is exposed to nutritional stress (Flier, Harris & Hollenberg 2000; Douyon & Schteingart 2002) but are unaffected by psychological stress (Kitaysky *et al.* 2005; Walpita *et al.* 2007), whereas GC level increase in both nutritional and psychological stress (Hayward *et al.* 2011).

Similarly, thermal stress causes an increase in GC levels and a decrease of both T3 and T4 (Marai & Haeeb 2010; Sejian, Maurya & Naqvi 2010). However, one should keep in mind that thermal stress is closely related to depression of food intake, and thus will be shown as a decrease of thyroid hormones (Pereira, Duarte & Negrão 2006; Sejian, Maurya & Naqvi 2010). While several studies on thermal stress have been conducted on domesticated animals (Alvarez & Johnson 1973; Borges *et al.* 2004; Sejian, Maurya & Naqvi 2010), studies on wild animals are underrepresented, likely due to logistic difficulties with obtaining such measurements in the wild (e.g. Washburn & Millspaugh 2002; Huber, Palme & Arnold 2003; Romero & Reed 2005; Johnstone, Reina & Lill 2012).

In the attempt to circumvent the problem, several studies inferred thermal stress indirectly, by relying only on behavioural responses, such as changes in habitat selection during the warmest periods and selection for thermal shelter (Sargeant, Eberhardt & Peek 1994; Dussault *et al.* 2004; Bjørneraas *et al.* 2011; Chapperon & Seuront 2011; Broders, Coombs & McCarron 2012; van Beest, Van Moorter & Milner 2012).

3.1.2 Combining physiological, behavioral and environmental information

Both purely physiological studies and purely behavioural studies are limited in their ability to establish the link between responses and triggers of stress. Recently, a few studies adopted interdisciplinary approaches relying on the integration between several physiological, behavioural and environmental information, thereby advancing the recent disciplines of ecophysiology (Ellis, McWhorter & Maron 2012; Tarszisz, Dickman & Munn 2014; Madliger & Love 2015). By integrating behavioral and physiological parameters, Hayward *et al.* (2011) and Ayres *et al.* (2012) established a link between anthropogenic disturbance and stress for killer whales and northern spotted owls, respectively. Using georeferenced fecal samples of woodland caribou and moose, Wasser *et al.* (2011) was able to test hypotheses related to the influence of predation, habitat quality and anthropogenic disturbance on either psychological or nutritional stress.

In addition to traditional physiological measures, advanced technology such as biologgers and biotelemetry, can provide additional information of an animal’s state and external environment (Owen-Smith, Fryxell & Merrill 2010; Wilmers *et al.* 2015). Remote monitoring allows scientists to study physiology, behavior and ecology of wild, cryptic and wide-ranging animals that previously have been difficult to study (Wilmers *et al.* 2015; Lennox *et al.* 2016). Therefore, by performing, for example, spatially-explicit analyses in a multiple stressor context, it is possible to answer the question “what is stressing the animal?” instead of “is the animal stressed?”. This approach gives a wider understanding of the potential threats the particular species is currently fronting, and improves our ability to predict how it likely will respond to future perturbations (Jachowski & Singh 2015).

4. Triggers and behavioural responses to stress

4.1 Physical stress

Broadly speaking, physical stress can be caused by factors like weather (temperature and precipitation; e.g. Shrestha *et al.* 2014), predation (natural predators and direct human disturbance; e.g. Stankowich 2008), parasites (e.g. Goldstein *et al.* 2005) and lack of food (e.g. Bastille-Rousseau *et al.* 2015).

Environmental temperature is an essential abiotic factor effecting an animal's space use and behaviour. Large herbivores can be sensitive to heat (van Beest, Van Moorter & Milner 2012; McCann, Moen & Harris 2013; van Beest & Milner 2013), and water availability (Rosenmann & Morrison 1967), especially for herbivores in arid- and semi-arid areas at lower latitudes where drought years might be more frequent and more severe (Simard 1997; Easterling *et al.* 2000; Duncan *et al.* 2012; Shrestha *et al.* 2014). As a behavioral response, they tend to seek for water and thermal shelter to reduce heat stress and dehydration (Cain III *et al.* 2006; van Beest, Van Moorter & Milner 2012). On the contrary, extreme or prolonged wet and cold periods can lead to increased stress of thermoregulation and in the worst case, decrease survival (Parker & Robbins 1985; Forchhammer & Boertmann 1993; Putman, Langbein & Sharma 1996; Gaillard *et al.* 2000; Hebblewhite 2005). In addition to change of weather patterns and altered temperatures, changed precipitation due to climate change is one of the major concerns today (e.g. Weladji *et al.* 2002; Hansen *et al.* 2011; Angelier & Wingfield 2013). Changed precipitation patterns at higher latitudes can lead to higher frequency of e.g. icing events and changes in snow cover (Klein 1999), which can increase the energy for digging for food and locomotion (Parker, Robbins & Hanley 1984; Forchhammer & Boertmann 1993; Kumpula & Colpaert 2003; Mysterud & Østbye 2006; Hansen *et al.* 2011), increase nutritional stress due to reduced access to forage, and ultimately affect population dynamics (Hansen *et al.* 2013).

Both predation from wild predators, hunting, and a range of other human activities can cause stress, and induce behavioral responses such as the fight-or-flight response (Stankowich 2008). Capturing wild animals for research or management purposes is a common practice. While capture and handling is definitively a source of stress for animals, a number of guidelines and protocols instruct on how to monitor and minimize capture-related stress (e.g. Arnemo, Kreeger & Soveri 2003; Arnemo *et al.* 2006; West, Heard & Caulkett 2014). Still, during handling both physical stress (such as trauma, surgery, intense heat/cold) and chemical stress (such as reduced oxygen supply, acid-base imbalance and anesthetic drugs) may be of concern (Arnemo & Caulkett 2007).

Parasite load vary with season and weather events, and can be a source of stress for large herbivores (e.g. Goldstein *et al.* 2005), which in turn can lead to change of fitness. For example, in *Rangifer* the increased insect harassment during warm periods (Gunn & Skogland 1997; Mörschel & Klein 1997; Hagemoen & Reimers 2002; Colman *et al.* 2003) can lead to changes in space use (Ion & Kershaw 1989; Watson, Davison & French 1994; Vistnes *et al.* 2008), decreased feeding rate (Colman *et al.* 2003), reduced body weight (Weladji & Holand 2003), and in extreme cases, can lead to death (Helle & Tarvainen 1984).

Nutritional stress caused by intraspecific competition for resources may affect herbivores at high population densities (Portier *et al.* 1998; Nellemann *et al.* 2000; Sinclair *et al.* 2007; White 2008; Simard *et al.* 2010). Also, while in some cases global warming is expected to increase the availability of trophic resources (Klein 1999; Tews, Ferguson & Fahrig 2007; Tyler 2010), in others it is expected to decrease it. The degradation of resources can thus potentially trigger nutritional stress, with possible consequences on increased predation risk (Leblond, Dussault & Ouellet 2013; Bastille-Rousseau *et al.* 2015). Habitat fragmentation can have similar effects, as it prevents access to important resources, and may confine animals to areas with lower nutritional quality (e.g. Panzacchi *et al.* 2015).

4.2 Psychological stress

Fear, which may be triggered by the actual or perceived threat posed by a predator, can in different degree affect the behavior of prey in the landscape (Brown 1999; Laundré, Hernández & Altendorf 2001; Holmes & Laundré 2006). The “landscape of fear” (Laundré, Hernández & Altendorf 2001; Laundré, Hernández & Ripple 2010) not only affects behavior, but also the stress levels of prey (Brown 1999; Laundré, Hernández & Altendorf 2001; Gobush, Mutayoba & Wasser 2008). For example, in habitat or features perceived as risky, prey tend to increase vigilance (often at the expenses of feeding rates; Caro 2005; Morrison 2011), change space use (often to sub-optimal habitat; Hernández & Laundré 2005; Laundré, Hernández & Ripple 2010), and increase stress levels (Gobush, Mutayoba & Wasser 2008). The predator has the ability to maintain and change a landscape of fear (Ripple & Beschta 2004), by e.g. reestablishing in an area (Laundré, Hernández & Altendorf 2001). Therefore, the degree of fear a prey associates with a certain habitat or features, is usually not permanent. In fact, the fear of being attacked keeps the animals alert, and increases their chance of survival in dangerous situations (Boissy 1995; Brown 1999).

Natural predators, such as wolves, are the basis of the fear-driven landscape (Ciuti *et al.* 2012). However, prey - especially from heavily hunted populations - tend to react to humans and non-lethal human activities in a similar way as natural predators (Frid & Dill 2002; Crosmary *et al.* 2012). Therefore, several species tend to avoid proximity to humans, human-dominated areas and sometimes also infrastructures such as roads, powerlines or trails (e.g. Panzacchi *et al.* 2015; Panzacchi *et al.* 2016) which in turn can lead to changed movement patterns, both at a short-term (e.g. Andersen, Linnell & Langvatn 1996) and long-term (e.g. Panzacchi, Van Moorter & Strand 2013) scale. Not only can stress levels increase when animals are directly exposed to human disturbance (Pereira, Duarte & Negrão 2006), but also when they use areas perceived as risky, such as areas with historically high poaching risk (Gobush, Mutayoba & Wasser 2008) or linear features with no human activity (Wasser *et al.* 2011). In response to human disturbance animals tend to increase vigilance (Wang *et al.* 2011; Ciuti *et al.* 2012). The prey faces a trade-off between vigilance and foraging (Brown 1999; Fortin *et al.* 2004; Caro 2005) where time spent feeding determines the level of nutritional stress (Creel, Winnie & Christianson 2009; Creel, Schuette & Christianson 2014). However, when some cases the prey’s fear of human activity can exceed the fear of natural predators (Ciuti *et al.* 2012), others use human disturbed areas as shelter to reduce predation risk by natural predators (Shannon *et al.* 2014).

5. Physiological consequences of stress

The stress physiology is complex and has been described in detail in a range of papers (e.g. Sapolsky, Romero & Munck 2000; Wingfield & Romero 2001; Arnemo & Caulkett 2007), and therefore in this review it will be summarized briefly. When a stressor operates on an animal, receptors in the body send signals to the hypothalamus in the brain. The hypothalamus further activates the sympathetic nervous system, which triggers the hypothalamus- pituitary-adrenal axis (HPA axis). In a stress situation the predominant hormonal response is the activation of the HPA axis, which is the vital regulator of adaption to stress (Reeder & Kramer 2005; Boonstra *et al.* 2014). The sympathetic nervous system activates an acute adaption, which initiates a vigorous behavior. The physiological responses are rapid; within 3 to 5 seconds the heart rate can be doubled and within 10 to 15 seconds the arterial blood pressure can increase to twice the normal levels (Arnemo & Caulkett 2007). The activation induces secretion of the stress hormones, primarily glucocorticoids (GCs) in form of cortisol (e.g. for primates, carnivores and ungulates) or corticosterone (e.g. rodents, birds and reptiles) (Romero 2004; Touma & Palme 2005). The GC secretion causes a range of physiological and behavioral changes that facilitate coping with the environmental stressor. To lead the body back to homeostasis, GCs trigger a negative feedback mechanism that inhibit further production of the stress hormones (Pozzi *et al.* 2008).

When the animal experiences chronic stress and the HPA axis is activated for long periods, to a return to homeostasis is inhibited (Boonstra 2004). Dantzer *et al.* (2014) characterizes chronically stressed individuals as having: *(i)* higher baseline CG levels; *(Cain III et al.)* higher frequency of acute GC increases; *(Cain III et al.)* increased amount of time to return GC levels back to baseline. Chronic stress can cause a decreased ability to cope with a stressor because of mechanisms named acclimation and facilitation (Romero 2004; Wingfield & Romero 2015). If the animal is exposed to a stressor for a prolonged period of time, it may get acclimated, i.e. GC secretion will be reduced and the animal will no longer respond to the active stressor. Even though this may seem beneficial, it might actually lead to a facilitation, i.e. the animal will have a poorer ability to cope with a new stressor than a non-acclimated animal. However, in this case too it is important to remember that the ability to cope with stress varies among e.g. species, reproductive mode, stressor, timing and duration of stressor (Sheriff, Krebs & Boonstra 2010b; Love, McGowan & Sheriff 2013).

The prolonged activation of the HPA axis has a range of physiological consequences, including the potential to suppress the immune system, growth, and trigger protein loss (Busch & Hayward 2009). During the vulnerable maternal and neonatal stage, the non-genetic maternal programming of the offspring takes place (Sheriff, Krebs & Boonstra 2010b; Love, McGowan & Sheriff 2013). Lab studies on mammals have shown that maternal and neonatal stress can have long-lasting detrimental consequences by causing changes in the programming and development of the offspring (Meaney, Szyf & Seckl 2007; Weinstock 2008; Mastorci *et al.* 2009) that can be detected also in adulthood (Romero 2004 - but see; ; Sheriff & Love 2013). Studies on snowshoe hare showed that maternal stress resulted in offspring with higher level of plasma-free cortisol, greater sensitivity to stress and lower immunity in adulthood (Sheriff, Krebs & Boonstra 2010b). Offspring of lab animals exposed to maternal stress are prone to depression, anxiety-like behavior, alteration in brain development and HPA function (Abe *et al.* 2007; Meaney, Szyf & Seckl 2007; Kapoor, Leen & Matthews 2008). Higher GC levels can also affect metabolic rates and digestive processes, which possibly can lead to higher maintenance costs because of increasing forage time and thus decreasing resting time (Wingfield *et al.* 1998; Sapolsky, Romero & Munck 2000). Given the importance of the topic, Love, McGowan and Sheriff (2013) urge the need for more studies on females and the programming of offspring related to maternal stress.

6. Can physiological responses affect fitness?

6.1 Individual level

There is a number of laboratory studies that have investigated the cort-fitness hypothesis (e.g. Dallman *et al.* 1992; Guimont & Wynne-Edwards 2006; Saul *et al.* 2012). Although stress science is a fast-growing topic, the amount of studies linking stress to fitness in natural settings is still poor, and to my knowledge especially studies in large herbivores are highly limited (see e.g. review; Bonier *et al.* 2009a). The limitations are likely connected to practical difficulties with monitoring physiological parameters in the wild. In addition, while in lab studies the duration, timing and intensity of the stressor can be carefully controlled, in wild populations this is often not possible (e.g. Sheriff, Krebs & Boonstra 2010b).

In general, researchers agree that acute stress of little to moderate magnitude will likely not have important negative effects on survival and reproduction in wild species (Tilbrook, Turner & Clarke 2000; Breuner, Patterson & Hahn 2008). On the contrary, ecologists and physiologists found evidence that chronic stress can cause detrimental effects on fitness, thus supporting the cort- fitness hypothesis (Tilbrook, Turner & Clarke 2000; Cabezas *et al.* 2007). For example, maternal stress has the ability to decrease the offspring ability to cope with stressors, thus decreasing individual fitness (Hayward *et al.* 2006; Love *et al.* 2008; Sheriff, Krebs & Boonstra 2010b; Haussmann *et al.* 2012). Sheriff, Krebs and Boonstra (2009) showed that snowshoe hare mothers gave birth to stillborn, and overall fewer and smaller babies after being exposed to stress.

Several studies show negative effects of stress on survival of birds (Suorsa *et al.* 2003; Blas *et al.* 2007; Kitaysky, Piatt & Wingfield 2007, but see; Comendant *et al.* 2003; Cote *et al.* 2006), lemurs (Pride 2005) and iguanas (Romero & Wikelski 2001). Also, negative effects on reproduction have been shown in a number of bird species (Lanctot *et al.* 2003; Angelier *et al.* 2007; Bonier *et al.* 2007; Kitaysky, Piatt & Wingfield 2007; Bonier *et al.* 2009b) and seals (Lidgard *et al.* 2008). However, scientists emphasize that the results are not universal due to complex and context-dependent relationships between type of stressors, GCs and fitness. Therefore, scientists urge for the need to more studies to formally test the cort-fitness hypothesis (Bonier *et al.* 2009a; Busch & Hayward 2009; Crespi *et al.* 2013).

6.2 Population level

Based on the information provided above, there is reason to believe that the physiology-fitness relationship can scale up from the individual to the population level. However, Madliger and Love (2014) pinpoint three important factors that need to be fulfilled to link GC levels to fitness at the population level: *(i)* levels must be consistent within individuals under stable energetic or environmental conditions; *(Cain III et al.)* individual GC levels must change in a similar (i.e. predictable) way in response to environmental changes; *(Cain III et al.)* levels must show a consistent relationship with fitness metrics within individuals. This requires investigations within different taxa, life stages etc., which require large datasets and long-term series, which only few studies have available (Madliger & Love 2015).

In a well-known, long-term study, Sheriff, Krebs and Boonstra (2010b) showed a decline in free-ranging snowshoe hare population size when mothers where exposed to maternal stress, and other researchers have found direct evidence of maternal stress to play a critical role in regulating population dynamics in free ranging vertebrates (reviewed in; Sheriff 2015). Stress responses act through generations (not only they transfer from mothers to offspring, but also from their grandmothers), and can thus affect population dynamics (Kirkpatrick & Lande 1989; Meaney 2001). Note that stress-related interferences during the maternal programming can also have the potential to affect the propensity of dispersal (Love, McGowan & Sheriff 2013).

Individual-based simulation models can be a very useful tool to explore potential effects of stress on population dynamics. Based on such models, Fefferman and Romero (2013) showed that high stress levels can alter the age structure of a population, which would rely preferentially on the oldest and most physically fit individuals for reproduction; this, ultimately would result in decreased population size. Although this is only a simulation-based model, it seems to explain some of the patterns found for example in a long-term study on snowshoe hare (Sheriff, Krebs & Boonstra 2011). If supported by other studies, these findings would have important conservation consequences, e.g. they indicate that anything that may impact (e.g. hunting) the oldest reproductive individuals would have a disproportionate effect on population size.

7. Case study: Rangifer

Reindeer and caribou *(i.e. Rangifer spp.)* have a circumpolar distribution, and can be either wild or semi-domesticated. Wild *Rangifer* in North America is defined as "caribou", and all other *Rangifer* in regions of northern Europe and Siberia, including semi-domestic animals of Eurasian origin in North America, are defined as "reindeer" (Bevanger 2004).

7.1 Triggers and effects of stress for *Rangifer*

Today, *Rangifer* is facing a range of challenges related to the increasingly human impacted and climate warming world. The species is well-known for being capable of the longest migrations among terrestrial animals (Bevanger 2004). However, as for most of the migratory species, these populations are now challenged due to blocked and hampered migratory routes caused by development of infrastructure (Wilcove & Wikelski 2008; Vors & Boyce 2009). In open landscapes such as mountain or tundra ecosystems the species is also known for being able to form large herds as an anti-predator strategy. This, together with the fact that several of the wild populations are subjected to hunting contributes to make the species particularly wary of human disturbance. In Norway, wild reindeer tend to strongly avoid roads, railways, industrial development such as hydropower, and human-dominated areas including tourist cabins and popular hiking trails (Nellemann *et al.* 2000; Nellemann *et al.* 2010; Panzacchi, Van Moorter & Strand 2013; Johnson & Russell 2014; Panzacchi *et al.* 2015; Panzacchi *et al.* 2016).

Climate warming is especially critical for *Rangifer* as it increases the frequency of icing events (Hansen *et al.* 2011) and insect harassment (Hagemoen & Reimers 2002). This can further lead to change of habitat (Vistnes *et al.* 2008) and lower nutritional intake (Pettorelli *et al.* 2005), which in turn can have consequences for fitness (White 1992). Finally, in some areas predation represents a major threat for the populations. The productive group (cows and calves) are especially vulnerable for disturbance during the calving season (Aastrup 2000; Wolfe, Griffith & Wolfe 2000), which ultimately can have negative stress effects, as described in chapter 6.1. An impressive load of papers has tested and reviewed the responses of *Rangifer* to these triggers of stress, however, most papers focus on the behavioral responses (e.g. Vistnes & Nellemann 2008; Reimers & Colman 2009; Reimers, Lund & Ergon 2011; Johnson & Russell 2014; Muhly *et al.* 2015).

7.2 Evidence of altered *Rangifer* GC levels triggered by stress

Some studies have investigating altered GC levels in *Rangifer* (e.g. Säkkinen *et al.* 2004; Macbeth 2013), however the number of published literature is limited, especially studies focusing on a multiple stressor context.

Freeman (2008) investigated how mountain caribou (*Rangifer tarandus caribou*) in British Columbia responded to motorized backcountry recreation by measuring GCs in feces. She found higher concentrations of fecal GCs in areas with disturbance, up to 10 km away from the motorized recreational areas. Wasser *et al.* (2011) performed a very comprehensive study on woodland caribou in western Canada, and monitored two physiological parameters (T3 and GCs) while performing a study on habitat use. They were able to test for specific hypotheses on the effect of human and predator disturbance on caribou stress levels, and showed that physiological and nutritional stress where positively affected by the degree of human disturbance (GCs levels decreased with distance to roads and increased with human activity; T3 levels the opposite effect). By including predator presence in the study, Wasser *et al.* (2011) could also show that caribou preferred safety from predation risk over nutrition. Joly, Wasser and Booth (2015) studied among other things nutritional stress in barren-ground caribou with respect to habitat quality, and their results support Wasser *et al.* (2011). They found a higher degree of nutritional stress at higher altitudes, where the quality of habitat and lichen abundance was lower; pregnant cows were the most affected by nutritional stress. The above mentioned studies sampled acute and chronic stress indicators from scats and therefore provide a non-invasive method to monitor population health in natural habitats.

8. Conclusion

Historically, stress has been investigated in a large amount of either purely ecological or purely physiological studies. This review focuses on stress especially in the context of a relatively new and very promising field of research: ecophysiology. Despite the underrepresented amount of studies on wild animals - and especially large herbivores - literature provides evidence for a range of possible severe consequences of stress and, in particular, chronic stress. Stress tends to be most critical for the reproductive units, and can scale up from affecting individual health and fitness, to negatively affect population dynamics.

This review shows that stress does matter, as it can affect both individuals and populations. In a world where the human footprint is rapidly increasing, there is urgent need for more studies adopting an ecophysiology approach, in order to trace back from stress responses to stressors. In particular, there is a need to understand the mechanisms and the consequences of stress on highly sensitive species, such as *Rangifer*, preferentially using non-invasive methods and multi-disciplinary approaches, especially in multiple-stressors contexts. Challenges related to the choice of appropriate methodological approaches and to the correct interpretation of results should be always kept in mind, and can be aided both by technological innovations and by the formulation of precise and testable hypotheses. However, understanding the link between triggers and consequences of stress is of crucial importance for conservation and management, and can facilitate human-wildlife coexistence in the future.

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