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Review article

Manipulating glucocorticoids in wild animals: basic and applied perspectives

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One of the most comprehensively studied responses to stressors in vertebrates is the endogenous production and regulation of glucocorticoids (GCs). Extensive laboratory research using experimental elevation of GCs in model species is instrumental in learning about stressor-induced physiological and behavioural mechanisms; however, such studies fail to inform our understanding of ecological and evolutionary processes in the wild. We reviewed emerging research that has used GC manipulations in wild vertebrates to assess GC-mediated effects on survival, physiology, behaviour, reproduction and offspring quality. Within and across taxa, exogenous manipulation of GCs increased, decreased or had no effect on traits examined in the reviewed studies. The notable diversity in responses to GC manipulation could be associated with variation in experimental methods, inherent differences among species, morphs, sexes and age classes, and the ecological conditions in which responses were measured. In their current form, results from experimental studies may be applied to animal conservation on a case-by-case basis in contexts such as threshold-based management. We discuss ways to integrate mechanistic explanations for changes in animal abundance in altered environments with functional applications that inform conservation practitioners of which species and traits may be most responsive to environmental change or human disturbance. Experimental GC manipulation holds promise for determining mechanisms underlying fitness impairment and population declines. Future work in this area should examine multiple life-history traits, with consideration of individual variation and, most importantly, validation of GC manipulations within naturally occurring and physiologically relevant ranges.

Key words: Corticosterone, cortisol, endocrinology, hormone, life history, stress

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Introduction

As exposure of wildlife to anthropogenic stressors intensifies (e.g. climate change, invasive species, chemical pollution, habitat fragmentation), investigation into the consequences of this exposure is shifting to the forefront of both basic and applied research (Wikelski and Cooke, 2006; Sih *et al*., 2010). Arguably, the most extensively studied organism-level response to stressors is the endogenous production and regulation of glucocorticoids GCs; (Cooke and O'Connor, 2010; Baker *et al*., 2013). Glucocorticoids are a class of steroid hormones that mediate physiological and behavioural responses to environmental challenges (Sapolsky *et al*., 2000). The production of GCs is regulated by the hypothalamic–pituitary–adrenal

(HPA) axis in mammals and birds and by the hypothalamic–pituitary–interrenal (HPI) axis in fishes, amphibians and reptiles. Comprehensively examined across taxa (mammals, Reeder and Kramer, 2005; birds, Siegel, 1980; reptiles, Guillette *et al*., 1995; fishes, Wendelaar Bonga, 1997; amphibians, Denver, 2009), the HPA/I axis initiates in response to an acute stressor in the hypothalamus with the release of corticotropin-releasing factor (CRF), which stimulates the pituitary to release adrenocorticotropic hormone (ACTH), which in turn stimulates the adrenal gland or interrenal cells of the head kidney to produce GCs (Fig. 1). Glucocorticoids (corticosterone in birds, non-human mammals, reptiles and amphibians; cortisol in fishes) then bind to glucocorticoid receptors (GRs) throughout the body, activating a cascade of physiological and behavioural changes (Fig. 1; Sapolsky *et al*., 2000). Via negative feedback at all organizational levels of the HPA/I axis (Fig. 1), GC production stops and circulating GC levels return to resting, pre-stressor levels. Thus, the focus on understanding the effects of GCs in animals inhabiting rapidly changing environments is not surprising given the established relationship between GCs and animal stress (Romero, 2004).

Wild populations now endure chronic exposure to natural stressors (e.g. winter, periods of low food availability, predation threat), in addition to anthropogenic stressors, whereby repeated and/or prolonged elevation of circulating GCs is possible (Sheriff *et al*., 2011; Boonstra, 2013; Wingfield, 2013; Dantzer *et al*., 2014; but see Dickens and Romero, 2013). Recurring elevations of GCs may lead to a chronically elevated baseline, which could subsequently influence the physiology, behaviour and fitness of an animal (Romero *et al*., 2009). Benchmark responses to chronic stressor exposure and chronically elevated GCs include reduced growth, immunocompetence, reproduction and survival. Notable reviews on the effects of supra-optimal hormone levels (and thus, justification for manipulating hormones in free-living systems; Ketterson *et al*., 1996) and exploration of how GCs mediate fitness outcomes from evolutionary perspectives (Breuner *et al*., 2008; Bonier *et al*., 2009; Meylan *et al*., 2012) provide excellent foundations for review of methodological aspects of this area of research. Understanding the diversity of approaches and applications of GC manipulation is important to gain insight into how field-oriented integrative biologists can continue to manipulate GCs to mimic *in vivo* conditions of stress experienced by wild animals and generate predictions relevant to ecology, evolution and environmental change.

Here, we first provide an overview of studies that have used exogenous GCs to examine the effects of elevated GCs on survival, physiological, behavioural, reproductive and intergenerational responses in wild vertebrates and demonstrate the range of approaches taken to manipulate GCs (Fig. 2 and Table 1). Administration of exogenous GCs simulates in a standardized manner (via dosage) the activation of GC-mediated processes following exposure to a stressor, but not the sensory perception of the stressor itself (which can be highly variable) nor the onset of the HPA/I. We acknowledge that manipulation of environmental/ecological factors (e.g. predator exposure, brood size) is an alternative and effective way to alter levels of GCs indirectly. We note the importance of physiological feedback in the vertebrate stress response (Fig. 1; Romero, 2004), the (at present) unknown influences of exogenous GCs on HPA/I feedback and GC receptor capacity, and also the growing use of GC receptor blockers (e.g. synthetic GCs, dexamethasone; Dickens *et al*., 2009a) and GC synthesis inhibitors (e.g. metyrapone; McConnachie *et al*., 2012a) in tandem with GC manipulation. However, we exclude such work here because it is beyond the scope of this paper. We focus on GC manipulation of wild species to ensure ecological and applied (e.g. conservation, resource management) relevance, given the potential for domesticated species and laboratory animals to have altered GC responses to stressors (e.g. in fishes; Lepage *et al*., 2001). We acknowledge that extensive laboratory research using model species [e.g. Norway rats (*Rattus norvegicus*), chickens (*Gallus domesticus*), rainbow trout (*Oncorhynchus mykiss*)] has been instrumental in learning about physiological mechanisms but note that such studies do not inform our understanding of ecological or evolutionary processes in the wild. Second, we summarize general findings gleaned from the literature to provide context for our third aim, which is to identify strategies to predict, mitigate and account for factors that drive the considerably variable results that can arise when experimentally manipulating GCs; variability that presently limits comparative analyses.

Understanding the extent and magnitude of GC-mediated effects on wildlife can build on both proximate and ultimate explanations for changes in animal abundance in altered environments. Do elevated GCs alter developmental and physiological processes that translate into fitness consequences? How do evolutionary trade-offs that shape inherent GC production and regulation influence the response to experimentally elevated GCs, and do such trade-offs vary across taxa? From an applied perspective, this information can advise conservation managers and policymakers of which individuals, populations or species are most susceptible to anthropogenic stressors and the ecological changes such stressors can elicit (Cooke *et al*., 2013; Madliger and Love, 2014).

Effects of glucocorticoids on fitness-relevant traits

Growth, immune function and survival

The effects of GC manipulation on growth, metabolism and immune function are well documented. Growth is often reduced following GC treatment in birds (Busch *et al*., 2008; Müller *et al*., 2009; Stier *et al*., 2009; Davies *et al*., 2013) and fishes (O'Connor *et al*., 2011, 2013; Midwood *et al*., 2014). Muscle-specific traits (e.g. mass, Busch *et al*., 2008; lipid content, O'Connor *et al*., 2013) are also reduced following GC manipulation. These reductions can influence completion of important developmental transitions (e.g. moulting in birds, Busch *et al*., 2008; overwinter survival in fishes, O'Connor *et al*., 2010). Altered growth trajectories may be driven by

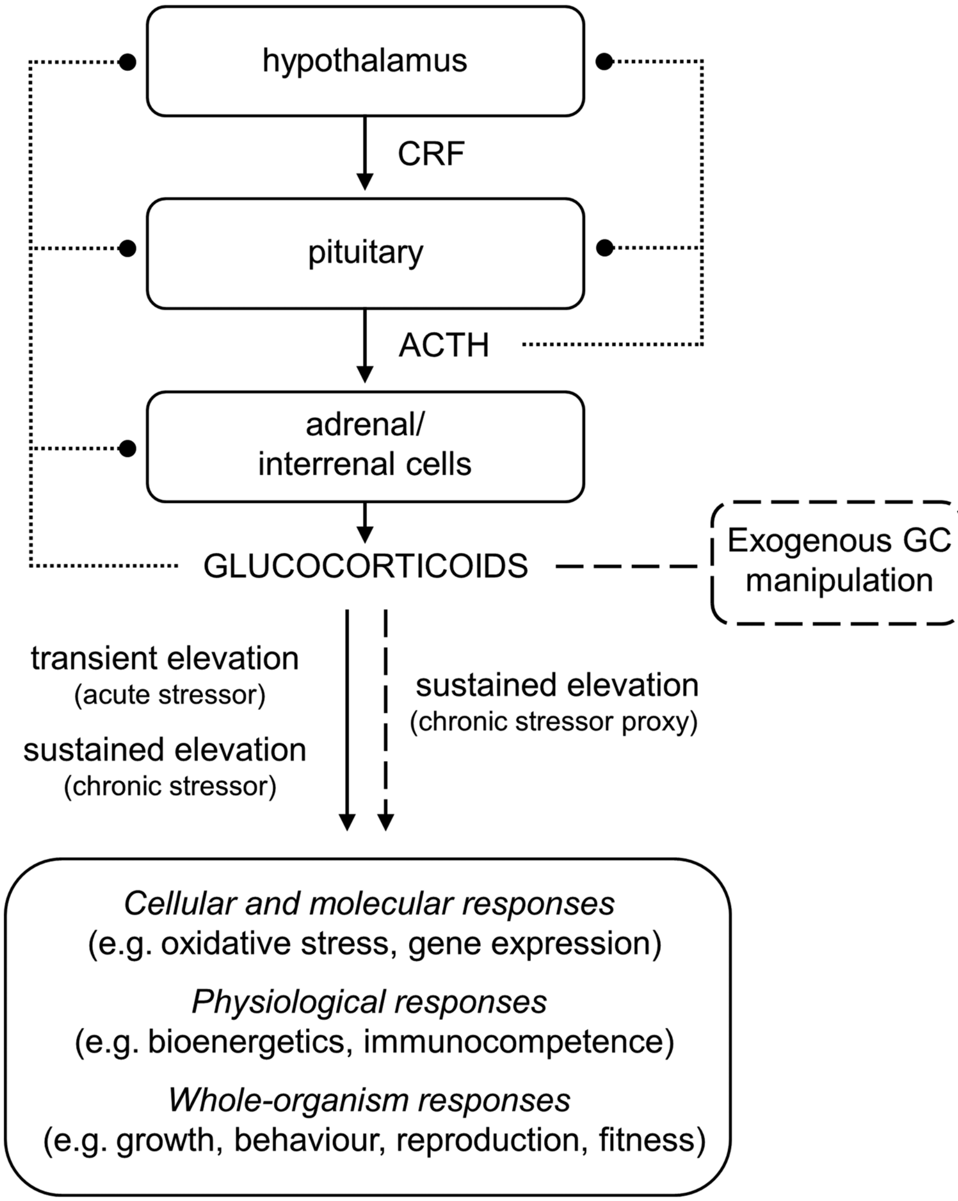

Figure 1: Overview of hypothalamic–pituitary–adrenal (HPA) or hypothalamic–pituitary–interrenal (HPI) axis. Stressor exposure stimulates production of corticotropin-releasing factor (CRF), resulting in release of adrenocorticotropic hormone (ACTH) from the pituitary. The ACTH binds to receptors on adrenal glands (mammals, birds) or interrenal cells (reptiles, fishes, amphibians), stimulating production of glucocorticoids (GCs). Concentrations of GCs are transiently elevated following exposure to an acute stressor. Via negative feedback (dotted lines) by both ACTH and GCs at all levels of the HPA/I axis, adrenal gland/interrenal cell GC production ceases. Chronic stressor exposure can weaken/disrupt the feedback mechanism and result in sustained GC elevation. Both transient and sustained elevation in GCs act on numerous physiological systems, resulting in changes at the cellular/molecular, physiological and whole-organism levels (continuous arrow). Experimental GC manipulation (dashed lines/arrow) bypasses activation of the HPA/I axis and elevates GCs in a manner mimicking chronic stressor exposure (i.e. sustained GC elevation). How exogenous GCs influence HPA/I axis functionality is not fully understood but is thought to influence negative feedback, GC receptor capacity and/or stressor perception. Paralleling endogenous GC production, exogenous GC manipulation also influences cellular/molecular, physiological and whole-organism traits.

underlying changes to metabolism. Glucocorticoids are considered to have a pivotal role in energy mobilization following stimulation of the HPA/I axis; however, the influence of exogenous GCs on circulating metabolites in wild vertebrates varies greatly. In fishes, plasma glucose can be elevated (O'Connor *et al*., 2009; Dey *et al*., 2010) or similar to untreated individuals (O'Connor *et al*., 2011). Plasma concentrations of protein and/or indicators of protein

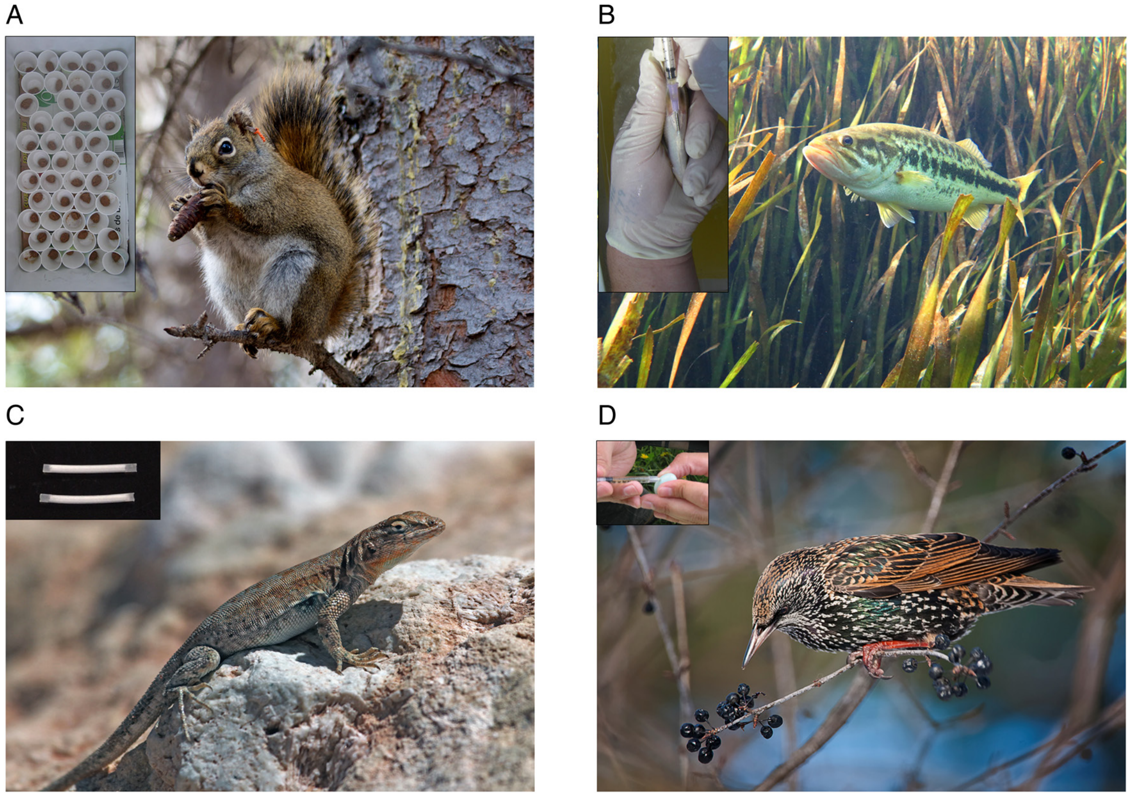

Figure 2: Examples of glucocorticoid (GC) manipulations that investigate effects of GCs on ecologically relevant traits in wildlife. (**A**) In mammals, Dantzer *et al*. (2013) fed wild red squirrels (*Tamiasciurus hudsonicus*) cortisol-laced peanut butter balls (inset) to corroborate findings of increased maternal GCs and offspring growth rates following exposure of mothers to natural and experimentally induced increases in conspecific densities. Photographs by Ben Dantzer. (**B**) In fishes, intraperitoneal injection of GCs (inset; photograph by Alex Nagrodski) in wild largemouth bass (*Micropterus salmoides*; photograph by Barbara am Ende) revealed how parental care, nest abandonment and susceptibility to infection can be altered by exogenous GCs administered during the breeding season (O'Connor *et al*., 2009). (**C**) In reptiles, GC-infused Silastic tubing (inset; photograph by Oliver Love) was implanted in free-ranging side-blotched lizards (*Uta stansburiana*; photograph by Ron Wolf) to assess how GCs influence home range size, general activity levels and competitive ability (DeNardo and Sinervo, 1994). (**D**) In birds, European starling (*Sturnus vulgaris*; photograph by Michael Cummings) eggs were injected with GCs (inset; photograph by Oliver Love) and raised in natural settings to explore how maternally derived hormones affected offspring condition, survival, hypothalamic–pituitary–adrenal function and begging behaviour (Love and Williams, 2008a, b).

mobilization (e.g. uric acid) are not affected by GC manipulation in a consistent manner (e.g. O'Connor *et al*., 2011; Davies *et al*., 2013). A potentially more functional metric of metabolism that could account for reductions in growth is standard metabolic rate, which is increased in largemouth bass (*Micropterus salmoides*) injected with cortisol (O'Connor *et al*., 2011). However, further examination of the relationship between plasma GC concentrations and metabolic rate is necessary, particularly in species exposed to thermal stressors, because the number of studies investigating standard metabolic rates following GC manipulation remains limited.

Chronic elevation of GCs is predicted to weaken immunocompetence and increase susceptibility to disease (Romero *et al*., 2009). Indeed, in birds considerable evidence supports this notion. Implantation of GC-filled Silastic tubing in American kestrels (*Falco sparverius*) enhances the swelling response to the plant toxin phytohaemagglutinin, but this effect was detected only after removal of the implant (Butler *et al*., 2010). Glucocorticoid manipulation is associated with a greater reduction in immunoglobulin levels in the common eider (*Somateria mollissima*) but has no impact on their T-cell immunity (Bourgeon and Raclot, 2006). Glucocorticoid treatment reduces the production of antibodies and resistance to oxidative stress in nestling barn owls (*Tyto alba*, Stier *et al*., 2009). Similar reductions in immunocompetence are observed in reptiles (e.g. phytohaemagglutinin swelling response, Berger *et al*., 2005; rate of wound healing, French *et al*., 2007), mammals (e.g. bacteria killing ability, Brooks and Mateo, 2013) and fishes (e.g. presence of external mould infection, O'Connor *et al*., 2009).

As the preceding paragraphs highlight, although the release and regulation of GCs are aimed at restoring homeostasis, chronically elevated GCs can disrupt this feedback system and

Table 1: Methods of glucocorticoid manipulation

Method	Taxa (references)	Description	Advantages and disadvantages
Silastic tubing	Birds* (Romero *et al.*, 2005), reptiles* (Juneau *et al.*, in press)	Silicone tubing filled with crystalline GCs and surgically inserted subcutaneously. Tubing is sealed at one, both or neither end and punctured with holes to facilitate diffusion of GCs	Effective control of dosage and GC release but costly and invasive
Osmotic pump	Birds* (Horton and Holberton, 2009)	Pump filled with crystalline GCs and surgically inserted subcutaneously. Pump is composed of osmotic and semi-permeable layers. Pump contains flow moderator to facilitate fixed delivery rates of GCs	Effective control of dosage and GC release but costly and invasive
Pellet	Birds* (Spée *et al.*, 2011)	Glucocorticoid is emulsified in a combination of cholesterol, cellulose, lactose, phosphates and stearates and formed into a pellet. The hardened pellet is surgically inserted subcutaneously, and GCs are released as it dissolves	Effective control of dosage and GC release but costly and invasive
Transdermal patch	Birds* (Patterson *et al.*, 2011), reptiles* (Knapp and Moore, 1997), amphibians* (Bliley and Woodley, 2012)	Crystalline GC dissolved in vehicle (e.g. sesame oil), applied to low-protein-binding filter paper and affixed to dorsal region. Lipophilic GCs are absorbed through the skin of species with lipid-rich epidermis	Cost effective and non-invasive but limited to species with a lipid-rich epidermis and where direct contact can be made with skin (e.g. in fishes, mucus secretion prevents contact)
Topical treatment	Birds* (Busch *et al.*, 2008), reptiles* (Meylan *et al.*, 2010)	Crystalline GC dissolved in vehicle (e.g. sesame oil, dimethyl sulfoxide) and applied directly onto dorsal region. Lipophilic GCs are absorbed through the skin of species with lipid-rich epidermis	Cost effective and non-invasive but often requires repeated application to attain desired GC concentrations; limited to species with lipid-rich epidermis and where direct contact can be made with skin (e.g. in fishes, mucus secretion prevents contact)
Food/drink	Birds* (Lõhmus *et al.*, 2006), mammals* (Brooks and Mateo, 2013), fishes (Barton *et al.*, 1987)	Crystalline GC dissolved in vehicle (e.g. sesame oil, dimethyl sulfoxide, ethanol) and added to food/water	Logistically accessible and non-invasive; however, variation in gut lining absorption and feeding/drinking rates and formation of feeding hierarchies can generate different GC levels among individuals
Injection (intra-arterial)	Fishes (Laurent and Perry, 1990)	Crystalline GC dissolved in vehicle (e.g. ethanol + saline) and injected into arterial cannula	Permits serial sampling, but uses invasive cannulation that requires holding animals in small enclosures, a possible confinement stressor. Best used to examine effects of acute elevation of GCs because diffusion into circulation is immediate
Injection (intramuscular)	Mammals* (Santema *et al.*, 2013), fishes* (Cull *et al.*, 2015)	Crystalline GC dissolved in vehicle (e.g. ethanol + saline, cocoa butter) and injected into musculature	Best used to examine effects of acute elevation of GCs because diffusion into circulation is often rapid when vehicle is liquid. In fishes, cocoa butter can be used in tropical species [e.g. checkered pufferfish, (*Sphoeroides testudineus*), Cull *et al.*, 2015]
Injection (intraperito-neal)	Birds (Gam *et al.*, 2011), fishes* (O'Connor *et al.*, 2009), reptiles* (Moore and Mason, 2001), amphibians* (Burmeister *et al.*, 2001)	Crystalline GC dissolved in vehicle (e.g. cocoa butter, coconut oil, vegetable shortening and vegetable oil mixture, ethanol + saline) and injected into intraperitoneal cavity	In temperate fishes, the temperature differential between the vehicle and holding water promotes the formation of a pellet that gradually releases GCs. Delivery rates can be inconsistent, and injury to organs is possible
Injection (egg)	Birds* (Love and Williams, 2008a, b), reptiles* (Warner *et al.*, 2009), fishes (Nesan and Vijayan, 2012)	Crystalline GC dissolved in vehicle (e.g. sesame/corn/peanut oil) that is injected directly into fertilized eggs	Bypasses the egg shell/membrane and directly delivers GCs into yolk. Facilitates investigation of interactive effects of maternally derived GCs and other compo-nents of maternal stress. Interfemale variation in egg GCs could influence desired GC levels

(*Continued*)

Table 1: continued

Method	Taxa (references)	Description	Advantages and disadvantages
Bath (egg/ embryo)	Fishes* (Gagliano and McCormick, 2009)	Crystalline GC dissolved into solution (e.g. ethanol) and mixed into vehicle that immerses unfertilized (e.g. in ovarian fluid) or fertilized eggs/embryos (e.g. in incubation water)	Facilitates investigation of interactive effects of maternally derived GCs and other components of maternal stress. Egg membrane permeability and hardening (e.g. of unfertilized vs. fertilized eggs) and interfemale variation in egg GCs could influence desired levels

Described in the table are the different GC methods used to date, the taxa for which the method is applicable, reference to a study using the method in said taxa, and the potential advantages and disadvantages of each method. Methods of GC manipulation that have been used in wild animals are indicated by an asterisk. Possible methods for the manipulation of glucocorticoids (GCs) vary among and within taxa. Glucocorticoids are either applied in the crystalline form (e.g. in Silastic tubing) or are first dissolved into a vehicle, such as cocoa butter, prior to application (e.g. for intraperitoneal injections). The type of GC used will vary by taxa (e.g. cortisol in fishes, corticosterone in birds and reptiles), and within a taxa different forms of the primary GC may be used (e.g. hydrocortisone vs. hydrocortisone 21-hemisuccinate salt). Benefits and limitations of different methodologies depend on the specific taxa and life stage examined, the invasiveness of the procedure and the desired duration of the GC elevation period. The desired effects of most manipulations are prolonged elevation (days to weeks) of circulating levels of GCs, however, some methods result in elevations that are shorter in duration (e.g. intra-arterial injection) or may need to be reapplied periodically to maintain elevated concentrations (e.g. topical treatment).

may compromise survival (Romero *et al*., 2009). In wild fishes, exogenous GC treatment reduced overall survival (Nagrodski *et al*., 2013b) and longevity (McConnachie *et al*., 2012a), with emergence of trends influenced by time passed since GC treatment (Nagrodski *et al*., 2013a). Multi-year monitoring revealed reduced survival in black-legged kittiwakes (*Rissa tridactyla*) following GC manipulation (Goutte *et al*., 2010). Sex-specific survival patterns are evident in common lizards (*Lacerta vivipara*); GC manipulation increases survival in males but has no effect in females (Cote *et al*., 2006). The effect of GC manipulation on survival can be absent in benign conditions but arise in the presence of an environmental stressor (e.g. winter conditions, O'Connor *et al*., 2010).

Behaviour

For virtually all behaviours examined, the administration of GCs produces results that vary depending on dosage, species and context, which highlights the complexity of the effect of physiological stressors on behavioural responses. In birds and herpetofauna, GC manipulation can increase foraging activity and food consumption rates (Kitaysky *et al*., 2003; Cote *et al*., 2006; Lõhmus *et al*., 2006; Crossin *et al*., 2012), but can also decrease (Busch *et al*., 2008) or have no effect on foraging behaviours (Bliley and Woodley, 2012). Activity levels can increase following GC manipulation in herpetofauna (Belliure and Clobert, 2004; Cote *et al*., 2006) and fishes (O'Connor *et al*., 2010), although carry-over effects can reveal latent reductions in activity (O'Connor *et al*., 2010). Glucocorticoid-mediated effects on activity may be species specific within a taxon, because activity can also be unaffected in herpetofauna (Bliley and Woodley, 2012; Wack *et al*., 2013) and fishes (Nagrodski *et al*., 2013a). Similar variation is observed with regard to thermoregulatory behaviour (i.e. basking), which decreases in ectothermic wall lizards (*Podarcis muralis*, Belliure and Clobert, 2004), increases in the live-bearing lizard *Hoplodactylus maculatus* (Cree *et al*., 2003) and does not change in gravid spotted skinks (*Niveoscincus ocellatus*, Cadby *et al*., 2010). There are also trait-specific effects of GC treatment. In checkered pufferfish (*Sphoeroides testudineus*), thermoregulatory behaviour but not swimming endurance was altered by GC injection (Cull *et al*., 2015).

When animals are exposed to chronic stress, costly reproductive behaviours are expected to be reduced in favour of behaviours that increase survival. Consistent with this prediction, aggression (DeNardo and Licht, 1993; McConnachie *et al*., 2012a) and competitive ability (measured as territory size, DeNardo and Sinervo, 1994; measured as time on territory, McConnachie *et al*., 2012a) are suppressed in GC-treated reptiles and fishes. Glucocorticoid manipulation appears to enhance anti-predator behaviours (Thaker *et al*., 2009; Trompeter and Langkilde, 2011) but impair learning (Kitaysky *et al*., 2003; Mateo, 2008). Courtship and mating behaviours in reptiles and amphibians can decrease (Burmeister *et al*., 2001; Moore and Mason, 2001) or increase (Gonzalez-Jimena and Fitze, 2012) following exogenous GC treatment. Reductions in aspects of parental care are frequently observed in birds treated with GCs, including food provisioning rates (Horton and Holberton, 2009), nest attendance (Spée *et al*., 2011) and incubation temperature (Thierry *et al*., 2013). Increased (Ouyang *et al*., 2013) and unchanged parental behaviours (Kitaysky *et al*. 2001) are reported as well, and effects can be sex and morph specific (Almasi *et al*., 2008, 2013). Understanding how reproductive behaviours are affected by GCs remains of particular interest, because these are the mechanisms affecting offspring success and, ultimately, individual fitness.

Reproduction

Laboratory-driven research shows that GCs suppress reproductive functions by mediating the production of reproductive hormones (Wingfield and Sapolsky, 2003), but results using wild-caught animals are less consistent. Elevated exogenous GCs correlate with a decline in prolactin levels in three species of wild birds [common eiders (*Somateria mollissima*), Criscuolo *et al*., 2005; black-legged kittiwakes (*Rissa tridactyla*), Angelier *et al.*, 2009; Adélie penguins (*Pygoscelis adeliae*), Spée *et al.*, 2011], which forms a component of the 'prolactin stress response' (e.g. Angelier and Chastel, 2009), but this relationship is not always evident (Crossin *et al.*, 2012). Likewise, GC treatment does not affect plasma androgens in male largemouth bass during brood care (O'Connor *et al.*, 2009) nor in red-sided garter snakes (*Thamnophis sirtalis parietalis*) despite reductions in reproductive behaviour in this species (Moore and Mason, 2001).

Literature describing the effects of adult GC treatment on gametic characteristics and reproductive success presently focuses on reproductive success in females rather than males. In snakes (Robert *et al.*, 2009) and placental reptiles (Meylan *et al.*, 2002, 2010; Cadby *et al.*, 2010), the probability of a successful clutch (e.g. live neonates) is significantly lower in GC-treated females. In birds (Salvante and Williams, 2003) and reptiles (Vercken *et al.*, 2007), clutch size is not influenced by maternal GC treatment. Adult pink salmon (*Oncorhynchus gorbuscha*) injected with exogenous GCs on spawning grounds release fewer eggs and a smaller proportion of their eggs compared with non-manipulated fish (McConnachie *et al.*, 2012a). While GC administration may have a considerable, direct impact on fitness via reproductive output, it can also have an indirect effect via offspring quality, because maternal GC treatment influences egg size (e.g. Lancaster *et al.*, 2008) and the hormonal composition of developing eggs (Love *et al.*, 2005; O'Connor *et al.*, 2013). Research on the resonating effects of maternal stress on surviving offspring is now growing, with maternally derived egg GCs as a candidate driver of intergenerational effects.

Intergenerational effects

Evaluation of offspring quality provides a comprehensive understanding of how increased levels of GCs impact wildlife across generations. In humans and rodents, the inter- and transgenerational effects of elevated GCs can be profound (reviewed by Khulan and Drake, 2012), but the understanding of how these processes manifest in wild animals remains a relatively new area of research. For oviparous species, a logistically simplified method for exploring hormonally driven intergenerational effects is the direct manipulation of egg GCs via hormone injection or bathing. Although these methods are an imperfect proxy for maternally induced increases in egg GCs, because epigenetic (Ho and Burggren, 2010) and potential maternal buffering components (Li *et al.*, 2012) are excluded, the applicability of egg injections/baths remains taxonomically broad. Importantly, manipulation of maternal or egg GCs can elicit similar responses; for example, in birds, GC-elevated females (Love *et al.*, 2005) and eggs (Love and Williams, 2008b) both result in female-biased clutches.

Effects of egg/maternal GC manipulation on offspring development are highly variable among and within taxa. Egg/maternal GC treatment can decrease (Gagliano and McCormick, 2009; Warner *et al.*, 2009), increase (Meylan and Clobert, 2005) or not influence offspring survival (Rubolini *et al.*, 2005). In reptiles, general measures of offspring growth can increase (Warner *et al.*, 2009), decrease (Meylan *et al.*, 2010) or show no change (Uller and Olsson, 2006) following egg/maternal GC treatment. Likewise, in birds, increased (Crossin *et al.*, 2012), decreased (Love *et al.*, 2005) and unchanged offspring body masses (Almasi *et al.*, 2013) are reported, as well as population-specific effects (Schultner *et al.*, 2013). Increases and decreases in avian offspring growth may be mediated by GC-mediated increases (Crossin *et al.*, 2012) and reductions (Horton and Holberton, 2009) in parental foraging/provisioning, respectively. Increases in growth rates are also observed in mammalian offspring reared from mothers with increased GCs (Dantzer *et al.*, 2013).

Generally, following GC treatment of eggs/mothers, offspring behavioural/performance responses are also variable. Juvenile birds reared from GC-treated eggs/mothers have elevated (Schultner *et al.*, 2013), dampened (Love and Williams, 2008a) or unaltered plasma GC levels (Almasi *et al.*, 2013) following exposure to a stressor. Baseline GC levels in juvenile Western garter snakes (*Thamnophis elegans*, Robert *et al.*, 2009) are also not affected by egg/maternal GC treatment. Egg/maternal GC treatment compromises offspring immune function (T-cell proliferation) in birds (Love *et al.*, 2005; Rubolini *et al.*, 2005). Begging intensity is decreased in yellow-legged gulls (*Larus michahellis*, Rubolini *et al.*, 2005) but increased in European starlings (Love and Williams, 2008b), along with flight muscle mass and performance (Chin *et al.*, 2009). Heart rate is increased in coral reef damselfish (*Pomacentrus amboinensis*, Gagliano and McCormick, 2009). Anti-predatory behaviour (shelter use) can increase in lizards (Uller and Olsson, 2006), and tendency to disperse is reduced but dependent on maternal condition (Meylan *et al.*, 2002). Not all behaviours are susceptible to egg/maternal GC manipulation; for example, sprinting/swimming endurance of reptiles remained unchanged for several species (Uller and Olsson, 2006; Robert *et al.*, 2009; Cadby *et al.*, 2010). Although again variable, adaptive implications of increases, decreases or no changes to the same trait can be contingent on whether the observed offspring trait is matched or mismatched to the maternal environment (Love *et al.*, 2013; Sheriff and Love, 2013), highlighting the significance of examining subsequent effects of GC manipulation in ecologically relevant conditions (see '*Considerations for the future use of glucocorticoid manipulations*' below).

How to interpret a 'mixed bag' of results

It is clear, given the extensively variable outcomes of exogenous GC manipulation, that results generated from laboratory-based biomedical and physiological research are not easily replicated in wild animals. This is not surprising when considering the manifold differences between laboratory and field environments (e.g. food availability, predation pressure, disease, behavioural repertoire). A major cause of variation in responses to GCs may be in the methodology itself; GCs represent only one step of the HPA/I axis (i.e. the end point GC elevation but not preceding hormonal signalling), and the use of different methods (Table 1) is apt to create variation within and among taxa. Although GCs are the major effector hormones of the stress response, experimental GC manipulation may not account for variation in GC receptor densities or the cascading reactions that release additional hormones, which generate negative feedback within the HPA/I axis (Fusani, 2008). Moreover, the range of methods available to manipulate exogenous GCs (Table 1) means that the medium of delivery (Quispe *et al.*, 2015), dosage, timing and duration of GC application contribute further to experimental variation. Dose-dependent behaviours (Burmeister *et al.*, 2001; Moore and Mason, 2001) underline the importance of dose validation, because the use of pharmacological doses of hormones and their effects may not be ecologically relevant (Fusani, 2008). Yet, variation in the validation of a dose as ecologically relevant is also evident; some studies report that manipulated GC levels are comparable to endogenous stress-induced levels (e.g. Nagrodski *et al.*, 2013a) or are a certain number of standard deviations away from baseline levels detected in wild animals (Love and Williams, 2008a, b). The duration of GC exposure (e.g. a spike of GC via intramuscular injection vs. continuous GC release via Silastic implant; Table 1), timing of trait examination (immediate vs. latent effects), invasiveness of the method (GC application can potentially cause stress), body temperature (for ectotherms) and comparison to adequate control/sham treatments could all influence the effects and interpretation of the GC manipulation. Additional factors to consider are the inherent differences among species, morphs, sexes and age classes, and examination of traits in an ecologically relevant context. Baseline and stressor-induced GC levels vary among species (within a taxon, Barton, 2000), morphs (Horton and Holberton, 2010), sexes (Kubokawa *et al.*, 2001), life-history strategy (Barry *et al.*, 2001) and age class (Mateo, 2006), which can produce variation in responses to GC manipulation. Even when these parameters are accounted for, the context in which animals are observed may have a significant effect on the response. Furthermore, the majority of studies involve the collection of animals from the wild followed by laboratory observations, where patterns may be an artefact of laboratory confinement because animals are not afforded the full range of behavioural options available in the field. Although the aforementioned factors delineated from patterns observed in the literature may be self evident, much research continues to be published using methods that do not effectively control for such factors prior to experimentation, resulting in a tendency to address factors driving variation after analyses contradict *a priori* predictions.

Considerations for the future use of glucocorticoid manipulations

Although there are numerous factors that could contribute to the variable responses to GCs detected among taxa, here we focus on the following three sources of variation that are relatively simple to incorporate and overcome with study design yet contribute significantly to enhancing the integration of experimental elevation of GCs and animal conservation: (i) encompassing multiple life-history parameters and individual variation; (ii) validating and publishing preliminary and final experimental methods; and (iii) continued collaboration among research fields.

Life history, time scale and individual variation

Aspects of an animal's life history (e.g. migration, senescence, alternative mating strategies) have shaped GC production and regulation but may also influence how exogenous application of GCs modulates an animal's behaviour, physiology and survival across its lifespan (Crossin *et al.*, 2015) and compared with conspecifics with alternative life histories (e.g. dominant vs. subordinate individuals, Øverli *et al.*, 2005). For example, Pacific salmon demonstrate chronically elevated baseline GCs during senescence (Baker and Vynne, 2014), at which time the neural and cellular regulation of GCs is thought to be degrading (reviewed by Carruth *et al.*, 2002) and the GC response to stressors is attenuated (Cook *et al.*, 2011). Also, early in development, salmon embryos demonstrate a hyporesponsive period whereby predicted increases in GCs following exposure to a stressor are not observed (Feist and Schreck, 2002). Diel fluctuations in GCs are also present in salmon (Thorpe *et al.*, 1987). Finally, within a species, iteroparous individuals have lower baseline GCs compared with semelparous individuals (Barry *et al.*, 2001). Accordingly, when choosing to manipulate GCs at a particular life-history stage or in a particular life-history strategy, one must be aware of the underlying regulatory processes occurring, because they could potentially attenuate or magnify predicted plasma GC elevations. Also, GC manipulation may eliminate these naturally occurring fluctuations in GCs, which may or may not be relevant for the environmental context (e.g. severe, prolonged stressor vs. repeated, acute stressor). This natural variation in circulating GCs must also be considered when determining the physiologically relevant range targeted by exogenous manipulation. Furthermore, these processes may mask (or enhance) secondary and tertiary effects but then manifest latent carry-over or intergenerational effects. Probably as a result of logistical constraints, most studies have focused on a single survival trait at a single life-history stage. Detection of potential masked or latent effects requires examination of multiple traits (e.g. locomotory and metabolic performance) across multiple life-history stages (e.g. hatching/metamorphosis, sexual maturation, senescence).

Glucocorticoid-mediated responses to short-term environmental stressors have been well documented in the literature (e.g. the 'emergency life-history stage' as defined by Wingfield *et al.*, 1998). More recent studies suggest that GCs can mediate phenomena operating over longer temporal scales and multiple life-history stages. O'Connor *et al*. (2014) recently defined carry-over effects as occurring 'in any situation where an individual's previous history and experience explains their current performance in a given situation'. This nuanced approach to carry-over effects is especially relevant for GC manipulations, which can have both short- (hours to days) and long-term influences (months to years) on animal physiology, behaviour and fitness. Broadening the traditional approach to carry-over effects (i.e. season to season) can facilitate broader application of relationships between GC levels in one state to a suite of metrics in a subsequent state. From a basic perspective, an individual's endocrine profile in one state can contribute to individual performance in a subsequent state (O'Connor *et al*., 2010; Midwood *et al*., 2014; Schultner *et al*., 2014). Tandem to incorporating life-history diversity and duration/carry-over effects is recognizing that even within a life-history strategy, there is interindividual variation in responses to stressors and exogenous GCs.

There is a growing appreciation for consistent individual variation in behaviour (i.e. personality), relationships between individual behaviours (i.e. behavioural syndromes, Sih *et al*., 2004) and support for associations between behavioural tendencies and physiological responses to stressors (i.e. coping style, Koolhaus *et al*., 1999). The ways in which these behavioural and physiological syndromes influence experimental manipulation of GCs should be of interest. Ranking individuals to establish personality may not always be feasible if it requires additional handling or housing that could alter behaviour (but see '*Collaborating among research disciplines*' below). Increasing sample sizes could help to balance the proportion of behavioural types being captured and reduce variation in response to exogenous GCs that may arise from inherent personality differences within a population; again, this option may not always be available when working with wild animals.

The GC manipulation studies reviewed above (see '*Effects of glucocorticoids on fitness-relevant traits*') were generally composed of single experiments within a particular biotic (e.g. age class, sex) and/or abiotic context (e.g. season, predation). To generate comprehensive knowledge of how increases in GCs affect wildlife, coordinated research is needed whereby multiple studies are carried out to track target animals prior to and across life stages after GC manipulation. Notable examples of such an approach are found across taxa (fishes, O'Connor *et al*., 2009, 2010, 2011, 2013; reptiles, Meylan *et al*., 2002, 2010; Meylan and Clobert, 2005; birds, Love *et al*., 2005; Love and Williams, 2008a, b). Using European starlings, Love *et al*. (2005) and Love and Williams (2008a, b) manipulated maternal and egg GCs, respectively, using ecologically relevant dosages and across years and breeding seasons, assessed various end points (body condition, clutch size and sex ratio) between generations (offspring growth, survival, immunocompetence and stress reactivity) and between abiotic states (low- vs. high-quality mothers via wing clipping).

Validations of glucocorticoid variant, dose and exposure route

Following selection of the appropriate sex, life-history stage and observation period, key to the ecological relevance of GC manipulation is validation of dose–response curves that are within an ecologically and physiologically relevant range (e.g. baseline egg GCs within 1.5 SD of the population mean, Love and Williams, 2008a, b; circulating GCs post-treatment not statistically different from levels detected in individuals chased to exhaustion, Nagrodski *et al*., 2013a). Dose validation ensures that effects are not resultant from supraphysiological elevations of limited ecological relevance. Pilot studies, where methods are employed on the same or similar species prior to or concurrent with field studies, can be used for informing dose deliveries and initial reference (e.g. Criscuolo *et al*., 2005). However, validation for a given species is necessary given documented examples of interspecific variation in GC manipulation outcomes (measured by cortisol in plasma) even among confamilials [e.g. half the dose used to achieve physiologically relevant values of cortisol for largemouth bass (O'Connor *et al*., 2013) yielded supraphysiological values for bluegill sunfish (*Lepomis macrochirus*, McConnachie *et al*., 2012b)].

Layered on the importance of dosage is the type of GC used as well as the delivery medium. For example, in teleost fishes the primary GC is cortisol (Bury and Sturm, 2007), but hydrocortisone mixed with coconut oil (O'Connor *et al*., 2010) and hydrocortisone 21-hemisuccinate mixed with cocoa butter (O'Connor *et al*., 2013) have been used experimentally to increase GCs in largemouth bass. It is unclear from currently published data whether one GC form and vehicle has advantages over another, and further work is needed to articulate the functional benefits of each.

The route of exposure is also important (see Table 1). For instance, intraperitoneal injection of GCs is used in fishes to increase egg cortisol levels but can result in increased female mortality and reduced progeny size, thus precluding or compromising intergenerational studies (Hoogenboom *et al*., 2011). Manipulation of teleost egg GCs has been accomplishing by bathing unfertilized eggs in ovarian fluid with a hydrocortisone solution (Sloman, 2010) or by microinjecting one-cell embryos with solutions of hydrocortisone first dissolved in ethanol then evaporated and reconstituted with water (Nesan and Vijayan, 2012).

Finally, as mentioned above, single vs. repeated administration of exogenous GCs has implications for the relevance of the stressor exposure being simulated. To enable consistency in experimental design, publishing outcomes of all dosages (concentration, type and brand of GC) and methodologies (Table 1) tested (e.g. by supplying online supplementary materials) would help to inform experimental design in future research.

Coupled with the need for dose validation is further exploration of how exogenously elevated GCs are influencing the

HPA/I axis itself in wild animals. Indeed, quantification of GC concentration can be confirmed in plasma (or other biological samples, Sheriff *et al*., 2011). Key secretagogues of GCs, CRF and ACTH, can also be measured in plasma and provide valuable information regarding negative feedback (Fig. 1). Determining HPA/I axis activity also entails sampling of other tissues. For example, genetic expression of CRF can be measured in the brain, or tissue-specific GR densities can by measured (Jeffrey *et al*., 2012). Accounting for changes in hormone receptors is especially important (Fusani, 2008); chronic stress and chronically elevated GCs reduce the expression and sensitivity of these receptors (Maule and Schreck, 1991; Dickens *et al*., 2009b; Jeffrey *et al*., 2012), and thus may influence secondary and tertiary effects of exogenous GC elevation.

Integration of research disciplines

The recent integration of behaviour and physiology into conservation biology has allowed conservation biologists to test hitherto untested hypotheses regarding the mechanisms that underlie phenomena of basic and applied interest (Wuchty *et al*., 2007; Cooke *et al*., 2012, 2014). The coalescing of research fields has been occurring for some time (e.g. ecophysiology, behavioural ecology, ecotoxicology, conservation physiology), and teams of scientists from diverse disciplines can produce more influential and novel research (Wuchty *et al*., 2007). However, often one has extensive training in only one field of the amalgamation and is entering as a novice into the other field (Sankar *et al*., 2007). One might argue that conservation physiology and conservation behaviour are two such fields whereby the majority of research is physiological and behavioural by nature but tends to be moulded to conservation issues *ad hoc*. Now, researchers in these fields are striving to design studies that use physiological and behavioural metrics to provide practical data that are easily translated to conservation issues (Cooke *et al*., 2014).

Collaboration across disciplinary lines is not always straightforward (Campbell, 2005). Many contemporary conservation problems necessitate an integrative approach in order to provide the data required for effective management (Reyers *et al*., 2010). Managers often need to know not only how wildlife is distributed in time and space, but also the reasons controlling individual variation within those patterns. Using wild Pacific salmon recreational fisheries in British Columbia as an example, researchers embraced an integrative approach by measuring plasma cortisol and glucose in upriver migrating individuals and determining migration rates via electronic tracking to evaluate the efficacy of revival devices following fishery capture (Donaldson *et al*., 2013). The researchers then conducted interviews to determine user-group perspectives on best practices (Donaldson *et al*., 2013). This multifaceted, integrative research programme has generated success, albeit not without challenges, via collaboration among natural scientists, conservation managers and engineers, among other experts (Cooke *et al*., 2012; Young *et al*., 2013).

Likewise, when experimentally altering GCs in wild animals with a goal of gleaning mechanistic insights into ecology, evolution and conservation, collaboration among natural scientists, conservation practitioners, industry and public stakeholder groups should be encouraged. An endocrinology expert can, for example, lend insight into the suitable design of dose validation studies, incorporate GC inhibitors and/or GC receptor blockers into such designs, and choose the most appropriate assays for sampling and measuring GCs. Behavioural ecologists and evolutionary biologists bring knowledge of experimental design that best captures the individual, population and ecosystem level effects of interest, and how these effects relate to environmental perturbations (e.g. predation, density, climate change). Geneticists can ensure proper crossing designs and analyses of molecular markers when planning intergenerational studies. Engineers designing animal tracking (telemetry) and data logging technology can provide novel opportunities to observe wild animals in natural settings before and after GC manipulation. The majority of studies reviewed here either used wild-caught animals manipulated and observed in laboratory settings or wild-caught animals manipulated and observed in the wild. Whether applicability to animal conservation is the primary or auxiliary goal of a study, the latter approach would be most conducive to collaboration with and uptake of knowledge by conservation practitioners. Having intimate knowledge of what data policymakers seek, conservation practitioners can guide a scientist's initial question and confirm whether an experimental approach is feasible in the wild (Cooke *et al*., 2012).

From mechanism to management

One must consider that even meticulously designed studies can produce variable results that are not easily applied to animal conservation. Discussions about the relevance of physiological and behavioural research (e.g. predictive value of GCs) to conservation managers and policymakers are abundant (Busch and Hayward, 2009; Cooke and O'Connor, 2010; Young *et al*., 2013; Dantzer *et al*., 2014; Madliger and Love, 2014), though little instruction is offered regarding how to extract meaningful information from highly variable data. Is it practical to use information from GC manipulations to inform conservation decisions? Presently, studies employing GC manipulations report varied effects on animal populations, ranging from increased, decreased and null effects, which makes generalization difficult. Furthermore, both U-shaped and bell-shaped relationships may exist between GC level and a given response variable, making generalization all the more difficult. Species- and context-specific studies of GCs are therefore the best means available to conservation managers who have an interest in the GC response of species under their protection. When such studies are not available, data from a similar or closely related species may be applicable, but with caution.

To put this into context, consider conservation and management activities that involve the translocation of animals.

Translocation involves the capture, confinement, transport and release of animals from one location to another, which can result in considerable stress (Dickens *et al*., 2009a). Use of controlled GC manipulation experiments may reveal which species, morphs, sexes or age classes may be most vulnerable to this stressor. Information on dose-dependent responses to GCs could be relevant for routinely monitored animals. Regular, minimally invasive or non-invasive measurement of GCs (via plasma, hair, feathers, faeces, etc., Sheriff *et al*., 2011) can be cross-referenced with a biologically relevant threshold, established by experimental GC manipulation, that indicates levels of GCs at which negative impacts are observed (Madliger and Love, 2014). Management action can then be prioritized based on whether GC levels in wildlife are above or below a critical stress threshold. Glucocorticoid-mediated maternal effects can be significant drivers of offspring quality, which can have implications for reproductive success. Intergenerational effects gleaned from experimental GC manipulation could help predict and/or explain patterns in population growth in animal systems that track mating events and monitor GC levels. Extending conclusions from experimental elevation of GCs to animal conservation at present is quite focused and species specific, but comparative conclusions may evolve with further experimental replication and consensus.

Conclusions

The reliability of GC concentrations as biomarkers of stress in wild animals has recently been questioned (Breuner *et al*., 2013; Dickens and Romero, 2013; Schoech *et al*., 2013). Future use of exogenous GCs to address both basic and applied questions should be approached with prior knowledge of natural ranges of GCs in wild animals and coupled with investigation of other predicted biomarkers of chronic stress. For example, the relationships between GCs and oxidative stress (Costantini *et al*., 2011) provide ample opportunity to use exogenous GCs to evaluate traditional biomarkers and also oxidative ecology in the context of animal conservation (Beaulieu *et al*., 2013). The scope for using experimentally elevated GCs to infer mechanisms driving population-level processes in wild animals will be a fruitful area of research with the continued implementation of collaborative and informed study designs.

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