THE ECOLOGY OF STRESS

The ecology of stress: effects of the social environment

Scott Creel*,[1], Ben Dantzer[2], Wolfgang Goymann[3] and Dustin R. Rubenstein[4]

[1]*Conservation Biology & Ecology Program, Department of Ecology, Montana State University, Bozeman, Montana, 59717 USA;* [2]*Department of Zoology, Michigan State University, East Lansing, Michigan, 48824, USA;* [3]*Abteilung Verhaltensneurobiologie, Max-Planck-Institut für Ornithologie, Eberhard-Gwinner-Straße, Haus 6a, D-82319, Seewiesen, Germany; and* [4]*Department of Ecology, Evolution and Environmental Biology, Columbia University, 10th Floor Schermerhorn Extension, MC 5557, 1200 Amsterdam Avenue, New York, New York, 10027 USA*

Summary

1. Many aspects of the social environment affect hypothalamic-pituitary-adrenal (HPA) axis function and increase circulating glucocorticoid concentrations. In this review, we examine the relationships between the social environment and the function of the HPA axis in vertebrates.

2. First, we explore the effects of the social environment on glucocorticoid secretion in territorial (primarily non-social) species, with an emphasis on the effects of variation in population density, as modified by environmental factors such as predation risk and food availability. In general, high population density or frequent territorial intrusions are associated with increased glucocorticoid secretion in a wide range of taxa, including mammals, birds, fish and reptiles, although there is considerable variability across species.

3. Second, we consider the effects of social interactions and dominance rank on glucocorticoid secretion in social species, mostly in birds and mammals. We review studies that have detected an association between social status and glucocorticoid levels – sometimes with higher glucocorticoid levels in low-ranking individuals, and sometimes with higher glucocorticoid levels in dominant individuals. The relationship between dominance and glucocorticoid levels varies among species, populations and years, in a manner that depends on the stability of the social hierarchy, environmental conditions, the type of breeding system, and the manner in which high rank is obtained and maintained.

4. Finally, we discuss the concept of allostasis and consider interactions between social effects and other environmental factors, noting that there is relatively little research on these interactions to date. For both non-social and social species, we identify priorities of future research. These priorities include more complete descriptions of HPA function that move beyond measurements of basal glucocorticoid concentrations (which will generally require field experiments), to studies that examine organizational effects of social stressors, that directly test the relationship between HPA function and fitness, and that examine how glucocorticoid responses affect population dynamics.

5. Although several lines of evidence suggest that glucocorticoid responses can affect the fitness of individuals and therefore can alter the dynamics of populations, the effect of glucocorticoid responses on population dynamics remains essentially unstudied.

Key-words: allostasis, dominance, glucocorticoid, hypothalamic-pituitary-adrenal axis, sociality, social behaviour, stress, territoriality

Introduction

Animals are faced with a constant flood of information from their external environment. Although much of this information can be ignored, some of it can be used in an adaptive fashion. In vertebrates, one of the primary mechanisms by which external environmental information elicits such an adaptive response is through initiating a physiological cascade of internal changes mediated in part through the hypothalamic-pituitary-adrenal (HPA) axis.

*Correspondence author. E-mail: screel@montana.edu
All authors contributed equally to the manuscript.

The HPA axis is the neuroendocrine pathway by which stress hormones (glucocorticoids) are released from the adrenal cortex. The structure and function of the HPA axis are reviewed elsewhere (e.g. Sapolsky, Romero & Munck 2000; Sapolsky 2002). The HPA axis integrates environmental information and the downstream release of glucocorticoids can potentiate an adaptive behavioural response (Monclús *et al.* 2005; Schulkin, Morgan & Rosen 2005) or alteration in life-history strategy (Wingfield *et al.* 1998; Boonstra 2005).

The social environment is one of the primary sources of information that can induce a physiological stress response. In both social and non-social animals, the frequency and type of interaction with conspecifics as well as status in social species can affect HPA axis activity. In this review, we examine the relationships between the social environment and the function of the HPA axis in vertebrates. First, we explore the effects of the social environment on glucocorticoid secretion in territorial species, with an emphasis on the effects of variation in population density, as modified by environmental factors such as predation risk and food availability. Second, we consider the effects of social interactions and dominance rank on glucocorticoid secretion in social species. Many studies have detected an association between social status and glucocorticoid levels – sometimes with higher glucocorticoids in low-ranking individuals, and sometimes with higher glucocorticoids in dominant individuals. Many studies also consider the particular traits associated with dominance or subordination that might be causally related to variation in glucocorticoid secretion. Other studies suggest that the general social environment (e.g. the stability or instability of social relationships and the type of dominance hierarchy) can affect the association between glucocorticoids and rank. Finally, we discuss the concept of allostasis and consider interactions between social effects and other environmental factors, noting that there is relatively little research on these interactions to date. Thus, this review reveals relationships between glucocorticoid secretion, environmental variables such as predation risk, population variables such as density or the rate of territorial intrusion and social variables such as dominance rank, and behavioural variables such as the rate of aggression. Clearly the HPA response is a physiological mechanism that might mediate a wide range of fitness effects. The review also reveals considerable variability among species in the response of glucocorticoid levels to these factors and suggests new hypotheses that might explain this variation.

Effect of the social environment on the stress axis in territorial vertebrates

NON-SOCIAL SPECIES: TERRITORIALITY

The patchy distribution of limited but defendable resources such as food, mates or preferable habitats can favour the evolution of territoriality. Territoriality is the exclusive use of an area (i.e. 'ecological' territoriality) or the active defence of an area from conspecifics using various visual, acoustic, or chemical signals that indicate ownership (i.e. 'behavioural' territoriality; Brown & Orians 1970). Signals advertising ownership may deter intrusions by conspecifics of the same gender or both genders and can also attract opposite-sex conspecifics, which can allow for the monopolization of mates and other limited resources.

Many vertebrate species exhibit either temporary or extended periods of territoriality. Although territoriality implies exclusiveness from conspecifics of the same or opposite gender, the true degree of non-sociality (i.e. avoidance of conspecifics) exhibited by territorial vertebrate species is variable. For example, males of many avian species breeding in temperate climates establish breeding territories but aggregate in large flocks at times outside of the breeding season (Nice 1941). The breeding territories of male songbirds are often defended from male but not female conspecifics, which results in male birds spending a significant portion of each year exclusive of other males. Similarly, females of some small mammal species (e.g. *Microtus, Clethrionomys,* and *Peromyscus* spp.) defend nesting territories during the breeding season, but will live in groups of related or unrelated individuals during the non-breeding season (Ostfeld 1990; Wolff 1993). At the other end of the continuum of non-sociality are species that defend year-round territories from both intra- and inter-sexual intruders. For example, both female and male North American red squirrels (*Tamiasciurus hudsonicus*) defend exclusive food-based territories year-round (Smith 1968). Female red squirrels are spontaneous ovulators, and they only appear to allow male intruders on their territories when they are in behavioural oestrous, which is approximately 1 day per year (Smith 1968; Lane *et al.* 2008). Thus, the degree of non-sociality in territorial vertebrate species can range from highly non-social (red squirrels) to tolerance of both sexes for most of the year except during the breeding season (temperate breeding avian species and some small mammal species). There is similar variation in the degree of non-sociality in species that actively defend mates (mate-defence polygyny) rather than actively defending a territory (resource-defence polygyny or monogamy). In mate-defence polygyny (e.g. impala, *Aepyceros melampus*), males typically attack other males during the mating season, but aggregate in large herds with little aggression outside of the mating season (Jarman 1974). Because social interactions can strongly affect the activity of the HPA axis, variation in the degree of non-sociality may interact with stress physiology. Here, we focus on the effects of the social environment on the activity of the HPA axis in vertebrate species that exhibit some degree of non-sociality due to territoriality (Fig. 1).
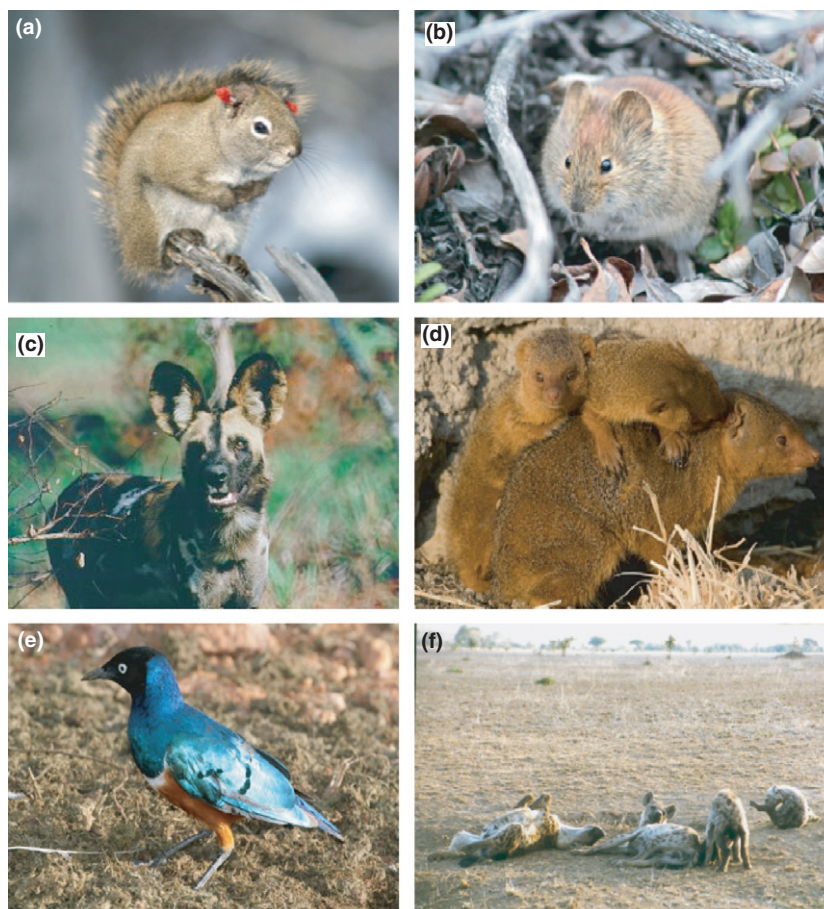
Fig. 1. (a, b) Population density and glucocorticoid levels are usually positively associated in non-social species, although the degree to which territorial vertebrate species are non-social is highly variable. For example, both male and female North American red squirrels (a) defend year-round food-based territories. In other small mammal species such as the northern red-backed voles (b), females only defend nesting territories during the breeding season (photos by R.W. Taylor). In many social species, behavioural dominance is strongly correlated with reproductive success but dominance is also associated with heightened glucocorticoid levels. For example, within groups of African wild dogs (c) and dwarf mongooses (d), only the behaviourally dominant individual of each gender is assured of breeding (photos by S. Creel). However, dominant wild dogs and dwarf mongoose also engage in more aggressive interactions and their glucocorticoid levels are higher than those of subordinates, which may impose fitness costs. In many social species, the relationship between social status and glucocorticoid levels can be complicated by both environmental variation and the method by which social status is acquired and maintained. (e) For example, in cooperatively breeding superb starlings, annual differences in rainfall and resource availability not only influence glucocorticoid levels, but they may do so differently in dominants and subordinates (photo by D. R. Rubenstein). (f) Unlike most other carnivores, social rank in spotted hyenas is inherited from the mother, which complicates the positive relationship between social status and age/size that is seen in many other species (photo by W. Goymann).

FACTORS AFFECTING ACTIVITY OF THE HPA AXIS IN TERRITORIAL SPECIES

In territorial vertebrates, population or breeding density is one of the best documented factors that influence the activity of the HPA axis. Christian (1950) first used Selye's description of stress (or general adaptation syndrome; Selye 1936) to describe how the adrenocortical response to population density might cause the density-dependent population cycles exhibited by some small mammal species. Christian (1950) hypothesized that increases in population density in small mammal species such as voles led to increased antagonistic social interactions, which caused an increase in adrenocortical activity. Christian further predicted that the consequences of this heightened adreno-cortical activity were a decrease or suppression of reproduction and an increase in mortality due to decreased resistance to disease or other limiting factors (Christian 1950; Christian & Davis 1964). As a result, population growth ceased or declined during peak population densities due to heightened mortality and decreased fecundity. Christian and colleagues (Christian 1950, 1956, 1961, 1964, 1971; Christian & Davis 1964, 1966) provided extensive empirical documentation in territorial mammalian species of the relationship between adrenal gland mass (a proxy of adrenocortical activity: Bronson & Eleftheriou 1964) and population density and/or the frequency of antagonistic interactions.

Christian's pioneering studies were instrumental in connecting how environmental factors influence the HPA axis

activity of individuals, which in turn affected population dynamics. Groundbreaking studies in a variety of mammalian taxa (primarily rodents) found significant positive relationships between population density and adrenal mass (reviewed by Christian 1971; To & Tamarin 1977) or *in vitro* adrenal secretion of glucocorticoids (Andrews 1968). However, Christian's research has been criticized because it was largely performed on captive animals often in a laboratory setting (Krebs & Myers 1974; Lee & McDonald 1985). Nonetheless, more recent studies in other mammalian species have documented a similar positive relationship between population density and plasma glucocorticoids (Boonstra & Boag 1992; m 1998) or faecal glucocorticoid metabolite concentrations (Novikov & Moshkin 1998; Harper & Austad 2004; Bian *et al.* 2011) in free-living individuals. For example, Boonstra & Boag (1992) found that populations of meadow voles (*Microtus pennsylvanicus*) at the highest densities had the highest free plasma corticosterone concentrations and lowest corticosterone-binding globulin concentrations. Support for this positive relationship between population density and stress axis activity in territorial mammalian species is not universal (e.g. To & Tamarin 1977; Harper & Austad 2004; Kuznetsov *et al.* 2004; Charbonnel *et al.* 2008), and we have little information about the relationship between population density and stress axis activity in some mammalian orders that include many solitary species (e.g. carnivores, of which more than 80% of species are solitary: Gittleman 1984).

The relationship between population density and the activity of the stress axis is best known from studies of mammals. This is not surprising given the initial focus of Christian and colleagues (see above). Although less well-studied than mammals, birds often show similar relationships between density and HPA function. With regard to stress physiology, most of the well-studied avian species breed in temperate regions exhibit territoriality only during the breeding season, and only defend territories from same-gender conspecifics. Although there are fewer studies of birds than mammals, a positive relationship between population density and plasma (Silverin 1998a) or yolk glucocorticoids (Love *et al.* 2008) has been reported for several species, while others have detected no relationship (Beletsky, Orians & Wingfield 1990, 1992). However, further support for the predicted positive relationship between density and stress axis activity in avian species may come from simulated territorial intrusion (STI) experiments. In these experiments, a territorial male is presented with an unfamiliar caged male (or a stuffed male) within his territory, paired with an audio playback of the species' song. Several studies in temperate-breeding birds have found that STIs cause a pronounced increase in plasma glucocorticoids (e.g. Silverin1993, 1998b; Van Duyse *et al.* 2004; Canoine & Gwinner 2005; Landys *et al.* 2007), whereas others have not found such a relationship (e.g. Harding & Follett 1979; Wingfield 1985; Pärn *et al.* 2008;

Scriba & Goymann 2010). Because antagonistic interactions and other territorial intrusions are predicted to increase as population density rises (e.g. Bretagnolle, Mougeot & Thibault 2008), we therefore would predict that population density is also positively correlated with stress axis activity in species that responded to STIs with elevated glucocorticoid production. To date, very few studies in avian species that exhibit year-round territoriality have directly tested the relationship between glucocorticoids and population density. However, some studies have found that STIs cause a significant increase in plasma glucocorticoids in bird species exhibiting year-round territoriality (e.g. Gill, Costa & Hau 2008; Landys *et al.* 2010), providing indirect evidence for a positive relationship between population density and stress axis activity.

Other taxa, including amphibians, reptiles and fish, also offer insights into the relationship between population density and HPA function. Amphibians and reptiles often defend resource-based territories and are non-social as adults. Many species only interact with conspecifics during the larval stage or during breeding as adults. Some studies in amphibians and reptiles also support the positive relationship between population or breeding density and stress axis activity. For example, increased population density during mating in anurans (Leary, Garcia & Knapp 2008) or nesting density in turtles (Jessop, Limpus & Whittier 1999) is associated with increased plasma glucocorticoids. High population density either were associated with increased or decreased plasma glucocorticoids in female side-blotched lizards (*Uta stansburiana*) depending upon the female reproductive tactic (Comendant *et al.* 2003). In contrast, experimentally increased densities in breeding salamanders did not elicit elevated plasma glucocorticoids (Cooperman, Reed & Romero 2004). It is important to note, however, that increased glucocorticoid concentrations during breeding aggregations might be driven by changes associated with reproduction that are not related to density (e.g. glucocorticoid concentrations rise during gestation in many mammals; Creel, Winnie & Christianson 2009; Dantzer *et al.* 2010; or glucocorticoid concentrations rise during intense mate competition in marsupials; Bradley, McDonald & Lee 1980; Bradley 1987). Evidence for positive effects of population density on stress axis activity in amphibians and reptiles also comes from laboratory studies. For example, heightened competition over burrows in captive spotted salamanders (*Ambystoma maculatum*; Cooperman, Reed & Romero 2004) or increased housing density in American alligators (*Alligator mississippiensis*; Elsey *et al.* 1990) was associated with increased plasma glucocorticoids (see also Hayes 1997; Glennemeier & Denver 2002). In some lizard species, forced antagonistic interactions with conspecifics in laboratory experiments can elevate plasma glucocorticoids (Klukowski & Nelson 1998; Schuett & Grober 2000; Yang & Wilczynski 2003), which suggests that stress axis activity would be elevated under high density conditions due to a heightened

frequency of antagonistic interactions. In many ways, such studies of forced interaction are similar to early studies of 'social stress' in captive animals that we discuss in the second part of this review.

Finally, it is well established that crowding increases stress axis activity in captive or hatchery reared fish (Barton & Iwama 1991), but we are aware of no studies examining the relationship between population or breeding densities and stress axis activity in free-ranging territorial fish. This is not surprising given the logistical difficulties of such a study. However, future studies in fish species in which males provide paternal care and actively defend brooding sites from conspecifics such as bluegill (*Leopomis macrochirus*; Neff & Knapp 2009) and smallmouth bass (*Micropterus dolomieu*; Hanson *et al.* 2009; Dey *et al.* 2010) should investigate how breeding or nesting density affects stress axis activity.

REMAINING QUESTIONS IN TERRITORIAL SPECIES

In the above section, we have detailed how population or breeding density increases HPA activity in vertebrate taxa and in some cases how forced antagonistic interactions between conspecifics can elevate stress axis activity. However, the positive relationship between population density or the frequency of antagonistic interactions and HPA axis activity is not universal across different taxa. Departures from the general pattern of increased density leading to increased HPA activity could be due to the confounding effects of reproductive condition, seasonality or recent extreme weather events on HPA axis activity or responsiveness (Kenagy & Place 2000; Romero 2002; Romero *et al.* 2008) or to the effects of trapping/handling stress on glucocorticoid levels (Kenagy & Place 2000; Sheriff *et al.* 2011a). As such, future studies examining relationships between population density and HPA axis activity should sample their study animals carefully to avoid these potentially confounding effects.

A central remaining question is to identify if the relationship between population density and HPA axis activity that has been found in many species is due to an increase in antagonistic interactions between conspecifics at high density, decreased per capita food abundance, or even increased attraction of predators. For example, food-abundance often co-varies with population density such that increased overall food abundance is associated with increased reproductive output and/or population density, but perhaps constant or decreased per capita food availability. As a result, determining the actual mechanism that induces heightened HPA axis activity under high population density conditions will require experimental manipulations of the potential causal variables, or careful sampling designs with multiple populations.

Few studies have experimentally manipulated population density, food-abundance or predator densities in free-living non-social territorial animals. In a recent study using a non-social species, the North American red squirrel, population density was positively correlated with faecal cortisol metabolite concentrations (B. Dantzer, unpublished data). Experimental increases in both actual (using long-term food supplementation) and perceived population density (using audio playbacks of territorial vocalizations to simulate high density conditions) also caused a significant increase in faecal corticosteroid metabolites (Dantzer *et al.* unpublished data). This suggests that, at least in this species, the actual variable causing changes in glucocorticoids (and also density-dependent behavioural responses; Dantzer *et al.* in press) is the perception of social competition and not food abundance or predator densities.

In addition to population density, predation risk may affect HPA axis activity in territorial species. For example, predator density affects plasma free glucocorticoid concentrations in snowshoe hares (*Lepus americanus*) (Boonstra *et al.* 1998; Sheriff, Krebs & Boonstra 2011b) and total plasma glucocorticoid concentrations in African stonechats (Scheuerlein, Van't Hof & Gwinner 2001). In elk, (*Cervus elaphus;* Creel, Winnie & Christianson 2009), predator density did not detectably affect faecal corticosteroid metabolites concentrations, although progesterone concentrations and calf production did decline in response to predation risk (Creel *et al.* 2007). To date, too few studies have examined the relationship between HPA activity and predation risk to infer general relationships with confidence. However, recently Zanette *et al.* (2011) simulated a strong increase in the perceived risk of predation using predator vocalization playbacks and observed behavioural changes in territorial female song sparrows, associated with a nearly 40% reduction in clutch size at fledgling. The impact of predation pressure in natural situations may be more subtle than in this experiment, because it simulated a situation with severe predation pressure by broadcasting predator vocalizations steadily for 130 days on a 4 day on/off basis (Zanette *et al.* 2011). This reduction in clutch size may be through a stress-mediated pathway because previous studies have found that glucocorticoids were elevated in response to increased predator abundance (Clinchy *et al.* 2004, 2011). This study experimentally confirms observational studies that have shown strong effects of predation risk on individual reproduction in wild populations, although these are not necessarily stress-mediated (Creel *et al.* 2007). We suggest that future studies examining relationships between population density and the activity of the stress axis should also consider how food abundance and predation risk co-vary with population density and HPA activity (see also McColl 1998).

As with studies of social species (see below), broader assessments of HPA function and tests for fitness effects in non-social species remain important. Although the initial focus of Christian and colleagues was to examine how population density or environmental variation influences the population dynamics of non-social animals through HPA axis activity, no studies that we are aware of have actually explored how HPA axis activity of individuals affects population dynamics as the focus of most field

studies to date has been on *individuals*. While it is reasonable to assume that effects on individual fitness often have consequences for population dynamics, it will be productive to return to the ideas of Christian and explore how the glucocorticoid responses of individuals to environmental variation can influence population or even community dynamics (Hawlena & Schmitz 2010). This will require careful experimentation of population densities and even HPA axis activity with tractable study species to examine if the glucocorticoid responses of individuals to environmental variation affect population density.

Effect of the social environment on the stress axis in group-living vertebrates

SOCIAL SPECIES: SOCIAL STATUS AND DOMINANCE RANK

Animals living in social groups often form dominance hierarchies. An individual's position within the dominance hierarchy can have strong effects on fitness, because social dominance often confers priority of access to mates, food and other resources (Fig. 1). In many cooperatively breeding birds and mammals, the probability of breeding is almost one for the socially dominant individual of each gender and almost zero for social subordinates. Given these clear benefits of social dominance, many early studies of aggression, rank and physiological stress responses were based on the hypothesis that low social status is stressful. Early research on captive rodents and primates supported this hypothesis (Bronson & Eleftheriou 1964; Louch & Higginbotham 1967; Manogue, Leshner & Candland 1975). In paired contests between laboratory rats, mice and monkeys, aggression increased glucocorticoid secretion in both winners and losers, but the effect was significantly stronger among losers. Thus, as field studies began to examine stress responses in the wild in the 1980s, a plausible hypothesis was that the 'stress of subordination' might underlie the reproductive suppression of social subordinates in many cooperatively breeding species.

However, social hierarchies and agonistic behaviour evolve to avoid the costs of overt aggression. This general explanation for the evolution of agonistic behaviour is predicated on the assumption that contests among group members can carry costs (Rubenstein & Shen 2009). The costs of engaging in agonistic or aggressive interactions (and more generally the costs of a given social position) are often not equal for both of the individuals involved, and this observation raises an interesting range of possibilities. If winning a direct contest provokes a weaker stress response than losing, but dominant individuals engage in more contests, then the total effect may be that dominants have higher mean circulating glucocorticoid levels than subordinates. In addition to direct contests, it is plausible that the maintenance of high rank requires more monitoring or 'policing' of the behaviour of others than is required for animals with low rank, simply due to differences in the

number of group mates who are subordinate to individuals of different rank. Observations of wild groups commonly show that dominant animals do engage in higher rates of aggressive and agonistic behaviour in many species (e.g. most social carnivores: Creel *et al.* 1997; Sands & Creel 2004), so it is plausible to hypothesize that social stress is greater for dominants than for subordinates, but the fitness costs are offset by the other benefits of high rank.

Given that one might plausibly hypothesize either positive or negative correlations between social status and glucocorticoid secretion, empirical data from wild populations are necessary to advance the science. Robert Sapolsky, one of the pioneers of social stress research in free-living animals, found that subordinate male olive baboons (*Papio anubis*) are more likely to be physiologically stressed than dominants and show chronically elevated levels of glucocorticoids (Sapolsky 1982, 1983). As a consequence of chronically elevated glucocorticoids, subordinate baboons are more likely to develop stress-related pathologies than dominants (Sapolsky, Alberts & Altmann 1997; Sapolsky & Spencer 1997). In follow-up studies, Sapolsky and coworkers discovered that this rank-related pattern in glucocorticoid physiology may be modified by styles of dominance (Ray & Sapolsky 1992), or may be suspended by environmental impacts, such as during a severe drought during which all members of the social group devoted most of their time to foraging, leaving little opportunity for social harassment (Sapolsky 1986). Most notably, Sapolsky (1992a) suggested that the relationship of glucocorticoid concentrations to rank depended on the stability or instability of baboon hierarchies. In stable hierarchies, the glucocorticoid levels of subordinates were higher than the glucocorticoid levels of high-ranking baboons, but this pattern was reversed during periods of social instability. Sapolsky's early results from free-ranging baboons supported the prevailing view from laboratory studies (e.g. Manogue, Leshner & Candland 1975) that subordinates are generally more likely to suffer from social stress than dominants. More importantly, these studies highlighted the role that social stability has on glucocorticoid levels in some species.

With the availability of non-invasive methods to measure hormone metabolites from urine or faeces, studies on the relationship between social rank and glucocorticoid levels of free-living animals have become more common over the past two decades. Some of these studies challenged the traditional view of the relationship between glucocorticoids and social rank in free-living animals that subordinates tend to have higher levels than dominants, arguing instead that dominants experience more psychosocial stress and often express higher levels of glucocorticoids than subordinates (Creel 2001). For example, glucocorticoid levels were higher in dominants than in subordinates in free-living African wild dogs (*Lycaon pictus*) and dwarf mongoose (*Helogale parvula*) (Creel, Creel & Monfort 1996; Creel *et al.* 1997). Both species are cooperative breeders and live in groups with '*despotic hierarchies*'

(Sapolsky 2005). Similarly, in cooperatively breeding African cichlid fish (*Neolamprologus pulcher*) dominants had higher glucocorticoid levels than subordinates (Mileva, Gilmour & Balshine 2010). The same pattern has been reported for several wild populations of cooperatively breeding primates (reviewed in Creel 2001) and gray wolves (*Canis lupus*; Sands & Creel 2004). In cooperatively breeding birds, dominants and subordinates often show similar glucocorticoid levels (e.g. Schoech, Mumme & Moore 1991; Wingfield, Hegner & Lewis 1991; Mays, Vleck & Dawson 1991; Malueg, Walters & Moore 2009). Together, these studies demonstrate that social rank has important effects on glucocorticoids in social species, but that the patterns differ among taxa and may vary with the stability and type of dominance hierarchy. Even in closely related pairs of species, pronounced differences have been observed. For example, dominant dwarf mongooses largely monopolize reproduction (Creel & Waser 1991; Creel *et al.* 1992), although dominant individuals have higher mean glucocorticoid levels than subordinates. When subordinate females do breed, their offspring are often killed, but social interactions with the breeding subordinate do not detectably change. In contrast, glucocorticoid levels are higher in subordinate females of alpine marmots (*Marmota marmota*), which are frequently attacked by dominant females (Hackländer, Möstl & Arnold 2003) and slender meerkats (*Suricata suricata*), who are subject to violent eviction from their group if they become pregnant (Young *et al.* 2006). Sapolsky (2005) reviewed the conditions under which social stress is stronger for dominants or stronger for subordinates and suggested several social conditions or individual traits that promote differences in social status related glucocorticoid patterns (resource inequity, maintenance of dominance, breeding style, stability of social ranks, subordinate coping strategies, subordinate avoiding mechanisms of dominants, subordinates' use of alternative strategies, stress of dominating mating, atmosphere of culture and personality). While much has been learned, further work is needed to fully disentangle the relationships between glucocorticoid secretion, social status and the behavioural causes and consequences of rank in social vertebrates (Creel 2001; Goymann & Wingfield 2004; Sapolsky 2005; Rubenstein & Shen 2009).

Social status and social interactions can be described in many ways. Some studies treat social status as a dichotomy, pooling subordinates into one category and comparing them to the top-ranked (alpha) individual in each group. Other methods produce a rank-order, treating social status as an ordinal variable. Still other methods consider quantitative variation, treating rank as a continuous variable. Most studies to date have tested for a categorical difference in the glucocorticoid levels of alphas and subordinates, or for a linear relationship between glucocorticoid levels and rank. Empirical research is just beginning to evaluate the possibility that glucocorticoid secretion may relate to social rank in a more complex

manner. A recent, long-term study of savannah baboons (*Papio cynocephalus*) illustrates this point well. Although the highest-ranking (alpha) males had elevated glucocorticoid levels, high-ranking males other than alphas tended to have lower glucocorticoid levels than low-ranking males (Gesquiere *et al.* 2011). Studies of other species have also reported that the glucocorticoid levels of alphas are elevated, with no detectable relationship between rank and glucocorticoids among non-alphas (e.g. in Yellowstone wolves; Sands & Creel 2004). Still other studies have found that the endocrine profiles of alphas and betas (second-ranked) animals are similar, with little relationship among lower ranks (for example in African wild dogs; Creel *et al.* 1997). Interestingly, the patterns that Gesquiere *et al.* (2011) observed for baboons were not affected by the stability or instability of the hierarchy, in contrast to the results of Sapolsky (1992a) for the same species.

LIVING IN SOCIAL GROUPS MAY REDUCE STRESS

An important, but often neglected, aspect in the discussion of the effect of the social environment on stress physiology is that the social environment may not only produce stress, but in fact it may reduce overall stress levels. For example, social support may buffer glucocorticoid levels in baboons (Alberts, Sapolsky & Altmann 1992; Ray & Sapolsky 1992; Virgin & Sapolsky 1997) and in greylag geese (*Anser anser*), the size of the family unit led to a decrease in the stress response during competitive feeding situations with other flock members (Scheiber *et al.* 2005; Scheiber, Kotrschal & Weiss 2009; see also a review on social buffering of the HPA-axis by Hennessy, Kaiser & Sachser 2009).

HOW SOCIAL STATUS IS ACQUIRED AND MAINTAINED MAY AFFECT THE RELATIONSHIP BETWEEN SOCIAL STATUS AND GLUCOCORTICOIDS

It is often assumed that success in aggressive interactions and the achievement of high dominance status are always a function of morphological and physiological characteristics. However, it has now become clear that social rank means different things in different species or even populations of the same species. Rank as a descriptor of social status does not specify the process by which social roles are obtained or maintained. Thus, behavioural strategies related to the acquisition and maintenance of rank, rather than the rank *per se*, are likely to determine the degree of social stress (and glucocorticoid levels) associated with a particular social status (von Holst 1998; Creel 2001; Goymann *et al.* 2001, 2003; Abbott *et al.* 2003; Goymann & Wingfield 2004; Sapolsky 2005).

In groups where dominance rank is inherited or dominance is achieved via queuing conventions social status is unlikely to have a major effect on glucocorticoid levels,

as long as there are no acute challenges (Goymann & Wingfield 2004; Sapolsky 2005). A similar scenario may occur in many 'high skew' cooperatively breeding species where a single dominant pair breeds and the other group members assist rearing the offspring (Vehrencamp 1984; Keller & Reeve 2004). In some species (e.g. many cooperatively breeding birds), adult subordinates are mainly offspring from prior years (e.g. Brown 1978). In other species, group structures are more complex and subordinates encompass a wide range of ages and degrees of genetic relatedness, including immigrants from other groups (e.g. in African wild dogs; Creel & Creel 2002). In cooperatively breeding species with high skew in reproductive success, reproductive suppression is experienced by most group members at some stage of their lives, and many individuals remain socially subordinate for their entire lives. Neuroendocrine mechanisms that operate mainly within the hypothalamic-pituitary-gondal axis are the prime mediators of reproductive suppression and glucocorticoid levels play only a minor role (e.g. Faulkes & Abbott 1997; Saltzman, Digby & Abbott 2009). Hence, similar to species with rank-inheritance or queuing conventions, rank-related patterns of glucocorticoid levels are unlikely to be the cause of reproductive suppression, and as long as there are no acute challenges, the correlation between rank and glucocorticoids could be positive, negative or neutral (Creel, Creel & Monfort 1996; Goymann & Wingfield 2004; Sapolsky 2005).

In contrast to stable social societies where rank is inherited or reproductive suppression is common, when there is conflict about reproduction in cooperative species, rank-related patterns of glucocorticoids may arise. For example, dominant pregnant female meerkats (*Suricata suricata*) aggressively target older and more distantly related subordinate females that represent a threat to their own reproduction. These subordinates show an impaired function of the hypothalamic pituitary gonadal axis, which may be caused by chronic elevation of glucocorticoid levels (Young *et al.* 2006). A similar situation occurs in many plural breeding species (where there are normally multiple breeding individuals within the group). Here, reproductive options exist for more than one breeding pair in a group and social dominance is acquired and maintained with low level or overt aggression, and subordinates are frequently threatened by dominants. Here, a social status related pattern of acute and chronic elevation of glucocorticoid levels is commonly observed in subordinates (Abbott *et al.* 2003; Goymann & Wingfield 2004; Sapolsky 2005). Such patterns are more likely to occur in societies with strong group cohesion as opposed to fission-fusion groups (Goymann & Wingfield 2004; Sapolsky 2005). In summary, current research suggests that it may not be the dominant or subordinate position itself, but rather the process by which social status is acquired and maintained that determines the physiological and psychosocial effects associated with a given social status (Sapolsky 1992b; Abbott *et al.* 2003; Goymann & Wingfield 2004).

INTERACTIONS BETWEEN SOCIAL AND ENVIRONMENTAL FACTORS

Social living is strongly influenced by ecological and environmental factors. In particular, resource distribution in time and/or space drives dispersal decisions, movement patterns and patterns of association in many taxa (Jarman 1974; Emlen & Oring 1977; Rubenstein & Lovette 2007; Jetz & Rubenstein 2010). These same ecological and environments factors also affect glucocorticoid levels in social species. In cooperatively breeding superb starlings (*Lamprotornis superbus*) (Fig. 1), annual differences in rainfall and resource availability not only influence glucocorticoid levels, but they may do so differently in dominant and subordinate individuals (Rubenstein 2007). However, these rank-related differences in glucocorticoid patterns may be more related to environmentally driven differences in levels of social conflict than to environmental factors directly (Rubenstein & Shen 2009). Similarly, in ring-tailed lemurs (*Lemur catta*), where social stressors and rank influenced glucocorticoid levels in captivity (Starling *et al.* 2010), socially-mediated glucocorticoid levels were also differentially impacted by food availability and environmental stress in the wild (Pride 2005). Although glucocorticoid levels are strongly influenced by social rank in savannah baboons (Gesquiere *et al.* 2011), environmental stressors also had strong effects on the patterns (Gesquiere *et al.* 2008). Thus, while social factors like rank and dominance interactions shape glucocorticoid levels in many species of birds and mammals, environmental factors like resource availability often interact with social factors to shape hormone profiles. One of the future goals in comparative studies of stress physiology in social species should be to disentangle the effects of social and environmental factors on hormone levels and social roles. So far, few studies have experimentally altered social (population density) or environmental factors (predator densities or food-abundance) in social species and investigated the consequences on demography, reproductive success and glucocorticoid secretion For example, food supplementation increased reproductive success in Florida scrub jays (*Aphelocoma coerulescens*). Breeding females supplemented with food started to reproduce earlier, laid larger clutches, and the survival of their offspring was increased (Schoech *et al.* 2008). Glucocorticoids possibly play a role in the mediation of this enhanced reproductive success, as jays supplemented with a high fat and high protein diet had lower glucocorticoid levels than controls and jays supplemented with a diet high in fats but low in proteins (Schoech, Bowman & Reynolds 2004; Schoech 2009). As a consequence, food supplementation may increase local population densities of this threatened species perhaps by lowering glucocorticoid levels and enhancing reproduction.

ALLOSTASIS, SOCIAL STATUS AND GLUCOCORTICOIDS

Separating the effects of social and ecological factors on glucocorticoid levels in free-living social animals may be difficult. The theoretical framework of allostasis has been proposed to help simultaneously study the effect of social and ecological factors on glucocorticoid levels in group-living species (Goymann & Wingfield 2004; Rubenstein & Shen 2009). Allostasis is a controversial theory that emerged from the biomedical literature (McEwen & Wingfield 2003) and has been applied more broadly to other biological disciplines, including studies of vertebrate social behaviour (Goymann & Wingfield 2004; Rubenstein 2007; Rubenstein & Shen 2009; Saltzman, Digby & Abbott 2009). Allostasis, which means achieving internal stability through bodily change of state, supports homeostasis by adjusting set-points to unpredictable stressors away from homeostatic baselines (Sterling & Eyer 1988). McEwen & Wingfield (2003) have used this allostasis framework to describe the physiological costs of coping with social and environmental challenges, and how physiological mediators such as glucocorticoids regulate responses (McEwen & Wingfield 2003). The allostasis framework has been extended by Romero, Dickens & Cyr (2009) in the reactive scope model to build from the allostasis model and address some of its criticisms. Together these models provide a starting place for exploring how predictable and unpredictable social and environmental stressors influence physiology and behaviour in social species.

Models of allostasis treat social interactions as a type of unpredictable social stressor (McEwen & Wingfield 2003; Goymann & Wingfield 2004; Romero, Dickens & Cyr 2009; Rubenstein & Shen 2009). Laboratory experiments have shown that unpredictable or uncontrollable stressors (such as electric shocks) provoke stronger glucocorticoid responses than the same stimuli when they are predictable or controllable (e.g. Weiss 1970). Although it is obvious that intense, short-term stressors like storms are unpredictable challenges that organisms cannot anticipate, many types of social interactions may also be relatively unpredictable. Animals that live in groups will experience affiliative social interactions daily (e.g. foraging, grooming, sleeping), and although these interactions may increase seasonally, they are still generally predictable events because animals can largely anticipate their occurrence. However, for social animals living within a dominance hierarchy that defines reproductive roles, changes in social status are often triggered by violent, escalated aggression. These escalated fights might be less predictable (although they are more likely under certain circumstances, such as the annual breeding period: Creel & Creel 2002; Young *et al.* 2006). In response to such interactions, an individual will rapidly shift its level of glucocorticoids to a new optimum in order to cope with the stressor. Thus, an acute social conflict might be analogous to a somewhat unpredictable environmental challenge (McEwen & Wingfield 2003; Goymann & Wingfield 2004; Romero, Dickens & Cyr 2009).

Allostasis models also specifically address the idea we described above that the physiological and psychosocial effects associated with a given social status are the result of the process by which social status is acquired and maintained rather than the resulting dominance rank *per se*. The process of rank acquisition is reflected in the level of allostatic load, or the cumulative physiological burden exacted on the body, as individuals adjust behaviour to aggressive social interactions (Goymann & Wingfield 2004). Allostatic load can be reflected in glucocorticoid levels (McEwen & Wingfield 2003; Goymann & Wingfield 2004; Rubenstein & Shen 2009). A comparative study by Goymann & Wingfield (2004) demonstrated that across a large sample of social bird and mammal species, the relative levels of glucocorticoids in dominants and subordinates are related to allostatic load and the way that rank is achieved and maintained in different societies. This work was extended theoretically and empirically by Rubenstein & Shen (2009) to predict the environmental conditions under which dominants or subordinates are expected to have higher allostatic load. This work also demonstrated that group structure (i.e. the ratio of breeders to non-breeders in a group) could also influence allostatic load and relative glucocorticoid levels. Together, these studies suggest that the allostatic load framework may help explain not only the different rank-related patterns seen in glucocorticoid patterns in vertebrates, but also the environmentally driven intra-specific variation in levels seen across years in long-term studies of individual species. The allostasis framework may also prove fruitful in studying the effects of factors on stress physiology in social species, such as the role of ontogeny and maternal effects during development.

SOCIAL ENVIRONMENT DURING ONTOGENY: PRENATAL AND POSTNATAL DEVELOPMENT

The effect that the social environment may have during the ontogeny of animals has received little attention in studies of free-living social species. The hormonal stress-axis of the mother and the offspring during early life may play a role in shaping the expression of phenotypic traits. Phenotypic plasticity, or the ability of an individual organism to alter its phenotype in response to changes in environmental conditions (Stearns 1989; Garland & Kelly 2006), is relatively understudied at both the functional and mechanistic levels in social species. In social species, individuals may adapt their phenotype to the social conditions encountered during ontogeny. A variety of laboratory studies have demonstrated that stressors acting on the mother during pregnancy or lactation (or during oogenesis in birds) may result in long-lasting effects on the offspring (reviewed in de Kloet *et al.* 2005; Catalani *et al.* 2011; Henriksen, Rettenbacher & Groothuis 2011). Whereas the mammalian literature generally takes a biomedical

perspective with the prevailing view that environmental stressors lead to pathologies, or deviations from the norm, the avian literature typically takes a more evolutionary perspective (Groothuis *et al.* 2005), with the prevailing view that environmental influences during early ontogeny (e.g. maternal effects) may help offspring to adapt to the current environment (Henriksen, Rettenbacher & Groothuis 2011). In captive animals, such as guinea pigs (Kemme, Kaiser & Sachser 2007, 2008), manipulations of the stability of social groups had no effect on HPA activity. Interestingly, however, male guinea pigs whose mothers lived in an unstable social environment during pregnancy and lactation had higher levels of testosterone later in life compared to males whose mothers lived in a stable social environment during this period. A study in spotted hyenas (Fig. 1) found that androgen metabolite levels are higher in dominant female spotted hyenas during pregnancy, which may affect offspring aggression (Dloniak, French & Holekamp 2006). However, the observed effect on aggressive behaviour was small, and potential effects on the HPA axis of the offspring were not investigated. A study of adoption in free-living spotted hyenas found that the influence of the social status of the surrogate mother on offspring behaviour was much stronger than the effects of the prenatal hormonal environment (East *et al.* 2009). In birds, development occurs in both the egg and during the nest stage (when direct hormonal effects from the mother are unlikely to occur). In cooperatively breeding Florida scrub-jays, parental provisioning rates directly influence baseline glucocorticoid levels in nestling (Rensel, Boughten & Schoech 2010b). The stress response in this species varies in different developmental stages (Rensel, Wilcoxen & Schoech 2010a) and is quite repeatable across different developmental periods (Rensel & Schoech 2011). Therefore, early life and developmental experiences in the nest may influence stress-physiology throughout adulthood.

Developmental effects on stress physiology in social species may not just be limited to circulating hormone levels. In studies of laboratory rats, variation in maternal care altered the expression of genes that regulate behavioural and hormonal stress responses, forming the basis of consistent individual differences in stress reactivity (Meaney *et al.* 1996; Meaney 2001). Similar programming may occur during adolescence. In guinea pigs, housing conditions from early adolescence through adulthood had profound effects on behaviour and hormone physiology of males: males that spent the adolescence period in mixed gender colonies showed a reduction in stress responsiveness compared to males that were housed with a single female during adolescence (Kaiser *et al.* 2007; Lürzel, Kaiser & Sachser 2010). It is unclear if these laboratory studies can be generalized to free-living animals, but it is possible that this kind of programming of the offspring stress responsiveness may be adaptive. For example, the social status of the mother, the stability of the social hierarchy she lives in, or the amount of alloparental care provided by helpers could influence offspring provisioning and/or care. This variation in offspring care may then transduce a social status related signal to the offspring, which could in turn, programme the offspring's reactivity to environmental stressors. Rank-related differences in maternal care that may potentially lead to such programming are known from wild populations (Pusey, Williams & Goodall 1987), and in wild baboons, persistent effects of female rank on offspring HPA activity have been demonstrated (Onyango *et al.* 2008). In summary, laboratory studies suggest that the social environment during embryonic development, in the nursing or nestling phase, and during adolescence may programme the hormonal stress response. Because it is currently unclear whether such programming may affect fitness or what consequences this programming may have on population demography, studies of free-living animals are needed to answer these questions.

Future directions

LINKING HPA FUNCTION AND FITNESS IN THE WILD

For both social and non-social species, much of our interest in relationships between social or environmental conditions and glucocorticoid concentrations is motivated by a desire to understand the physiological mechanisms by which the environment affects fitness. However, it is difficult to establish causal relationships between glucocorticoid levels and social behaviour or environmental conditions. Likewise, understanding the relationship between glucocorticoids and fitness is not straight-forward. Prolonged elevated baseline levels of glucocorticoids are commonly viewed to be detrimental, costly and decrease fitness (Sapolsky, Romero & Munck 2000). However, there is little consistent evidence for a negative association between elevated baseline glucocorticoids and fitness (Bonier *et al.* 2009a). Part of the variation among species in the glucocorticoid/fitness relationship could be attributed to a variety of demographic, social (e.g. social rank, age, group size) or environmental factors (e.g. resource availability). Additionally, seasonal patterns of glucocorticoid release could also obscure the relationship. For example, many of the studies of HPA-fitness relationships reviewed by Bonier *et al.* (2009a,b) were conducted in the breeding season. Although many species show elevated baseline levels of glucocorticoids during breeding (Romero 2002), this does not necessarily indicate that these breeders are chronically stressed. Rather, elevated levels of glucocorticoids during breeding may play a role in the regulation of enhanced metabolic needs during reproduction. During breeding, elevated baseline levels of glucocorticoids may actually be predictive for high reproductive success in some species (Bonier *et al.* 2009b; Ouyang *et al.* 2011). Just as the accumulation of studies across a range of species and conditions altered our understanding of relationship between HPA function and rank, we suggest that studying the relationship between HPA function and fitness across a range

of species and conditions will yield new insights. Studies along ecological or social gradients (e.g. variation in population density or variation in group size) will be of particular value.

HYPOTHALAMIC-PITUITARY-ADRENAL FUNCTION AT MULTIPLE LEVELS

In addition to looking at glucocorticoids in different life history stages, it may also be important to look at other components of the HPA-axis. Studies that incorporate a range of methods [baseline glucocorticoid measurements, glucocorticoid responses to acute stressors, adrenocorticotropic hormone (ACTH) challenge and dexamethasone suppression] will be of particular value. For example, baseline and maximal stress-induced glucocorticoid levels bind to different types of receptors (Romero 2004) and may have fundamentally different effects on behaviour. In cooperatively breeding, superb starlings, baseline, maximal levels and stress responses tended to show similar patterns in individuals of different social rank (Rubenstein 2007), but the same may not be true in all species. What may be most relevant to understanding the relationship between glucocorticoids and fitness in social species is the response to stress and the feedback regulation of glucocorticoid release (reviewed in Romero 2004), which has been demonstrated for baboons (Sapolsky & Altmann 1991; reviewed in Sapolsky, Romero & Munck 2000; Sapolsky 2002). Although dominant baboons typically expressed lower baseline glucocorticoid levels than subordinates, when faced with a stressor, glucocorticoid levels not only increase much faster in dominants than in subordinates, but dominants also terminated the release of glucocorticoids more quickly after cessation of the stressful event (Sapolsky & Altmann 1991; Sapolsky 1993). These differences between dominants and subordinates were neurally driven and could not have been elucidated simply with studies of circulating hormones levels. When injected with corticotropin-releasing factor (CRF), the hypothalamic peptide that induces release of ACTH from the anterior pituitary, dominants responded with a larger increase in ACTH than subordinates, which then led to a much faster increase in glucocorticoid production. Shutting down the adrenocortical stress response via negative feedback was more efficient in dominants. Sapolsky demonstrated this by administering dexamethasone, a synthetic glucocorticoid that artificially stimulates negative feedback of the HPA axis (Sapolsky & Altmann 1991; Sapolsky 1993). To our knowledge, these data are the only ones relating negative feedback regulation of the HPA-axis with fitness and social status in a free-living vertebrate. Data from marine iguanas (*Amblyrhynchus cristatus*) suggest that individuals with an effective negative feedback regulation were more likely to survive a severe environmental stressor than individuals with a less effective negative feedback regulation (Romero & Wikelski 2010). Thus, for baboons and marine iguanas, the effectiveness of negative feedback regulation

of the HPA-axis can be a predictor of fitness. These studies demonstrate that field studies can examine not only circulating glucocorticoid levels, but also feedback mechanisms. Broad inferences will not be possible until more studies have been performed, because HPA sensitivity can vary with age, and despite their generally inhibitory effects on CRF, glucocorticoids can have locally positive feedbacks on CRF release (e.g. in the central amygdala, which is involved in social behaviour: Schulkin, Morgan & Rosen 2005).

Conclusion

In summary, the increase in the number of studies of glucocorticoids in free-living vertebrates in the past two decades has greatly influenced our understanding of stress physiology. However, many exciting avenues for future research exist. More complete descriptions of HPA function and a better understanding of the complex relationships between glucocorticoids and fitness will be fundamental. Determining these relationships will require long-term studies of organisms with known ages in different life history stages and demographic, social and environmental contexts, as well as comparisons among populations or experimental manipulations of the putative causal variables that affect HPA axis activity. Maternal and organizational effects on neuroendocrine and epigenetic components of stress physiology in free-living animals are also areas ripe for exploration. To achieve these and other goals, we must move beyond simply assaying plasma glucocorticoid or faecal glucocorticoid metabolite levels. Studies should simultaneously examine natural and experimentally induced stress responses and the associated negative feedbacks. Moreover, studies of glucocorticoid receptors and binding globulins are mostly lacking in field studies and would help to fully understand the complexities of stress physiology. Much of what we know about stress comes originally from the biomedical literature. For several decades, extending concepts from biomedical research to studies in the wild has been a productive way to learn how individuals respond to unpredictable social and environmental challenges, and how these responses influence fitness or population demography. While much has been learned, well-identified avenues for future research remain.

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