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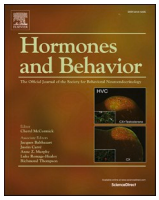

Expanding the frame around social dynamics and glucocorticoids: From hierarchies within the nest to competitive interactions among species☆

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ABSTRACT

The effect of the social environment on individual state or condition has largely focused on glucocorticoid levels (GCs). As metabolic hormones whose production can be influenced by nutritional, physical, or psychosocial stressors, GCs are a valuable (though singular) measure that may reflect the degree of "stress" experienced by an individual. Most work to date has focused on how social rank influences GCs in group-living species or how predation risk influences GCs in prey. This work has been revealing, but a more comprehensive assessment of the social environment is needed to fully understand how different features of the social environment influence GCs in both group living and non-group living species and across life history stages. Just as there can be intense within-group competition among adult conspecifics, it bears appreciating there can also be competition among siblings from the same brood, among adult conspecifics that do not live in groups, or among heterospecifics. In these situations, dominance hierarchies typically emerge, albeit, do dominants or subordinate individuals or species have higher GCs? We examine the degree of support for hypotheses derived from group-living species about whether differential GCs between dominants and subordinates reflect the "stress of subordination" or "costs of dominance" in these other social contexts. By doing so, we aim to test the generality of these two hypotheses and propose new research directions to broaden the lens that focuses on social hierarchies and GCs.

1. Introduction

The relative role of biotic and abiotic environmental features in affecting individual animals or their populations is a central focus of ecology. The biotic environment includes a sundry of social interactions that an individual has with other individuals either of the same or different species. The social environment is diverse, extending beyond traditionally considered stable adult conspecific interactions, it can include social interactions among individuals that come together either briefly or for longer periods of time to mate, among parents and their offspring, among siblings, or in agonistic interactions among conspecifics (Frank, 2007). It can also describe interactions among heterospecifics, such as interactions during competition over some limited resource or between predators and their prey (Fig. 1).

Assessing the impacts of these multifaceted features of the social environment on animals is challenging, but measures of glucocorticoids (GC) are one way to do so because they respond to environmental changes (or the anticipation of those challenges), including all of the different features of the social environment (Creel et al., 2013a, 2013b). GCs are a group of steroid hormones (cortisol and corticosterone) produced by the hypothalamic-pituitary-adrenal (HPA) axis (in mammals, birds, reptiles: Norris and Carr, 2013) or hypothalamic-pituitary-interrenal (HPI) axis (in fish and some amphibians, Norris and Carr, 2013). GCs have a diversity of impacts on individuals through both non-genomic and genomic mechanisms (Sapolsky et al., 2000; Landys et al., 2006; Hau et al., 2016). For example, GCs can have widespread effects on features of organismal physiology such as water balance (Landys et al., 2006) or the mobilization of energy to fuel organismal function through gluconeogenesis in the liver (Kuo et al., 2015) or lipid metabolism (Landys et al., 2006). GCs also impact a variety of behaviors including most social behaviors from parental care to cooperative behaviors exhibited by group-living species (Raulo and Dantzer, 2018). They are metabolic hormones whose production can increase in response to situations that require elevated energetic expenditure

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(reproduction, aggression, movement), but they can also increase in response to exposure to nutritional, physical, or psychosocial stressors (Sapolsky, 2005; Romero and Wingfield, 2015) and there is overlap in these categories such as aggression being a physical stressor that requires increased energetic expenditure. Accordingly, GCs are often used as a measure of "stress", though this definition is quite narrow given that they have important metabolic functions in the absence of exposure to stressors (Landys et al., 2006; Romero et al., 2009, 2015). Nonetheless, because GCs typically increase in response to exposure to different types of stressors (Romero and Wingfield, 2015), their concentrations in an individual could therefore act as an integrator (or "tip of the iceberg") of the degree of challenges an individual experiences in the social realm (*sensu* Cohen et al., 2012) by reflecting the cumulative exposure of individuals to these stressors. The latter could also be interpreted as a type of "social allostatic load" where experiences with different types of social stressors (beyond those previously described for the acquisition and maintenance of dominance described by Goymann and Wingfield, 2004) exert an additive toll on the physical state of on an individual (McEwen and Wingfield, 2003, 2010). The cumulative effects of social interactions could also push an individual into "homeostatic overload" (*sensu* Romero et al., 2009).

Understanding how the social environment affects GCs (or how GCs affect responses to the social environment, discussed below) is also likely important to understand the broader ecological and evolutionary consequences of variability in the social environment. This is because, depending on the duration of increase, GCs can exert impacts on individual health, survival, and reproduction. Although acute increases in GCs can promote adaptive phenotypic plasticity to cope with certain environmental conditions or stressors (Wingfield et al., 1998; Breuner et al., 2008; Bokony et al., 2009; Bonier et al., 2009; Hau et al., 2010; Dantzer et al., 2013; Middlemis Maher et al., 2013), there is also evidence that chronic elevations in GCs may be detrimental (Sapolsky et al., 2000; McEwen, 2008) even in wild animals. For example, recent meta-analyses show that individuals with elevated baseline plasma GCs exhibited lower survival and reproduction (Sorenson et al., 2017; Schoenle et al., 2021) and experimental increases in GCs can reduce both survival and reproduction (Bonier and Cox, 2020; Schoenle et al., 2021). Further, a recent longitudinal study in wild female baboons showed that those exhibiting chronic elevations in fecal GC metabolites had a reduced lifespan (Campos et al., 2021). Although it is important to consider that survival is only one component of fitness, the relationship between GCs and fitness is likely context-dependent (Bonier et al., 2009; Dantzer et al., 2016; Schoenle et al., 2018; Sapolsky, 2021), and that an association between GCs and fitness does not mean that GCs are causing a reduction in fitness (Bonier and Martin, 2016; Dantzer et al., 2016). These studies illustrate that individuals with chronic elevations in GCs due to features of their social environment could experience some fitness cost either directly due to elevated GCs or through some other mechanism that is associated with elevated GCs and lower fitness (i.e., the "third unmeasured trait" problem or environmental co-variance: Bonier and Martin, 2016; Dantzer et al., 2016). This emphasizes the value of measuring GCs if one is interested in understanding how variability in

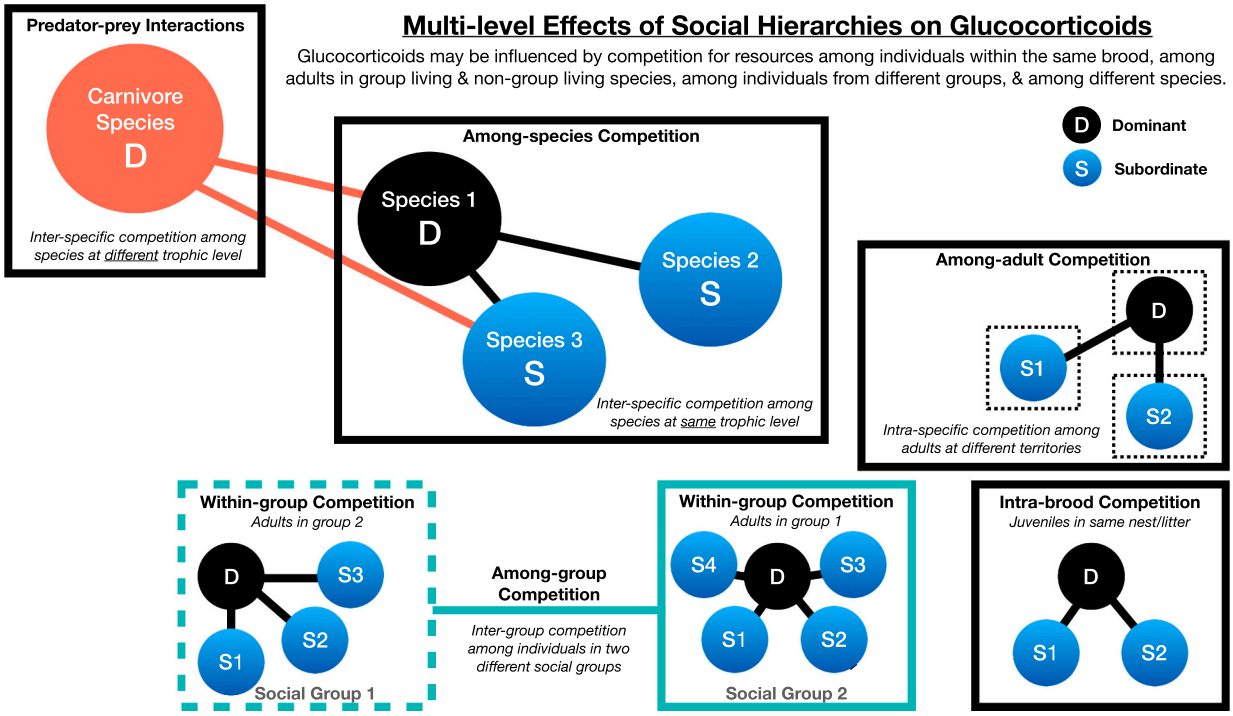

Fig. 1. The social environment can affect glucocorticoids (GCs) through competitive interactions that establish hierarchical relationships (dominants or subordinates) at many different levels. This includes competitive interactions among members of the litter/brood ("intra-brood conflict"), interactions among adults in both group-living ("within-group competition") or solitary species ("among-adult competition"), among adults in group-living species that live in two different social groups ("among-group competition"), and among individuals of different species, either through competitive (non-consumptive) interactions between heterospecifics ("among-species competition") or through consumptive interactions ("Predatory-prey Interactions"). In these situations, there is a dominant individual (D) and subordinate individual (S) where the dominant individual "wins" the interaction and the subordinate loses. Here, we illustrate the multi-level perspective about how these different components of the social environment may influence different measures of GCs where these different levels may each by themselves or in interaction with others affect individual GCs. Most work on this topic to date focuses on how GCs are influenced by within-group competition (dominant vs. subordinate GCs in group-living species), predator-prey interactions (effects of predation risk on prey GCs), and to a lesser degree the effects of among-adult competition on GCs in solitary species (effects of conspecific density on GCs of adults). However, the social environment is much more diverse and consideration of these different levels of the social environment will be important to understand the how social hierarchies cause variation in GCs. There is also a strong need to integrate how positive social interactions at one level of the social environment might buffer individuals from the distressing aspects of competitive interactions at another level, which are not shown here.

the social environment affects individuals, especially as measures of GCs can now be obtained from a variety of tissue types in many animal species (Sheriff et al., 2011).

Despite a long-history of interest in documenting how GCs, or the HPA axis in general, responds to the social environment (e.g., effects of crowding on HPA axis in rodents: Christian, 1950, 1956), to date, most recent work has focused on understanding how GCs are associated with social status or rank among adults in group-living species (Creel, 2001; Abbott et al., 2003; Goymann and Wingfield, 2004; Sapolsky, 2005; Creel et al., 2013a, 2013b; Beehner and Bergman, 2017) or the effects of predation risk on GCs in prey (Hawlena and Schmitz, 2010; Travers et al., 2010; Clinchy et al., 2013; Zanette et al., 2014). However, GCs may also play an important role in facilitating behavioral responses to a diversity of stimuli in the social environment from parental care to cooperation among unrelated individuals (Raulo and Dantzer, 2018). Here, we aim to expand the focus of the effects of the social environment in two different realms: the first focuses on within-brood competition, asking if GCs respond to social dominance hierarchies among juvenile siblings as they do to social dominance hierarchies among adult individuals in group-living species. We focus specifically on this topic of within-brood competition given that it is common in the literature yet often not integrated with studies of the effects of social hierarchy or status on GCs in other group-living species. The second focuses on the influence of social interactions between adult conspecifics and heterospecific individuals in a competitive situation. Heterospecific interactions could include two herbivorous species competing for preferred feeding or nesting sites in herbivorous species, two ectothermic species competing for a preferred site to optimize thermoregulation, two carnivorous species competing for exclusive access to carrion, etc. Although there has been much work focusing on competition over the most crucial resource (life) among predators and prey, less work has focused on these other more benign competitive interactions between heterospecifics. For both foci, we examine if differences between dominants and subordinates are explained by the "stress of subordination" where subordinates (or losers of the competitive interaction) have higher GCs than dominants (or winners of the competitive interaction) or the "costs of dominance" where dominants have higher GCs than subordinates (Fig. 2: sensu Creel, 2005; Creel and Sands, 2013; Muller et al., 2021). These two hypotheses largely assume that the differences in GCs between subordinates and dominants are expected to be sustained (chronic), though they may only occur during specific time periods (e.g., Young et al., 2006; Cavigelli and Caruso, 2015). Additionally, these two hypotheses also assume that the chronic elevations in GCs are detrimental, which may or may not be the case, as we discuss below.

Our goal is quite simple and similar to a recent call that advocates inclusion of interactions among heterospecifics rather than only conspecifics when defining social behavior (Oliveira and Bshary, 2021). We advocate for a multi-level or hierarchical view of understanding how the social environment generates variation in GCs (Fig. 1). Rather than only focusing on how social status/rank or predation risk impact GCs within an individual, what is the relative impact of intra-brood competition, social status, predation risk, and conspecific or heterospecific competition over resources on GCs? It may be that predation risk or social status do in fact have much more profound impacts on GCs within an individual, more so than one of these other levels of the social environment. However, we do not know this at this time due to the lack of studies addressing these issues from a more comprehensive perspective. As a direct consequence, we also do not know if changes in GCs caused by one of these levels has carry-over impacts on the physiological stress response to other levels. For example, if intra-brood competition causes changes in GCs early in life or inter-specific competition causes elevations in GCs in the loser/subordinate of the interaction, do these influence their subsequent physiological stress response to predation risk or

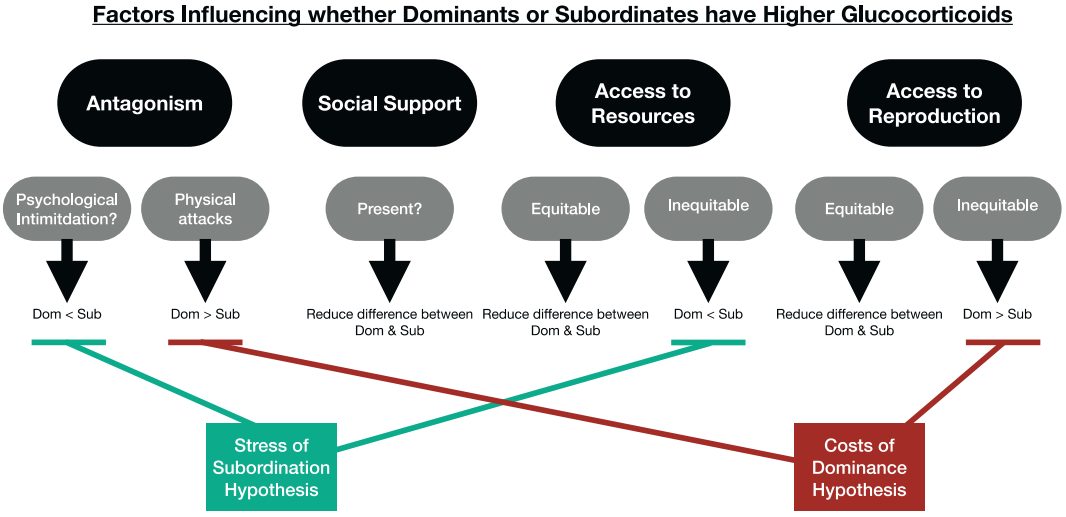

Fig. 2. Overview of factors that can predict whether or not dominants or subordinates have higher baseline or integrated (fecal, urine, hair, feather, etc.) glucocorticoids (GCs). Here, dominant and subordinate status may be between individuals from the same nest (intra-brood), pair-bonded individuals, within the same group of conspecifics in social species, among conspecifics in solitary species, or among heterospecifics. *Antagonism* refers to whether the dominant individual uses physical attacks or psychological intimidation to establish or maintain dominance over the subordinate individual. *Social Support* describes whether subordinates have other group members to gain support following attacks from the dominant or to reduce the rate of aggression they receive from the dominant. *Access to Resources* refers to whether the subordinate and dominant have equal access to a resource. *Access to Reproduction* describes whether subordinates are able to breed at a frequency that is similar as dominants (which can influence GCs). The "Costs of Dominance Hypothesis" is supported if dominants have higher baseline or integrated GCs than subordinates, such as reflecting the energetic costs of frequent physical attacks on subordinates or having a higher reproductive rate. The "Stress of Subordination" Hypothesis is supported if subordinates have higher baseline or integrated GCs than dominants, such as if they receive psychological intimidation from dominants or have less access to a resource (e.g., elevated baseline or integrated GCs could reflect nutritional stress in subordinates). The presence of social support and equal access to resources or reproductive opportunities can all moderate the difference in baseline or integrated GCs between dominants and subordinates, such as reducing the magnitude of difference in baseline or integrated GCs between dominants and subordinates. Importantly, none of these features are mutually exclusive and dominant or subordinate baseline or integrated GCs can be influenced through all these different factors. This figure was generated using concepts published elsewhere (Creel, 2001; Sapolsky, 2005; Creel and Sands, 2013).

intra-specific competition experienced later in life? Answering these questions will be difficult, but posing them at least moves the field of comparative endocrinology towards a better understanding of why individuals, populations, species, or higher order taxonomic groupings vary in their HPA axis activity or GCs, although other features of the environment (such as individual state, abiotic conditions, etc.) also have important impacts on HPA axis activity and GCs.

2. Glucocorticoids: measurement, duration of exposure, & consequences

Before discussing how GCs respond to different types of social interactions, there are three issues related to the measurement of GCs and their impacts on animal health and fitness that need to be briefly outlined. First, the studies we review below use a diversity of GC measures that we classify into three categories. Point estimates of GCs from blood samples are often used to estimate *baseline GCs* if the samples were obtained within 3 min of the animal being captured or restrained (Romero and Reed, 2005). *Stress-induced GCs* is used to refer to those point estimates of GCs obtained >3 min after the animal was captured or restrained and are therefore usually elevated in response to the stress of capture/handling and are considered acute increases. Other studies used measures of *integrated GCs* obtained by estimating GCs themselves or GC metabolites in fecal, urine, feather, hair, or saliva samples (Sheriff et al., 2011). These are referred to as integrated GCs here because they are thought to reflect baseline and stress-induced GCs over some specific time period (Sheriff et al., 2011). Below, we refer to the measure of GCs as baseline, stress-induced, or integrated GCs for each study unless it was a review paper or this information was not available. We briefly note here that our review focuses on measures of GCs that are available in the literature (mostly baseline or stress-induced GCs or integrated GCs), but we agree with other reviews on this topic (Creel et al., 2013a, 2013b) that other measures of the HPA axis (e.g., efficacy of negative feedback, GC receptors, stress responsiveness) will be essential to understand how the social environment affects individuals. Unfortunately, these measures are not readily available for many species at this time so we focus on GCs.

Second, the typical assumption in studies about how placement in a social hierarchy affects GCs is that elevated GCs are detrimental or represent pathology. This assumption that "high GCs are detrimental" is inherent to the two major hypotheses (stress of subordination vs. costs of dominance) where the subordinate or dominant individual with elevated GCs is assumed to be experiencing some cost. This assumption is based upon decades of research in humans and laboratory animals suggesting elevated baseline GCs have adverse consequences (Sapolsky et al., 2000; Romero, 2004; McEwen, 2008), with some support from studies in free-living animals (Sorenson et al., 2017; Bonier and Cox, 2020; Campos et al., 2021; Schoenle et al., 2021). However, as we noted above (Introduction) and below (Future directions), acute elevations in GCs can mediate adaptive phenotypic plasticity to cope with the environmental challenge that is inducing the increase in GCs (e.g., Dantzer et al., 2013; Middlemis Maher et al., 2013). We do not seek to resolve this debate here, but merely emphasize that more empirical work is needed to test hypotheses about how GCs affect survival and reproduction across ecological gradients (see also Boonstra, 2013; Beehner and Bergman, 2017).

The final consideration that is closely related to the second point is that the duration of the increase in GCs can be either *acute* or *chronic*. Acute increases in GCs may occur over minutes or hours whereas chronic elevations in GCs occur over longer periods of time (days, weeks, months). Whether or not the increase in GCs is acute or chronic may be closely tied to the effect of elevated GCs on animal health and fitness. The current hypothesis, that needs to be tested empirically, is that *acute* increases in GCs may be adaptive whereas *chronic* increases in GCs are maladaptive (McEwen, 1998; Sapolsky et al., 2000; McEwen and Wingfield, 2003; Romero et al., 2009; but see Boonstra, 2013). This is often best illustrated by the effects of elevated GCs on the immune system (Dhabhar and McEwen, 1997), such as observational studies in humans suggesting that acute treatment with GCs improves outcomes for patients infected with COVID-19 whereas chronic treatment with GCs in such patients is detrimental (Robinson and Morand, 2021). Where appropriate and when the information is available, we note below whether the increase in GCs caused by a feature of the social environment was acute or chronic.

3. Winners, losers, & glucocorticoid responses to social competition

We first review how GCs respond to the social environment, focusing on the most basic interaction in terms of dyadic social competition where one individual is defeated. In this realm, one of the participants is a "winner" and the other a "loser" of the interaction or competition for some resource. This could describe competition among two individuals for social rank in group-living species where there is a winner (dominant) and loser (subordinate) or in predator-prey interactions where the winner (dominant) eats and the loser (subordinate) dies. It can also describe intra-brood conflict in species that produce more than one offspring at a time (polytocous species) and exhibit parental care where two siblings compete for a resource (food from parents, preferred location in nest) where once again there is a winner/dominant (gets resource) and loser/subordinate (does not get resource). Competitive interactions among conspecifics or heterospecifics can also be included here where two individuals (outside of a nest or place of birth) compete for a resource and there is once again a winner or loser. The outcome may result from a direct antagonistic interaction between two individuals or a situation where the subordinate or loser avoids confrontation based upon prior experience or some cue and therefore still does not gain the resource. Thus, for simplicity, we characterize an individual as losing (also referred to here as a subordinate) if they do not gain access to the resource, with or without physical confrontation.

The impact of losing an antagonistic social confrontation or losing access to a resource on GCs has been best described in the formation of social dominance hierarchies in male laboratory rats. We use these studies to summarize how GCs respond to social interactions and their subsequent impacts on behavior. Our interpretation is that these studies have been mostly focused on how antagonistic social interactions cause *chronic* elevations in GCs (reflected in baseline GCs or integrated GCs), although we also briefly discuss some of the elegant work on the acute changes in GCs following these social interactions. Importantly, we note that this is a relatively narrow discussion of the responses of GCs to antagonism in one species, often only in males, and in the laboratory where individuals are forced to interact with one another and cannot escape the situation. The latter may be particularly important given that the rats in these studies are often forced to engage and escalate physical interactions, unlike free-living animals (Creel and Sands, 2013). This in addition to the fact that laboratory rodents have been under artificial selection for >100 years, which likely has selected for "tameness" and consequently resulted in changes in the HPA axis that is presently observed in laboratory rodents (e.g., Albert et al., 2008).

In rats, antagonistic interactions between two males who are unfamiliar with one another are staged where they compete for food or water (e.g., Timmer and Sandi, 2010). These dyadic interactions can cause an acute increase in baseline and stress-induced GCs in both individuals that promotes aggression (Haller et al., 1998; Kruk et al., 2004; Haller et al., 2014). For example, in staged encounters between male rats, both the winner and loser experienced acute increases in baseline GCs for nearly 3 h after the fight, but the baseline levels only in the loser remained elevated for another 2 h after those in the winner declined back to near their pre-fight levels (Schuurman, 1980). Other studies in male rats illustrate that the higher baseline GCs in subordinates (losers) than dominants (winners) is maintained for ~6 weeks after establishment of social rank (Dijkstra et al., 1992). Inhibition of the production of

GCs (such as using metyrapone), which should reduce both baseline and stress-induced GCs, decreases aggressiveness of individual rats in these encounters (Haller et al., 2000; Mikics et al., 2004). The individual who is defeated (loser) experiences a chronic increase in GCs that subsequently increases submissive behavior or reduced aggression whereas GCs return to their typical levels in the winner (Haller et al., 1996; Haller, 2014; Weger et al., 2018). The elevation in baseline and/or stress-induced GCs in the loser following defeat contributes to the maintenance of the social hierarchy by promoting submissiveness (e.g., Weger et al., 2018). Thus, at least in rats, in a dyadic antagonistic interaction, baseline GCs initially increase in both individuals and promote aggressiveness (i.e., an acute increase in GCs), but GCs continue to stay elevated in the defeated individual (i.e., a chronic increase in GCs) and promote submissiveness and reduced aggressiveness. The outcome from these studies make a simple but important point: the direction of the association between GCs and dominance or subordinance depends upon when they are measured during a conflict. Baseline and/or stress-induced GCs are acutely increased in both individuals following the antagonistic interaction, but often only chronically increased in the defeated individual.

Do the same patterns exist in other species or in other social contexts where individuals compete over some resource? Answering these questions is challenging. Firstly, determining if/how baseline or stress-induced GCs respond in the acute phase of the antagonistic interaction and following it when the winner is established is not possible in many free-living species. However, the same patterns observed in rats seem to be present in other vertebrates (Summers et al., 2005; Summers and Winberg, 2006). For example, from mammals to fish to lizards, aggressive encounters cause acute elevation in GCs (measured either as baseline or stress-induced plasma GCs or different measures of integrated GCs) in both winners and losers (Goymann et al., 1999; Øverli et al., 1999; Woodley et al., 2000; Summers et al., 2005; Wittig et al., 2015). Following antagonistic interactions between two snakes (where adults are largely non-social except during breeding), the loser has higher stress-induced GCs than the winner 1 h after the encounter (Schuett et al., 1996). In a variety of species, chronic administration of exogenous GCs (which should increase baseline GCs over short time periods) can reduce aggression (Øverli et al., 2002; Summers et al., 2005; DiBattista et al., 2005) and administration of a GC receptor antagonist (mifepristone), which should elevate circulating baseline GCs due to the antagonist preventing negative feedback, reduced aggressive attacks/displays in lizards (DiBattista et al., 2005). We briefly note that interpreting the behavioral effects following administration of GC receptor antagonists like mifepristone (as in DiBattista et al., 2005) is tricky because administration of mifepristone should increase circulating baseline GCs but their effects on the number of GC receptors is often unknown. As a result, the increased aggression due to administration of a GC receptor antagonist (that should increase baseline GCs by preventing negative feedback) suggests that the effects of GCs on aggressive behavior can occur through a non-genomic mechanism (Mikics et al., 2004; Sandi and Haller, 2015). In social cichlid fish exhibiting a dominance hierarchy, males that are ascending the dominance hierarchy exhibit increases in baseline GCs (Culbert et al., 2018), but those that lose their high social rank exhibit a rapid increase in stress-induced GCs (Maruska et al., 2013). Similarly, in male frogs during the mating season, vocalizations from other males cause an acute increase in baseline GCs (Leary, 2014), but chronic elevations of baseline GCs (via treating males with exogenous GCs) caused an increase in subordinate-like behavior where males reduced vocalizations and engaged in satellite male behavior (Leary and Crocker-Buta, 2018). These studies illustrate similarities with studies in rats where acute challenges raise different measures of GCs (either baseline or stress-induced plasma GCs or integrated GCs) in dominants and subordinates (dominants being those that are ascending the hierarchy), but only stay elevated in those that become subordinate (those that lose their rank) that in turn promotes submissive or subordinate behavior. Although there is clearly more work to do on this topic, these results collectively suggest that losing a competitive interaction for a resource or a loss in rank causes chronic changes in GCs, which in turn affect subsequent social behavior.

Our focus however is on exploring the question of whether or not losing battles for a resource or becoming a subordinate either among siblings, adult conspecifics in non-group living species, or among heterospecifics, impacts GCs, measured either as baseline, stress-induced, or integrated GCs. For example, if two ungulate species compete for the same food resource or two small mammal species compete for the same burrow/nest site, does the loser of the interaction experience an increase in GCs? Similarly, in polytocous species that provide parental care, when siblings compete for a resource, does the loser experience an increase in GCs? Here, we review the impact of the different levels of social competition on GCs (Fig. 1). To help guide this discussion, we will first present two hypotheses proposed for group-living species to explain when subordinates (losers) would have higher GCs than dominants (winners) or when dominants have higher GCs than subordinates (Fig. 2). As we noted above, if these elevations in GCs in subordinates or dominants are chronic (reflected in a sustained increase in baseline GCs or integrated GCs), they may carry costs to the individual's fitness, though this is often assumed rather than explicitly tested.

4. Responses of GCs to social competition: patterns and insights from social dominance hierarchies in group-living species

Differences in GCs between dominants and subordinates in highly social group-living species are often explained as reflecting either the costs of dominance or stress of subordination (Fig. 2: Creel, 2005; Creel and Sands, 2013; Muller et al., 2021). Baseline or integrated GCs are expected to be chronically higher in subordinates than dominants if they reflect the stress of subordination (Fig. 2). Studies in laboratory rats (where males defend small territories from other males: Modlinska and Pisula, 2020) discussed above predict that losers (subordinates) should have chronically higher GCs than winners especially if the winner and lose are still near one another (von Holst, 1998; Abbott et al., 2003). Sapolsky (1982, 1983) showed that in groups of group-living olive baboons (*Papio anubis*), subordinates had chronically higher baseline GCs than dominants, presumably reflecting the stress of subordination. Furthermore, Abbott et al. (2003) showed that subordinates had higher integrated GCs than dominants in 7 group-living primate species (6 were in captivity) if they experienced social stress (e.g., physical violence or "psychological intimidation" from dominants, inequitable access to food).

By contrast, baseline or integrated GCs may be elevated in dominants rather than subordinates due to the costs of dominance (Fig. 2). For example, dominants may experience energetic/metabolic demands (reflected in increased baseline or integrated GCs) if they use physical punishment to establish or enforce a dominance hierarchy or because of their increased reproductive activity. As unpredictability can lead to elevated baseline and stress-induced GCs (Weiss, 1970; Zimmer et al., 2020; Guindre-Parker and Rubenstein, 2021) or changes in the glucocorticoid receptor (Hofmeister and Rubenstein, 2016), elevated GCs in pugnacious dominants could also reflect psychological stress due to outcome uncertainty during frequent conflicts. For example, dominants can have higher stress-induced or integrated GCs than subordinates in cooperatively breeding species such as African wild dogs (*Lycaon pictus*), dwarf mongooses (*Helogale parvula*) and grey wolves (*Canis lupus*: Creel, 2001; Sands and Creel, 2004). At least for African wild dogs and dwarf mongooses, this may be because dominants direct high levels of aggression towards subordinates, suggesting a cost of dominance (Creel, 2001, 2005), at least during the mating season (Creel and Sands, 2013).

Subsequently, Goymann and Wingfield (2004) and Sapolsky (2005) outlined the specific conditions under which we might expect subordinates or dominants to have higher GCs. Goymann and Wingfield (2004) showed that the degree of challenges in the social environment

(similar to Abbott et al., 2003) could predict whether subordinates or dominants had higher GCs (measured as either baseline or stress-induced plasma GCs or integrated GCs). For example, if dominants achieved their high status through costly antagonistic interactions and/or had to frequently re-assert their dominance using such displays, they may have experienced increased "wear and tear" (allostatic load) that manifests itself in higher GCs compared to subordinates. Similarly, Sapolsky (2005) predicted that dominants should have chronically higher GCs than subordinates if they frequently use physical violence to enforce the social hierarchy or police the reproductive activity of subordinates. A qualitative review of associations between social rank and GCs (largely using integrated GCs) in primates patterns support this prediction where the social rank that had higher GCs was the one that seemed to require greater energetic demands associated with aggression or reproduction (Beehner and Bergman, 2017). On balance, Sapolsky (2005) proposed that subordinates should have chronically higher GCs than dominants if dominants use psychological intimidation to enforce the hierarchy or restrict subordinates' access to food (though we note that psychological intimidation is usually poorly defined in this literature). Additionally, subordinates may reduce their GCs by avoiding interactions with dominants or seeking social support with other group-members (Sapolsky, 2005), a hypothesis that was upheld by a comparative study in measuring integrated GCs in primates (Abbott et al., 2003). These contributions were important because some of these studies (Goymann and Wingfield, 2004) placed less emphasis on treating dominance as a categorical variable (GCs in dominants vs. subordinates) and thinking more about costs of dominance or stress of subordination as continuous variable.

Work in group-living species has revealed other nuanced effects of social rank on different measures of GCs. For example, GCs in subordinates or dominants need not be chronically elevated over long periods of time but could be chronically elevated during specific and shorter periods of time of the year or during specific life history stages. For example, in group-living spotted hyenas (*Crocuta crocuta*), subordinate females have higher integrated GCs than dominant females but only when dominants are not lactating (Goymann et al., 2001). In cooperatively breeding meerkats (*Suricata suricatta*) and alpine marmots (*Marmota marmota*), subordinate females may only have higher stress-induced or integrated GCs when the dominant female is pregnant due to high levels of physical aggression from the dominant female towards subordinate females during pregnancy (Hackländer et al., 2003; Young et al., 2006; Dantzer et al., 2017). Sex is also an important factor to consider when investigating social hierarchy on GCs in group-living species (Creel et al., 1996; Creel et al., 1997). For example, in primates, dominant males have higher integrated GCs than subordinates males but this pattern is reversed in females where dominant females exhibit lower integrated GCs than subordinates (Cavigelli and Caruso, 2015; Beehner and Bergman, 2017; Müller et al., 202l; Levy et al., 2020). In group-living primate species, the stability of the social group may also override the effects of social rank (Sapolsky, 1992; but see Gesquiere et al., 2011). Additionally, in some primates (Gesquiere et al., 2011) but not others (Müller et al., 2020), there may only be a difference in integrated GCs between the top-ranked male and second-ranked male. Finally, in nearly all of these studies, there is an assumption that social rank should be considered as a dichotomous variable where the researchers assess if GCs in the dominant individual differs from all subordinates (but see Goymann and Wingfield, 2004). This may be an appropriate classification for situations where there is an obvious winner vs. loser (e.g., two offspring in the same nest competing for dominance or two individuals competing for access over a resource), but it may be a tenuous assumption in more social species that live in groups. In such species, dominance hierarchies may instead be a continuum rather than a dichotomy (e.g., a social hierarchy among subordinates), so do GCs vary as a linear function of rank? The few studies on this topic (all of which used integrated GCs) are mixed (Creel et al., 1997; Sands and Creel, 2004; Gesquiere et al., 2011; Campos et al., 2021). For example, integrated GCs varied as a linear function of rank in males but not females in the same baboon species (Gesquiere et al., 2011; Levy et al., 2020; Campos et al., 2021) and model selection analyses indicated that models that treated rank as a categorical variable were preferred over those that treated rank as a continuous variable (Levy et al., 2020). Nonetheless, as Levy et al. (2020) have recently emphasized, future studies that are able to collect detailed behavioral data necessary to put social rank on a continuum should investigate whether GCs vary as a linear function of rank rather than treating rank as a categorical variable (dominant vs. subordinate).

This body of research on group living animals has been incredibly helpful in understanding how GCs (especially measures of integrated GCs) are affected by rank of an individual in the social hierarchy within a group and whether the differences in GCs reflect the stress of subordination or costs of dominance. We now examine if similar patterns emerge by focusing on hierarchies among siblings within the same brood and among conspecifics or heterospecifics.

5. Competition beyond social rank as a cause of variation in GCs

Below we focus on how the social environment, composed of both conspecifics and heterospecifics, can elicit changes in the GCs of individuals. Interactions with conspecifics (among adults or juveniles/nestlings of the same species) or heterospecifics could elicit a change in GCs through competition over some resource (food, water, mates, nest/burrow, etc.). The specific mechanism could be through interference competition, exploitative competition, or apparent competition. For example, GCs may be elevated in two individuals of one or different species that battle over access to some resource (interference competition) or where an individual from one or two different species loses access to a preferred food resource (exploitative competition). GCs may also be elevated in individuals of species 1 because species 2 increases in abundance, thus supporting larger populations of their shared predator (apparent competition).

Here, we mostly focus on interference and exploitative competition, where losers or subordinates are those that lose an antagonistic interaction or lose access to a resource. The *stress of subordination* hypothesis would be supported if losers/subordinates had higher GCs (baseline or integrated GCs) and the *costs of dominance* hypothesis would be supported if dominants had higher GCs (baseline or integrated GCs), which could be due to high ranking individuals having to frequently reassert their dominance through physical confrontations (Fig. 2). Although the focus here is on baseline or integrated GCs, we also cover studies that measured stress-induced GCs as they were often the only GC measure available.

6. Intra-brood conflict and competition: effects on GCs

In polytocous species that provide parental care, offspring compete for resources provided by parents, such as food, water, parental interaction/attentiveness towards offspring, or some other resource. In some species, offspring can compete directly for these resources, eventually forming a dominance hierarchy within the nest. In others, offspring may compete for access to a specific place in a nest that provides the greatest access to a resource. Here we discuss whether the hierarchy formed among siblings in these species reflects the stress of subordination (subordinate baseline or integrated GCs $>$ dominant baseline or integrated GCs) or costs of dominance (dominant baseline or integrated GCs $>$ subordinate baseline or integrated GCs). We note that nearly all of the examples discussed below occurred in bird species where the parents of the siblings are defending small territories as the observations occurred during the breeding season, although there are some exceptions such as the cooperatively breeding Florida scrub jay (*Aphelocoma coerulescens*) or colonial seabird species.

These patterns have been best studied in altricial bird species, largely because hatching asynchrony (where one individual hatches before

another) creates an age- and size-based dominance hierarchy (Magrath, 1990; Mock and Parker, 1997). The dominant nestling can also be aggressive towards subordinates, potentially culminating in siblicide (Mock et al., 1990; Mock and Parker, 1997). These patterns are suggestive of a "despotic hierarchy" among siblings, similar to what can occur among adults of group-living species (Sapolsky, 2005).

There are a few caveats in such bird species to mention before discussing GC differences between dominant or subordinate nestlings. First, because the HPA axis matures after hatching, assessing differences in HPA axis activity or any measure of GCs in species with hatching asynchrony needs to carefully consider that differences between first and later hatched chicks is merely due to age differences (Love et al., 2003a). Second, first and later laid eggs can vary in their contents, including GCs (e.g., being higher in eggs laid later: Groothuis and Schwabl, 2008), such that any GC differences in subordinate and dominant nestlings may be influenced by differential maternal deposition into the egg. However, cross-fostering studies have suggested that differences in stress-induced GCs between first, second, and last-hatched eggs are, indeed, due to post-hatching environmental experiences rather than egg contents (Diaz-Real et al., 2016).

We first focus on whether GC differences between dominant and subordinates from the same brood (due to intra-brood competition) support the stress of subordination hypothesis. Here, subordinates (later-hatched) are expected to experience both nutritional and psychosocial stress from inequity in access to food and due to receiving aggression from their dominant (first-hatched) sibling (Fig. 2). If subordinates from the same brood have higher baseline or integrated GCs due to nutritional stress, this hypothesis would predict that 1) nestling body condition should correlate negatively with baseline or integrated GCs, 2) food-supplementation should lower nestling baseline or integrated GCs whereas food-restriction should increase them, 3) effects of hatch order on nestling baseline or integrated GCs should be eliminated if body condition is controlled for statistically, and 4) dominants (first hatched) should have lower baseline or integrated GCs than subordinates (later hatched). While the evidence is mixed, there are many examples that align with these predictions. For example, in Florida scrub jays, heavier nestlings had lower baseline GCs and breeding pairs who were provided with supplemental food on their territory produced nestlings with lower baseline GCs (Rensel et al., 2011; see also Young et al., 2017). Other studies, mainly in territorial bird species, find similar patterns where body condition, mass, or growth is inversely correlated with either baseline or stress-induced GCs (Sockman and Schwabl, 2001; Müller et al., 2010; Poisbleau et al., 2010; Braasch et al., 2014) or where natural or experimental food restriction increases baseline or stress-induced GCs in dominants, subordinates, or both (Nuñez-de la Mora et al., 1996; Kitaysky et al., 1999; but see Williams et al., 2008). Eraud et al. (2008) showed that later hatched chicks in collared doves (*Streptopelia decaocto*) had higher baseline GCs than earlier hatched chicks, but these differences were absent when a measure of body condition was controlled for statistically. These data suggest that in at least some bird species, nestling baseline GCs could reflect the stress of subordination due to inequity in access to nutrition (nutritional stress). A rare study in mammals where offspring compete for the maternal food source (access to teats) also supports the interpretation. In group-living spotted hyenas, offspring compete for access to a teat and those with the least access to teats (loser or subordinate) have higher integrated GCs than those with greater access (Benhaiem et al., 2013). Despite the expectation that dominant siblings should have lower GCs than subordinates because the former often has greater access to food, in several bird species, first hatched (dominants) actually have higher baseline or stress-induced GCs than later hatched chicks (Schwabl, 1999; Love et al., 2003b; Rensel et al., 2011). Other studies do not find any clear pattern on the effects of hatching order on baseline or stress-induced GCs (Sockman and Schwabl, 2001; Blas et al., 2005; Brewer et al., 2010; Müller et al., 2010) or that subordinate nestlings do indeed have higher baseline GCs than dominant nestlings (Young et al., 2017). Some studies of captive birds where food is provided ad libitum to parents are particularly revealing as yet again first hatched nestlings still have higher levels of baseline and stress-induced GCs than later hatched individuals (Schwabl, 1999; Love et al., 2003b).

Baseline or integrated GCs in nestlings/juveniles seem to be affected by access to food, supporting the hypothesis that differences in GCs between subordinates and dominants within the same brood are driven by nutritional stress. However, dominant (first hatched) nestlings that should have better access to food resources than subordinates often have higher baseline or integrated GCs rather than lower. How do we explain these incongruencies? Do these results for some bird species support the hypothesis that differences in baseline or integrated GCs between dominant and subordinate siblings reflect the costs of dominance? In particular, if dominant siblings use physical means to establish, enforce, or maintain the dominance hierarchy, they may have higher baseline or integrated GCs than subordinates whereas subordinates may have higher baseline or integrated GCs than dominants if dominants use psychological intimidation rather than physical violence (Sapolsky, 2005). In nestling birds, physical violence could manifest itself in terms of physical attacks from the dominant towards subordinate or through direct competition during begging for food from parents (Roulin and Dreiss, 2012).

Testing these predictions is challenging because of the lack of data on how dominance hierarchies are established or enforced in nestling birds and the challenge of quantifying psychological intimidation. Given that many bird species have hatching asynchrony where there is a substantial difference in age, size, and development between dominant (first hatched) and subordinate (later hatched) nestlings, we might expect little physical confrontation between dominant and subordinate nestlings. Indeed, in several bird species with hatching asynchrony, there is little to no aggression ever observed among the nestlings (e.g., Love et al., 2003b; Rensel et al., 2011). Interestingly, in these latter two species (American Kestrels, Florida scrub jays), baseline and/or stress-induced GCs are still higher in first hatched nestlings (here termed dominant given their priority access to food) despite the lack of physical antagonism observed. It is possible that continuous behavioral observations of nestlings would reveal some direct antagonistic interactions among siblings that establishes a dominance hierarchy, especially if these occur over brief periods of time.

Studies of bird species where there is obligate or facultative siblicide may provide some insight about how within-nest dominance hierarchies affect GCs. Boobie species nest in open areas such that the establishment, maintenance, and enforcement can be readily observed and its impacts on GCs have been well-documented. Here, the costs of dominance hypothesis would predict that the dominant (first hatched chick) would have higher GCs than the subordinate (later hatched) given that physical antagonism is used in the maintenance and enforcement of the dominance hierarchy. However, subordinate nestlings often have higher baseline and/or stress-induced GCs than dominant nestlings in boobies with either obligate or facultative siblicide (Nuñez-de la Mora et al., 1996; Tarlow et al., 2001; but see Ramos-Fernández et al., 2000). For example, blue-footed boobies (*Sula nebouxii*) produce two chicks with the first hatched chick (~4 days older) enforcing a dominance hierarchy with repeated physical attacks and harassment on the later hatched chick (Ramos-Fernández et al., 2000); further, the subordinate nestling has higher baseline GCs than the dominant nestling (Nuñez-de la Mora et al., 1996). Thus, even if physical assertions of dominance are frequent in this species, subordinate nestlings still had higher baseline and/or stress-induced GCs, suggesting that these GCs differences reflect the stress of subordination perhaps because the subordinate experiences physical, psychosocial and/or nutritional stress.

A final way to examine if the stress of subordination or costs of dominance explain GC differences between dominant and subordinate siblings is in bird species with variability in the degree of hatching asynchrony. For example, in nests with greater hatching synchrony, one might predict that dominant individuals would have higher baseline or

integrated GCs than subordinates (supporting the costs of dominance hypothesis) due to the need to enforce the hierarchy with physical confrontations rather than merely age- or size-based differences where the dominant-subordinate relationship may be maintained without physical aggression. Additionally, there is some evidence that nests with greater levels of hatching synchrony exhibit higher instability in the sibling dominance hierarchy (Gilby et al., 2011), which could lead to dominant individuals having higher GCs than subordinates (Sapolsky, 2005). Black-legged kittiwakes (*Rissa tridactyla*) are a colonial seabird species that exhibits within species variation in hatching asynchrony; in synchronously hatching nests, one nestling was dominate and delivered high levels of aggression to subordinate nestlings, but subordinates did not suffer a reduction in growth compared to typically asynchronous nests (Merkling et al., 2014a), and there were no differences in baseline GCs between dominant and subordinate individuals (Merkling et al., 2014b). On the other hand, as hatching asynchrony increased, subordinate nestlings also received more attacks from the dominant nestling and grew slower (Merkling et al., 2014a). In line with the stress of subordination hypothesis, subordinate nestlings also had higher baseline GCs than dominants in highly asynchronous nests (Merkling et al., 2014b). These results suggest differences in GCs (here baseline GCs) between dominant (first-hatched) and subordinate (second-hatched) nestlings are reflective of the stress of subordination, especially in highly asynchronous nests where subordinates have little access to food and are frequently attacked. Additionally, they suggest that the ability of subordinates to gain access to food in synchronous nests may result in them having similar baseline or integrated GCs to dominants despite the observation that they received high levels of aggression.

In summary, baseline and/or stress-induced GCs often differ between dominant and subordinate siblings and, similar to studies of adults in group-living species, empirical studies do not provide a clear picture on whether these differences reflect the stress of subordination or costs of dominance. On the one hand, there is inequitable access to food where first hatched or dominant nestlings have greater access than later hatched or subordinate nestlings and baseline and/or stress-induced GCs are often higher in nestlings with less access to food. Thus, subordinates may experience nutritional stress in addition to psychosocial stress from physical attacks or psychological intimidation, supporting the stress of subordination hypothesis (Fig. 2). On the other hand, in several bird species, dominants have higher baseline and/or stress-induced GCs than subordinates, perhaps because they use physical means to establish, maintain, or enforce the dominance hierarchy. However, physical assertions are rarely observed among nestlings in many species despite dominants having higher GCs than subordinates. Furthermore, in boobies where the dominant nestling frequently physically attacks the subordinate, it is subordinates who have higher baseline and/or stress-induced GCs than dominants. Clearly, more comparisons are needed to identify if there are any general patterns emerging about GC differences between subordinate and dominant nestlings and careful observational studies to characterize dominance behaviors in nestlings.

7. Interference competition among conspecifics: impacts on GCs

In addition to interactions among juvenile conspecifics, competitive interactions among adult conspecifics are another aspect of the social environment that are widely known to influence GCs (Fig. 1). Their effects have been relatively well-documented in both group-living and non-group living species, though the focus often differs. In group-living species, most studies focus on differences in GCs (usually measured as integrated GCs) between dominants and subordinates and these are reviewed elsewhere (Creel, 2001; Abbott et al., 2003; Goymann and Wingfield, 2004; Creel, 2005; Sapolsky, 2005; Creel et al., 2013a, 2013b; Beehner and Bergman, 2017). In non-group living species, the focus is instead on examining the influence of conspecific population density on GCs, which was initially started with studies of the effects of crowding on the HPA axis in laboratory rodents (Christian, 1950, 1956). More recent studies in free-living animals that do not live in groups have found widespread support for a positive association between conspecific density and GCs (usually measured as integrated GCs) in many species (Creel et al., 2013a, 2013b; Newman et al., 2015), though there are exceptions (Cooperman et al., 2004; Blondel et al., 2016; Edwards et al., 2020). Similar patterns are also documented in group-living species, such as meerkats and zebra where increased group size is associated with elevated integrated GCs among group members (Dantzer et al., 2017; Seeber et al., 2018) or in group-living primates where increased inter-group interactions are associated with elevated integrated GCs (Schoof and Jack, 2013).

Here, we focus on how social interactions (winning or losing competition) among adult conspecifics influence GCs to test if these patterns reflect the stress of subordination or costs of dominance (Fig. 2). We first note that these types of interactions may be very different from the staged dyadic and iterative interactions between two conspecifics described in rats or other species where both the winner and loser experience an acute increase in GCs, but only the loser experiences a chronic increase in baseline or integrated GCs (discussed above). Here, the interactions among free-living conspecifics may be infrequent or seasonal and losers may be able to avoid the winner, whereby the outcome of these interactions on the GCs of winners and losers is not clear. The stress of subordination hypothesis would predict that losers (subordinates) of a competition for a resource would have higher baseline or integrated GCs, perhaps because of the loss of access to a resource or due to physical attacks or psychological intimidation by the winner (dominant) of the interaction (Fig. 2). The costs of dominance would predict that the winner (dominant) would have higher baseline or integrated GCs than the loser (subordinate) due to it frequently using physical violence to assert dominance and GCs acting as a mechanism of energy mobilization needed for heightened expression of territorial behavior (Fig. 2).

Most studies investigating the effects of conspecific density on GCs in non-group living species find that, among individuals, increased conspecific density is associated with elevated GCs. However, in studies that track if GCs change within-individuals across a gradient of density show that integrated GCs are elevated in some individuals under high densities but lowered in others (Guindre-Parker et al., 2019). The elevations in GCs when density is increased could reflect an increase in antagonistic interactions that cause GCs in both the winner and loser of those interactions to increase. Similar to group-living species or among siblings in birds (discussed above), documenting these aggressive interactions and their acute effects on GCs is challenging. Consequently, many studies investigate how antagonistic interactions among conspecifics affect their GCs use an experimental approach where a conspecific competitor or its cues (a model, audio playback, or live individual in a cage) is temporarily introduced on the territory of another individual (simulated territorial intrusion). Here, the territorial owner has a resident advantage and can be considered the winner or dominant individual in this interaction and the intruder is the loser and the resident is the winner because the intruder is removed at the end of the simulated territorial intrusion.

In studies of fish, bird, amphibian, and reptile species that are territorial, a version of the simulated territorial intrusion paradigm is often used to gauge the impact of a competitive interaction on GCs. Here, the challenged individual (winner or dominant) generally experiences an increase in baseline and/or stress-induced GCs compared to a control stimulus (Klukowski and Nelson, 1998; Pinxten et al., 2004; van Duyse et al., 2004; Gill et al., 2008; Charlier et al., 2009; Landys et al., 2010; Newman and Soma, 2011; Deviche et al., 2014; Leary, 2014; Ros et al., 2014), though this is not always the case (Wingfield and Lewis, 1993; Davis and Marler, 2003; Remage-Healey and Bass, 2005; Lynn et al., 2007; Scriba and Goymann, 2010; Fokidis et al., 2011; de Assis et al., 2012). Other studies in territorial fish comparing the change in stress-induced GCs in response to a mirror image of an individual vs. an actual opponent show that stress-induced GCs rise equally in both

conditions even if there is no winner when an individual is exposed to its mirror image (Ramos et al., 2021). These results are consistent with studies in territorial male rats (discussed above) where an acute antagonistic interaction can cause an acute but temporary elevation in GCs in the winner of the dyadic interaction.

Unfortunately, most studies using this paradigm do not measure the effects of the simulated intrusion on GCs of the intruder such that the effects on the loser cannot be identified. In one study in non-social spotted salamanders (*Ambystoma maculatum*) in captivity where baseline GCs were measured in the winner (resident) and loser(s) (intruders), the effects of competition among conspecifics for a resource (burrow) depended upon the number of intruders/competitors (Cooperman et al., 2004). The resident salamander (who initially resided in the burrow) and intruder had similar baseline GCs if only one intruder was introduced, whereas the resident had higher baseline GCs if four intruders were introduced. However, in a separate study in captive birds using a similar paradigm where 1 to 5 birds were allowed to intrude into the cage of a resident bird, residents and intruders had similar baseline GCs 30 min after the conclusion of the intrusion (Nephew and Romero, 2003). Only when 5 intruders were added to the cage of the resident did the intruders have higher baseline GCs than the resident (Nephew and Romero, 2003). Although these results are interesting, they are again somewhat limited by the fact that the interactions were forced and the participants could not escape from one another (as discussed above for laboratory rats).

Taken together, these results would appear to partially support the costs of dominance hypothesis where individuals winning antagonistic interactions for access to a resource exhibit higher baseline and/or stress-induced GCs than the loser. This would differ from studies in rats and other species described above where the loser or subordinate had a chronic increase in GCs. Again, it is worth noting that in interactions between free-living individuals, the eventual winner and loser may never interact with one another again. For example, the loser could avoid the winner, perhaps preventing the chronic increase in their baseline and/or stress-induced GCs that would be predicted from the iterative dyadic interactions between two individuals in the laboratory. This would be consistent with the prediction from Sapolsky (2005) that dominants may have similar or higher GCs than subordinates if they use physical means to enforce the dominance hierarchy and subordinates can avoid dominants. However, this conclusion seems premature because the effects of these staged interactions on GCs in the loser/subordinate are often unknown. Additionally, the STI paradigm where an individual is presented with an "intruder" (vocalization or physical model of a conspecific or both vocalization and model) may not reflect what happens in an actual dyadic interaction between two individuals. Specifically, in these types of STI experiments, the "intruder" does not respond to the focal individual with a full suite of behaviors (intruders may be caged, or a taxidermy model), which could influence the GC response of the focal individual who does not receive sensory feedback from the fake intruder indicative of them being defeated. At this point, studies on this topic show that challenged individuals exhibit increased baseline GCs and sometimes the winner has higher baseline GCs (Cooperman et al., 2004) whereas other times the loser has higher baseline GCs (Nephew and Romero, 2003). As such, support for the costs of dominance and stress of subordination hypotheses cannot be evaluated and more studies using forced conflicts or interactions among adult conspecifics over resources or simulated territorial intrusions that measure changes in GCs in both the winner and loser are needed.

8. Interference competition among heterospecifics: impacts on GCs

The final component of the social environment that can influence GCs that we will discuss are interactions between individuals of two different species that compete for the same resource. For example, group-living social carnivores in parts of Africa compete for prey or antagonize one another in a non-predatory context, different bird species compete for access to food resources during the breeding season or in mixed-species flocks in the non-breeding season where individuals are gregarious, and animals compete for priority access to carrion or a preferred site of basking/resting/nesting. In these situations, individuals of one species often win the competition for the resource while the other loses, setting up another situation where some individuals of one species are dominant and those from another species are subordinates. Here, subordinates are considered those who are excluded from an area or resource or those who lose aggressive interactions. The consequences of these inter-specific interactions are a central focus of ecology (Connell, 1983; Schoener, 1983), yet the impacts on GCs are less studied except in predator-prey interactions. As mentioned above, the effects of heterospecifics on GCs could either be through interspecific aggression during interference competition or through exploitative competition where individuals of one species indirectly prevents individuals from another species from accessing a resource (though we note neither of these are mutually exclusive explanations). For example, individuals of species 1 that is competitively superior to species 2 could drive away individuals of species 2 from a preferred habitat or a food source through direct aggression, by stealing their food, or depleting shared resources.

Here, we again focus on examining support for the costs of dominance vs. stress of subordination hypotheses (Fig. 2). If individuals from the competitively superior species (dominant/winner) have higher baseline or integrated GCs, this would support the costs of dominance hypothesis whereas if individuals from the competitively inferior (loser or subordinate) species has higher baseline or integrated GCs, this supports of the stress of subordination hypothesis. However, testing these hypotheses is challenging because we need to know which species is competitively superior over the other species. One way to directly establish these identities is through behavioral observations among individuals of two species, such as individuals from species 1 aggressively driving individuals from species 2 away from a certain area or stealing their food, or observations showing that the presence of species 1 displaces individuals from species 2 (e.g., in social carnivores in Africa: Caro and Stoner, 2003). However, such data are often not available and so differences in body size may be used where the larger species is assumed to be competitively superior. This assumption is based upon observations that size is often a major predictor of the outcome of antagonistic interactions between individuals of two different species that share the same habitat or have a similar diet (e.g., McCormick and Weaver, 2012). This is also the case in the establishment of a social hierarchy when there is a vacancy in the dominant position in group-living species such as meerkats where the older or heavier individual is more likely to acquire dominance (Clutton-Brock et al., 2006; Hodge et al., 2008), or in the linear hierarchies of haremic fish such as angelfish (*Centrophyge bicolor*: Ang and Manica, 2010) and blue-banded gobies (*Lythrpnus dallil*: Rodgers et al., 2007). For sake of simplicity and in the absence of direct behavioral observations, we assume that the larger species is competitively superior (dominant/winner) or, in the case of human-wildlife interactions, we assume humans are the dominant/winner.

We can dissect this discussion through a few different ways. First, we can ask if the presence or abundance of individuals of one species elicits a change in baseline or integrated GCs in the other species. In the few studies that have been conducted, the answer seems to be yes and no. For example, in separate studies of different ungulate species in USA and Italy, the abundance of one large ungulate species is positively associated with integrated GCs in another smaller ungulate species (both species live in small groups), though this is only during mild winters (Atwood et al., 2020) or in the summer (Formenti et al., 2018). This increase in integrated GCs in the smaller ungulate species is perhaps due to resource competition from the larger ungulate species, such as the density of elk or red deer (*Cervus elphaus*) being positively associated with integrated GCs in the smaller mule deer (*Odocoileus hemionus*) or Apennine chamois (*Rupicapra pyrenaica ornata*). Similarly, the presence

of the noisy miner (*Manorina melanocephala*) in parts of Australia seems to exclude smaller bird species through direct aggression and the presence of noisy miners in small forest patches may increase one marker of physiological stress (the ratio of heterophil to lymphocytes: Davis et al., 2008) in one of these smaller bird species, the superb fairy-wren (*Malurus cyaneus*: Bain et al., 2019). Other observational studies in small mammals did not find that the presence or abundance of individuals of a larger species increased GCs in individuals of a smaller species. For example, integrated GCs in deer mice (*Peromyscus maniculatus*), which are largely non-social, were not higher when they experienced increased abundance of a larger species (voles: *Microtus* spp.: Eleftheriou et al., 2021). Similarly, in a study of free-living non-social wildcats (*Felis silvestris*), the presence of smaller (European pine marten: *Martes martes*) or larger (European red fox: *Vulpes vulpes*) competitor species did not influence integrated GCs in the wildcats (Piñeiro et al., 2015). Other studies comparing GCs in individuals from one species living on islands versus those on the mainland may also provide insight. For example, in territorial birds and mammals, individuals on islands have lower baseline (Müller et al., 2007) or stress-induced GCs (Clinchy et al., 2004) or smaller adrenal glands (To and Tamarin, 1977), but not all studies find this pattern (e.g., no difference in integrated GCs: Stewart et al., 2020). Although these reductions in GCs in the island populations compared to the mainland may reflect "release" from predators, it could also reflect the effects of release from heterospecific competition.

Experimental studies where individuals are housed with conspecifics, heterospecifics, or predators would be ideal to examine the impacts of heterospecifics on baseline or integrated GCs relative to these other factors. Unfortunately, these types of studies are too rare and inconclusive. For example, Chase et al. (2016) showed that whole body GCs in juvenile tidewater gobies (*Eucyclogobius newberryi*) were similar if they were housed with conspecifics or with individuals from a native heterospecific (*Gasterosteus aculeatus*) that was observed to be competitively superior (outcompetes the gobies for food). In a rare experimental study in common voles (*Microtus arvalis*) placed in semi-natural field enclosures, Liesenjohann et al. (2013) investigated how the presence of individuals from a different heavier vole species (*Microgus agrestis*) affected integrated GCs of pregnant or lactating common voles compared to the presence of similar-sized conspecifics or a possible predatory species (shrew). They showed that pregnant common voles exhibited higher integrated GCs when paired with shrews (predator) compared to when paired with conspecific or heterospecific voles. However, lactating common voles with dependent pups paired with competitors (conspecifics or heterospecifics) did have higher integrated GCs than lactating females in the enclosures with the predator (shrew). These results in voles highlight how the presence of competitors (either conspecific or heterospecific) can elicit a more pronounced elevation in GCs relative to a predator.

Another way we can examine how heterospecifics affect GCs is by focusing more narrowly on the presence of invasive species and ask if their presence elicits a change in baseline or integrated GCs in an endemic species. Although relatively few studies have addressed this issue, the answer is unequivocal. From amphibians to lizards to mammals, the presence of an invasive (heterospecific) species is associated with an elevation in baseline or integrated GCs in the endemic species (Jessop et al., 2015; Narayan et al., 2015; Santicchia et al., 2018), though we note in some studies these effects are nuanced such as wolves (*Canis lupus*) having higher integrated GCs if living in sympatry with free-ranging domestic dogs only if they were in small packs (Molnar et al., 2015). In other studies investigating how the presence of an introduced species affects baseline and stress-induced or integrated GCs in endemic species, the effects of the introduced species may be more due to their role as a predator rather than a competitor (e.g., Berger et al., 2007; Narayan et al., 2013; Graham et al., 2012, 2017). However, some studies clearly demonstrate how an introduced species that competes with an endemic species can elevate GCs in the latter. For example, non-social lace monitor lizards (*Varanus varius*) and the introduced European red fox (*Vulpes vulpes*) compete for food in Australia and lizards in areas with high fox densities had higher baseline GCs (Jessop et al., 2015; but see Anson et al., 2013). This increase in the monitor baseline GCs is perhaps due to increased competition for food when foxes were abundant (Anson et al., 2013) and this is interesting given that these adult lizards are typically heavier than adult foxes. In an experimental study using field enclosures, Narayan et al. (2015) showed that non-social ground frogs (*Platymantis vitiana*) in enclosures with the heavier invasive cane toad (*Rhinella marina*) had higher integrated GCs than those without cane toads, though we note cane toads may not only be a competitor of ground frogs but also a predator (*sensu* Narayan et al., 2013). In non-social Eurasian red squirrels (*Sciurus vulgaris*), the presence of the larger introduced North American grey squirrel (*Sciurus carolinensis*) is associated with higher integrated GCs in the smaller endemic red squirrel and experimental removal of grey squirrels leads to reductions in red squirrel integrated GCs (Santicchia et al., 2018). How these changes in GCs in the endemic species occur is not clear. It could reflect the stress of subordination whereby the introduced species is competitively superior and elevates GCs of the endemic species through direct aggression or by out-competing the endemic species for some preferred resource. For example, the North American mink (*Neovison vison*) was introduced into the United Kingdom and competes and aggressively attacks two endemic mustelid species (Harrington et al., 2009), which could cause their GCs to be elevated although this has not been documented. By contrast, in Eurasian red squirrels, the North American grey squirrel is larger but antagonistic interactions between individuals of these two species are rare (Wauters and Gurnell, 1999) and so the elevations in GCs of the endemic red squirrel may be caused by increased food competition when in sympatry with grey squirrels (Wauters et al., 2002).

Finally, we can ask if a particular cosmopolitan species that has invaded every known habitat and is competitively superior to every other species regardless of body size (humans) elicits an increase in baseline or integrated GCs in other species. This has been recently covered in several different meta-analyses covering baseline and stress-induced GCs or integrated GCs (Dantzer et al., 2014; Iglesias-Carrasco et al., 2020; Injaian et al., 2020) so we only briefly mention how the presence of humans can be associated with elevated GCs. For example, a recent meta-analysis showed that various measures of human activity (light at night, human noise or density, etc.) are not associated with elevated baseline and stress-induced GCs in vertebrates, though this conclusion is mostly generated from studies in birds (Iglesias-Carrasco et al., 2020; Injaian et al., 2020) and future studies need to consider how the social system of a species modifies the impacts of human activity on their GCs. However, the effects of humans on GCs of other animals are complex as individuals that are particularly sensitive to human stimuli may preferentially avoid colonizing human-dominated landscapes (Lowry et al., 2013). Additionally those individuals that settle in urban areas may eventually exhibit modifications to their HPA axis to cope with chronic human disturbances (Dickens and Romero, 2013) such that GCs of individuals in human-dominated landscapes are not chronically elevated. Studies that experimentally expose animals to the cues of humans are best poised to address this question and they show that human presence or their cues increases either baseline or integrated GCs (e.g., Blickley et al., 2012; Kleist et al., 2018; Injaian et al., 2019). Also, capitalizing on the reduction in outdoor human activity and associated changes in wildlife behavior (e.g., Derryberry et al., 2020; Manenti et al., 2020) during the 2020 COVID-19 pandemic may yield unique insights into the relationship between human presence and wildlife GCs. Here, if humans are considered to be the winner/dominant of the interaction with other animals, at least some of these studies support the stress of subordination hypothesis.

Collectively, these studies illustrate how the presence and abundance of heterospecifics can affect GCs (measured as baseline or stress-induced GCs or integrated GCs) in a variety of species. Testing whether these

results support the stress of subordination or costs of dominance hypothesis is tricky. On the one hand, several of the above studies show that the presence of a competitively superior species (larger species or perhaps humans) seems to elicit an increase in baseline or integrated GCs in the other smaller or competitively inferior species. Moreover, the uncertainty or unpredictability of interactions with invasive species (including humans) may contribute to the elevated GCs observed in endemic species. However, similar to the issue presented above for conspecific interactions, the effects of heterospecific interactions on the GCs of the winner or dominant species (here being the competitively superior or invasive species) are often not known. For example, if Eurasian red squirrels have higher integrated GCs when in the presence of the larger North American grey squirrel (Santicchia et al., 2018), do grey squirrels also experience in elevation in integrated GCs when in the presence of red squirrels? So while the studies reviewed above illustrate how the loser or subordinate species often exhibits an increase in GCs in the presence of the winner or dominant species, perhaps supporting the stress of subordination hypothesis, this is again premature because we cannot compare GCs in the loser/subordinate to those of individuals in the winner/dominant species. Additionally, congruent with the considerations for within-nest dominance hierarchies, at this point it is not clear if a rise in baseline or integrated GCs exhibited by the loser or subordinate species is due to some physical interaction between individuals or a reduction in access to resources, like food. Thus, future studies on this topic must consider not only *if* heterospecific interactions result in a change in baseline or integrated GCs in the winner/dominant species versus the loser/subordinate species, but also *how* – is it resource limitation or is it reflecting physical or even psychological stress?

9. Future directions

Above we have highlighted how multiple components of the social environment may influence different measures of GCs beyond simply social rank or dominance status in group-living species or predator-prey interactions among heterospecific species. We summarize how interactions among juveniles from the same brood/litter can generate variation in GCs, as can competitive interactions between conspecifics and heterospecifics in both group-living and solitary species (Fig. 1). We note that the focus of some of these areas of research have primarily focused on one measure of GCs, such as studies of within-brood competition and sibling hierarchies has primarily focused on measures of baseline GCs whereas studies of social rank or heterospecific competition has focused on measures of integrated GCs. Nonetheless, these studies using diverse measures of GCs indicate that the social environment can cause variation in baseline and/or stress-induced GCs and integrated GCs through multifarious means and they can provide an additional way to test the generality of the costs of dominance and stress of subordination hypotheses (Creel, 2001; Sapolsky, 2005). Doing so can help us better understand the generalizability of these two hypotheses. For example, in comparisons of GCs between dominant and subordinate individuals in group-living species, dominants may have higher baseline or integrated GCs not because of social rank but because of increased reproductive activity (e.g., in meerkats: Barrette et al., 2012). Above, we highlighted how despite the absence of asymmetry in reproductive activity (such as between dominant and subordinate nestlings), dominants can have higher GCs than subordinates. We now summarize a few possible areas of future research for this more holistic view of the effects of the social environment on GCs.

1) **The two main hypotheses to explain how the social environment causes variation in GCs (stress of subordination and costs of dominance) are not mutually exclusive.** In some ways, the conclusion of this review is equivocal as it does not provide a clear picture of whether baseline or integrated GCs reflect the stress of subordination or costs of dominance. Baseline or integrated GCs (and sometimes stress-induced GCs) may be higher in subordinates than dominants because subordinates are receiving more physical aggression from their dominant counterparts (which could also elevate GCs in dominants: Sapolsky, 2005) or receiving less food, both of which may happen simultaneously. For example, GCs may increase in both dominants and subordinates with increasing number of siblings in the nest or with the number of adult conspecifics or heterospecifics. This increase in GCs in both dominants and subordinates could be interpreted as being due to increased antagonism (reflecting costs of dominance) or due to reduced per capita food availability (reflecting stress of subordination). Moreover, increased food-availability in the surrounding environment may reduce the effects of exploitative competition by alleviating nutritional stress in subordinates, but also simultaneously increase interference competition by elevating the amount of aggression dominants exhibits towards subordinates (e.g., Dubuc et al., 2017). These confounds affect our ability to understand how the social environment affects GCs and is similar to how challenging it is to address if elevated predation risk influences prey either through GC-mediated reproductive suppression or by altering the foraging behavior in prey (Creel et al., 2009). Future studies employing individual-level food-supplementation of subordinates will be helpful to test the predictions from these two hypotheses. For example, if subordinates that are provided with food continue to experience increased physical antagonism from dominants and they still exhibit elevated baseline or integrated GCs compared to dominants, this would support the stress of subordination hypothesis. This type of experiment would also provide insight into the mechanism (nutritional, physical, or psychosocial stressors) by which dominants elicit a change in subordinate GCs. Here, subordinates may have higher baseline or integrated GCs not because of nutritional stress but due to exposure to physical/psychosocial stressors from the dominant individual(s).
2) **Is direct physical aggression required for competition with conspecifics and heterospecifics to increase subordinate GCs?** Above we have described how interactions among conspecifics (either juveniles or adults) or heterospecifics (adults) can, at least in some species, increase different measures of GCs. These effects can occur through interference competition or exploitative competition (or some combination) where individuals engage in antagonistic interactions or one individual loses access to a resource, respectively. In studies of the subtle or non-consumptive effects of predators on prey, the mere possibility of the presence of a predator (or its cues) may elicit an increase in prey baseline or integrated GCs (Travers et al., 2010; Clinchy et al., 2013; Zanette et al., 2014). This is similar to the psychological intimidation subordinates received from dominants described by Sapolsky (2005) for group-living species. Here, we can also ask if the presence of competitors either of the same or different species can elicit a sustained elevation in baseline or integrated GCs through psychological intimidation (i.e., do competitors have non-consumptive effects on each other?). For example, does exposure to cues of a species that is thought to be competitively-dominant over another species affect baseline or integrated GCs in that other species? If so, it is possible to test the prediction from Sapolsky (2005) that when dominants can use psychological intimidation to enforce or reassert dominance, subordinates should have higher baseline or integrated GCs (Fig. 2). Assessing this prediction will require greater definition of psychological intimidation, but studies that provide subordinates with supplemental food could also address if physical/psychosocial stress from dominants or nutritional stress causes changes in subordinate baseline or integrated GCs.
3) **Does dominance status among pair-bonded individuals influence GCs?** Another component of the social environment that we did not discuss above due to a lack of study is the effects of dominance hierarchies or within-pair competition within pair-bonded individuals. If there is priority access to food or another resource within a pair-bond, it will also be possible to examine if GCs respond to this type of hierarchy and provide another way to test the

generality of the stress of subordination and costs of dominance hypotheses. For example, in pair-bonded New Zealand robins (*Petroica australis*), males have priority access to food over females, which sometimes includes aggressive attacks (Steer and Burns, 2008). Similar to subordinates avoiding dominants in group-living species (Sapolsky, 2005), female robins avoid the male partner during specific times of year (Menzies and Burns, 2010). Other studies in social carnivores show that the dominant female may have priority-access to food (Watts and Holekamp, 2007) or that the amount of aggression pair-bonded individuals received from their partner can vary according to their degree of monogamous behavior (being higher if they are less monogamous: Botterill-James et al., 2017). This type of within-pair hierarchy and aggression also provides the opportunity to test predictions if GCs reflect the stress of subordination and costs of dominance. For example, do subordinate female New Zealand robins have higher baseline or integrated GCs than their male partners due to reduced access to food or experiencing aggression? Such studies can again help to identify when GCs are higher in subordinates or dominants beyond social hierarchies that are found in group-living species.

4) **Does the degree of social support affect GCs of subordinates outside of interactions among adults in group-living species?** Abbott et al. (2003) and Sapolsky (2005) highlighted that the stress of subordination may be lessened in adult subordinates of group-living species if they receive support from other group members. Other studies have emphasized how social buffering (often quantified as affiliative grooming between two individuals) could reduce measures of GCs in highly social primate species (Engh et al., 2006), but also other non-primate species like laboratory rats (Kikusui et al., 2006; Raulo and Dantzer, 2018). Do similar phenomenon occur in solitary species or among juveniles competing for the same resources? Just as in our conceptual model presented in Fig. 1 where we emphasize the need to consider antagonistic interactions at multiple levels, there is also the need to consider how social interactions at one level of the social environment could buffer individuals from stress at other levels. For example, in solitary species, individuals with adjacent territories may mutually benefit through stable social neighborhoods as time and energy spent on territory defense is reduced due to the adjacent territory owners being "dear enemies" (Siracusa et al., 2017, 2019, 2021). We may view this as a sort of subtle or indirect social support where individuals experiencing increasing conspecific density (and therefore elevated competition) do not experience as pronounced of an increase in baseline or integrated GCs if they have a stable social neighborhood full of familiar individuals. Moreover, juveniles of polytocous species could mitigate the effects of subordination on baseline or integrated GCs if they have greater social support in the form of more siblings. For example, above we described how several studies show that dominant nestling birds (first-hatched) have higher baseline GCs than subordinates (later hatched), yet some of the studies showing no effect of hatching order on baseline GCs are in species producing >2 offspring (Blas et al., 2005; Müller et al., 2010; Braasch et al., 2014). This presents the possibility that the effects of subordination on baseline or integrated GCs may be reduced if the subordinates have more siblings (social support) in the nest, which is somewhat analogous to a type of within-nest Allee effect. However, we note that while the presence of more siblings may lessen the effects of subordination on GCs in the subordinate nestlings, it also illustrates our first point above about the lack of mutual exclusivity in whether baseline or integrated GCs reflect the stress of subordination or costs of dominance. Although more siblings may provide subordinates with greater social support and/or dilute their exposure to attacks from the dominant nestling and may therefore lower their GCs, more siblings should also increase sibling competition for food, potentially generating greater nutritional stress. Future studies will need to better address whether social interactions at multiple levels of our framework (Fig. 1) can buffer individuals from the effects of external stressors at other levels. This will also require creative ways to quantify positive social interactions between individuals in species that are not highly social or who do not engage in allogrooming (e.g., linear distance between two perching/roosting individuals, node centrality in social networks).

5) **Do effects of one part of the social environment on GCs carry over to influence the outcome of other types of social interactions?** In several species, including in-depth studies in laboratory rats, individuals are more likely to lose a dyadic interaction with a conspecific if they have higher baseline or integrated GCs at the start of the competition or fight (Sloman et al., 2004; DiBattista et al., 2005; Gilmour et al., 2005; Earley et al., 2013; Cordero and Sandi, 2007). Additionally, given that the effects of dominance/subordination status of juveniles can influence their baseline or integrated GCs, this may have long-term consequences on their HPA axis and behavior as adults given that a variety of studies highlight how early developmental conditions influence the HPA axis (Harris and Seckl, 2011). For example, rats that experienced stress early in life (during adolescence) exhibited higher levels of aggression in competitive interactions later in life (Cumming et al., 2014). Furthermore, the effects of stress or elevated GCs are not restricted to an individual but can instead spread among conspecifics and affect their GCs or physiological state (Buchanan and Preston, 2014; Martin et al., 2015; Noguera et al., 2017). This suggests that the effects of one part of the social environment on the baseline or integrated GCs of an individual may have carry-over effects for that individual or other nearby conspecifics, though testing this hypothesis is required. For example, future studies could examine if the social status of nestling birds affects their HPA axis into adulthood or predicts the outcome of future contests with conspecifics as an adult. Other studies could examine if heterospecific interactions that lead to elevated baseline or integrated GCs impact performance in subsequent competitions with conspecifics.

6) **What are the relative impacts of different competitive interactions on GCs?** Few studies have examined the relative impact of the different components of the social environment on any measure of GCs (Fig. 3A). For example, is the relative increase in baseline or integrated GCs for an individual who loses a competitive interaction with a conspecific greater than if they lose a competitive interaction to a heterospecific? Are the effects of elevated predation risk on prey GCs greater than the effects of increased conspecific density in the prey species? Ignoring interactions between predators and prey, the degree of niche overlap (such as diet) may predict the relative impact of these different features of the social environment on GCs (Fig. 3B). For example, social status within a nest may have a large influence on baseline or integrated GCs relative to social status among two heterospecifics. This is because of the very strong overlap in diet among offspring who consume food brought by parents whereas heterospecifics can exhibit dietary differentiation (Fig. 3B). Heterospecific interactions that lead to changes in baseline or integrated GCs may actually be quite rare given that many species that experience inter-specific competition may eventually reduce the degree of conflict through niche differentiation (MacArthur, 1958), by segregating what they eat (Schoener, 1986), and/or when or where they are active (Berryman and Hawkins, 2006). This is not always possible among conspecifics in the same nest or group or pair-bonded individuals such that the effects of conspecifics on GCs may be stronger than heterospecifics. Future studies examining the relative impacts of heterospecifics vs. conspecifics on baseline or integrated GCs are necessary (such as Liesenjohann et al., 2013; Chase et al., 2016) to test these predictions. In studies that are adequately powered statistically, one way forward may be to use hierarchical mixed-effects models to partition the variance in baseline or integrated GCs caused by conspecifics vs. heterospecifics from the multilevel viewpoint we described above. Doing so could also include how

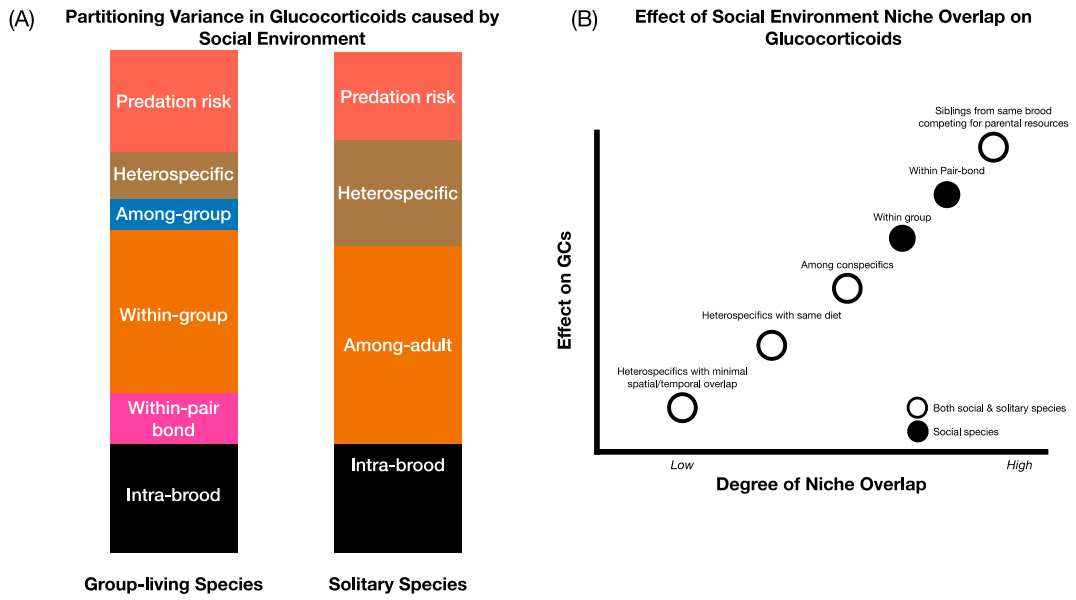

Fig. 3. (A) To fully characterize the impact of the social environment on any measure of glucocorticoids (GCs), we need studies that partition the variance in GCs according to these different levels of the social environment. These differ between solitary and social (group-living) species such as the latter being influenced by dominant/subordinate relationships among conspecific group members or within pair-bonds. We note here that we are quite liberal in what we consider a "group-living species". Here, we classify species as group-living where two opposite-sex individuals that exhibit a pair-bond during the mating season or outside of the mating season. It is not a requirement for group-living species to exhibit pair-bonding, nor is it a requirement for species that exhibit pair-bonding to live in a group larger than the two pair-bonded individuals. In species that exhibit pair-bonding but do not otherwise live in a group, the "within-group" effect on GCs would be zero whereas other species that exhibit pair-bonding and live in a group with other adult conspecifics, this effect may be non-zero. By contrast, solitary species are those that do not exhibit pair-bonding and do not live in groups. (B) The relative effect of the different components of the social environment on GCs may depend upon the degree of niche overlap. For example, there may be a relatively large difference between dominant and subordinate baseline GCs among nestling birds relatively to a smaller difference between dominant and subordinate individuals of different species. This reflects the degree of niche overlap, being highest among conspecific individuals in the same nest where they are only consuming food from their parents.

measures of social support at one level (such as among group members) might buffer individuals from the consequences of antagonistic interactions on baseline or integrated GCs at another level (such as among heterospecifics), as discussed above.

7) **When the outcome of social interactions is more unpredictable, does it lead to a greater changes in GCs?** The predictability of stressors may influence the magnitude of the stress response (Taborsky et al., 2021). For example, unpredictable stimuli can lead to pronounced elevations in GCs compared to those that are more predictable in rats (Weiss, 1970) and in wild bird species, individuals experiencing unpredictable environments exhibit higher GC production in response to stress (Zimmer et al., 2020; Guindre-Parker and Rubenstein, 2021) or changes in the glucocorticoid receptor (Hofmeister and Rubenstein, 2016). Although we described above why heterospecific interactions may be too rare to elicit changes in GCs, the outcome of competitive interactions with heterospecifics (even if rare) may be more unpredictable and may therefore lead to a stronger stress response than those with conspecifics. Conspecifics often have stereotyped display sequences or specific cues/signals that can reflect their condition or ability to win a contest (Laidre and Johnstone, 2013). This may reduce direct physical antagonistic interactions because it provides all parties with some predictive information about the likely outcome of the competition. However, interactions among heterospecifics may instead lead to escalated challenges because a lack of such stereotyped displays or cues/signals, especially in situations where individuals of one species encounter individuals of another introduced species. In such situations, it is possible that competitive interactions among heterospecifics leads to a greater change in baseline or integrated GCs than competitive interactions with conspecifics, reflecting the greater level of unpredictability of encounters with heterospecifics than conspecifics.

8) **GCs are affected by the social environment, but what are the consequences?** The studies reviewed above merely highlight that the social environment can elicit a change in baseline or stress-induced GCs or integrated GCs, yet studies about the consequences of the shift in these different measures of GCs in dominants/winners and subordinates/losers have been infrequent. We might expect that acute elevations in baseline or integrated GCs in dominants or subordinates leads to adaptive phenotypic plasticity, as other studies illustrate how elevations in baseline or integrated GCs can induce adaptive plasticity in behavior, morphology, or life history (Wingfield et al., 1998; Boonstra, 2013; Dantzer et al., 2013; Middlemis Maher et al., 2013). For example, central infusion of GCs in individual rats that lose fights (subordinates) can promote submissiveness and reduce aggressiveness, which is presumably an adaptive behavioral response to avoid future aggression from the dominant individual (Weger et al., 2018). In nestling birds, elevated baseline GCs in later hatched individuals (subordinates) may facilitate an adaptive behavioral response by promoting submissiveness to the dominant nestling (Vallarino et al., 2006) or increasing begging behavior (Kitaysky et al., 2001; Loiseau et al., 2008; Perez et al., 2016). So while it is useful to examine if elevated baseline or integrated GCs reflect the stress of subordination or the costs of dominance, it will be crucial to also examine the consequences of the elevated baseline or integrated GCs on other traits including survival and reproduction. It is of course likely that the effects of elevated baseline or integrated GCs depend to some degree upon whether the increase is acute or chronic. These issues have already been emphasized for studies about the relationship between different measures of GCs and rank in primates (Beehner and Bergman, 2017). The key question to move the field forward is to focus on the benefits of elevated baseline or integrated GCs due to subordination or dominance rather than their supposed costs.

10. Conclusions

Our goal was to expand the consideration of how social dynamics influence different measures of GCs, and, in reviewing different components of the social environment, we argue that there is more support that baseline or integrated GCs reflect the stress of subordination rather than the costs of dominance. Testing these two hypotheses will require creative experiments, such as alleviating nutritional stress in subordinates (described above) as well as a better understanding of the physical or psychological battles between dominants and subordinates. For example, in a group-living species where subordinates are thought to have higher baseline or integrated GCs than dominants due to psychological intimidation, it may be possible to examine if the differences in baseline or integrated GCs between dominants and subordinates are flipped by experimentally causing dominants to be aggressive. This could be induced experimentally by increasing the degree of reproductive conflict within the group, such as promoting asynchrony of litters produced by dominants and subordinates that promotes direct aggression by the dominant towards the subordinate (Cant et al., 2014). Here, the dominant individual may need to switch from using psychological intimidation to physical means to enforce the dominance hierarchy, providing the opportunity to test if dominants have higher baseline or integrated GCs than subordinates when using physical aggression compared to psychological intimidation (Sapolsky, 2005). Similarly, by supplementally feeding subordinate (later hatched) nestling birds, the dominant nestling may switch to physical attacks to enforce the dominance hierarchy. Unfortunately, experimental approaches seem to be rare when examining how social status affects any measure of GCs.

The goal of this review was merely to highlight that when seeking to understand how the social environment influences any measure of GCs, it will be important to expand the frame beyond well-studied within-species adult social hierarchies and consider how interactions among conspecifics at different ages (from the juvenile to adult stage) and among heterospecifics influence GCs. There is also a strong need to incorporate how positive social interactions at one level of the social environment might buffer individuals from competitive interactions at another level. Additionally, it will be useful to document if the effects of different levels of the social environment (Fig. 1) on GCs depend upon the measure of GCs used (baseline or stress-induced plasma GCs or the different ways to quantify integrated GCs). We have reviewed how these features of the social environment affect GCs but it is clear more work is needed to understand the causes of variation in GCs from an inclusive hierarchical perspective.

Data availability

No data was used for the research described in the article.

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