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Glucocorticoids, male sexual signals, and mate choice by females: Implications for sexual selection

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ABSTRACT

We review work relating glucocorticoids (GCs), male sexual signals, and mate choice by females to understand the potential for GCs to modulate the expression of sexually selected traits and how sexual selection potentially feeds back on GC regulation. Our review reveals that the relationship between GC concentrations and the quality of male sexual traits is mixed, regardless of whether studies focused on structural traits (e.g., coloration) or behavioral traits (e.g., vocalizations) or were examined in developmental or activational frameworks. In contrast, the few mate choice experiments that have been done consistently show that females prefer males with low GCs, suggesting that mate choice by females favors males that maintain low levels of GCs. We point out, however, that just as sexual selection can drive the evolution of diverse reproductive strategies, it may also promote diversity in GC regulation. We then shift the focus to females where we highlight evidence indicating that stressors or high GCs can dampen female sexual proceptivity and the strength of preferences for male courtship signals. Hence, even in cases where GCs are tightly coupled with male sexual signals, the strength of sexual selection on aspects of GC physiology can vary depending on the endocrine status of females. Studies examining how GCs relate to sexual selection may shed light on how variation in stress physiology, sexual signals, and mate choice are maintained in natural populations and may be important in understanding context-dependent relationships between GC regulation and fitness.

1. Introduction

A fundamental aspect of life history research involves the trade-off between reproduction and survival, or current and future reproduction, and how life history strategies evolve across varying ecological and environmental contexts to maximize fitness (Stearns, 1989, 2000). Glucocorticoids (GCs) figure prominently in such tradeoffs because of their pleiotropic actions and central role in regulating life history traits (Breuner et al., 2008; Ricklefs and Wikelski, 2002; Wingfield et al., 1998). For example, one recurrent theme in GC-related research is that low GC reactivity (i.e., production of GCs in response to stressors) promotes investment in reproduction at the cost of survival while high GC reactivity promotes survival at the cost of reproduction (Breuner et al., 2008; Wingfield et al., 1998; Wingfield and Sapolsky, 2003).

While GC regulation may be expected to vary in a manner that optimizes fitness, baseline levels of GCs or levels associated with the acute stress response can be negatively, positively, or unrelated to fitness estimates (reviewed by Bonier et al., 2009; Breuner et al., 2008). One prominent hypothesis to explain inconsistencies in GC-fitness relationships proposes that they are context-dependent (see Bonier et al., 2009 for additional explanations). The general idea is that if the optimal stress response differs across environmental or ecological contexts then the relationship between endocrine traits and fitness may vary from weak to strong, or shift from negative to positive (Breuner et al., 2008; Taff and Vitousek, 2016; Vitousek et al., 2018).

Here we use this conceptual framework to build a case for understanding the role of GCs in modulating traits thought to evolve under sexual selection. We are interested in first establishing a basic understanding from the accumulating empirical studies regarding the association between circulating GC traits (e.g., baseline, stress-induced levels) and sexual traits known to be under sexual selection. This knowledge then provides a foundation for considerations regarding how sexual selection can feedback as a source of selection on GC traits. For example, a central tenet of sexual selection is that it drives the evolution of traits that can compromise survival (Andersson, 1994). We thus ask whether sexual selection potentially drives correlated evolutionary responses in GC physiology (*sensu* Adkins-Regan, 2005; Hau et al., 2016; McGlothlin and Ketterson, 2008; Vitousek et al., 2019; Zera

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et al., 2007). Of course, such an evolutionary response requires heritable variation in both the conventional sexually selected traits (behavior, morphology) as well as the GC physiological traits. The latter requires significantly more future research effort, though the existing artificial selection studies on this topic suggest significant heritability for multiple aspects of GC physiology (e.g., Baugh et al., 2012, 2017a; Evans et al., 2006; Pottinger and Carrick, 2001; Roberts et al., 2007b).

Despite evidence that elevated GCs redirect resources towards survival at the expense of reproduction (i.e., concepts of the CORT-trade-off hypothesis, see Breuner et al. 2008; Patterson et al., 2014) and a growing understanding of how the stress response relates to fitness, there has been little emphasis on how circulating GCs influence phenotypic targets of sexual selection. For example, of the 30 studies examining GCs in relation to performance measures provided in Breuner et al. (2008) only one examined sexual signals or interpreted the effects in the context of mate acquisition (i.e., Roberts et al., 2007b). Similarly, studies examining stress-fitness relationships often focus on variation in GCs of males or females that successfully mated and produced offspring, thereby omitting non-breeding individuals. For example, of the 41 studies measuring proxies for fitness in terms of reproductive success (as opposed to survival estimates) reviewed in Bonier et al. (2009), we determined that only three (~7%) considered the stress physiology of unmated males or females (e.g., Kotrschal et al., 1998; Lancaster et al., 2008; Lanctot et al., 2003). This is important because in many species a large proportion of reproductively competent adult males fail to effectively compete for, attract, or acquire mates (reviewed in Emlen and Oring, 1977; Janicke and Morrow, 2018; Nonacs and Hager, 2011). If variance in male mating success is related to variation in GC levels, exclusion of males that do not acquire mates could increase type I and II errors for GC-fitness relationships. In contrast, variance in mating success is often lower in females than males (Clutton-Brock, 1988), but the strength of sexual selection and how it potentially impacts the stress response is contingent upon the strength of female preferences for male traits.

Here, we review endocrine stress physiology in the context of both intra- and intersexual selection. Our overview focuses primarily on variation in GC levels because aspects of the stress response that are likely to be important in understanding GC-fitness relationships (e.g., speed of onset, negative feedback, and peak levels attained, Zimmer et al., 2019) or factors regulating the stress response (binding proteins, see Breuner and Orchinik, 2002; receptor distributions, Baugh et al., 2017b) remain largely unstudied in the context of sexual selection (but see Almasi et al., 2010; Jennings et al., 2000; Spencer and MacDougall-Shackleton, 2011; Wada et al., 2008). We first focus on whether GC levels correlate with sexual signals of males. Our overview draws from research on a broad range of organisms to understand how GCs are linked to sexually selected male traits, whether certain types of sexual signals (i.e., structural versus behavioral) are more likely to be affected by GCs, and whether GC-effects, when they occur, are studied in developmental/organizational and/or activational contexts. We then shift our focus to females (signal receivers) where we review evidence that GC's affect mate choice decisions.

One central theme propelling the current review, especially in terms of activational effects of GCs, is that elevated GCs can reduce investment in reproductive behavior, and yet many reproductive behaviors are directly linked to GC production. For example, male reproductive behaviors often involve aggressive contests with other males, are energetically demanding, or increase the risk of predation (Andersson, 1994), all of which are known to activate the HPA/I axis regulating GC production (Creel et al., 2001; Emerson, 2001; Harris and Carr, 2016). Indeed, the source of variation in circulating GCs may not matter in terms of its impact on courtship signals of males, but the bidirectional nature of these hormone-behavior relationships link GCs to various aspects of sexual selection (i.e., intrasexual competition and costs of signaling) that may be critical in understanding the agents of selection that potentially shape the stress response.

1.1. Glucocorticoids and sexual signals in males

Perhaps the most studied potential role of GCs in sexual selection focuses on intraspecific competition and suppression of reproductive behavior (reviewed by Creel, 2001). In many social mammals, for example, reproduction in male contest losers is suppressed and dominant contest winners monopolize females (Creel, 2001). Intraspecific interactions can dramatically impact GC levels and chronically elevated GCs often suppress the production of gonadal steroids that are critical for the expression of reproductive behavior (reviewed by Creel, 2001; Creel et al., 2013; Goymann and Wingfield, 2004; Young et al., 2006). Based on these effects, one prominent hypothesis for suppression of reproductive behavior involves GC production in subordinate contest losers (reviewed by Creel, 2001). However, support for this hypothesis in social mammals appears to be weak. For example, GCs are more often elevated in dominant males and there is little evidence that reproductive suppression is mediated by elevated GCs (Creel, 2001; Sands and Creel, 2004). Outside of mammalian social dominance hierarchies there seems to be more support for elevated GCs or low androgens in contest losers, but again these patterns are highly variable and inconsistent (Adkins-Regan, 2005; Creel et al. 2013; Earley and Hsu, 2008; Hsu et al., 2006).

Rather than focusing on complete suppression of reproduction, several lines of research have shifted the emphasis to more subtle effects of GCs on male reproductive behavior. For example, given that elevated GCs can decrease the energy directed towards reproduction and the production of gonadal steroids (Chand and Lovejoy, 2011; Greenberg and Wingfield, 1987; Sapolsky, 1992; Wingfield and Sapolsky, 2003), which are often critical for the expression of male secondary sexual traits, GCs are likely to be a major modulator of male sexual signals (Buchanan, 2000). Evidence of GC-mediated effects on male sexual signals is, however, mixed and somewhat controversial. For example, while an early review of the topic emphasized cases where GCs are potentially involved in regulating the expression of male sexual traits (Husak and Moore, 2008) a recent *meta*-analysis revealed little evidence that various metrics of stress, including circulating GC levels, were related to male sexual traits but reported evidence that females prefer "unstressed" males (Moore et al., 2016). So little work has been done in terms of GC effects on male traits and attractiveness that the results are potentially subject to type II errors (Garamszegi, 2016). The analysis also spans a broad range of both structural and behavioral traits that introduce noise in the analysis (Buchanan et al., 2016). For example, given that GCs are well known to modulate neural motor activity (Joels, 1997; Moore and Miller, 1984; Moore and Rose, 2002; Rose et al., 1995; Remage-Healey and Bass, 2006a, 2007), one possibility is that sexual behaviors are more likely to be affected by GCs than structural traits (Leary, 2016). This may be important in terms of mate choice studies showing how females are homing in on dynamic performance aspects of male motor behavior, rather than fixed structural cues, to assess prospective mates (Barske et al., 2011; Baugh and Ryan, 2010c; Coleman et al., 2004; Hogan and Staddard, 2018). In other words, GCs may be affecting how structural traits are actively advertised rather than their overall physical appearance, and this may be the more consequential phenotypic level in terms of sexual selection.

To examine the role of GCs in sexual selection, we assembled studies examining GCs in relation to structural traits (i.e., integumentary derivatives) versus behavioral traits (i.e., those that involve motor output). Studies were extracted from previous reviews on the topic by Buchanan (2000), Husak and Moore (2008) and Moore et al. (2016), and from forward citations of these reviews using Google Scholar. We included studies that examined sexually selected traits in males only (but see Henderson et al. 2013; Taff et al., 2019; Weiss et al., 2013 for GC-related effects on female signals) and for which direct or indirect estimates of GCs were provided. Although any trait that potentially influences mate acquisition may be subject to sexual selection, we focused primarily on studies that examined at least one trait that is

Table 1
Studies examining relationships between GCs (or indirect estimates of GCs) and sexually selected traits in males.

Species	Measured sexual signaling traits	Summary of main findings	Androgens measured?	Correlative or experimental		Expected effect on attractiveness	Source
Structural Traits							
Squamate reptiles							
Sand lizard, *Lacerta agilis*	Size of badge (flank coloring) and mobility	High baseline plasma GCs associated with larger badges (reflecting increased fighting ability) at end of reproductive season but high GCs decreased mobility in androgen-administered males	No	Correlative	↓	High GCs should decrease reproductive success via decreased mobility	Lindsey et al. (2016)
Common lizard, *Lacerta vivipara*	Carotenoid-based coloration	Baseline and chronically elevated plasma GCs increased redness when food was abundant	No	Correlative (baseline) and experimental (chronic, A)	↑	High GCs should increase attractiveness	Fitze et al. (2009)
Common lizard, *Lacerta vivipara*	Carotenoid-based coloration	Food restriction abolished red color enhancement when plasma GCs were high (follow up to Fitze et al., 2009 above)	No	Correlative and experimental (chronic, A and E)	–		Cote et al. (2010)
Common lizard, *Lacerta vivipara*	Carotenoid/ melanin-based coloration	GC administration negatively affected ventral carotenoid and melanin-based coloration but food availability did not (developmental framework)	No	Experimental (A and E)	↓	High GCs should decrease attractiveness	San-Jose and Fitze (2013)
Anole, *Anolis carolinensis*	Melanin-based body color, rate of courtship signaling, perch site selection in contest winners/ losers	Traits were unrelated to baseline plasma GC's but related to androgens	Yes	Correlative	–		Greenberg and Crews (1990)
Anole, *Anolis carolinensis*	Dewlap size and bite force	Traits unrelated to baseline plasma GCs but related to androgens	Yes	Correlative	–		Husak et al. (2007)
Mexican boulder spiny lizard, *Sceloporus pyrocephalus*	Coloration	Duller males tended to have higher baseline plasma GCs, unrelated to androgens	Yes	Correlative	↓	High GCs should decrease attractiveness	Calisi and Hews (2007)
Fence lizard, *Sceloporus undulatus*	Coloration, signaling behavior and aggression	Traits unrelated to baseline and chronically elevated plasma GCs (developmental and activational frameworks)	No	Correlative (baseline) and experimental (chronic, A)	–		MacLeod et al. (2019)
Birds							
Zebra finch, *Taeniopygia guttata*	Carotenoid-based beak coloration	Chronically elevated plasma GCs associated with repeated handling resulted in redder hues in beaks (developmental framework)	No	Correlative	↑	High GC's should increase attractiveness	McGraw et al. (2011)
Zebra finch, *Taeniopygia guttata*	Color reflectance in legs, beaks and cheek patches	No difference in measured traits for lines selected for divergent peak plasma GC levels and no relation to androgens (developmental framework)	Yes	Correlative and experimental (artificial selection of lines for divergent GC levels)	↓	*Females preferred males with low GCs even though not related to measured traits	Roberts et al. (2007a)
Zebra finch, *Taeniopygia guttata*	Body size, dominance ranking, color reflectance	Lines selected for divergent peak GC levels did not differ in signal quality or dominance, but lines selected for low GCs were larger, unrelated to androgens (developmental framework)	Yes	Correlative and experimental (artificial selection of lines for divergent GC levels and E)	↓	High GCs may decrease size associated mating advantages	Roberts et al. (2007b)
House finch, *Haemorhous mexicanus*	Carotenoid-based plumage redness	Redder males have more GCs in feathers (developmental framework)	No	Correlative	↑	High GCs expected to increase attractiveness	Lendvai et al. (2013)
Red grouse, *Lagopus lagopus*	Comb area	Degree to which administered androgens and parasites impacted ornamentation depended on GCs – high GCs in feathers increased parasite development and decreased androgen-mediated ornamentation (developmental framework)	Yes	Correlative and experimental (E)	↓	High GCs should decrease attractiveness	Bortolotti et al. (2009)
Red grouse, *Lagopus lagopus scoticus*	Carotenoid-based coloration	High feather GCs associated with reduced coloration (developmental framework)	No	Correlative and experimental (E)	↓	High GCs should decrease attractiveness	Mougeot et al. (2010)
Barn swallow, *Hirundo rustica*	Tail length	Larger ornaments related to low plasma GCs	No	Correlative and experimental (E)	↓	High GCs should decrease attractiveness	Saino et al. (2002)
Barn swallow, *Hirundo rustica erythrogaster*	Melanin-based coloration	No relationship between breast brightness and plasma GCs or responsiveness (developmental and activational frameworks)	No	Correlative and experimental (E)	–		Jenkins et al. (2013)
	Structural coloration of plumage		No	Correlative	–		Sarpong et al. (2019)

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Table 1 (*continued*)

Species	Measured sexual signaling traits	Summary of main findings	Androgens measured?	Correlative or experimental		Expected effect on attractiveness	Source
Tree swallow, *Tachycineta bicolor*		Iridescent (structural) coloration did not predict baseline plasma GCs prior to or after molt (developmental framework)					
Red-winged blackbird, *Agelaius phoeniceus*	Carotenoid-based epaulet size	No relationship between baseline plasma GCs and epaulet size	No	Correlative	–		Merrill et al. (2014)
Red-winged blackbird, *Agelaius phoeniceus*	Reflectance of carotenoid-based epaulet color	Epaulet hue and red chroma did not vary in feather GCs from museum specimens but higher brightness was associated with lower GCs (developmental framework)	No	Correlative	↓	High GCs should decrease attractiveness	Kennedy et al. (2013)
Pied flycatcher, *Ficedula hypoleuca*	Forehead patch size and black plumage coloration	High fecal GC metabolites associated with reduced patch size but unrelated to coloration	No	Correlative	↓	High GCs expected to lower dominance rank due to reduced patch size but increase territorial behavior	Lobato et al. (2010)
Collared flycatcher, *Ficedula albicollis*	Forehead and wingpatch size and song	Higher stress physiology estimate (heat shock protein 70) was related to longer and more versatile songs but unrelated to other traits	No	Correlative	↑	High stress responsiveness should increase attractiveness	Garamszegi et al. (2006)
Common yellowthroat, *Geothlypis trichas*	Melanin and carotenoid-based coloration	Higher stress responsiveness (higher acute plasma GCs) was associated with males with with larger masks and more colorful bibs	No	Correlative and experimental (E)	↑	Higher GCs reflect males with increased capacity to cope with stress	Henschen et al. (2018)
Crested auklet, *Aethia cristatella*	Feather crest ornament length	High baseline plasma GCs related to shorter crests	No	Correlative and experimental (E)	↓	High GCs should decrease attractiveness	Douglas et al. (2009)
Red-backed fairy wren, *Malurus melanocephalus*	Plumage coloration	Plasma GCs and androgens not related to coloration	Yes	Correlative and experimental (E)	–		Barron et al. (2013)
Red bishop, *Euplectes orix*	Plumage coloration	Higher GC estimates (heterophil/lymphocyte ratios) were negatively related to coloration in 2 seasons but positively related to coloration in 1 season, plasma androgens unrelated to coloration	Yes	Correlative	↑↓	High GCs may decrease or increase attractiveness	Edler and Friedl (2010)
Northern cardinals, *Cardinalis cardinalis*	Carotenoid-based plumage coloration	Higher GC estimates (heterophil/lymphocyte ratios) were positively related to coloration	No	Correlative	↑	High GCs should increase attractiveness (but see alternative interpretation by authors)	Maney et al. (2008)
Red junglefowl, *Gallus gallus*	Comb size	Plasma GCs and androgens not related to comb size	Yes	Correlative and experimental (E)	–		Parker et al. (2002)
Barn owl, *Tyto alba*	Phaeomelanic coloration	GC administration produced feathers with less coloration, but natural plasma GCs were not related to coloration (developmental and activational frameworks)	No	Correlative and experimental (A)	↑	High GCs should increase attractiveness	Roulin et al. (2008)
Barn owl, *Tyto alba*	Phaeomelanic and eumelanic coloration	GC administration produced feathers with less eumelanin but not phaeomelanins, but baseline plasma GCs were unrelated to both. Darker individuals show lower GC response to stressor (developmental and activational frameworks)	No	Correlative and experimental (A and E)	?	Not clear if females prefer males with lower eumelanin, but males prefer females with more melanin	Almasi et al. (2010)
King penguin, Aptenodytes patagonicus	Reflectance of beak spot and size of auricular feather patch	Baseline plasma GCs were not related to measured traits but birds with more beak UV hue mounted a greater acute GC response	No	Correlative	↑	High GC reactivity should be associated with increased attractiveness	Viblanc et al. (2016)
Mammals							
Mandrill, *Mandrillus sphinx*	Facial red coloration	Fecal GCs unrelated to coloration, but fecal androgens positively related to coloration	Yes	Correlative	–		Setchell et al. (2010)
Human, *Homo sapiens*	Composite aspects of facial attributes	Females preferred faces representative of males with low salivary GCs; high androgens offset negative effects of high GCs	Yes	Correlative	↓	*High GCs associated with decreased attractiveness to females	Moore et al. (2011)
Human, *Homo sapiens*	Composite aspects of facial attributes		Yes	Correlative	↓	*High GCs associated with decreased attractiveness to females	Rantala et al. (2012)

(*continued on next page*)

Table 1 (*continued*)

Species	Measured sexual signaling traits	Summary of main findings	Androgens measured?	Correlative or experimental		Expected effect on attractiveness	Source
		Positive relationship between plasma androgens and facial attractiveness that were strongest in males with low plasma GCs					
Behavioral Traits							
Fish							
Electric fish, *Brachyhypopomus gauderio*	Electric organ discharge (EOD) characteristics	GC administration reduced EOD amplitude and duration, but effects of increased plasma GCs during social challenges negated by increased plasma androgens	Yes	Correlative and experimental (A and E)	↓ –	High GCs should decrease attractiveness if not accompanied by increased androgens	Gavassa and Stoddard (2012)
Amphibians							
Great Plains toad, *Bufo cognatus*	Vocal attributes	High plasma GCs, but not androgens, predicted short call duration and GC administration decreased call duration independently of androgens	Yes	Correlative and experimental (A)	↓	*Females preferred calls characteristic of males with low GCs	Leary et al. (2006)
Woodhouse's toads, *Bufo woodhousii*	Vocal attributes	Plasma GCs, but not androgens, were positively related to vocal effort	Yes	Correlative	↑	High GCs should increase attractiveness	Leary et al. (2008)
Green treefrog, *Hyla cinerea*	Vocal attributes	Plasma GCs and androgens unrelated to vocal attributes	Yes	Correlative	–		Leary et al. (2015)
Green treefrog, *Hyla cinerea*	Vocal attributes	Plasma GCs and androgens unrelated to vocal attributes	Yes	Correlative	–		Crocker-Buta and Leary (2018b)
Green treefrog, *Hyla cinerea*	Vocal attributes	High plasma GCs better predictor of low vocal effort than low androgens	Yes	Correlative	↓	High GCs should decrease attractiveness (*unpubl summary of female preferences presented in paper)	Crocker-Buta and Leary (2018a)
Green treefrog, *Hyla cinerea*	Vocal attributes	GC administration decreased vocal effort independently of plasma androgens	Yes	Experimental (A)	↓	High GCs should decrease attractiveness	Leary and Crocker-Buta (2018)
Treefrog, *Hypsiboas albopunctatus*	Call rate	Plasma GCs not related to call rate	No	Correlative	–		Titon et al. (2016)
Smith frog, *Hypsiboas faber*	Call rate	High plasma GC related to increased call rate, unrelated to plasma androgens	Yes	Correlative	↑	High GCs should increase attractiveness	de Assis et al. (2012)
Bombay night frog, *Nyctibatrachus humayuni*	Vocal effort	Urinary metabolite GC and androgens unrelated to vocal effort	Yes	Correlative	–		Joshi et al. (2017)
Squamate reptiles							
Sand lizard, *Lacerta agilis*							see Lindsey et al. (2016) above
Anole, *Anolis carolinensis*							see Greenberg and Crews (1990) above
Anole, *Anolis carolinensis*							see Husak et al. (2007) above
Fence lizard, *Sceloporus undulatus*							see MacLeod et al. (2019) above
Common Lizard, *Lacerta vivipara*	Aggression, tongue extrusions, chases, approaches and copulation attempts with females	GC administration increased all measured traits except aggression. Plasma GCs measured in separate experiment.	No	Experimental (A)	↓	*High GCs should increase reproductive success but females showed reduced preference for GC-treated males	Gonzalez-Jimena and Fitze (2012)
Birds							
Collared flycatcher, *Ficedula albicollis*							see Garamszegi et al. (2006) above
Brown-headed cowbird, *Molothrus ater*	Vocal repertoire	High plasma GCs related to high repertoire size	No	Correlative	↑	High GCs should increase attractiveness (energetic)	Merrill et al. (2013)
	Vocal attributes		Yes		↓		

(*continued on next page*)

Table 1 (*continued*)

Species	Measured sexual signaling traits	Summary of main findings	Androgens measured?	Correlative or experimental		Expected effect on attractiveness	Source
European starling, *Sturnus vulgaris*		Males subject to nutritional stress during development tended to have higher peak plasma GCs, spent less time singing, longer latencies in evoked singing, and sang fewer song bouts that were unrelated to androgens		Correlative and experimental (E)		High GCs (or poor nutrition) should decrease attractiveness	Buchanan et al. (2003)
Zebra finch, *Taeniopygia guttata*	Vocal attributes	Males with longer and more frequent vocalization had lower total and free baseline plasma GCs (developmental and activational frameworks)	No	Correlative	↓	High GCs should decrease attractiveness	Wada et al. (2008)
Zebra finch, *Taeniopygia guttata*	Vocal attributes	High GCs during development reduce growth rate, song duration and complexity	No	Correlative and experimental (E)	↓	High GCs should decrease attractiveness (* shown in Spencer et al., 2005)	Spencer et al. (2003)
Zebra finch, *Taeniopygia guttata*	Neural development and vocal attributes	High GCs during development reduce volume of song control nuclei and number of syllables in song	No	Correlative and experimental (A and E)	↓	High GCs decrease male attractiveness (* shown in Spencer et al., 2005)	Buchanan et al. (2004)
Zebra finch, *Taeniopygia guttata*	Song learning accuracy complexity, performance and output	Nutritional stress during development elevated baseline plasma GCs and some aspects of HPA-axis function, but did not affect song learning or or aspects of song	No	Correlative and experimental (A and E)	–		Kriengwatana et al. (2014)
Song sparrow, *Melospiza melodia*	Vocal repertoire	Larger GC responses during restraint associated with larger song repertoires but unrelated to song rate (developmental and activational frameworks)	No	Correlative	↑	High GC reactivity associated with increased attractiveness	Grunst and Grunst (2014)
Song sparrow, *Melospiza melodia*	Vocal complexity	High GC reactivity during restraint associated with fewer syllables in song (developmental and activational frameworks)	No	Correlative	↓	High GC reactivity associated with decreased attractiveness	MacDougall-Shackleton et al. (2009)
Song sparrow, *Melospiza melodia*	Vocal complexity	Lower GC response to restraint associated with more complex song,. more effective negative feedback related to lower heterophil to lymphocyte ratios, song unrelated to sensitivity to exogenous ACTH (developmental and activational frameworks)	No	Correlative	↓	High GC reactivity associated with decreased attractiveness	Schmidt et al. (2012)
Song sparrow, *Melospiza melodia*	Vocal complexity	Food restriction and GC administration during development reduced song complexity but not performance, food restriction decreased song learning, Food restriction but not GC administration was associated with smaller song control nuclei (developmental framework)	No	Experimental (A and E)	↓	High GCs should decrease attractiveness	Schmidt et al. (2013)

Studies that measure both structural and behavioral traits are represented in both categories and summarized when first described. To simplify the results, not all measured variables provided in the citations are described in the summary (e.g., immune responses, body condition estimates, social manipulation, parasite loads). The expected effect of high GCs (during development or in adulthood) on attractiveness to females is only specified when a significant relationship between GCs and traits were found (indicated with arrows to indicate increase or decrease, and a dash when no relationship was detected). Studies that were clearly designed to address "developmental" (i.e., organizational) effects of GCs are specified; all other studies, in our interpretation, were designed to examine "activational" effects of GCs in adults. Cases in which female preference tests were actually performed are bolded with asterisks. Designation of experimental studies (versus correlative studies) refers to procedures in which GCs were altered either experientially (i.e., exposure to stressors) or through administration of GC's (designated with an "E" and "A", respectively, in column 5).

potentially assessed by females when making mate choice decisions or male mating behaviors that clearly affect the probability of acquiring mates.

We found a total of 54 studies meeting these criteria (Table 1). We present the main findings of these studies, specify if androgens were also examined, whether the available data is experimental (e.g., whether GCs were administered or altered via exposure to stressors) or correlative, the expected effect on attractiveness when an effect was detected, and whether females were tested to determine if they actually discriminate among males with varying GC levels. Many studies focus on GC exposure during development and how it influences expression of the measured trait later in life (e.g., the Developmental stress hypothesis associated with birdsong, Buchanan et al., 2004; Nowicki et al., 1998) whereas other studies focus on how changes in GCs in adulthood potentially alter the expression of sexually selected traits (e.g., concepts of the Energetics–hormone vocalization model developed for frogs, Emerson, 2001). We thus note, when possible, whether studies aligned with a developmental/organizational or activational framework.

The 54 studies examined represent 33 species, with 33 studies that examined structural traits and 26 studies that examined behavioral traits, five of which examined a combination of traits belonging to both categories. Squamate reptiles and birds were represented in both categories, whereas primates were only represented in the structural category and fish and amphibians were only represented in the behavioral category. Most studies were done in birds (32 studies), followed by squamate reptiles (nine), amphibians (nine), primates (three), and fish (one).

1.1.1. Structural traits

Studies on structural traits focused primarily on integumentary coloration (25/33 studies) and ornament/body size (Table 1). Ten of the 33 studies examining structural traits did not find an association between GCs and the structural trait. In the 23 cases that did, results suggested that elevated GCs reduced male attractiveness or reproductive success in 12 cases and increased attractiveness or reproductive success in six cases. The remaining five studies found that the GC-trait relationship varied between years (Edler and Friedl, 2010), that greater stress reactivity was associated with more attractive males (Henschen et al., 2018; Viblanc et al., 2016), that there was a GC effect with uncertain impacts on mate choice by females (Almasi et al., 2010), or that there was no clear relationship between GCs and the measured traits but that females actually preferred males with low GCs (Roberts et al., 2007a). This latter study represents one of only three studies examining structural traits that specifically assessed whether females discriminate among males with varying GC levels (in this case, lines artificially selected for divergent peak GC levels in birds). Only two other studies examined female preferences in relation to GCs, both of which showed a preference by women for facial characteristics of men with lower GC levels (Table 1).

While most studies in the structural category provided justification to support the predicted effects on male attractiveness, they did not test whether GC relationships with the male phenotype translate into variation in mate choice by females. Female preference tests are critical because the variance in male trait values subject to GC effects may be insufficient or irrelevant for female perception and discrimination (just noticeable differences) or mate choice execution under real world conditions (just meaningful differences). Female preference tests are particularly important when GCs appear to be related to suites of traits that have opposing effects on mate choice by females. For example, three studies found that high GC levels were positively associated with carotenoid-based coloration suggesting that higher GCs should increase male attractiveness (Fitze et al., 2009; Lendvai et al., 2013; McGraw et al., 2011, Table 1). However, high GCs can also decrease melanin-based coloration, which is expected to decrease male attractiveness (see Calisi and Hews, 2007; San-Jose and Fitze, 2013, Table 1). In contrast, three studies found that higher GCs were related to decreased carotenoid-based coloration, suggesting that higher GCs should reduce male attractiveness (Kennedy et al., 2013; Mougeot et al. 2010; San-Jose and Fitze, 2013, Table 1) and one study found that the negative effects of high GCs on melanin-based coloration potentially increases male attractiveness (Roulin et al., 2008). In this latter study (performed in barn owls), males potentially prefer females with higher melanin-based coloration and females potentially prefer males with lower melanin. Hence, GC-mediated effects on melanin-based coloration could select for higher or lower GCs depending upon whether the direction of selection is determined primarily through mate choice by females or males (see Almasi et al., 2010). GC relationships with coloration can be mixed even in studies on a single species. For example, in a series of studies performed on the common lizard, *Lacerta vivipara,* GC-coloration relationships varied depending upon whether food was abundant or restricted, illustrating the importance of nutritional state in phenotypic expression (Cote et al., 2010; Fitze et al. 2009; San-Jose and Fitze, 2013).

1.1.2. Behavioral traits

Studies examining relationships between GCs and behavioral traits were dominated by analysis of vocalizations (20/26 studies) followed by various other mating behaviors (i.e., push-up displays of lizards, attempted copulations, aggression), and, finally, electric organ discharge (EOD) characteristics of electric fish (Table 1). Similar to structural traits, the relationships between GCs and behavioral traits were highly variable. For instance, of the 20 studies examining vocalizations, the results from 10 studies suggested that high GCs should decrease male attractiveness to females, 5 suggested that high GCs should increase attractiveness, and 5 reported no relationship (Table 1). Interestingly, studies on vocalization take two very different approaches to understanding GC-mediated effects on their expression – one that focuses on activational effects of GCs on calling (mostly in anuran amphibians) and the other that focuses on developmental stress and organizational effects of GCs on neural substrates underlying vocal production in birds. The former is rooted in the energetic demands of display (stemming from concepts of the Energetics-hormone vocalization model; Emerson, 2001) while the other is rooted in the Developmental stress hypothesis (Buchanan et al., 2004; Nowicki et al., 1998; Table 1). Indeed, there is evidence for activational effects of GCs on vocal motor output (Remage-Healey and Bass, 2004, 2006b, 2007) and organizational effects of GCs on neural development (Buchanan et al., 2003, 2004; Spencer and MacDougall-Shackleton, 2011) indicating that both scenarios are equally plausible but only one is typically emphasized in studies on these two taxonomic groups.

As with structural traits, only a small fraction of studies directly assessed female preferences for behavioral traits; two in frogs (Leary et al., 2006; the other is unpublished but summarized in Crocker-Buta and Leary (2018a), one in lizards (Gonzalez-Jimena and Fitze, 2012), and two in birds (Spencer et al., 2005; Roberts et al., 2007a, the latter of which is included in both categories because the traits that females used to select males could be structural or behavioral). All of these studies showed decreased female preferences for males with high GCs. Interestingly, one study showed that female preference for males with high GCs decreased even though the effect of GCs on male behavior were expected to increase their mating success (Gonzalez-Jimena and Fitze, 2012), emphasizing the importance of mate choice trials in understanding the potential role of GCs in sexual selection (see also Roberts et al., 2007a).

1.1.3. Across category considerations

Most studies, regardless of whether they focused on structural or behavioral traits, were correlative or, if experimental, were experiential in nature (Table 1). Several recent studies emphasize the problems associated with interpreting such data. In zebra finches, for example, isolation stress (i.e., housing individuals separately) increased GCs and

altered vocal characteristics, suggesting that GCs contribute to vocal modifications (Perez et al., 2012). However, GC administration did not result in the full suite of vocal modifications shown in isolation (Perez et al., 2012; see also Sehrsweeney et al., 2019 for example in red squirrels, *Tamiasciurus hudsonicus*, involving vocalizations that advertise territorial ownership). Similarly, the effects of nutritional stress on vocalization in birds can yield different results than GC administration (Schmidt et al., 2013; reviewed by Crino and Breuner, 2015). However, even direct manipulation of GCs can be misleading. In electric fish, for example, cortisol injections simulating GC secretion during intraspecific contests caused decreases in EOD amplitude and duration that potentially decrease attractiveness to females (Gavassa and Stoddard, 2012). However, when males interact their GC levels are elevated and yet their EODs are not affected because concordant elevations in androgens appear to negate the effects of elevated GCs on EOD features (see Gavassa and Stoddard, 2012; reviewed in Gavassa et al., 2013). Together, these results emphasize the importance of collecting both correlative and experimental data to understand how the stress response and GCs modulate sexually selected traits.

Work on electric fish also illustrates the importance of examining GCs in conjunction with androgens. For example, because elevated androgens can negate the negative effects of elevated GCs on sexually selected traits (reviewed in Gavassa et al., 2013), positive relationships between GCs and androgens may explain cases where no correlation between GCs and the measured trait were found (see Table 1). Elevated GCs can also inhibit androgen production thereby modifying trait expression, or GCs can modify sexual traits independently of suppressive effects on androgen production, effectively masking androgenic effects on sexually selected traits (Leary and Crocker-Buta, 2018; Leary and Knapp, 2014; Leary et al., 2006). Any of these scenarios may apply to the 54 studies examined, 22 of which included measures of androgens (Table 1). Studies that simultaneously measure aspects of GC regulation and androgens are likely to lead to a clearer understanding of GC-trait relationships. For example, variation in the relationships between GCs and male sexual traits could be related to variation in negative feedback in the HPA axis, receptor-mediated inhibition of GCs on the HPG axis, or binding protein levels that can regulate exposure of target tissues to GCs (see Wada et al., 2008; Kriengwatana et al. 2014).

Discrepancies among studies in relationships between GCs and male sexual traits are likely to be attributable, at least in part, to thresholding effects of GCs on trait expression (see Emerson, 2001; Romero, 2002). For example, because male sexual traits are often costly to produce (Andersson, 1994) and GCs play a central role in mobilizing energy reserves (Laugero, 2001; Sapolsky et al., 2000), moderate elevations in circulating GCs may be required to meet the metabolic demands associated with an increase in the magnitude or intensity of such traits (e.g., concepts of the "Energetic-hormone vocalization model", Emerson, 2001 and the "Energy mobilization hypothesis", Romero, 2002). However, above some level, GCs are predicted to decrease investment in reproductive behavior, leading to reduced expression of male sexual traits (see Emerson, 2001). It is the two sides of this "tipping point" associated with GC threshold effects that may account for variation in the relationships between GCs and sexually selected traits shown in Table 1.

Work in anuran amphibians illustrates how these threshold effects can result in disparate relationships between GCs and sexually selected traits. For example, in two species of anurans (*Bufo woodhousii*, Leary et al., 2008 and *Hypsiboas faber*, de Assis et al., 2012) natural variation in GC levels were positively correlated with estimates of vocal effort (see also Emerson and Hess, 2001 for interspecific comparison of 4 frog species) suggesting that mate choice by females may favor males with higher GCs (Table 1). However, in the two studies in which exogenous GCs were administered in anurans, results revealed that high GCs decreased vocal effort (*Bufo cognatus*, Leary et al., 2006; *Hyla cinerea*, Leary and Crocker-Buta, 2018). In both of these species, reproductive strategies (alternative mating tactics) were critical in elucidating GC-vocal relationships. For example, in *H. cinerea*, males compete with one another using aggressive acoustic signals that stimulate GC production (Leary, 2014). Contest losers are typically the smallest males with the largest GC response to aggressive signals and who adopt non-calling mating tactics (Leary, 2014; Leary and Harris, 2013). In this species, high GCs are causally associated with the adoption of non-calling mating tactics but GC effects on calling behavior depend on the social-acoustic environment so that in the absence of vocal competitors males with high GCs call, but in the presence of vocal competitors they adopt a non-calling "satellite" mating tactic (Leary and Crocker-Buta, 2018). Hence, by altering the social-acoustic environment, GC-vocal relationships can be examined in satellite males (Crocker-Buta and Leary, 2018a). Inclusion of satellite males in hormone-call analysis dramatically increased the upper range of GCs found in males in natural choruses and revealed negative correlations between GC levels and vocal attributes (Crocker-Buta and Leary 2018a), mirroring the negative effects of GC injections on call parameters (Leary and Crocker-Buta, 2018), which was not detected when satellite males were excluded from the analysis (Crocker-Buta and Leary, 2018b; Leary et al., 2015).

These studies in anurans highlight that courting males can have a very narrow range of circulating GCs that preclude detection of GC-vocal relationships, but by examining a greater range of GC levels (i.e., by sampling males adopting alternative mating tactics) negative relationships between GCs and vocal attributes become apparent. These relationships may be more widespread in anurans and other taxa, but may not be detected in systems where there are not opportunities to sample the courtship signals of males with high GCs. These findings also suggest that elevated GCs are not likely to *cause* an increase in courtship signaling, but positive correlations may exist because elevated GCs are required to meet the metabolic demands of increased courtship signaling – this is a central concept of the Energetics-hormone vocalization model (Emerson, 2001) and probably applies to many positive associations between GCs and sexually selected traits. Similarly, dominant males often have higher GCs as a consequence of increased aggressive interactions with other males (Creel et al., 2013) which may lead to positive correlations between GCs and sexually selected traits (Laubach et al., 2013; Lindsey et al., 2016). Alternatively, males with more elaborate ornaments may be advertising their ability to cope with stressful situations with a greater stress response (Henschen et al., 2018).

1.1.4. Summary and future research on GCs and male sexual signals

Our overview indicates that the relationship between GCs and sexual traits is complex and varies from species to species and trait to trait (see also Moore et al., 2016). More studies have examined GC relationships with coloration than any other sexual trait but coloration also shows the most complex and inconsistent relationships with GCs (see also Moore et al., 2016). For example, carotenoid and melanin-based traits are often opposing in terms of how high GCs potentially affect them and are often conflicting in terms of whether mate choice by females should select for males with higher or lower levels of GCs. Whether sexual selection on color-based traits plays any role in shaping the stress response is thus unclear. Experimental manipulation of GCs are required to better understand GC-color relationships and mate choice trials are needed to tease apart the significance of GC effects on carotenoid-based versus melanin-based coloration.

A particularly intriguing aspect of melanin-based coloration is that it is linked to genetic correlations and pleiotropic actions on behavioral traits (McKinnon and Pierotti, 2010; Ducrest et al., 2008; Santostefano et al., 2019) that may increase survival (Almasi et al., 2008; reviewed by Crino and Breuner, 2015). For example, variation in GC sensitivity in barn owls is linked to melanin-based coloration and male provisioning behavior to offspring, suggesting that varying environmental conditions could maintain variation in GC-related traits (Almasi et al., 2008). Such effects fall under the "CORT-adaptation hypothesis" (Bonier et al., 2009a), which proposes that increased GCs mediate behaviors that enhance reproductive output.

Vocalizations are the second most studied sexual signal in terms of how they relate to GCs and, similar to coloration, were highly variable (see also Moore et al., 2016), However, discrepancies in GC-vocal relationships seem better understood, at least in an activational context, because of the well-established metabolic costs of vocalization and expected "cause-effect" relationships described in the Energetics-hormone vocalization model (Emerson, 2001). Vocalizations are also better studied and understood in terms of developmental/organizational effects than any other trait, at least in birds. Green treefrogs, *H. cinerea*, Great plains toads, *Bufo cognatus*, and zebra finches, *Taeniopygia guttata* represent the only cases, to our knowledge, where there is correlational data on GC-sexual trait relationships, experimental manipulation of GCs, control of androgens and body condition as factors contributing to GC relationships with male sexual signals, and where female discrimination and preferences for males with varying GCs have been shown (see citations in Table 1). Vocalizations thus provide strong evidence for GC-mediated effects and the results suggest that females prefer males with low GCs. However, there is little evidence supporting the hypothesis that GCs play a more prominent role in modulating behavioral traits compared to structural traits (see also Moore et al., 2016).

One particularly difficult aspect of interpreting studies examining GC relationships with male sexual traits is that the temporal frame for measuring GC concentrations and sexual traits is often not clearly described. This was especially problematic for structurally-based traits where, for example, GC levels may play a central role in coloration during specific periods of development (i.e., molt in birds, see Romero et al., 2005; Kennedy et al., 2013). In contrast, coloration in some animals (i.e., lizards) may change rapidly and in conjunction with changes in hormone levels (Taylor and Hadley, 1970). We recommend that, regardless of the type of trait examined, future studies more clearly lay out the organizational/activational basis for examining relationships between GCs and sexually selected traits. For example, studies examining GC relationships with songbird vocalizations are clearly set in a developmental context. Hence, manipulation of GCs and measures of sexually selected traits are offset temporally and justified in doing so. In contrast, studies examining GC-coloration relationships often do not clearly describe whether the measured traits are expected to be modified during development or modulated by GCs later in life. This is important because organizing effects may uncouple the relationship between hormone levels and traits in adults or alter the responsiveness of target tissues to GCs later in life (Moore, Hews and Knapp, 1998).

Another problem with interpreting studies relating GCs to sexually selected traits is that it is often difficult to discern if measures of GCs represent acute or chronically elevated GC levels. This is important because chronically elevated GCs often negatively affect gonadal steroids that are critical in the expression of sexually selected traits. Moreover, chronically elevated GCs are expected to negatively impact fitness while the acute stress response is expected to enhance fitness (Breuner et al., 2008). Delineating these two categories, particularly for studies examining activational effects of GCs, was often difficult either because sufficient information was not provided or determining what constitutes acute versus chronic elevations in GCs is problematic.

Together, our overview suggests that the direction of the relationship between GCs and male sexual signals is highly variable (see also Moore et al., 2016). Nonetheless, there are several cases where both correlative and experimental approaches indicate a negative effect of GCs on sexually selected traits and all mate choice tests that have been performed indicate female preferences for males with low GC levels. Such results suggest that mate choice by females could drive correlated responses for low GC profiles in male signalers. However, we emphasize how misleading simple measures of GC concentrations can be in terms of how they translate into selection on various aspects of the stress response (reviewed by Bonier et al., 2009; Bonier and Martin, 2016). In particular, we do not know whether there is indirect selection on GC regulation. For instance, individual males that are more efficient foragers or more effective at assimilating nutrients may be favored if GCs are related to body condition and are a primary source of variation in signal expression (Leary et al., 2004, 2006). We note, however, that even if sexual selection acts indirectly on GC regulation it is unlikely to favor a single hormonal phenotype. For instance, just as sexual selection can drive the evolution of multiple reproductive strategies it may also drive diversity in endocrine regulation (i.e., high/low GC concentrations or variation in GC reactivity) that potentially translates into individuals that vary in short term prospects of reproduction versus long term survival (see also Blas et al., 2007; Breuner, et al., 2008). Studies examining other aspects of the stress response (e.g., cumulative GC exposure, strength of negative feedback, ability to mount subsequent stress responses) could provide insight into how sexual selection influences the expression of sexually selected traits.

1.2. Glucocorticoids and sexual behavior in females

There are several lines of evidence suggesting a role for GCs in modulating aspects of mate choice by females. For example, when ecological challenges are introduced in a mating context–which often increases the costs of mate acquisition–females in many species adjust their behavior in ways that minimize these costs, often resulting in weakened or absent species-typical preferences and more permissive mate choices (Dill et al., 1999; Hingle et al., 2001; Willis et al., 2012). Because this topic of how challenges and "stressors" in a phenomenological sense (i.e., context- and state-dependent mate choice) modulate mating preferences have been reviewed elsewhere (Cotton et al., 2006; Hunt et al., 2005; Jennions and Petrie, 1997), and because such designations may not always be associated with an endocrine response (reviewed in Romero, 2004), we restrict our review here to the subset of studies that test for a GC link.

When we expand female reproductive behavior beyond merely mate choice, there is evidence in a variety of vertebrates that stress, experiential and hormonal, is an ecologically important aspect of mating behavior. Mate searching and sampling, for example, are associated with some or all of the following: (1) increased locomotor activity and associated search costs (Baugh and Ryan, 2010a; Gall et al., 2019; Rinktamäki et al., 1995), which have been linked to weakened female preferences (Forsgren 1992; Milinski and Bakker, 1992) and elevated GCs (Breuner et al., 1998; Sandi et al., 1996); (2) increased conspicuousness to predators and fear responses, which can weaken female preferences (Baugh and Ryan, 2010b; Dill et al., 1999; Forsgren, 1992; Willis et al., 2012), and elevate GCs (Cockrem and Silverin, 2002; Vitousek et al., 2014; reviewed in Clinchy et al., 2013); and (3) reduced food consumption and caloric deficits which can weaken female preferences (Hingle et al., 2001; Houston et al., 2007; Jönsson, 1997), and have also been linked to elevated baseline GCs (Kriengwatana et al., 2014). These environmental stressors are known to influence variation in mate sampling and preferences in females, though there is little empirical work directly connecting (experimentally or correlatively) the GC status of females to their mate choice behavior.

Another reason to explore the relationship between GCs and female mate choice behavior involves the physiological linkages between the components of metabolic pathways involved in the HPA/I axis and the behaviors that support reproductive efforts in females (Wingfield and Sapolsky, 2003). For example, sexual reproduction is among the most energetically demanding chapters in the life histories of female vertebrates, wherein energy expenditures during the breeding season can be an order of magnitude higher in females than males (Ryan et al., 1983). As a consequence, peak reproductive readiness in females is often associated with naturally elevated GC levels. In anurans GCs decline precipitously and rapidly following oviposition (Bastien et al., 2018; Baugh et al., 2018; Gall et al., 2019), and a similar pattern is present in mammals where a surge in GCs during parturition is essential for the initiation and maintenance of labor (Thorburn et al., 1977). It is therefore seemingly paradoxical that elevated GCs are often associated

with reduced investment in current reproductive efforts (Angelier et al., 2009; Horton and Holberton, 2009; Kitaysky et al., 2001; Schoenle et al., 2017) and even inducing reproductive failure at surpraphysiological levels (O'Connor et al., 2009; Silverin, 1986). Do elevated GCs abolish, dampen or have no effect on female proceptivity as would be predicted by the idea that the HPA/I axis is antagonistic to the HPG axis (Bókony et al., 2009; Husak and Moore, 2008; Toufexis et al., 2014; but see Wingfield and Sapolsky, 2003)? Perhaps more intriguing, is there any empirical support for the idea that GCs modulate the expression of intraspecific preferences in females and thus the strength of sexual selection on male traits?

One challenge in this regard is that for many vertebrates, such as songbirds and mammals, the energetic demands and role of GCs are dominated by pre- and post-copulatory life history chapters, such as migration, molt, nesting, incubation and provisioning (Bonier et al., 2007; Wingfield, 2003; Wingfield et al., 2004). Because these activities can be divorced from mate selection they complicate the study of GC-mediated mate choice *per se*. Hence, an evaluation of GCs and female mate choice in organisms with simpler breeding life histories and tractable mate choice assays may be particularly useful. Anuran amphibians offer some important advantages in this regard. Generally, many female anurans do not migrate or undergo a seasonal molt prior to mate choice, do not build nests, and do not rear and provision altricial offspring (Wells, 2007). A female's willingness to copulate (receptivity), or the more common measure of willingness to select a mate (proceptivity) as well as mate discrimination can be measured precisely using phonotaxis tests which can experimentally isolate single male display traits (Gerhardt, 1995). Moreover, such female choice behaviors are highly replicable across years (Ryan, 2011; Ryan et al., 2019), do not require gonadal hormone implants or even gonads in some cases (Diakow et al., 1978), allow for unconfounded repeated measures, and thus provide the opportunity to characterize female preferences at the individual level (Baugh and Ryan, 2009; Gerhardt et al., 2000; Ryan et al., 2019).

Further, for studies focused on the activational roles played by GCs, we suggest that it is relevant to focus on both male signal traits and female preference traits that are dynamic in nature—traits whose expression can be modulated across time scales relevant for GC action (minutes to hours; Gasser et al., 2010; Sandi et al., 1997). For example, female preferences for dynamic male vocal traits (e.g., temporal features) are also dynamically expressed across brief time courses and can vary within- and among-females (Baugh et al., 2010c). Such dynamic decision making behavior is a measure of *choosiness* in females—in other words, how females actually execute their mate choice preferences in real time.

1.2.1. Glucocorticoids and female sexual proceptivity

Elevated GCs in breeding females might suggest a lack of sensitivity to HPA/I activity in the context of mate choice behavior. Indeed, a recent study in Cope's gray treefrogs (*Hyla chrysoscelis*) showed that what is presumably a potent stressor (capture, handing and cardiac puncture for blood sampling) did not suppress female sexual proceptivity (positive phonotaxis towards the playback of male calls); in fact, 100% of females tested within minutes of this standardized stressor exhibited robust and species-typical phonotaxis towards male calls and subsequently resumed amplexus with mates and oviposited (Gall et al., 2019). Their approach latencies, however, were approximately twice as long as control females, which is interpreted as an indicator of dampened sexual motivation and has been shown to be state-dependent (Baugh and Ryan, 2009, 2017). Consistent with this idea, unmanipulated females that had naturally higher GC concentrations also exhibited significantly slower approaches (Gall et al., 2019). This same dampening effect of elevated GCs was observed in a study of mate choice in female túngara frogs (*Physalaemsus (=Engystomops) pustulosus*), which also demonstrated slower approaches for females with naturally elevated GCs (Fig. 1). In contrast to these findings, Davis and Leary (2015) found no effect of circulating or experimentally elevated GCs on female approach latencies in green treefrogs.

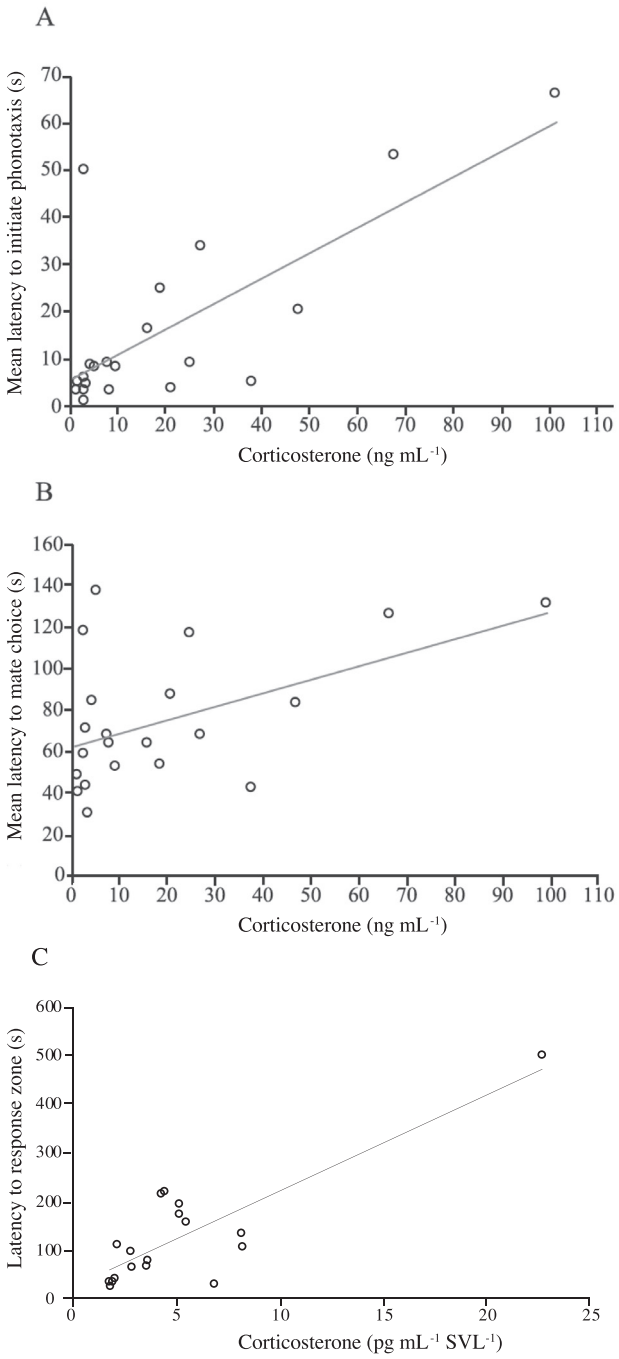

Fig. 1. In female *H. chrysoscelis* there is a positive correlation between plasma GCs and the latency to initiate phonotaxis *(a)* as well as to complete a mate choice *(b)* (from Gall et al., 2019). Similarly, in female *P. pustulosus* there is a positive correlation between water-borne GCs and the latency to complete mate choice *(c)* ($r = 0.76$, $p < 0.001$, $n = 18$). Untransformed hormone concentrations are depicted and statistical analyses were performed on $\log_{10}$ transformed values, which did not change the significance of the effects. Likewise, correcting for correlated levels of estradiol and omitting a statistical outlier (in *b)* did not change the significance of the effects.

It is interesting to note that the positive correlations observed in *P. pustulosus* frogs and *H. chrysoscelis* appear to be largely driven by females with the highest GC concentrations exhibiting the longest latencies (Fig. 1). This might suggest a non-linearity in GC-motivation

relationships and help explain the lack of such an effect in the green treefrog study which lacked outlier phenotypes. Together, these anuran proceptivity studies are consistent with the broader literature on this topic showing that, aside from supraphysiological levels (O'Connor et al., 2009), elevated GCs generally do not inhibit sexual proceptivity and underscores the idea that extreme endocrine phenotypes might be particularly informative in terms of hormone-behavior relationships (Williams, 2008). It is important to note that reproductively ready female anurans have a brief time horizon for securing a male mate, after which point they oviposit and sacrifice their annual fitness (Bastien et al., 2018; Gall et al., 2019; Lynch et al., 2005). Hence, the sensory-motor systems underlying female mate choice behavior in anurans may be buffered against the impact of seasonally elevated GCs (reviewed in Wingfield and Sapolsky, 2003) to ensure mate acquisition and fertilization of a maturing clutch.

Similar to work in frogs, a recent study in common lizards (*Zootoca vivipara*) demonstrated that females that were administered exogenous GCs were less likely to mate, exhibited more aggression towards potential male partners and displayed less proceptive behavior toward males (tongue extrusion and approaches) (Romero-Diaz et al., 2019). Lizard and anuran studies thus indicate a dampening effect of elevated GCs on female proceptivity, though they differ in that the lizard study suggests exogenous GCs can lead to decreased copulation, not merely slower approaches.

Work on anurans highlight the fact that hormone-behavior relationships are rarely simple and one-dimensional. For example, though individual female treefrogs with lower GC levels during reproductive readiness (pre-oviposition state) expressed higher sexual proceptivity (faster approaches), one day later (post-oviposition state) all females exhibited substantially lower GC levels and yet were unanimously non-proceptive (Gall et al., 2019). This suggests that GCs modulate sexual proceptivity in a state-dependent manner (i.e., high GCs appear to dampen sexual motivation only during peak sexual readiness), which in this case coincides with peak gonadal steroid concentrations immediately prior to oviposition (Bastien et al., 2018; Gall et al., 2019). Therefore, as with male signalers and GCs, it is important that future studies dissociate the contributions of other endocrine systems (Diakow et al., 1978), especially gonadal steroids which can be positively correlated with GCs. Additionally, the modulating effect of GCs on behavior could be non-linear (Hau and Goymann, 2015). For example, moderate GC declines may elevate proceptivity but large declines may abolish it. These hormonal dynamics are unstudied in the context of mate choice.

1.2.2. Glucocorticoids and mate choice preferences in females

To our knowledge there are only a handful of studies that have assessed, correlatively or experimentally, the effects of GCs on female mating preferences. There is a deeper body of literature, however, on the HPA axis and decision making in general, particularly in humans (reviewed in Starcke and Brand, 2012). While the findings from these human studies vary in terms of whether stress confers advantages or disadvantages in human decision making performance, there appears to be a common thread indicating that decision making under experiential stressors with a GC correlate often leads subjects to make suboptimal decisions, typically characterized by an overexploitation of current options and more haphazard decision making compared to control subjects (Keinan, 1987; Lenow et al., 2017). Interestingly, males and females can differ in how decision making tradeoffs are resolved (van den Bos et al., 2009), with some evidence that stress can induce disassortative mating preferences in women (Lass-Hennemann et al., 2010). These results suggest the importance of GCs in the cognitive processes of decision making and we think such approaches could be fruitfully imported in animal studies of decision making in a mate choice context.

There have been a few correlative studies testing the effect of how natural levels of GCs may modulate mate selection. For example, female marine iguanas (*Amblyrhynchus cristatus*) with naturally higher plasma GCs in response to a 30-min restraint stressor assessed fewer displaying males, suggesting that a more reactive HPA axis may also be interfering with mate sampling and decision making (Vitousek and Romero, 2013). Similarly, a few recent studies in anurans measured naturally varying levels of GCs in female gray treefrogs (*H. versicolor, H. chrysoscelis*) during mate choice (Bastien et al.. 2018; Baugh et al., 2019; Gall et al., 2019). In contrast to the marine iguanas, these studies showed that the robust species-typical preferences for attractive male advertisement signals (longer call durations; Gerhardt and Huber, 2002) were intact in females with naturally elevated GCs and uncorrelated with circulating or excreted GCs. Moreover, GC concentrations were unassociated with the duration of mate sampling following dynamic alteration of male call playback (a proxy for the thoroughness of sampling effort) (Bastien et al., 2018). It appears that naturally varying levels of progesterone are a better predictor of dynamic mate sampling in female *H. versicolor*. Likewise, studies on *H. chrysoscelis* indicate that natural plasma GC concentrations are not only unassociated with auditory behavior but also not linked with the processing of male call frequencies in the peripheral auditory system. That too appears to be modulated by a gonadal steroid, estradiol in this case (Gall et al., 2019; Baugh et al., 2019).

To our knowledge, there are only three studies to date that have measured female mating proceptivity and preferences following experimental manipulation of GCs. In the first study, oestrus female mice were administered exogenous corticosterone and subsequently tested for male odor proceptivity using a y-maze olfactometer (Kavaliers and Ossenkopp, 2001). Whereas control females exhibited robust interest in male odors compared to blanks, GC-injected females showed a marked dose-related decrease in this behavior. Specifically, females at an intermediate dose (5 mg kg^{-1}) exhibited no proceptivity, while females at a lower and higher GC dosage had intact but significantly attenuated proceptivity compared to controls. These effects were present rapidly after GC administration (10 min) and absent shortly thereafter (60 min). The investigators further established that the GC-facilitated decline in sexual proceptivity is likely mediated by NMDA and GABA receptor mechanisms. These results suggest an inhibitory role for GCs on female sexual motivation and underscore the transient nature of this modulatory effect. Though this mouse study did not test for intraspecific preferences, we assume the ablation of a preference for male odors compared to blanks would also translate into a lack of preference among different male odors, though this remains to be tested. In the second study, exogenous corticosterone was administered to reproductively ready female green treefrogs (*H. cinerea*) at three different dosages and tested in a phonotaxis chamber to assess preferences for calls that varied in rate (Davis and Leary, 2015). Results revealed that females receiving the highest dosages exhibited a reduced preference for high call rates compared to control groups and lower dosage treatment groups. This is a surprising behavioral effect given that the preference for higher call rates in this species and many other acoustically communicating species is robustly present under normal conditions (Gerhardt, 1987; Gerhardt and Huber, 2002). Reduced female choosiness under conditions of elevated GCs may represent a 'making the best of a bad situation' strategy. For example, elevated GCs could favor reduced mate sampling because GCs negatively impact attentional-cognitive processes that lead to haphazard and thrifty decision making (Keinan, 1987; Lenow et al., 2017). This could be adaptive if GCs reduce the physiological time horizon for viable gametes that would otherwise go unfertilized (Bastien et al., 2018). Experimental manipulations are needed in this area. The third study found that female lizards administered exogenous corticosterone did not differ from control females in their mate choice preferences (familiar versus unfamiliar males), despite exhibiting reduced sexual proceptivity (Romero-Diaz et al., 2019). Collectively, these studies emphasize the importance of distinguishing GC effects on female sexual receptivity versus mate choice preferences, which may be uncoupled

mechanistically.

1.2.3. Summary and future research on GCs and female mate choice

The paucity of studies on this topic makes it clear that there is a need for broader and deeper future research efforts. Taxonomically, we currently have very shallow coverage, with no experimental tests of GCs on female choice in birds or fishes. This is surprising given the breadth of studies that independently evaluate GCs or sexual behavior in songbirds. One methodological challenge in this regard is the ability to assay songbird proceptivity and preference under physiologically natural conditions (e.g., without the use of hormone implants; Nagle et al., 1993), and yet manipulate the HPA axis without the added stressor of handling. Methods to non-invasively introduce moderate, rapid and transient elevations in GCs, as has been performed in other contexts in songbirds (Breuner et al., 1998) and frogs (Hu et al., 2008), would permit experimental studies that eliminate unwanted secondary stressors and may aid in controlling for other hormone fluctuations that are correlated with GCs over longer timeframes (e.g., gonadal steroids). Similarly, methods to non-invasively measure the resulting endocrine status of females could allow researchers to repeatedly sample female proceptivity and mate choice across relevant time courses and a range of contexts. This would permit, for example, the measurement of individual female preference functions (Gerhardt et al., 2000) and how they may be modulated by circulating GCs, including how GCs might impact the consistency (within-individual variance) of such female preference functions, not merely mean effects. Such non-invasive measurement methods are currently validated and available for aquatic organisms such as amphibians (Bastien et al., 2018; Baugh et al., 2018; Gabor et al., 2013; Narayan, 2013) and fishes (reviewed in Fischer et al., 2014; Scott and Ellis, 2007).

These tools could be further combined with upstream manipulations of the HPA axis, such as the use of secretagogues like ACTH and CRH, or the experimental manipulation of negative feedback via synthetic GCs such as dexamethasone—methods often used in the study of stress in songbirds and other taxa in non-mate choice contexts (Baugh et al., 2017b,c; Romero, 2004). Likewise, understanding the links between GC receptor expression and HPA reactivity (Baugh et al., 2017b,c; de Kloet, 1991; Dickens et al., 2009) and its influence on mate choice would be highly beneficial. For instance, despite decades of research on the neural basis for the production and perception of song in oscines, and despite the widespread distribution of GC receptors in brain regions that control these critical sexual signaling processes (Senft et al., 2016), little experimental effort has been focused on understanding how GCs modulate neural function and behavior in either sex. Measurements of binding globulins and their potential to buffer females from what otherwise might be strong inhibitory effects of GCs could be a fruitful avenue for future study, as would linkages between the HPA axis and other fast-acting neuromodulators such as serotonin which are known to influence female mate choice preferences (Zhang et al., 2013).

There is clearly a need to better characterize the temporal coupling of GCs and traits important in sexual selection. For example, many of the female sexual behavior-GC studies described earlier evaluated acute stressors and generally showed a lack of any robust dampening of sexual receptivity despite impacts on female preferences. Activationally, we should expect a time lag (e.g., hours or days) for behavioral consequences of elevated GCs given the genomic implications of GC action on classical cytosolic receptor systems. However, the limited evidence points to quite rapid effects, potentially mediated through non-genomic membrane-bound receptor systems (Orchinik and McEwen, 1994), including rapid and transitory effects of elevated GCs on receptivity in female mice (< 60 min; Kavaliers and Ossenkopp, 2001), female green treefrogs (< 100 min; Davis and Leary, 2015), and male salamanders (< 8 min; Moore and Orchinik, 1991).

Lastly, we think there is immense scope for organizational studies of GCs on the development of female sexual behavior. There is increasing empirical support that exposure to stress and GCs during early life can have profound and enduring behavioral effects in adults (Welberg and Seckl, 2001; Woodgate et al., 2010; reviewed in Monaghan and Haussmann, 2015). In theory, these lasting behavioral effects could arise due to associated changes to brain regions involved in the endocrine regulation of the HPA axis function (Matthews et al., 2004; Meaney et al., 2007; Spencer et al., 2009) and sexual behavior (Hu et al., 2008; Marasco et al., 2016; Schmidt et al., 2013). Because GC-behavior relationships, especially for higher level behavioral traits (complex behavior suites), might be principally non-activational in nature (Koolhaas et al., 2010), experimental tests of HPA/I programming during early life and the consequences it has for sexually selected traits in adults could provide valuable insights.

2. Conclusions and implication for GCs and sexual selection

Given the interest in understanding how variation in the endocrine stress response evolves, and the agents of selection that potentially shape it, it is imperative that we understand the role of GCs in sexual selection. The study of GCs and sexual selection remains in its infancy, particularly for intersexual selection. As with the study of sexual selection at large, there are far more studies focused on the conspicuous courtship signals of males than the mate choice behaviors of females. Nonetheless, some general patterns do emerge. First, when we selectively examine systems in which male courtship traits are dynamically expressed (e.g., temporal properties of vocalizations and electric signals) and in which GCs have been experimentally manipulated, there is a trend for elevated GCs to diminish the attractiveness of these signals. For example, across all studies, female preference tests were performed in 7 studies and all showed female preferences for males with low GCs (Table 1), suggesting that mate choice by females may favor males with low GC levels (see also Moore et al., 2016). However, whether this translates into selection for low stress reactivity is a very different question. For example, low stress reactivity is unlikely to represent the only successful strategy, particularly when it is expected to decrease survival because of its link to increased risk-taking behavior (Baugh et al., 2017b), which would be especially costly for signalers apt to produce conspicuous courtship displays in the presence of stressors such as predation risk (Bernal et al., 2007; Dapper et al., 2011; Leary et al., 2006; Leary and Crocker-Buta, 2018). We thus predict that sexual selection favors diverse hormonal phenotypes and that these hormonal phenotypes are, in many cases, represented by males with diverse reproductive strategies (i.e., alternative mating tactics).

On the female receiver side, the small set of studies suggest a moderate dampening effect of elevated GCs on female sexual proceptivity–even very high plasma GCs and potent stressors are often ineffective at abolishing sexual proceptivity. Likewise, emerging evidence suggests that elevated GCs may also attenuate species typical preferences for attractive male traits. Whether there are general patterns across species in the sensitivity of the sexes to GCs in sexual behavior is unknown. However, given the time-constrained fecundity of females compared to males in many vertebrates, and the often elevated levels of GCs at peak sexual readiness, we might assume that female proceptivity is less sensitive to GC elevations (Wingfield and Sapolsky, 2003). These ideas will require further study, preferably in a system where the behavioral task is the same for both sexes (e.g., Baugh and Ryan, 2017) and will expand our understanding how GCs potentially alter the strength of sexual selection on male traits.

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Appendix A. Supplementary data

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