Neuroscience and Biobehavioral Reviews 151 (2023) 105241

Contents lists available at ScienceDirect

Neuroscience and Biobehavioral Reviews

journal homepage: www.elsevier.com/locate/neubiorev

Coping styles vary with species' sociality and life history: A systematic review and meta-regression analysis

Renée A. Duckworth [a,*], Kathryn C. Chenard [a], Lexis Meza [a], Maria Carolina Beiriz [a,b]

[a] Department of Ecology and Evolutionary Biology, University of Arizona, Tucson, AZ 85721, USA
[b] Department of Ecology and Natural Resources, Universidade Federal do Ceará, Fortaleza, CE 60440-900, Brazil

ARTICLE INFO

Keywords:
Personality
HPA axis
Stress response
Glucocorticoid
Aggression
Boldness
Anxiety
Fear

ABSTRACT

Despite a long history of animal studies investigating coping styles, the causal connections between behavior and stress physiology remain unclear. Consistency across taxa in effect sizes would support the idea of a direct causal link maintained by either functional or developmental dependencies. Alternatively, lack of consistency would suggest coping styles are evolutionarily labile. Here, we investigated correlations between personality traits and baseline and stress-induced glucocorticoid levels using a systematic review and meta-analysis. Most personality traits did not consistently vary with either baseline or stress-induced glucocorticoids. Only aggression and sociability showed a consistent negative correlation with baseline glucocorticoids. We found that life history variation affected the relationship between stress-induced glucocorticoid levels and personality traits, especially anxiety and aggression. The relationship between anxiety and baseline glucocorticoids depended on species' sociality with solitary species showing more positive effect sizes. Thus, integration between behavioral and physiological traits depends on species' sociality and life history and suggests high evolutionary lability of coping styles.

1. Introduction

It has long been recognized that there are consistent differences among individuals in how they cope with stress, and studies have identified repeated patterns of correlated behavioral and physiological responses that vary along a continuum of proactive and reactive coping styles (Cockrem, 2007; Koolhaas et al., 1999). In the classic descriptions, proactive individuals take more risks, are bolder, more aggressive and have lower physiological stress reactivity, whereas reactive individuals take fewer risks, are less bold and aggressive and have higher physiological stress responses (Ebner and Singewald, 2017; Koolhaas et al., 1999; Sih et al., 2004; Steimer and Driscoll, 2003). These axes were initially defined in studies of laboratory rodents and the original axes of behavioral variation and stress reactivity were verified in these taxa via selection for high and low aggression lines (Benus et al., 1991; de Boer et al., 2017). In these studies, researchers found that selective breeding for high and low attack latencies produced lines that not only differed in their aggressiveness, but that also differed in both baseline and stress-induced glucocorticoid levels (Korte et al., 1992; Veenema et al., 2003). From these foundational studies, the concept of coping styles has been refined over the years as researchers have realized that the type and magnitude of a behavioral response may vary independently of one another (Koolhaas et al., 2007a, 2007b). In more recent years, researchers have focused on trying to understand the links between any consistent differences in behavior (referred to as personality traits here) and variation in glucocorticoid levels and have also included personality traits such as activity, exploration and sociability in their definitions of proactive and reactive phenotypes (e.g. Santicchia et al., 2022). Given the diversity of behaviors that researchers now include in assessments of individual variation in coping style, in this review, we take a broad approach and, instead of defining coping styles by specific behavioral traits, we focus on trying to understand which behavioral traits are consistently linked to physiological stress response across taxa.

The concept of coping styles is now widely used in studies of animal personality (Grace and Anderson, 2014; Kern et al., 2016; Martins et al., 2007; Overli et al., 2007; Zidar et al., 2017), yet the mechanisms linking consistent differences in behavior to differences in glucocorticoid variation remain unclear (Carere et al., 2010). There are three possible scenarios: 1) behavioral variation causes variation in stress physiology, 2) variation in stress physiology causes behavioral variation, or 3) the two are not causally linked but both are organized early in development and are often correlated (Carere et al., 2010). Under the first two, a

* Corresponding author.
E-mail address: rad3@arizona.edu (R.A. Duckworth).

https://doi.org/10.1016/j.neubiorev.2023.105241
Received 5 December 2022; Received in revised form 15 May 2023; Accepted 17 May 2023
Available online 20 May 2023

direct causal link should lead to more consistent patterns in effect size across species. While under the third scenario, the relationship between glucocorticoid and behavioral variation may be more evolutionarily labile.

Consistent differences in behavior cause animals to perceive and interact with their environments differently (Bergmuller and Taborsky, 2010; Duckworth, 2006; Stamps and Groothuis, 2010). As such, behavioral differences may be a cause rather than a consequence of differences in stress physiology (Carere et al., 2010; Koolhaas et al., 2010), especially for behavioral traits that enable individuals to construct a less stressful environment. For example, more aggressive individuals are expected to exert more control over their environment [1]. Similarly, bolder, less fearful individuals are less likely to be alarmed easily by novel stimuli and this may diminish the likelihood that they will show an elevated reaction to stressors. Under these scenarios, consistent differences in behavior may be determined early in life, but the links between behavior and stress physiology are not formed until later in life (Duckworth et al., 2018).

Alternatively, it is possible that personality variation and physiological stress reactivity are both organized early in development (Besson et al., 2016; Duckworth, 2015; Fish et al., 2004). A perturbed developmental environment can increase prenatal offspring glucocorticoid exposure causing a permanent increase in activity of the hypothalamic-pituitary-adrenal (HPA) axis (Seckl and Meaney, 2004; Weaver et al., 2004). However, how and whether HPA axis programming causes variation in personality traits is unclear (Groothuis and Schwabl, 2008). It could be that the physiological stress response and personality traits are influenced simultaneously, but separately, by stressors during development (Glover et al., 2010). Developmental stressors have been shown to alter the structure and function of the limbic system (Weinstock, 2008), the area of the brain most frequently linked to the types of personality traits, like fear and aggression, that are commonly associated with coping styles (Adelstein et al., 2011; Adrian-Ventura et al., 2019; de Boer et al., 2017; Van Schuerbeek et al., 2011). Given that this is also the site of the hypothalamus and hippocampus, which are key structures in HPA axis programming (Bale, 2015; Charil et al., 2010), it makes sense that developmental stress could simultaneously impact stress physiology and personality traits (Duckworth et al., 2018). However, the extent that HPA axis programming itself directly causes consistent individual variation in behavioral traits is unknown, although direct effects have been suggested for studies of developmental influences on aggression (Ahmed et al., 2014; Aubin-Horth et al., 2012; Walker et al., 2018) and anxiety (de Kloet et al., 2004; Welberg and Seckl, 2001).

Which of the above causal mechanisms best explains the links between behavioral traits and stress physiology has important implications for our understanding of how variation in these links might evolve. It could be that they reflect universal functional, selective, or developmental constraints that lock species into fixed patterns of covariation (Arnold, 1994). For example, under the first hypothesis, what we call "behavioral control" (Table 1), behavioral variation causes variation in glucocorticoid levels, and so the directionality of the link should be highly consistent across taxa assuming that the function of the behavior is consistent. This assumption is most clearly met for aggression because more aggressive individuals can often exert more control over their environment [1]. In social species, higher aggression can enable control of the social environment through either exclusion of rivals or establishment of a stable dominance hierarchy in a group (Sapolsky, 2004), and, in nonsocial species, it enables control of environmental variation if more aggressive individuals acquire more resources or higher quality territories (Duckworth, 2006; Stamps and Krishnan, 1997; Watson and Miller, 1971). Indeed, the widely held prediction for coping styles is that more aggressive individuals will have lower glucocorticoid levels (Koolhaas et al., 1999). However, variation in species' social structure could impact the strength of this relationship if aggression's role in exerting control of the environment is stronger (or possibly even weaker) in social versus non-social species (Creel et al., 2013). Alternatively, if the function of aggression is not consistently related to individual's ability to exert control over their environment, then we may observe no consistent relationship across species between glucocorticoid levels and variation in aggression.

In cases where both behavior and stress physiology are organized early in development, the evolutionary lability of coping styles depends on the causal link between HPA axis programming and behavioral variation. If variation in personality traits is directly caused by variation in HPA axis programming, then links between behavior and stress physiology might be universal across taxa. For this hypothesis, which we refer to as 'physiological control', we would expect to observe consistency in both the magnitude and direction of correlations between personality traits and stress reactivity across taxa (Table 1). It should be noted that, while such consistency in the relationship between stress reactivity and behavioral traits supports the idea of physiological control, there is still the possibility that other factors play a role in producing this link. For example, an individual's early experiences may create feedbacks between behavioral and glucocorticoid responses that channel them into mutually reinforcing co-expression (Duckworth et al., 2018). However, we think that the latter explanation would produce less consistency in correlations among taxa than the former.

Finally, it may be that, even though glucocorticoid programming is evolutionarily ancient and occurs in a similar way across taxa (Thayer et al., 2018; e.g. higher early developmental stress exposure leads consistently to higher stress reactivity of offspring later in life), how developmental stress influences personality traits may depend on species' social structure or life history. In this case, which we refer to as the 'evolutionary lability' hypothesis, there would be no consistent causal link between HPA axis programming and personality traits, and their pattern of covariation should instead be highly variable across taxa. If supported, we expect that both social structure and life history variation may play a role in determining the direction and strength of links between personality variation and physiological measures of HPA function (Table 1).

Both baseline and stress-induced glucocorticoid levels and risk-taking behavior (e.g. boldness and fearfulness, referred to here as anxiety-related traits) vary depending on where species are on the slow-

Table 1
Summary of hypotheses and predictions for why effect sizes may vary across species.

Hypotheses	Causal links	Consistent effect sizes across taxa?	Key behavioral traits	Most important covariates			
				Dev. mode	*Soc. structure*	*Life history*	*Subgroups*
Behavioral control	behavioral types construct their environment and this influences stress physiology	Yes	Aggression		X		
Physiological control	stress-induced physiology determines behavior	Yes	Anxiety	X			
Evolutionarily labile	behavioral variation and stress physiology evolve independently - no universal causal links	No	All personality traits		X	X	
Non-standard methods across studies	Variable results due to methodological issues	No	All personality traits				X

fast life history continuum (Ghalambor and Martin, 2001; Hau et al., 2010; LaManna and Martin, 2016; Møller and Garamszegi, 2012; Vitousek et al., 2019). Slow species are longer-lived, have slower growth and invest more in parental care compared to fast species; generally, slow species prioritize adult survival over current reproduction and are more risk-averse (Badyaev and Ghalambor, 2001; Ricklefs and Wikelski, 2002). Numerous studies have shown that glucocorticoid levels across species vary in relation to species' life history. For example, a study comparing avian taxa found that stress-induced glucocorticoid levels were higher in species with higher adult survival rates (Hau et al., 2010); presumably, this enhances survival by facilitating physiological responses that reduce immediate risks. Moreover, in a large comparative study of glucocorticoid variation across vertebrates, Vitousek et al. (2019) found that species with more lifetime reproductive attempts (species on the faster end of the continuum) had higher stress-induced glucocorticoid levels during breeding. There is also abundant evidence that life history variation influences variation in risk-taking behavior. In a comparative study investigating individual variation in boldness to a perceived predator in 133 species of birds, Møller and Garamszegi (2012) found that faster species show more variance in risk-taking behavior.

Finally, whether species have altricial or precocial offspring is another life history axis that may influence the link between stress reactivity and personality variation. The timing of development of different parts of the brain relative to birth is species-specific (Clancy et al., 2007; Dobbing and Sands, 1979). In precocial species, the period of maximal brain growth and a large proportion of neuroendocrine development takes place before birth or hatching. In contrast, in altricial species, the period of rapid growth and brain development mostly occur in the early postnatal period (Charvet and Striedter, 2011). This difference means that, in altricial species, the relative timing of the impact of stress on development of various neuroendocrine systems may be less coordinated compared to precocial species (Lupien et al., 2009), ultimately decreasing the covariation between HPA axis programming and determination of personality traits. As such, consistent links between personality traits and HPA function may be more prevalent in precocial compared to altricial species.

In the last two decades, there has been a surge of interest in testing for links between behavioral variation and glucocorticoid levels across a diversity of wild and non-model organisms. These studies have produced mixed results with some finding no links and others finding both positive and negative patterns of covariation (Westrick et al., 2019). These studies provide a unique opportunity to assess whether there is evidence for these various hypotheses and to determine whether variation in effect size across studies is due to the evolutionary lability of the link between stress reactivity and personality traits or whether it reflects methodological issues or lack of standardization across studies (Table 1). To summarize existing evidence for links between glucocorticoid variation and personality traits and to examine potential correlates, we conducted a meta-analysis of studies that investigate individual variation in animal personality traits and their links to either baseline and/or stress-induced glucocorticoid levels. Variation in baseline and stress-induced glucocorticoid levels were considered separately because there is considerable evidence that these two aspects of HPA axis variation are shaped by distinct selection pressures and are regulated somewhat independently (Denver, 2009; Vitousek et al., 2019). Given the wide variety of definitions of coping styles found in the literature (Zidar et al., 2017) and that at least one of our hypotheses makes predictions about personality traits in general, we include studies that examine variation in multiple personality traits, including activity, aspects of anxiety (e.g., exploratory behavior [coded in our study as 'fear of the unknown'], neophobia and fear of predators; see below for detailed explanations of these categories), aggression and sociability. To test our hypotheses (Table 1), we also collected data on variation in species' sociality and life history traits as well as potentially confounding variables across studies.

2. Methods

2.1. Literature search

We performed a systematic literature search according to the Preferred Reporting Items for Systematic reviews and Meta-Analyses (PRISMA; Moher et al., 2009; Fig. 1). After completing a preliminary reading to determine a list of keywords, we conducted an online database search on titles, abstracts and key words, in the *Scopus* database on 30 March 2022, using the following key word combinations: (corti* OR glucocort* OR "stress react*" OR "stress respons*" OR HPA OR "hypothalamic–pituitary–adrenal axis" OR "heart rate") AND ("Open field" OR bold* OR shy OR docil* OR explor* OR aggres* OR "Coping style*" OR domina* OR fear* OR proactiv* OR reactiv* OR behavioral AND flexib* OR neophob* OR "Tonic immobility" OR "Novel object" OR "Novel arena" OR "Novel environment" OR vigilan* OR risk-prone OR risk-averse) AND NOT (human* OR child* OR infant* OR patient* OR women OR plant* OR insect*). Some of our search terms were very broad (e.g. "stress react*" and "stress respons*"), which allowed us to capture a greater number of relevant studies; however, this meant our initial results included many species outside our focal group of vertebrates. Adding terms to exclude particular taxonomic groups (e.g. insects, plant) resolved this issue.

This search yielded 1,919 articles (Fig. 1). Two authors (M.B. and L. M.) screened article abstracts using the inclusion and exclusion criteria outlined below. Other sources of articles came from reference lists of key review papers (McMahon et al., 2021; Koolhaas et al., 1999, Koolhaas et al., 2011, and Cockrem, 2007), as well as *Scopus* lists (forward search) of citing publications of these articles. After screening titles and abstracts, these other sources provided 132 additional papers. Excluding duplicates and initial screening based on the inclusion/exclusion criteria (see below for details), resulted in a total of 436 studies that were examined in their full text versions. Relevant data from 71 papers were extracted and included in the meta-analysis (Table 2).

From the collected papers, we extracted data on the magnitude and direction of the relationship between any of the behavioral variables and measures of baseline ($n = 45$), long-term ($n = 11$) or stress-induced ($n = 38$) corticosterone (see below for definitions). We used the program Comprehensive Meta-analysis (version 3.3.070; Borenstein, 2022) as well as standard formulas (Peterson and Brown, 2005) to calculate effect sizes (Fisher's Z). If results were provided in a nonstandard way or there was insufficient information, we obtained data from the authors or by using WebPlotDigitizer (Rohatgi, 2014) to extract raw data from figures to calculate correlation coefficients. When necessary, we changed the direction of the correlation so that higher values always indicated a more intense behavioral response. This was necessary for studies which coded behavior as a measure of boldness or exploratory behavior and for which we re-coded it as an anxiety-related behavior. Thus, if the original relationship between boldness and glucocorticoid levels was positive (indicating that bolder individuals had higher levels), we entered the coefficient as negative (indicating that less fearful individuals had higher levels).

2.2. Inclusion and exclusion criteria

Studies were included in the data set only if they fulfilled the following criteria: 1) subjects were non-human vertebrates that had not been bred for domestication or been selected for behavioral or physiological traits. Under this criterion, we did include model lab organisms because even though they are considered "domesticated" compared to their wild relatives, they have not explicitly been selected to lose fear of humans. Domesticated farm animals and pets were excluded, but zoo animals were included. We restricted our study to non-domesticated animals because our goal was to understand how correlations might evolve in populations that have not undergone specific anthropogenic selection on fear and anxiety traits. 2) Both stress response and

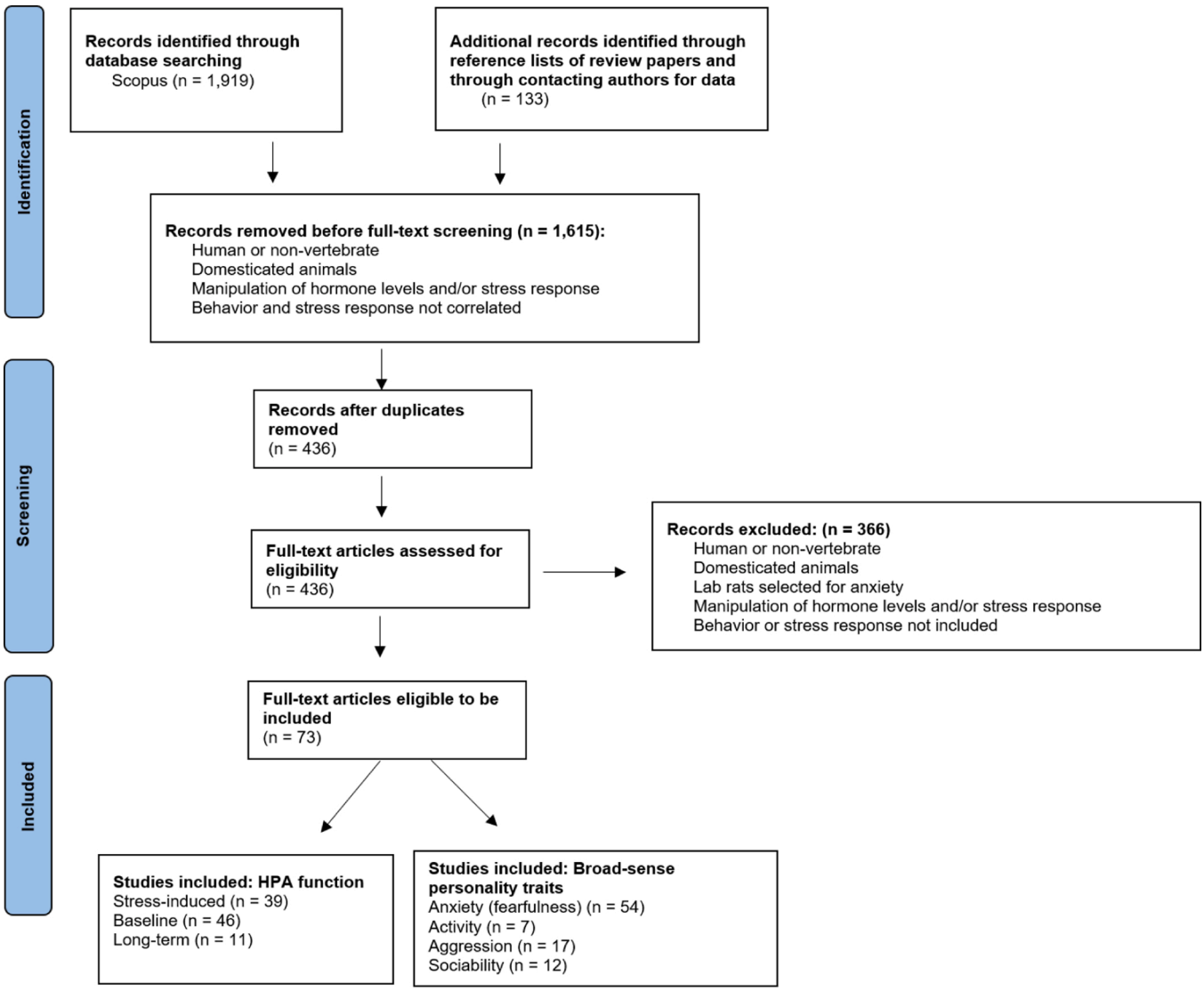

Fig. 1. Flow diagram based on recommendations of Preferred Reporting Items for Systematic Reviews (PRISMA).

behavioral variation were within the normal species range. This criterion meant that we excluded studies in which hormone levels were manipulated through injection or implants as well as studies which altered behavior or stress response through surgical or other means of manipulating the brain. 3) We only included studies in which the stress response and behavior were measured independently during the same life stage.

2.3. *Categorizing personality traits*

We categorized behavioral variables based on definitions outlined here, which largely follow recommendations by Réale et al. (2007) and Garamszegi et al. (2013). We coded anxiety-related traits using both 'broad-sense' and 'narrow-sense' categorizations where the former combines various measures of fearfulness into a single "anxiety" category and the latter distinguishes between neophobia, fear of predators, and fear of the unknown. Many tests of exploratory behavior fell into this latter category. Thus, tests that measured individual responses to novel objects, a novel environment, or a simulated or real predator as well as open field tests were all combined as expressions of anxiety in the broad-sense because they are all behaviors in which individuals vary in their hesitancy to interact with various aspects of their environment. Behaviors were categorized in the narrow-sense as neophobia if they were measured as exploration of a novel object, as 'fear of a predator' if they were assessed in response to a known predatory threat, and 'fear of the unknown' if they were assessed as an individual's willingness (or hesitancy) to explore a novel environment which represents an unknown level of risk. We excluded all studies that measured behavior in response to a food reward in the narrow-sense, but not the broad-sense categories. Fear of the unknown included behaviors that were measured as an animal's movement into or through a novel environment where the potential threats are not obvious. Therefore, this category included measures that other researchers often referred to as "exploratory behavior" or "boldness." It also included many of the behaviors measured in open field tests such as the time it took to move from a familiar or closed environment into a novel environment. These studies typically almost always capture a balance between variation in individual neophilia and fear of an unknown environment. We are assuming here that, even though some individuals/species may be attracted to novelty (have a high curiosity), that an unknown and previously unexplored environment is always inherently risky in that the individual doesn't have full knowledge of potential risks. We also included vigilance behavior in this category. "Fear of a predator" included studies that measured responses to specific visually observed predators, including humans (such as flight initiation distance studies for birds), as well as responses to chemical or auditory predator cues.

Table 2
Summary of studies included in the meta-analyses.

Study citation	Species	Class	Sex	Age	Sample	Source	Covariates?
Stress-induced							
Activity							
Arnold et al. (2016)	*Cyanistes caeruleus*	Aves	both	mixed	plasma	wildcaught	y
Aubin-Horth et al. (2012)	*Gasterosteus aculeatus*	Pisces	male	adult	water	wildcaught	y
Careau et al. (2014)	*Taeniopygia guttata*	Aves	female	adult	plasma	captive	y
Careau et al. (2020)	*Taeniopygia guttata*	Aves	male	adult	plasma	captive	y
Currylow et al. (2017)	*Astrochelys radiata*	Reptilia	both	adult	plasma	wild	n
Medina-Garcia et al. (2017)	*Melopsittacus undulatus*	Aves	male	mixed	plasma	captive	n
Aggression							
Aubin-Horth et al. (2012)	*Gasterosteus aculeatus*	Pisces	male	adult	water	wildcaught	y
DeCaluwe et al. (2013)	*Neofelis nebulosa*	Mammalia	male	adult	fecal	captive	n
Hanson et al. (2009)	*Micropterus dolomieu*	Pisces	male	adult	plasma	wild	y
Huang et al. (2020)	*Cardinalis cardinalis*	Aves	female	adult	fecal	wildcaught	n
Kralj-Fiser et al. (2010)	*Anser anser*	Aves	male	adult	fecal	wild	n
Anxiety							
Alfonso et al. (2019)	*Dicentrarchus labrax*	Pisces	both	adult	plasma	captive	n
Archard et al. (2012)	*Brachyrhaphis episcopi*	Pisces	both	adult	water	wildcaught	y
Arnold et al. (2016)	*Cyanistes caeruleus*	Aves	both	mixed	plasma	wildcaught	n
Atwell et al. (2012)	*Junco hyemalis*	Aves	both	adult	plasma	wildcaught	n
Aubin-Horth et al. (2012)	*Gasterosteus aculeatus*	Pisces	male	adult	water	wildcaught	y
Baugh et al. (2013)	*Parus major*	Aves	both	adult	plasma	wild	n
Baugh et al. (2017)	*Parus major*	Aves	both	adult	plasma	wildcaught	y
Beerling et al. (2011)	*Rattus norvegicus*	Mammalia	male	adult	plasma	captive	n
Brashears et al. (2020)	*Bothrochilus boa*	Reptilia	both	adult	plasma	captive	n
Bousquet et al. (2015)	*Anas platyrhynchos*	Aves	female	adult	plasma	captive	n
Careau et al. (2014)	*Taeniopygia guttata*	Aves	female	adult	plasma	captive	y
Cavigelli and McClintock (2003)	*Rattus norvegicus*	Mammalia	male	adult	plasma	captive	n
Cavigelli et al. (2007)	*Rattus norvegicus*	Mammalia	male	adult	plasma	captive	n
De la Roca et al. (2020)	*Dicologlossa cuneata*	Pisces	both	juvenile	plasma	captive	n
Fürtbauer et al. (2015)	*Gasterosteus aculeatus*	Pisces	female	adult	water	wildcaught	y
Herr et al. (2017)	*Agkistrodon piscivorus*	Reptilia	both	mixed	plasma	wild	n
Hoglund et al. (2020)	*Sparus aurata*	Pisces	both	juvenile	plasma	captive	n
Huang et al. (2020)	*Cardinalis cardinalis*	Aves	both	adult	fecal	wildcaught	n
Jacques-Hamilton et al. (2017)	*Malurus cyaneus*	Aves	both	adult	plasma	wildcaught	y
Keiling and Suski (2019)	*Micropterus salmonoides*	Pisces	both	adult	plasma	captive	y
Lendvai et al. (2011)	*Passer domesticus*	Aves	female	adult	plasma	wild	y
Mazza et al. (2019)	*Myodes glareolus*	Mammalia	both	adult	fecal	captive	y
Medina-Garcia et al. (2017)	*Melopsittacus undulatus*	Aves	male	mixed	plasma	captive	n
Mell et al. (2016)	*Zootoca vivipara*	Reptilia	male	adult	plasma	wildcaught	n
Moyers et al. (2018)	*Haemorhous mexicanus*	Aves	both	adult	plasma	wild	y
Qu et al. (2018)	*Ochotona curzoniae*	Mammalia	both	mixed	plasma	wildcaught	y
Rangassamy et al. (2016)	*Mus spicilegus*	Mammalia	both	adult	fecal	captive	n
Raoult et al. (2011)	*Argyosomus japonicus*	Pisces	both	juvenile	plasma	captive	n
Rosengren et al. (2017)	*Salmo salar*	Pisces	both	juvenile	plasma	captive	n
Seltmann et al. (2012)	*Somateria mollissima*	Aves	female	adult	plasma	wild	n
Thomson et al. (2016)	*Oncorhynchus mykiss*	Pisces	both	adult	plasma	captive	n
Tudorache et al. (2015)	*Danio rerio*	Pisces	both	juvenile	plasma	captive	n
Sociability							
Crino et al. (2017)	*Taeniopygia guttata*	Aves	female	adult	plasma	wildcaught	y
Kralj-Fišer et al. (2010)	*Anser anser*	Aves	male	adult	fecal	wild	n
Medina-Garcia et al. (2017)	*Melopsittacus undulatus*	Aves	male	mixed	plasma	captive	n
Ray and Sapolsky (1992)	*Papio anubis*	Mammalia	male	adult	plasma	wild	n
Long-term							
Aggression							
Takeshita et al. (2018)	*Macaca fuscata*	Mammalia	female	adult	fecal	wild	y
Westrick et al. (2019)	*Tamiasciurus hudsonicus*	Mammalia	both	adult	fecal	wild	y
Anxiety							
Bensky et al. (2017)	*Gasterosteus aculeatus*	Pisces	both	adult	water	wildcaught	n
Fanson et al. (2013)	*Elephas maximus*	Mammalia	both	adult	fecal	captive	n
Hare et al. (2014)	*Urocitellus richardsonii*	Mammalia	both	mixed	fecal	wildcaught	n
Inoue-Murayama et al. (2018)	*Callithrix jacchus*	Mammalia	both	adult	hair	captive	n
Laudenslager et al. (2011)	*Chlorocebus sabaeus*	Mammalia	female	adult	hair	captive	n
Montiglio et al. (2012)	*Tamias striatus*	Mammalia	both	adult	fecal	wildcaught	y
Westrick et al. (2019)	*Tamiasciurus hudsonicus*	Mammalia	both	adult	fecal	wild	y
Zohdy et al. (2017)	*Microcebus rufus*	Mammalia	both	adult	fecal	wild	y
Sociability							
Fanson et al. (2013)	*Elephas maximus*	Mammalia	both	adult	urine	captive	n
Soltis et al. (2003)	*Saimiri sciureus*	Mammalia	both	adult	urine	captive	n
Takeshita et al. (2018)	*Macaca fuscata*	Mammalia	female	adult	fecal	wild	y
Tkaczynski et al. (2019)	*Macaca sylvanus*	Mammalia	both	adult	fecal	wild	n
Baseline							
Activity							
Arnold et al. (2016)	*Cyanistes caeruleus*	Aves	both	mixed	plasma	wildcaught	y
Grand et al. (2012)	*Loxodonta africana*	Mammalia	female	adult	plasma	captive	n

(*continued on next page*)

Table 2 (*continued*)

Study citation	Species	Class	Sex	Age	Sample	Source	Covariates?
Medina-Garcia et al. (2017)	*Melopsittacus undulatus*	Aves	male	mixed	plasma	captive	n
Aggression							
Chang et al. (2012)	*Kryptolebias marmoratus*	Pisces	both	adult	water	captive	n
Potticary and Duckworth (2020)	*Sialia mexicana*	Aves	female	adult	plasma	wild	n
Esattore et al. (2020)	*Cervus elaphus*	Mammalia	male	adult	plasma	captive	n
Garamszegi et al. (2012)	*Ficedula albicollis*	Aves	male	adult	fecal	wild	y
Grand et al. (2012)	*Loxodonta africana*	Mammalia	female	adult	plasma	captive	n
Huang et al. (2020)	*Cardinalis cardinalis*	Aves	both	adult	fecal	wildcaught	n
Kralj-Fiser et al. (2010)	*Anser anser*	Aves	male	adult	fecal	wild	n
Li et al. (2020)	*Kryptolebias marmoratus*	Pisces	both	adult	water	captive	n
Pärn et al. (2008)	*Luscinia svecica*	Aves	female	adult	plasma	wild	n
Sands & Creel (2004)	*Canis lupus*	Mammalia	both	adult	fecal	wild	n
Schweitzer et al. (2017)	*Amatitlania siquia*	Pisces	both	adult	water	captive	n
Westergaard et al. (2003)	*Macaca mulatta*	Mammalia	female	juvenile	plasma	wild	y
Anxiety							
Arnold et al. (2016)	*Cyanistes caeruleus*	Aves	both	mixed	plasma	wildcaught	n
Atwell et al. (2012)	*Junco hyemalis*	Aves	both	adult	plasma	wildcaught	n
Baugh et al. (2013)	*Parus major*	Aves	both	adult	plasma	wild	n
Baugh et al. (2017)	*Parus major*	Aves	both	adult	plasma	wildcaught	n
Bousquet et al. (2015)	*Anas platyrhynchos*	Aves	female	adult	plasma	captive	n
Brashears et al. (2020)	*Bothrochilus boa*	Reptilia	both	adult	plasma	captive	n
Cavigelli and McClintock (2003)	*Rattus norvegicus*	Mammalia	male	adult	plasma	captive	n
Cavigelli et al. (2007)	*Rattus norvegicus*	Mammalia	male	adult	plasma	captive	n
Chang et al. (2012)	*Kryptolebias marmoratus*	Pisces	both	adult	water	captive	n
Chmura et al. (2016)	*Marmota flaviventris*	Mammalia	both	adult	fecal	wild	y
Clary et al. (2014)	*Urocitellus richardsonii*	Mammalia	female	adult	fecal	wild	y
Dosmann et al. (2015)	*Urocitellus beldingi*	Mammalia	both	adult	fecal	wild	y
Fürtbauer et al. (2015)	*Gasterosteus aculeatus*	Pisces	female	adult	water	wildcaught	y
Garamszegi et al. (2012)	*Ficedula albicollis*	Aves	male	adult	fecal	wild	y
Grand et al. (2012)	*Loxodonta africana*	Mammalia	female	adult	plasma	captive	n
Guenther et al. (2014)	*Cavia aperea*	Mammalia	both	mixed	plasma	captive	y
Herr et al. (2017)	*Agkistrodon piscivorus*	Reptilia	both	mixed	plasma	wild	n
Hoglund et al. (2020)	*Sparus aurata*	Pisces	both	juvenile	plasma	captive	n
Holding et al. (2020)	*Otospermophilus beecheyi*	Mammalia	both	adult	fecal	wild	y
Huang et al. (2020)	*Cardinalis cardinalis*	Aves	both	adult	fecal	wildcaught	n
Lavergne et al. (2019)	*Lepus americanus*	Mammalia	both	mixed	fecal	wildcaught	n
Lendvai et al. (2011)	*Passer domesticus*	Aves	female	adult	plasma	wild	y
Maren et al. (1993)	*Rattus norvegicus*	Mammalia	male	adult	plasma	captive	n
Keiling and Suski (2019)	*Micropterus salmonoides*	Pisces	both	adult	plasma	captive	y
Mazza et al. (2019)	*Myodes glareolus*	Mammalia	both	adult	fecal	captive	y
Medina-Garcia et al. (2017)	*Melopsittacus undulatus*	Aves	male	mixed	plasma	captive	n
Moyers etal (2018)	*Haemorhous mexicanus*	Aves	both	adult	plasma	wild	y
Muraco et al. (2013)	*Poecilia latipinna*	Pisces	male	adult	water	wildcaught	n
Pritchard et al. (2020)	*Vicugna vicugna*	Mammalia	female	adult	fecal	wild	y
Qu et al. (2018)	*Ochotona curzoniae*	Mammalia	both	mixed	plasma	wildcaught	y
Rangassamy et al. (2016)	*Mus spicilegus*	Mammalia	both	adult	fecal	captive	n
Seltmann et al. (2012)	*Somateria mollissima*	Mammalia	both	adult	fecal	wild	y
Tudorache et al. (2015)	*Danio rerio*	Pisces	both	juvenile	plasma	captive	n
Vobrubova et al. (2021)	*Rattus rattus*	Mammalia	male	adult	fecal	wildcaught	n
Sociability							
Crino et al. (2017)	*Taeniopygia guttata*	Aves	female	adult	plasma	wildcaught	y
Grand et al. (2012)	*Loxodonta africana*	Mammalia	female	adult	plasma	captive	n
Kralj-Fišer et al. (2010)	*Anser anser*	Aves	male	adult	fecal	wild	n
Medina-Garcia et al. (2017)	*Melopsittacus undulatus*	Aves	male	mixed	plasma	captive	n
Ray and Sapolsky (1992)	*Papio anubis*	Mammalia	male	adult	plasma	wild	n
Rimbach et al. (2022)	*Rhabdomys dilectus*	Mammalia	female	adult	plasma	captive	n
Rimbach et al. (2022)	*Rhabdomys pumilio*	Mammalia	female	adult	plasma	captive	n
Seltmann et al. (2012)	*Somateria mollissima*	Mammalia	both	adult	fecal	wild	y

By categorizing the behaviors this way, all of the narrow sense "anxiety" behaviors were expected to vary in the same direction as the broad sense category of anxiety. In other words, a more intense expression of "fear of the unknown" is also a more intense expression of anxiety; whereas, if we were to categorize these behaviors in the same way as other researchers (e.g. using exploratory or boldness), a more intense expression of behavior would correspond to a lower intensity of anxiety. Thus, this categorization allowed us to orient the relationships between the broad and narrow sense behavioral categories and measures of stress in the same way.

Other behaviors that we included in this study were "activity", which included assessment of the general intensity of movements in a familiar environment without any social or environmental challenge, and "sociability", which included the propensity for conspecifics to interact with one another in a nonaggressive way. Finally, we included "aggression" as any trait that depicted the intensity of an antagonistic behavior toward a conspecific (including a mirror image). We excluded studies that focused solely on dominance rank estimates without measures of aggression because dominance, while often related to aggression, is an outcome of behavioral interactions and not a personality trait per se (Duckworth, 2014). Moreover, some studies categorized fear responses as aggression if they involved focal individuals attacking a potential predator. We re-categorized these variables as a fear response and included them in our narrow sense "fear of a predator" category. We originally also searched for studies that assessed the relationship between behavioral flexibility and glucocorticoid response, however, we only found two studies that met our criteria and so we did not include this category.

2.4. Categorizing HPA function

We categorized measures of glucocorticoids as baseline, long-term, or stress-induced. Baseline measures included studies where researchers collected blood, fecal, urine or water (in the case of many fish studies) from animals that were either undisturbed or sampled within a short enough timeframe that handling would not yet have elevated glucocorticoid levels. Typically, baseline samples refer to a sample taken at a single point in time, but because some studies combined multiple samples from an individual over a long period (several weeks or months) or used tissues (e.g. hair) that integrate glucocorticoid levels over a long time period, we also included a category for long-term glucocorticoids. Finally, we categorized glucocorticoid measures as stress-induced if they were taken after an individual was subject to handling or other stressor and sampled at a time interval that was expected to reflect the peak glucocorticoid response (Cockrem, 2013).

2.5. Subgroup designations

Some studies measured coping styles in only a single sex or age group, while others combined these groups. Therefore, we extracted data on age class as 'adult', 'juvenile' or 'mixed' and sex as 'male', 'female' or 'mixed'. We also included in our dataset information on potentially confounding variables. Studies often vary in the method by which they sample glucocorticoids with many studies using plasma samples while other studies used noninvasive sampling of feces, hair, urine or water (for fish). Therefore, we included information about 'sample type' as a potentially confounding covariate in our dataset. We also included 'animal source' as a potentially confounding covariate. For the latter, we categorized animals as 'captive' if they were born and reared in captivity, as 'wild caught' if they were wild animals placed in captivity for the study, or 'wild' for animals studied in the wild.

2.6. Life history and social traits

To test hypotheses about the evolution of coping styles, we compiled life-history and social structure data on all species from the primary literature, including the articles in our study, as well as from. public databases (e.g., AnAge (de Magalhaes and Costa, 2009); FishBase (Froese and Pauly, 2022); Birds of North America (Billerman et al., 2022)). Traits included mean body mass, maximum longevity, mean time to maturity, and the average number of reproductive events per year (litters, clutches, etc.). Species were also classified by their social structure (group living, pair-living, solitary). When species' social structure changed between breeding and nonbreeding seasons, we used the breeding season social structure designation. We also categorized species as territorial or non-territorial. Species were categorized as territorial if they maintained territories for even part of the year. Finally, we used the primary literature and above-mentioned online databases to assess whether species' developmental mode was altricial or precocial.

We used principal component analysis to reduce our three highly inter-correlated life history variables (see Table S1 for correlation matrix) and body mass (all log-transformed) to a single variable that corresponds to slow versus fast life history variation. The first principle component had an eigenvalue of 2.65 and explained 66.3% of the variance and corresponded to 0.48 (longevity), 0.56 (time to maturity), − 0.49 (average annual reproduction) and 0.46 (body mass). Therefore, higher PC1 scores indicate slower species and lower scores indicate faster species.

2.7. Statistical analyses

To assess phylogenetic independence of the data (Adams, 2008; Lajeunesse, 2009), we used the geiger package in R (Pennell et al., 2014; version 4.1.3) to test effect sizes for phylogenetic signal by estimating Pagel's λ. We estimated this separately for the three datasets (aggression and baseline as well anxiety and both baseline and stress-induced glucocorticoids) which all had at least 10 species, by constructing sub-trees including only the species in these datasets using www.timetree.org (see Fig. S1 for tree of all species used in the study). For these analyses, we calculated mean effect sizes if there were more than one study on the same species. The parameter λ is estimated using maximum likelihood and ranges from 0 to 1. When λ approaches zero, this reduces all internal branches to zero, resulting in a 'star phylogeny' (Felsenstein, 1985), indicating that traits are statistically independent of the phylogenetic structure. All three estimates of Pagel's λ were not significantly different from 0 ($\lambda < 0.001$; $P = 1.0$ for all three), so no further phylogenetic methods were used.

Analyses were performed using Comprehensive Meta-Analysis (Borenstein, 2022). While we were able to obtain correlation coefficients for the majority of studies, there were also a number of studies that used more complex models that included covariates. A typical assumption of meta-analyses is that the studies included all have a similar structure and thus are directly comparable to one another (Borenstein et al., 2021). Studies that include covariates violate this assumption; however, leaving them out can increase sampling error and may bias and/or reduce the generalizability of effect size estimates (Peterson and Brown, 2005). Therefore, we opted to include studies with covariates and to explicitly assess whether inclusion of these studies altered our results.

To assess overall evidence that more proactive (e.g. more aggressive and less fearful) individuals have both lower baseline and stress-induced glucocorticoid levels, an overall mean effect size was calculated for relationships between each behavior and stress category based on calculating Fisher's Z of individual studies and weighting by study variance (Borenstein et al., 2021). We used random effects models for all analyses because we were interested in generalizing results across a variety of situations and the included studies are unlikely to be functionally equal (Borenstein et al., 2010; Kelley and Kelley, 2012). We used I^2 to assess heterogeneity of effect sizes (Higgins and Thompson, 2002).

If a study provided results separately for different sets of individuals (e.g., for different species, sexes, or age categories), we included either subgroups (for sex and age) or, for the one study on two species (Rimbach et al., 2022), treated them as independent studies. For studies that assessed multiple measures of the same behavior (e.g. many studies assessed either multiple measures of anxiety or assessed a subcategory of anxiety using multiple tests), we combined results calculating the weighted average of the calculated effect sizes for the same relationship. One study (Schweitzer et al., 2017) used principle component analysis to categorize individuals as either 'proactive' or 'reactive'. We included this study as measuring aggression as this was the behavior that loaded highest on the principle component used. Twenty-four studies assessed both baseline and stress-induced glucocorticoids. Even though the relationship between these measures and behavioral traits are expected to be distinct, including these overlapping studies in our analysis as separate studies violates assumptions of independence because there may be an association between results from the same individuals in the same study. Therefore, to assess this possibility, we analyzed the correlation in effect sizes across studies that reported relationships for both baseline and stress-induced glucocorticoids and found that the relationship was weakly negative and non-significant ($r = -0.35$, $P = 0.093$) confirming that there was no strong positive covariation among these measures.

To determine whether social structure, territoriality, developmental mode and/or life history variation were important moderators of effect size, we used meta-regression analyses for broad-sense categories with at least 10 studies available. We first used subgroup analysis to identify potentially confounding factors by assessing whether overall effect size differed among studies that did and did not include covariates, and whether effect sizes were influenced by sample source (e.g. fecal versus plasma) or animal source (e.g. wild versus captive). We also examined whether sex and age subgroups were important predictors of effect size.

We included subgroup variables in further analyses if they showed any tendency to modulate effect sizes as indicated by $p < 0.15$.

For assessing moderators of the relationship between both stress-induced and baseline glucocorticoids with anxiety, we used a backwards stepwise selection process where we fit a full model with all variables of interest and sequentially removed variables based on their significance in the model, removing variables with the highest p-values first. We first ran a full model which included social structure, territoriality, developmental mode, and life history variation. However, for stress-induced glucocorticoids and anxiety, models including both social structure and territoriality had problems with collinearity, so we ran two separate full models, one that included territoriality and one for social structure. These models also included age and covariates based on the results of the subgroup analysis. For assessing moderators of the relationship between baseline glucocorticoids and aggression, because we had a much smaller sample size, we also ran two separate initial models which included species' social structure and territoriality separately.

3. Results

3.1. Effect sizes and heterogeneity

In general, we found weak relationships between glucocorticoid levels and behavioral traits (Fig. 2). Only three effect sizes differed significantly from zero: the relationship between measures of long-term glucocorticoids and aggression which was weakly positive and the relationship between baseline glucocorticoids and both aggression and sociability which were weakly negative (Fig. 2B & C). None of the effect sizes for the relationship between stress-induced glucocorticoid levels and behavioral traits differed from zero (Fig. 2 A). However, there was moderate to high heterogeneity among studies as indicated by I^2 values (Fig. 2).

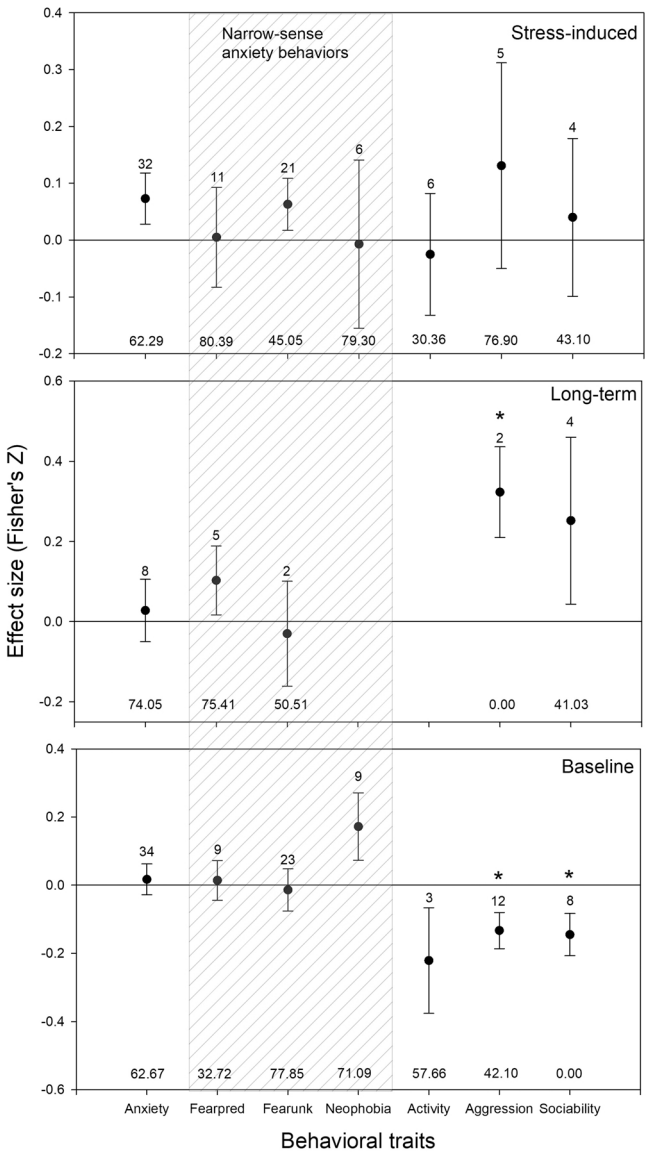

Fig. 2. Effect sizes for the relationship between behavioral traits and stress-induced (upper), long-term (middle), and baseline (lower) corticosterone. Shown are means and standard errors (SE). Sample size (number of studies) is indicated above each bar and I^2 values showing the amount of heterogeneity among studies are shown at the base of each panel. Hashed box indicates the breakdown of values for analysis of narrow-sense behaviors which are combined for the anxiety category. Stars above bars indicate effect sizes that are significantly different from zero ($p < 0.05$).

3.2. Subgroup analysis

For broad-sense behaviors for which we had at least 10 studies, variation in effect sizes was not explained by use of covariates (i.e. studies that included covariates in models assessing the relationship between behavioral and glucocorticoid variation), the type of sample analyzed for glucocorticoids, or animal source (Tables 3–5). Moreover, there was little evidence for age class and sex influencing the relationship between glucocorticoids and behaviors. There were two potential exceptions to this general pattern. For the relationship between stress-induced glucocorticoid response and anxiety, studies without covariates did have a weak overall positive effect size while studies with covariates did not differ from zero (Table 3). There was also some potential influence of age as adults showed a slightly stronger positive effect size than juveniles (Table 3) and this pattern was proved robust even after accounting for variation in life history (see meta-regression results below). While the between-group heterogeneity did not reach significance in any of these cases, given the low number of studies, we lacked the power to identify small differences among these groups.

3.3. Meta-regression of broad-sense behaviors

3.3.1. Stress-induced glucocorticoids and anxiety

The final model contained both life history variation and the subgroup age ($Q = 43.40$, $df = 3$, $p < 0.0001$) and explained 94% of the between-study variance. Whether or not studies used covariates (coefficient $= -0.044 \pm 0.078$ SE, 95%CI [−0.20, 0.11], $z = -0.57$, $p = 0.567$), developmental mode (coefficient $= -0.054 \pm 0.092$ SE, 95%CI [−0.23, 0.12], $z = -0.59$, $p = 0.553$), species' territoriality (coefficient $= 0.059 \pm 0.062$ SE, 95%CI [−0.06, 0.18], $z = 0.95$, $p = 0.340$), and species' social structure ($Q = 0.73$, df=2, $p = 0.696$) were not important moderators and were omitted from the final model. The relationship between stress-induced glucocorticoids and anxiety was strongly influenced by life history variation – slower species showed a positive association between stress reactivity and anxiety while fast species showed a negative relationship (coefficient $= 0.095 \pm 0.019$ SE, 95%CI [0.06–0.13], $z = 4.96$, $p < 0.0001$, Fig. 3 A). In studies that contained juveniles, there was a tendency for the relationship between stress reactivity and anxiety to be more negative compared to studies that contained only adults ($Q = 5.52$, $df = 2$, $p = 0.063$; Fig. 3B).

3.3.2. Baseline glucocorticoids and anxiety

Both species' social structure and developmental mode were significant predictors of the relationship between baseline glucocorticoids and anxiety (social structure: ($Q = 10.62$, $df = 2$, $p = 0.005$; developmental mode: coefficient $= -0.199 \pm 0.100$ SE, 95%CI [−0.39, 0.002], $z = -1.98$, $p = 0.047$; Fig. 4). Territoriality was also a potential moderator with territorial species having lower effect sizes than non-

Table 3
Subgroup analyses of the relationship between stress-induced glucocorticoid response and anxiety.

Moderator variables	Sample size (# studies)	Meta-analysis						Between group heterogeneity		
		Fisher's Z	se	z	p	95% CI L	95% CI U	Q	df	p
Covariates?								**2.670**	**1**	**0.102**
No	21	0.124	0.052	2.390	0.017	0.022	0.225			
Yes	11	-0.015	0.067	-0.223	0.824	-0.147	0.117			
Type of sample								2.487	2	0.288
Fecal	3	-0.128	0.140	-0.920	0.358	-0.402	0.145			
Plasma	26	0.103	0.051	2.024	0.043	0.003	0.203			
Water	3	0.037	0.153	0.243	0.808	-0.263	0.337			
Source of animals								0.169	2	0.919
Captive	17	0.070	0.065	1.078	0.281	-0.057	0.197			
Wild	5	0.116	0.120	0.968	0.333	-0.119	0.352			
Wild-caught	10	0.058	0.076	0.763	0.445	-0.091	0.208			
Age								**4.318**	**2**	**0.115**
Adult	23	0.119	0.050	2.375	0.018	0.021	0.218			
Juvenile	5	0.057	0.107	0.534	0.593	-0.152	0.266			
Mixed	4	-0.126	0.107	-1.174	0.240	-0.335	0.084			
Sex								2.575	2	0.276
Both	20	0.022	0.054	0.414	0.679	-0.083	0.128			
Female	6	0.158	0.109	1.454	0.146	-0.055	0.372			
Male	7	0.175	0.099	1.772	0.076	-0.019	0.369			

Between group heterogeneity tests in bold indicates groups that met criteria for inclusion in meta-regression analysis ($p < 0.15$)

Table 4
Subgroup analyses of the relationship between baseline glucocorticoids and anxiety.

Moderator variables	Sample size (# studies)	Meta-analysis						Between group heterogeneity		
		Fisher's Z	se	z	p	95% CI L	95% CI U	Q	df	p
Covariates?								0.146	1	0.702
No	20	0.033	0.062	0.533	0.594	-0.088	0.154			
Yes	14	-0.002	0.067	-0.028	0.977	-0.134	0.130			
Type of sample								0.735	2	0.692
Fecal	12	0.058	0.077	0.758	0.449	-0.092	0.209			
Plasma	19	-0.021	0.065	-0.320	0.749	-0.147	0.106			
Water	3	0.065	0.145	0.446	0.656	-0.219	0.349			
Source of animals								2.107	2	0.349
Captive	14	0.090	0.073	1.231	0.218	-0.053	0.232			
Wild	11	-0.065	0.078	-0.836	0.403	-0.218	0.088			
Wild-caught	9	0.015	0.084	0.175	0.861	-0.150	0.180			
Age								2.058	2	0.357
Adult	26	0.041	0.053	0.765	0.444	-0.063	0.145			
Juvenile	2	0.183	0.237	0.770	0.441	-0.282	0.647			
Mixed	6	-0.106	0.105	-1.010	0.313	-0.312	0.100			
Sex								0.993	2	0.609
Both	20	0.003	0.057	0.057	0.954	-0.108	0.114			
Female	7	0.129	0.119	1.081	0.280	-0.105	0.363			
Male	8	-0.005	0.093	-0.051	0.959	-0.187	0.178			

territorial species (coefficient = −0.229 ± 0.122 SE, 95%CI [−0.47, 0.01], z = −1.87, p = 0.062; Fig. 4A). Relative to group-living animals, solitary species generally showed a higher mean effect size (coefficient = 0.471 ± 0.147 SE, 95%CI [0.18, 0.76], z = 3.20, $p = 0.001$; Fig. 4B). Pair-living species also showed a positive effect size, however, it did not differ relative to group-living species (coefficient = 0.153 ± 0.132 SE, 95%CI [−0.11, 0.41], z = 1.16, $p = 0.246$). In general, precocial species had a lower mean effect size compared to altricial species (Fig. 4C). Effect sizes across studies did not differ in relation to species' life history (coefficient = −0.031 ± 0.029 SE, 95%CI [−0.09, 0.02], z = −1.08, p = 0.279). Overall, the model explained 38% of the between-study variation and substantial unexplained variance remained (test that unexplained variance is zero: $Tau^2 = 0.022$, $I^2 = 47.11\%$, $p = 0.002$).

3.3.3. *Baseline glucocorticoids and aggression*

The final model included only species' life history variation (Q = 3.56, df = 1, $p = 0.059$) with only a small amount of the between-study variance explained ($R^2 = 0.21$; $Tau^2 =$, $I^2 = 0.00\%$). However, including developmental mode did produce a model that explained a higher proportion of the between-study variance ($R^2 = 0.42$; Q = 5.54, df = 2, $p = 0.062$). In general, slower species had more strongly negative effect sizes compared to faster species (coefficient = −0.061 ± 0.032 SE, 95% CI [−0.12, 0.002], z = −2.6, $p = 0.059$; Fig. 5). In the full model, species' social structure (Q = 0.23, df = 2, $p = 0.890$) and territoriality (coefficient = 0.075 ± 0.217 SE, 95%CI [−0.35, 0.50], z = 0.35, $p = 0.730$) were not important moderators of effect size.

4. Discussion

Despite a long history of studies that investigate the links between behavioral traits and stress physiology, we still have a poor understanding of the underlying mechanisms linking them. Consistency across taxa in the magnitude and direction of correlations among these traits would support the idea that there is a direct causal link and that covariation of these traits is due to either functional, selective or developmental constraints (Arnold, 1992; Maynard Smith et al., 1985). In our meta-analysis of more than 70 studies of the links between personality traits and glucocorticoids, we found little evidence for this. With the possible exception of aggression and sociability in relation to baseline glucocorticoids, there was little evidence for consistent effect

Table 5
Subgroup analyses of the relationship between baseline glucocorticoids and aggression.

Moderator variables	Sample size (# studies)	Meta-analysis						Between group heterogeneity		
		Fisher's Z	se	z	p	95% CI L	95% CI U	Q	df	p
Covariates?								0.002	1	0.966
No	10	-0.136	0.061	-2.211	0.027	-0.256	-0.015			
Yes	2	-0.129	0.138	-0.936	0.350	-0.401	0.142			
Type of sample								3.227	2	0.199
Fecal	4	-0.126	0.091	-1.387	0.165	-0.305	0.052			
Plasma	5	-0.277	0.101	-2.742	0.006	-0.475	-0.079			
Water	3	-0.047	0.078	-0.606	0.545	-0.201	0.106			
Source of animals								0.293	2	0.864
Captive	5	-0.104	0.085	-1.227	0.220	-0.270	0.062			
Wild	6	-0.168	0.092	-1.837	0.066	-0.348	0.011			
Wild-caught	1	-0.166	0.187	-0.889	0.374	-0.532	0.200			
Age								1.849	1	0.174
Adult	11	-0.113	0.053	-2.120	0.034	-0.217	-0.008			
Juvenile	1	-0.388	0.196	-1.983	0.047	-0.772	-0.005			
Sex								0.072	2	0.964
Both	3	-0.110	0.093	-1.181	0.238	-0.293	0.073			
Female	6	-0.146	0.096	-1.517	0.129	-0.336	0.043			
Male	5	-0.129	0.099	-1.306	0.192	-0.323	0.065			

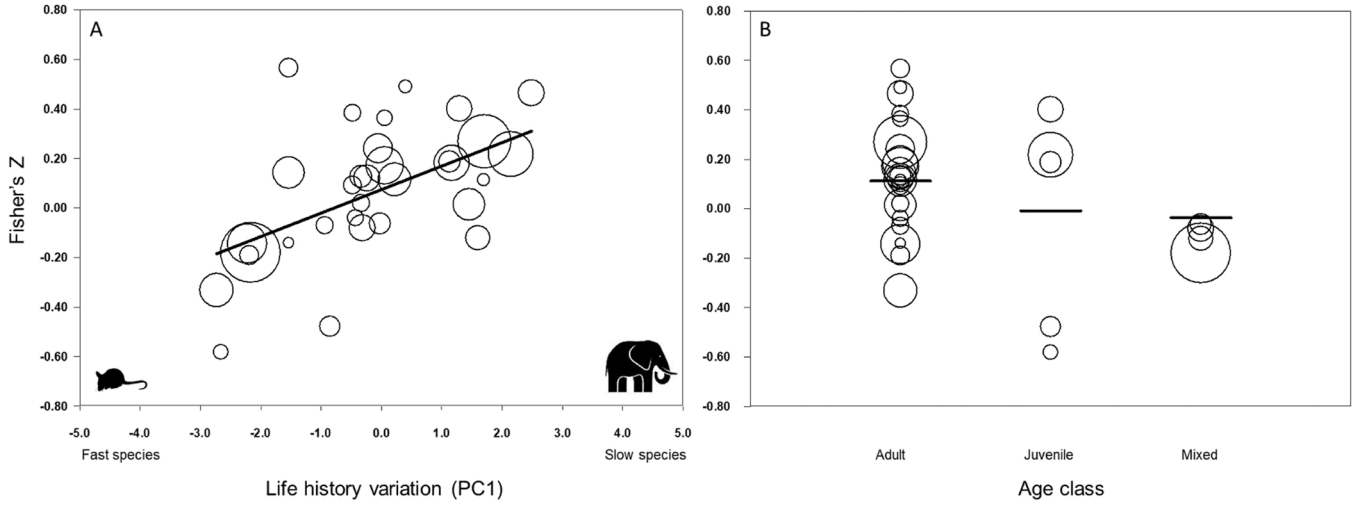

Fig. 3. Influence of life history variation and age on the relationship between stress-induced glucocorticoid levels and anxiety behaviors. A. Slower species are more likely to show a positive relationship between stress-induced glucocorticoids and fearfulness; whereas faster species show a negative relationship. Higher values of PC1 indicate species that are longer-lived, mature at a relatively later age, have a higher body mass and have lower annual reproduction compared to lower values of PC1. B. Studies that included juveniles showed a tendency to have lower effect sizes compared to studies that did not. Horizontal lines indicate group means. Size of circles indicate weight of study in analyses.

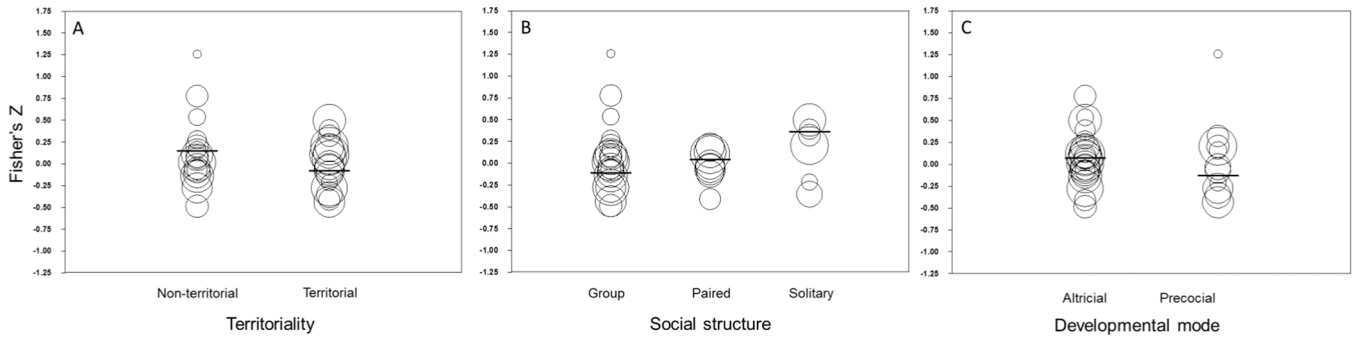

Fig. 4. Influence of A. territoriality, B. social structure, and C. developmental mode on the relationship between baseline glucocorticoid levels and anxiety behaviors. Horizontal lines indicate group means. Size of circles indicate weight of study in analyses.

sizes across studies and taxa. Instead, particularly for the relationship between anxiety and stress-induced glucocorticoids, we found that there was a high amount of heterogeneity among studies and this heterogeneity was related to species' variation in life histories and social structure.

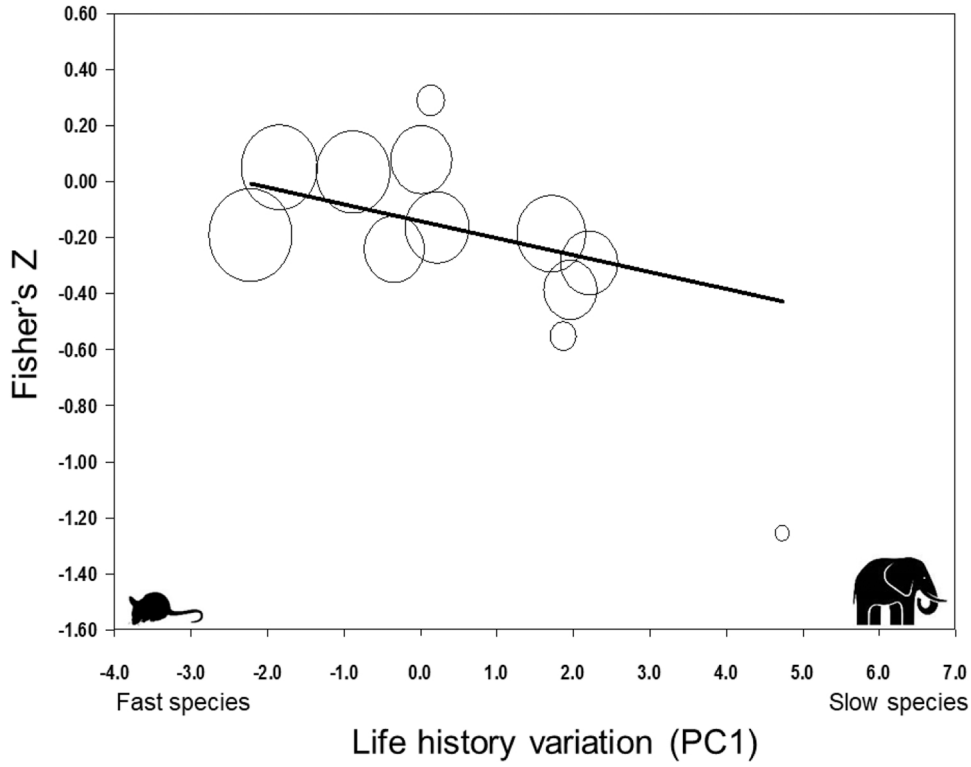

Fig. 5. Influence of life history variation on the relationship between baseline glucocorticoid levels and aggression. Higher values of PC1 (x-axis) indicate species that are longer-lived, mature at a later age, have a higher body mass and have lower annual reproduction compared to lower values of PC1. Size of circles indicates weight of study in analyses.

4.1. Anxiety and stress-induced glucocorticoids

The fact that there was a high heterogeneity in effect size for anxiety-related behaviors (Fig. 2) suggests there is no universal causal relationship between anxiety traits and stress-induced glucocorticoids. Instead, we found strong evidence that the nature of the relationship between them evolves as a part of species' life histories. Specifically, in slow species more fearful individuals have higher stress reactivity, whereas in fast species, less fearful, bolder individuals have higher stress reactivity. This finding raises the questions: what are the costs and benefits of higher stress-induced glucocorticoid levels and how might they influence evolution of the link between stress reactivity and behavior?

The phenotypic consequences of individual variation in glucocorticoid levels has been most extensively studied in the context of maternal programming of offspring HPA axis, where offspring exposed to maternal stress early in development have altered expression of glucocorticoid receptors in the brain (Chaby, 2016; Harris et al., 2013; Meaney, 2001; Meaney and Szyf, 2005; Meaney et al., 2007; Seckl and Meaney, 2004). Prenatal stress exposure has been shown to stably decrease hippocampal glucocorticoid receptor expression and increase both basal and stress-induced glucocorticoid responses (Meaney et al., 2007). Increased glucocorticoid levels can enhance an individual's response to risky or stressful situations (Denver, 2009; Hermans et al., 2014), but this comes at a cost (Korte et al., 2005; Sapolsky et al., 2000). Over the long term, higher circulating glucocorticoids can lead to poorly regulated metabolic function, can suppress reproduction, digestion and immune responses and can have potentially negative impacts on the brain (Hau et al., 2016; Kim and Haller, 2007; Korte, 2001; Meaney et al., 2007; Oitzl et al., 2010). Our results suggest that the evolutionary consequences of these costs and benefits may be different for species that vary in their life histories.

A recent meta-analysis across 14 species found that HPA-axis sensitivity to prenatal stress is conserved such that it leads to higher glucocorticoid responses regardless of a species' overall life history strategy (Thayer et al., 2018). This prior work, in conjunction with our present study (Fig. 3 A), suggests that what is evolving across species is not how variation in HPA programming occurs, but instead, it is how personality traits are linked to this HPA axis programming. Thus, one possible explanation for the observed positive relationship between effect size and life history variation (Fig. 3 A) is that, in slow species, prenatal stress may lead to production of offspring that have both higher stress reactivity and higher fearfulness; whereas, in fast species, prenatal stress produces individuals that are bolder, less fearful and have higher stress reactivity. This may be because, in fast species, an individual born into a stressful or riskier environment may benefit by simultaneously being bolder in the face of environmental challenges and having a stronger glucocorticoid response to increase their competence in reacting to them. However, for slower species, because they are long-lived, it may be beneficial for individuals born into a challenging environment to be more cautious and to take fewer risks (Ghalambor and Martin, 2001; Roff, 1993; Stearns, 1992; Williams, 1966); these more fearful individuals may also benefit by having higher glucocorticoid responses when they do encounter stressors. Thus, one potential explanation for the relationship between effect sizes and life history is that species' life history influences which personality traits are favored in stressful environments and this secondarily leads to variable correlations with HPA axis programming – which itself appears to be uniform across taxa (Thayer et al., 2018) with more stressful environments leading to production of offspring with higher glucocorticoid responses. The extent that glucocorticoid programming can explain these findings is an important topic for future research. Overall, our results support the idea that there are no absolute constraints linking stress-induced glucocorticoid levels and behavioral traits.

4.2. Anxiety and baseline glucocorticoids

Interestingly, the only case where species' social structure influenced the relationship between behavior and glucocorticoids was for anxiety and baseline levels. In this case, solitary species were more likely to show a positive effect size compared to group-living species. While variation in anxiety-related behaviors are not social behaviors per se – after all, an individual can be fearful in complete isolation – they can still be modulated in response to social context (Kerman et al., 2018; Mainwaring et al., 2011; St. Lawrence et al., 2021). In solitary species, individuals must monitor the environment and detect threats completely on their own; whereas, in many group-living species individuals can rely on collective vigilance (Blumstein, 2006; Childress and Lung, 2003; Townsend et al., 2011). Given that HPA programming is consistent across taxa (Thayer et al., 2018), our results may indicate that it is more important to produce more fearful offspring when encountering stressful environments for solitary species than it is for group-living species. Overall, our findings suggest the need for additional studies that assess how variation in coping styles may differ across species with variable social structure.

We also found that developmental mode was an important moderator of the link between baseline glucocorticoids and anxiety behaviors. Precocial species had more consistently negative effect sizes compared to species with altricial offspring. This is consistent with the idea that early developmental effects may be important in determining the links between glucocorticoid levels and behavioral traits as there is more overlap in peak brain growth in regions that jointly influence HPA programming and personality traits in precocial species. However, unlike the meta-regression model for anxiety and stress-induced glucocorticoids, there was substantial variance that remained unexplained suggesting there may be additional factors that are important in explaining species' differences in the relationship between fearfulness and baseline glucocorticoids. For example, genetic effects might be crucial in determining the relationship between glucocorticoid levels and behavior across taxa (Veenema et al., 2003). Moreover, some have suggested that baseline glucocorticoid levels are not be highly repeatable within individuals (Bonier et al., 2009; Schoenemann and Bonier, 2018) and this may obscure our understanding of how they are associated with other traits.

4.3. Aggression and baseline glucocorticoids

Aggression and sociability were the only behaviors for which we found some consistency of effect sizes across studies. Some of the most compelling evidence for coping styles is from studies of divergent selection lines for aggression in rodents, where more aggressive individuals generally show lower physiological stress responses compared to less aggressive individuals (Koolhaas et al., 1999; Veenema et al., 2003). While these laboratory studies support the idea that there is a causal link between aggression and glucocorticoids, Koolhaas et al. (2010) suggested that differences among individuals in physiological stress response are mainly a consequence rather than a cause of differences among individuals in behavior. This interpretation is consistent with prior studies that have found that baseline glucocorticoid levels are less repeatable across individuals (Schoenemann and Bonier, 2018) which may indicate a strong influence of current environmental conditions. Future work could assess these ideas by manipulating environmental quality for both aggressive and non-aggressive individuals and observing whether baseline glucocorticoids better reflect behavioral phenotype or environmental quality.

Interestingly, a similarly negative effect size was also observed for sociability where, within a species, more sociable individuals were also more likely to have lower baseline glucocorticoids. While often thought of as opposing traits, both higher aggression and higher sociability indicate an individual's willingness to engage more readily with conspecifics and social aggression and social bonding have been shown to be modulated by similar oxytocin pathways (Crespi, 2016). Therefore, perhaps the key to understanding lower baseline glucocorticoid levels in relation to variation in social traits, is that both higher aggression and higher sociability enable individuals to exert greater control of their environments. In general, interpreting these patterns requires a deeper understanding of why individuals vary in baseline glucocorticoids levels, a topic of current debate (Baugh et al., 2014; Bonier et al., 2009; Dingemanse et al., 2010a, 2010b; Romero and Reed, 2008; Schoenemann and Bonier, 2018).

Life history variation was a significant moderator of the strength of the relationship between aggression and baseline glucocorticoids. Specifically, species on the slower end of the life history continuum were more likely to show strong negative effect sizes compared to faster species. Thus, in slower species, more aggressive individuals generally have lower baseline glucocorticoid levels, whereas, in fast species, there is no relationship between the two. Factors that could help explain this pattern is if species with slower life histories were generally more sociable or territorial than species with faster life histories as this might provide for more opportunities for aggressive control. However, in our models, there was no independent influence of variation in either species' sociality or territoriality on effect sizes. Thus, our original idea that the relationship between aggression and glucocorticoid levels would be most likely moderated by species' social structure was not supported. Instead, our findings raise the possibility that, for species that are longer-lived or that take a longer time to reach maturity, more aggressive individuals may have more opportunities to exert control over their environment. Future work assessing the causal links between aggression and baseline glucocorticoid levels would be useful in assessing this possibility.

4.4. Subgroup analyses and potentially confounding variables

Whenever different studies investigating the same topic find widely variable results, there is always the possibility that this reflects methodological issues or lack of standardization across studies. We did not find any evidence of this in our study. Neither the type of sample used for assessment of glucocorticoid levels nor the source of the animals used (captive versus wild) had a strong impact on effect sizes. Moreover, we also did not find strong evidence that effects sizes varied by age or sex. The only exception to this was a non-significant trend in the meta-regression analysis of stress-induced glucocorticoids and anxiety traits (Fig. 3B). Studies that included juveniles tended to have more negative effect sizes compared to studies that used only adults. One other potential moderator of effect size in this same analysis was whether studies used covariates (Table 3). While our subgroup analysis showed that studies that did use covariates had a tendency to have lower effect sizes than studies that did not, this was more likely due to the particular subset of taxa used in these studies. In the meta-regression, use of covariates was no longer important once species life history was taken into account suggesting that studies that did not include covariates were more often on species at the faster end of the life history continuum. Thus, overall, the results of our subgroup analysis suggest that differences in methodology across studies is not likely to explain variation in effect sizes, and it also points out where further evidence would be useful, particularly for potential age-related affects modulating the relationship between stress-induced glucocorticoids and anxiety-related traits. The possibility of age as an important mediator of this relationship is particularly intriguing given that older individuals may be more willing to take risks given expectation of fewer opportunities for future reproduction (Biro and Stamps, 2008; Møller and Nielsen, 2014; Thornhill, 2010). As such, life history theory predicts that this should result in systematic age-related differences in boldness towards predators and this may influence correlations with glucocorticoid responses (Seltmann et al., 2012).

One additional caveat pertains to the results from studies that measured long-term glucocorticoid levels. While we did not have

enough studies in this category to do as thorough an investigation of moderators as we did for baseline and stress-induced glucocorticoids, it did show some important differences from our other analyses. In particular, there often seems to be an assumption that measures of glucocorticoids over the long term are equivalent to baseline levels. However, the only significant effect size result for long-term glucocorticoids was with aggression and it varied in the opposite direction compared to measures of baseline. While the long-term data was limited in sample size, these preliminary findings suggest that studies based on long-term measures of glucocorticoids should not necessarily be assumed to vary with behavioral traits in the same way that baseline levels do.

Our study also points out other areas where we need more information. Overall, there were few studies on reptiles and we found no studies on amphibians that met our inclusion criteria. This gap in the coping style field doesn't necessarily reflect a lack of interest in stress physiology in these groups. There are numerous studies investigating glucocorticoids in amphibians and reptiles (Cockrem, 2013; Eikenaar et al., 2012; Moore and Jessop, 2003; Moore et al., 1991; Overli et al., 2007; Telemeco et al., 2019); however, they either are not explicitly relating glucocorticoid levels to behavioral traits, or they often used hormone implants or injections to manipulate glucocorticoids and so we could not include them in this study (Denardo and Licht, 1993; Thaker et al., 2010; Yang and Wilczynski, 2003). Our study also revealed that there are fewer studies that assess glucocorticoids in relation to social traits than for anxiety traits, especially for stress-induced levels. This is somewhat surprising given that, for some of the earliest studies of coping styles, aggression was a main focal trait (Benus et al., 1991; Koolhaas et al., 1999; Overli et al., 2007). While studies of aggression and glucocorticoid levels are still quite frequent in laboratory rodents, it would be useful to have more of these studies across a diversity of animals. Finally, despite several authors including differences in activity levels in their definition of coping styles (Keiling and Suski, 2019; Mazza et al., 2019), there were few studies that assessed its relationship with glucocorticoid levels. However, this is at least in part because of our stringent definition of activity. We coded behavior as 'activity' only if it was measured in a familiar environment; whereas, in some studies, researchers reported activity levels as separate from exploratory behavior in their novel environment tests, even though, in practice, the two may be difficult to separate (Perals et al., 2017).

Finally, it is important to note that ideas about coping styles were explicitly developed to explain consistent individual differences in behavior (Koolhaas et al., 1999). While many of the studies in our meta-analysis included some assessment of repeatability of behavior or referred to prior work that measured repeatability, we assumed that all of the behaviors fit the definition of 'personality trait'; however, future work that explicitly assesses both repeatability of behavior and the glucocorticoid response (e.g. Duckworth and Sockman, 2012) as well as correlations between them would be useful in determining the stability of hormone-behavior relationships (Ball and Balthazart, 2008). Moreover, since meta-analysis requires comparison of studies that are similar in structure we focused on studies that provide simple correlations between phenotypic variation in behavior and glucocorticoid levels. As more studies are published that partition variation into between- and within-individual components (Dingemanse et al., 2010a, 2010b; Stamps and Krishnan, 2014), new insights may be gained from future meta-analyses that aim at assessing correlations at the within-individual level.

5. Conclusion

Meta-analysis cannot determine causal mechanisms between stress physiology and behavioral traits, but it can at least shed light on whether there is consistent directionality in these relationships. Overall, for anxiety-related behaviors, we found most support for the evolutionary lability hypothesis and, for aggression, some support for the behavioral control hypothesis. We found little support for the idea of physiological control as studies of the link between anxiety-related behaviors and glucocorticoids showed highly variable results that were related to either life history variation or species' sociality. This does not mean that, within a particular species, physiological mechanisms that underlie variation in glucocorticoid responses are not ever causally linked to variation in behavior. It simply means that there are no universal causal links where physiological variation determines behavioral variation. Instead, any developmental and/or physiological integration of proximate pathways linking the HPA axis to behavioral traits are evolutionarily flexible and likely shaped by current selection. Such flexibility is consistent with the idea that maternal programming of the HPA axis is a common response to developmental stress and that what evolves across species is not how the HPA axis is programmed, but how behavioral traits are linked to this programming (Duckworth et al., 2018; Potticary and Duckworth, 2020). Thus, our results suggest that there might be different developmental mechanisms underlying associations between stress physiology and distinct behavioral traits across taxa. Future studies elucidating these links across a diversity of non-model organisms are needed to assess this idea.

This raises the question of how we should define coping styles, and, in particular, proactive and reactive types. Even though multiple correlated physiological and behavioral traits are typically thought of as comprising coping styles (de Boer et al., 2017; Ferrari et al., 2013; Overli et al., 2007), empirical findings have made it clear that links between stress physiology and behavioral traits are complex and not related in the same ways across all taxa leading to refinements of the original ideas (Coppens et al., 2010; Koolhaas et al., 2007; Qu et al., 2018; Steimer and Driscoll, 2003; Westrick et al., 2019; Zidar et al., 2017). A meta-analysis of correlations among personality traits found that most were weak, and, while anxiety-related traits were generally positively correlated within a species, aggression varied largely independently of these traits (Garamszegi et al., 2013). Thus, lack of strong covariance among the behavioral traits most often associated with coping styles (aggression and boldness/fearfulness) in combination with our findings of a lack of consistent relationship between personality traits and glucocorticoid levels suggests that there is not a universal 'coping style' structure among animals. This is not to say that the concept is not useful – after all, there is no question that personality traits often do covary with stress physiology. However, instead of coping styles reflecting specific repeated combinations of behavioral traits, the picture emerging is that of a suite of behavioral and physiological traits that are recombined in different ways depending on species' sociality and life history.

Acknowledgements

We thank Claudio Carere and Dario Maestripieri for organizing the workshop at the Ettore Majorana Foundation and Centre for Scientific Culture that led to this special issue. We are grateful to Alex Badyaev, Matthew Moelling, Matt Jenkins, Juliana Kosters, and Stephen Cooke for discussions of these ideas and comments on earlier drafts. We are also grateful to two anonymous reviewers for their constructive comments. Funding was provided to MCB by a Study Abroad Award from the Projeto Institucional PrInt/CAPES/UFC and to KCC for a Dissertation Fellowship from the Marshall Foundation.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.neubiorev.2023.105241.

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