The role of glucocorticoids in the vertebrate response to weather

Robert de Bruijn, L. Michael Romero*

Department of Biology, Tufts University, Medford, MA 02155, USA

ARTICLE INFO

ABSTRACT

Changes in the environment related to inclement weather can threaten survival and reproductive success both through direct adverse exposure and indirectly by decreasing food availability. Glucocorticoids, released during activation of the hypothalamic-pituitary-adrenal axis as part of the stress response, are an important candidate for linking vertebrate coping mechanisms to weather. This review attempts to determine if there is a consensus response of glucocorticoids to exposure to weather-related stimuli, including food availability, precipitation, temperature and barometric pressure. The included studies cover field and laboratory studies for all vertebrate taxa, and are separated into four exposure periods, e.g., hours, days, weeks and months. Each reported result was assigned a score based on the glucocorticoid response, e.g., increased, no change, or decreased. Short-term exposure to weather-related stimuli, of up to 24 h, is generally associated with increased glucocorticoids (79% of studies), suggesting that these stimuli are perceived as stressors by most animals. In contrast, the pattern for exposures longer than 24 h shows more variation, even though a majority of studies still report an increase (64%). Lack of glucocorticoid increases appeared to result from instances where: (1) prolonged exposure was a predictable part of the life history of an animal; (2) environmental context was important for the ultimate effect of a stimulus (e.g., precipitation limited food availability in one environment, but increased food in another); (3) prolonged exposure induced chronic stress; and (4) long-term responses appeared to reflect adaptations to seasonal shifts, instead of to short-term weather. However, there is a strong bias towards studies in domesticated laboratory species and wild animals held in captivity, indicating a need for field studies, especially in reptiles and amphibians. In conclusion, the accumulated literature supports the hypothesis that glucocorticoids can serve as the physiological mechanism promoting fitness during inclement weather.

1. Introduction

Changes in an environment can have important repercussions for organisms living in that environment. One important category of environmental change is related to climate, as animals are exposed to changes in weather. Weather parameters that may affect animals include temperature, precipitation, and barometric pressure, each of which can have direct and indirect effects on food availability. All four of these parameters can change relatively predictably on a seasonal basis, or very rapidly and unpredictably during inclement weather, such as a storm. Changes in these parameters pose both direct and indirect challenges to organisms. For example, changes in weather can pose a direct threat to survival (Bumpus, 1899; Childs, 1913; Frazar, 1881; Odum and Pitelka, 1939) and reproductive success (Astheimer et al., 1995). On the other hand, many animals also use weather-related changes in their environment as cues for timing life history stages, such as breeding (Wingfield et al., 2011; Wingfield and Ramenofsky, 2011) and migration (Ramenofsky and Wingfield, 2007). The effects of weather-related changes on vertebrates have been the topic of scientific research for centuries, yet much is still unknown about the mechanisms that link animals to their environment and help them adapt to and cope with these changes (Wingfield et al., 2017). Understanding the interaction between animals and their environment has become even more important in recent decades as climate change is impacting both long-term predictability and short-term volatility of weather-related parameters (Romero and Wingfield, 2016; Wingfield et al., 2011).

The stress response, a concept first introduced about 80 years ago (Cannon, 1932; Selye, 1946), is a key physiological mechanism that helps animals cope with a variety of stressors. One of the main mediators of a stress response is glucocorticoid secretion (Sapolsky et al., 2000). Glucocorticoids, and thus the stress response, are important candidates for linking vertebrate coping mechanisms to weather-related changes in the environment and are the focus of this review. Our goal was to determine whether evidence from the literature supports a role for glucocorticoids in transducing inclement weather conditions to physiological and behavioral coping responses.

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* Corresponding author.
E-mail addresses: RobertdeBruijn@cunet.carletonc.ca (R. de Bruijn), michael.romero@tufts.edu (L.M. Romero).

1.1. Acute stress

Animals respond to potentially noxious stimuli with a suite of behavioral and physiological changes, collectively called the stress response (Sapolsky et al., 2000). A major component is the hypothalamic-pituitary-adrenal (HPA-) axis, which is activated slowly over minutes to hours (Sapolsky et al., 2000). Activation of the HPA-axis consists of a hormonal cascade, culminating in the release of glucocorticoids from adrenal or interrenal tissue, depending upon the species. The main glucocorticoid in fish and most mammals is cortisol, whereas in rodents, amphibians, reptiles and birds it is corticosterone (both abbreviated as CORT).

At basal concentrations CORT is thought to be important for regulating normal daily and seasonal metabolic, behavioral, and physiological adjustments (Landys et al., 2006; Romero and Wingfield, 2016). A minimum concentration of CORT is necessary for survival, as adrenalectomized rats cannot cope even with mild stressors (Darlington et al., 1990). Additionally, many species seasonally modulate basal CORT concentrations (Romero, 2002), which may help animals fine-tune their physiology to differential demands during different life history stages.

Once an animal perceives a stressor, CORT concentrations start to increase above basal. Increases in plasma CORT in response to a stressor have been measured in all vertebrate taxa, although the speed of the response appears to differ between the taxonomic groups (Cockrem, 2013). For example, while CORT had not increased in response to capture in amphibians after 10 min (Mosconi et al., 2006), in birds CORT responses to capture have been found in less than three minutes (Romero and Reed, 2005). At stress-induced levels, CORT is thought to shift an animal's behavior and physiology towards what is called an emergency life-history stage (Wingfield et al., 1998). The stress response thus temporarily interrupts normal life-history functions in order to redirect and mobilize energy in order to allow the animal to adequately respond to the stressor, after which the animal can return to normal activities (Wingfield et al., 1998). Once the threat has passed, the HPA-axis quickly shuts off via a negative feedback loop, where CORT effectively shuts down its own production (Dallman and Bhatnagar, 2001; Romero, 2004; Sapolsky et al., 2000) and the animal returns to a normal life-history stage (Wingfield et al., 1998).

1.2. Chronic stress

Whereas the acute increase in CORT is considered to be an adaptive response that helps animals cope with stressors, repeated or chronic exposure to CORT is associated with negative consequences (Sapolsky et al., 2000). Chronic stress occurs when the mediators of stress, such as CORT, become disruptive themselves (Romero et al., 2009). For example, prolonged exposure to CORT can disrupt reproduction (Berga, 2008), suppress the immune system (Dhabhar and McEwen, 1997) and dysregulate the HPA-axis itself (Dickens and Romero, 2013). Eventually the stress response will become maladaptive and thus hamper instead of aid in survival (McEwen, 1998).

Unfortunately, there is no consensus CORT response for chronic stress, as prolonged or repeated exposure to a variety of stressors can result in increases, decreases or no changes in CORT (Dickens and Romero, 2013). Consequently, there is no generic or diagnostic CORT profile of a chronically stressed animal, although individual species may show consistent profiles. Furthermore, there is no clear consensus in the literature about when elevated CORT concentrations shift from indicating a beneficial acute response to a detrimental chronic response. This is especially a problem because CORT levels can vary significantly between species and across seasons, which means that direct comparisons between absolute values are difficult.

1.3. Examining the CORT response to weather-related stimuli

In this review, we aimed to examine what is known about CORT responses of animals to different ecological stimuli associated with changes in weather. Because we are interested in the relationship between CORT and weather-related stimuli, it is important to keep in mind that the focus of this review is not just on basal levels of CORT. Instead we will discuss CORT levels after exposure to one of the stimuli of interest. This will include both acute and long-term changes in CORT associated with acute and long-term exposure. Unfortunately, there is no consensus in the stress literature about what constitutes acute versus long-term responses. For example, it seems obvious that elevated levels of CORT after 30 min of restraint are indicative of acute stress and that changes in CORT after exposure of over a month would constitute chronic stress. However, very little is known about when this shift happens. Furthermore, while long-term changes in CORT levels may indicate chronic stress, this is not consistently true (Dickens and Romero, 2013) and will ultimately depend on whether or not such a change has negative effects on fitness. We have therefore decided to focus on including only the first CORT measurement after exposure to a stimulus and thus assume that any changes found reflect the impact of that stimulus. Note, however, that the first measurement might be defined as basal or baseline in the specific study, but except under very acute conditions, that sample likely reflects the longer-term chronic stress. We thus hoped to further clarify the role of CORT as an important physiological mechanism linking vertebrates and their environment. We were especially interested in comparing correlational with experimental studies and in comparing the responses of free-roaming animals to the response of captive wild animals. The overall goal was to determine whether there is a consensus response across different types of weather-related stimuli, stimulus exposure durations, taxonomic groups, and study types (i.e., utilizing domesticated laboratory, wild captive, or free-ranging animals).

2. Methods

2.1. Paper selection

Included studies were identified using Scopus, Web of Science and Google Scholar by using the following search terms: glucocorticoid/cortisol/corticosterone, stress, temperature/cold/hot, precipitation/rain/snow, barometric/air pressure and food availability/food restriction/starvation, in any combination with Amphibian/Reptile/Fish/Bird/Mammal. Furthermore, we backtracked references from papers found in these database searches to cast as wide a net as possible. Our focus was on primary literature, as we were mainly interested in articles that reported both detailed methodology and CORT measurements.

2.2. Criteria for inclusion

In order to be able to judge the effect of the stimuli of interest on changes in CORT, we excluded articles if a stimulus was combined with any other stimulus, or if a stimulus was examined during physiological life history stages that could possible confound the effects on CORT, such as pregnancy and hibernation. We further restricted our search to exclude papers where the effect of a stimulus of interest was combined with injections of drugs or chemicals, for example exogenous CORT, where stimuli were examined in combination with infectious diseases, or forced exercise, and we excluded studies using selectively bred lines. Finally, we focused our search on literature after 1970. A total of 385 data points from 316 studies met these criteria and form the basis for this review.

2.3. Duration of exposure

In order to further analyze the role of CORT in response to weather-

related stimuli, we separated studies based on the time period in which the stimulus was experienced. As it is unclear when CORT concentrations shift between baseline, stress induced, and chronic levels, as described above, we decided to separate exposure times into four different categories, namely less than 24 h (Hours), between one and seven days (Days), from a week up to a month (Weeks) and longer than a month (Months), which also includes seasonal patterns. Combined with the fact that weather-related data are often reported on the same time scales, we feel that these categories represent the most useful time periods to study the CORT response to weather-related stimuli.

2.4. Nature of the study – free-living, wild captive, domestic laboratory

The nature of the study can have an important impact on the implications of the results. Studying animals in their natural environment is likely to give the best representation of how they will respond to and be able to cope with weather-related events. However, by definition such studies will be correlational and it may therefore be difficult to separate the effects of the stimulus of interest from any confounding factors. It is also often difficult to track individual animals, which may further introduce confounding factors. Researchers have attempted to minimize such limitations by introducing experimental manipulations in field studies, by bringing animals into captivity, or a combination of both. While field manipulation studies allow researchers to study the responses of free-roaming animals to specific stimuli, such studies often incur considerable cost and are subject to substantial technological limitations, which may explain why we discovered relatively few such studies. Laboratory-based experimental studies allow for much better control of the stimulus of interest and, when designed properly, allow researchers to significantly reduce or even eliminate any potentially confounding factors. However, while captivity makes it easier to track individual animals, captivity itself can have considerable effects on HPA-axis functioning (Baker et al., 1998; Cockrem and Silverin, 2002; Dickens and Romero, 2009; Lattin et al., 2012). Similarly, domesticated animals show attenuated HPA-axis functioning (e.g., Kunzl and Sachser, 1999), which can already be apparent in the first captive bred generation (e.g., Cabezas et al., 2012). To summarize: while field correlational studies may provide direct insights into how animals naturally respond to changes in their environment, this comes at a cost to specificity; conversely, while laboratory-based experimental studies (using either wild captive or domesticated species) allow for the most control of the stimulus of interest, the effect of captivity or domestication raises questions about the applicability of the findings of such studies to free-roaming animals in their natural environment. We therefore separated studies into four different categories: field manipulation, field correlation, wild in captivity and domesticated laboratory studies.

2.5. Glucocorticoid sampling method

While most studies measure CORT in plasma samples, in recent years several techniques have become available that have made it possible to measure CORT in feces (Palme, 2005; Wasser et al., 2000), urine (Germano et al., 2012; Narayan, 2013), hair (e.g., Davenport

et al., 2006) and feathers (Bortolotti et al., 2008; Romero and Fairhurst, 2016). Each of these techniques has advantages, such as non-invasive sampling, and disadvantages, such as they often give a more integrated measure of CORT over a longer period of time (Sheriff et al., 2011). Furthermore, these measures of CORT can be influenced by a variety of factors, such as food and water intake (Kalliokoski et al., 2015; Morrow et al., 2002), bacterial degradation (e.g., Goymann, 2012) and sample exposure to the environment (e.g., Wilkening et al., 2016). Regardless of any difficulty in correlating CORT in these other biological matrices to blood, each study is presumed to be internally consistent. By reducing all results to a simple increase, decrease, or no change (see below), we capture that internal consistency and minimize any potential confounds arising from unknown connections to CORT in the blood. While the number of studies using such alternative methods is currently few, we attempted to evaluate if sampling method is an important covariate in any response patterns.

2.6. Synthesis of findings

In order to examine the effects of each stimulus on CORT responses, we assigned each study a score of "1" if an increase in CORT was reported, a "0" if no correlation was reported, and a "−1" if a decrease in CORT was reported. We then averaged the responses for each stimulus for each time period (i.e., Hours, Days, Weeks, Months) the stimulus was applied, to evaluate whether the literature supports a consensus CORT response. However, even if a consensus response exists, the average can result from any combination of increases, decreases or no changes and therefore does not provide any information about the variation in reported responses. For example, 10 studies with no change would give the same average response as 5 studies with an increase and 5 studies with a decrease in CORT. Consequently, we graphed each individual study around the average response, thus giving a visual representation of the spread in responses. It is important to note that some papers have contributed multiple data points. This can be due to a single study testing multiple species or time points, or because the response to more than one stimulus was examined. Since we were specifically interested in the response in every species and at every time point, we decided to treat each reported result as an individual data point. Finally, although variance can be calculated for ordinal data, such as the scores in this review, with only 3 potential responses the variance itself is not very informative. It will either span or not span all 3 responses. An overview of the total number of studies included in this review for each weather-related stimulus and separated by taxonomic group is given in Table 1.

2.7. Statistical analysis

This review is not a meta-analysis of the CORT responses to weather-related stressors. In order to perform such a meta-analysis, we would require effect sizes for the studies included. However, most studies in the stress literature do not report effect sizes, which makes this currently impossible. Instead, the review focused on whether or not overall patterns exist in the CORT responses to weather-related stimuli.

Table 1
Stressor and taxonomic breakdown. Overview of the number of studies for each stimulus separated by taxonomic group. Dashes represent categories, which did not turn up any results in the literature search, likely because these stimuli are not expected to directly affect those taxonomic groups. Total numbers are given for each stimulus and taxonomic group.

	Food Availability	Temperature Cold	Temperature Heat	Precipitation	Barometric Pressure	Taxa Totals
Amphibians	8	1	6	–	–	15
Reptiles	6	10	2	3	–	21
Fish	39	19	17	–	–	75
Birds	70	34	15	24	3	146
Mammals	36	42	30	20	–	128
Stressor Totals	159	106	70	47	3	385

Table 2
Food availability. List of the studies that have measured CORT responses after a decrease in food availability. Papers are grouped by exposure time, study type, Taxon, and the biological matrix from which CORT was measured ("body" indicates CORT was measured from the entire body of the individual). See text for descriptions of Study Type (manip. = manipulative, corr. = correlational). For response, −1 = CORT decrease; 0 = no change in CORT; 1 = CORT increase.

	Study Type	Taxon	CORT matrix	Response	Reference
Hours	Field manip.	Birds	Blood	1	(Saino et al., 2003)
	Field corr.	Birds	Blood	1	(Jenni-Eiermann et al., 2008)
	Wild captive	Birds	Blood	−1	(Kitaysky et al., 2005)
	Wild captive	Birds	Blood	1	(Lynn et al., 2003)
	Wild captive	Birds	Blood	1	(Strochlic and Romero, 2008)
	Wild captive	Birds	Blood	1	(Krause et al., 2017)
	Wild captive	Fish	Blood	0	(Hoseini et al., 2014)
	Domestic lab	Birds	Blood	0	(Wall and Cockrem, 2009)
	Domestic lab	Birds	Blood	1	(Freeman et al., 1980)
	Domestic lab	Birds	Blood	1	(Lynn et al., 2010)
	Domestic lab	Birds	Blood	1	(Scanes et al., 1980)
	Domestic lab	Birds	Blood	1	(Nir et al., 1975)
	Domestic lab	Birds	Blood	1	(Geris et al., 1999)
	Domestic lab	Mammals	Blood	1	(Djordjevic et al., 2008a,b)
	Domestic lab	Mammals	Blood	1	(Ogias et al., 2010)
	Domestic lab	Mammals	Blood	1	(Ventura, 1982)
	Domestic lab	Mammals	Blood	1	(Murphy and Wideman, 1992)
	Domestic lab	Fish	Blood	0	(Barcellos et al., 2010)
Days	Field manip.	Birds	Blood	0	(Angelier et al., 2015)
	Field manip.	Birds	Blood	1	(de la Mora et al., 1996)
	Field corr.	Birds	Blood	1	(Barrett et al., 2015)
	Wild captive	Birds	Blood	0	(Schwabl, 1995)
	Wild captive	Birds	Blood	0	(Will et al., 2014)
	Wild captive	Birds	Feather	0	(Will et al., 2014)
	Wild captive	Birds	Blood	1	(Astheimer et al., 1992)
	Wild captive	Birds	Blood	1	(Yadav and Haldar, 2014)
	Wild captive	Birds	Blood	1	(Lendvai et al., 2014)
	Wild captive	Birds	Blood	1	(Sears and Hatch, 2008)
	Wild captive	Reptiles	Blood	−1	(French et al., 2007)
	Wild captive	Fish	Blood	0	(Sinnett and Markham, 2015)
	Wild captive	Fish	Blood	1	(Hoseini et al., 2014)
	Wild captive	Fish	Body	1	(Piccinetti et al., 2015)
	Wild captive	Fish	Blood	1	(Abdelghany, 1993)
	Wild captive	Amphibian	Blood	−1	(Crespi and Denver, 2005)
	Wild captive	Amphibian	Body	1	(Crespi and Denver, 2005)
	Domestic lab	Birds	Blood	1	(Rees et al., 1985)
	Domestic lab	Birds	Blood	1	(Freeman et al., 1981)
	Domestic lab	Birds	Blood	1	(Mench, 1991)
	Domestic lab	Mammals	Blood	1	(Johansson et al., 2008)
	Domestic lab	Mammals	Blood	1	(Djordjevic et al., 2003)
	Domestic lab	Mammals	Blood	1	(Nishiyama et al., 2008)
	Domestic lab	Mammals	Blood	1	(Lerner et al., 1986)
	Domestic lab	Mammals	Blood	1	(Tang et al., 1984)
	Domestic lab	Mammals	Blood	1	(Makino et al., 2001)
	Domestic lab	Mammals	Blood	1	(Lonati-Galligani, 1988)
	Domestic lab	Mammals	Blood	1	(Hao et al., 2000)
	Domestic lab	Mammals	Blood	1	(Suemaru et al., 1986)
	Domestic lab	Fish	Blood	0	(Elabd et al., 2016)
	Domestic lab	Fish	Blood	0	(Ramsay et al., 2009)
	Domestic lab	Fish	Blood	0	(Breves et al., 2016)
	Domestic lab	Fish	Blood	0	(Kim et al., 2014)
	Domestic lab	Fish	Blood	1	(Barcellos et al., 2010)
	Domestic lab	Amphibian	Body	1	(Glennemeier and Denver, 2002)
Weeks	Field manip.	Birds	Blood	−1	(Madliger et al., 2015)
	Field manip.	Birds	Blood	0	(Williams et al., 2008)
	Field manip.	Birds	Blood	1	(Schoech et al., 2004)
	Field corr.	Birds	Blood	0	(Krause et al., 2016)
	Field corr.	Birds	Blood	1	(Krause et al., 2016)
	Field corr.	Birds	Blood	1	(Kitaysky et al., 2007)
	Field corr.	Birds	Feather	1	(Will et al., 2014)
	Field corr.	Mammals	Feces	1	(Schoof et al., 2016)
	Wild captive	Birds	Blood	−1	(Kitaysky et al., 2005)
	Wild captive	Birds	Blood	−1	(Le Ninan et al., 1988a)
	Wild captive	Birds	Blood	−1	(Bauer et al., 2011)
	Wild captive	Birds	Blood	0	(Bauer et al., 2011)
	Wild captive	Birds	Blood	0	(Valle et al., 2015)
	Wild captive	Birds	Blood	0	(Bridge et al., 2009)
	Wild captive	Birds	Blood	1	(Will et al., 2014)
	Wild captive	Birds	Blood	1	(Kempster et al., 2007)
	Wild captive	Birds	Blood	1	(Pravosudov and Kitaysky, 2006)
	Wild captive	Birds	Blood	1	(Fokidis et al., 2011)

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Table 2 (*continued*)

	Study Type	Taxon	CORT matrix	Response	Reference
	Wild captive	Birds	Blood	1	(Fokidis et al., 2012)
	Wild captive	Birds	Blood	1	(Kitaysky et al., 2001)
	Wild captive	Birds	Blood	1	(Kitaysky, 1999)
	Wild captive	Birds	Blood	1	(Kitaysky et al., 2006)
	Wild captive	Birds	Blood	1	(Strochlic and Romero, 2008)
	Wild captive	Mammals	Feces	−1	(Taillon and Cote, 2008)
	Wild captive	Reptiles	Blood	0	(Cote et al., 2010)
	Wild captive	Reptiles	Blood	1	(Webb et al., 2017)
	Wild captive	Amphibian	Body	1	(Warne and Crespi, 2015)
	Domestic lab	Birds	Blood	0	(Spencer et al., 2003)
	Domestic lab	Birds	Blood	1	(Carsia et al., 1988)
	Domestic lab	Birds	Blood	1	(Carsia and McIlroy, 1998)
	Domestic lab	Birds	Blood	1	(Carsia and Weber, 2000)
	Domestic lab	Birds	Blood	1	(Savory and Mann, 1997)
	Domestic lab	Birds	Blood	1	(Marasco et al., 2015)
	Domestic lab	Birds	Blood	1	(de Jong et al., 2002)
	Domestic lab	Mammals	Blood	1	(Stewart et al., 1988)
	Domestic lab	Mammals	Blood	1	(Garcia-Belenguer et al., 1993)
	Domestic lab	Mammals	Blood	1	(Chacon et al., 2005)
	Domestic lab	Mammals	Blood	1	(Diaz-Munoz et al., 2000)
	Domestic lab	Mammals	Blood	1	(Ventura, 1982)
	Domestic lab	Mammals	Blood	1	(Conn et al., 1995)
	Domestic lab	Mammals	Blood	1	(du Dot et al., 2009)
	Domestic lab	Mammals	Blood	1	(Challet et al., 1995)
	Domestic lab	Mammals	Blood	1	(Marinkovic et al., 2007)
	Domestic lab	Mammals	Blood	1	(Johansson et al., 2008)
	Domestic lab	Mammals	Blood	1	(Ling and Bistrian, 2009)
	Domestic lab	Mammals	Blood	1	(Lonati-Galligani, 1988)
	Domestic lab	Mammals	Blood	1	(Belda et al., 2005)
	Domestic lab	Fish	Blood	−1	(Small, 2005)
	Domestic lab	Fish	Blood	0	(Caruso et al., 2011)
	Domestic lab	Fish	Blood	0	(Breves et al., 2016)
	Domestic lab	Fish	Blood	0	(Gavassa and Stoddard, 2012)
	Domestic lab	Fish	Blood	0	(Caruso et al., 2011)
	Domestic lab	Fish	Blood	0	(Caruso et al., 2011)
	Domestic lab	Fish	Blood	0	(Sumpter et al., 1991)
	Domestic lab	Fish	Blood	0	(Kim et al., 2014)
	Domestic lab	Fish	Blood	0	(Holloway et al., 1994)
	Domestic lab	Fish	Blood	1	(Peterson and Small, 2004)
	Domestic lab	Fish	Blood	1	(Gimbo et al., 2015)
	Domestic lab	Fish	Blood	1	(Barcellos et al., 2010)
	Domestic lab	Fish	Blood	1	(Costas et al., 2011)
	Domestic lab	Fish	Blood	1	(Kelley et al., 2001)
	Domestic lab	Fish	Blood	1	(Vijayan et al., 1996)
	Domestic lab	Fish	Blood	1	(Sangiao-Alvarellos et al., 2005)
	Domestic lab	Fish	Blood	1	(Caruso et al., 2012)
	Domestic lab	Fish	Body	1	(Chase et al., 2016)
	Domestic lab	Fish	Body	1	(Wunderink et al., 2012)
	Domestic lab	Amphibian	Body	0	(Crespi et al., 2004)
	Domestic lab	Amphibian	Body	1	(Hu et al., 2008)
Months	Field corr.	Birds	Blood	1	(Wingfield et al., 1999)
	Field corr.	Birds	Blood	1	(Herring and Gawlik, 2013)
	Field corr.	Birds	Blood	1	(Doody et al., 2008)
	Field corr.	Birds	Blood	1	(Le Ninan et al., 1988b)
	Field corr.	Birds	Blood	1	(Franci et al., 2015)
	Field corr.	Birds	Blood	1	(Walker et al., 2005)
	Field corr.	Birds	Blood	1	(Kitaysky et al., 2007)
	Field corr.	Mammals	Blood	1	(Ortiz et al., 2001)
	Field corr.	Mammals	Feces	1	(Berghanel et al., 2016)
	Field corr.	Reptiles	Blood	1	(Romero and Wikelski, 2001)
	Wild captive	Birds	Blood	0	(Heath and Dufty, 1998)
	Wild captive	Birds	Blood	0	(Valle et al., 2015)
	Wild captive	Birds	Blood	1	(Pravosudov et al., 2001)
	Wild captive	Birds	Blood	1	(Cherel et al., 1988)
	Wild captive	Birds	Blood	1	(Lyons and Roby, 2011)
	Wild captive	Reptiles	Blood	0	(Neuman-Lee et al., 2015)
	Wild captive	Reptiles	Blood	0	(Carsia et al., 2012)
	Wild captive	Amphibian	Blood	1	(Reeve et al., 2013)
	Wild captive	Amphibian	Body	1	(Crespi and Warne, 2013)
	Domestic lab	Birds	Blood	1	(Hocking et al., 1999)
	Domestic lab	Birds	Blood	1	(Rajman et al., 2006)
	Domestic lab	Birds	Blood	1	(Marasco et al., 2015)
	Domestic lab	Birds	Blood	1	(Kubikova et al., 2001)
	Domestic lab	Mammals	Blood	1	(Stewart et al., 1988)
	Domestic lab	Mammals	Blood	1	(Stewart et al., 1988)

Table 2 (*continued*)

Study Type	Taxon	CORT matrix	Response	Reference
Domestic lab	Mammals	Blood	1	(Wan et al., 2003)
Domestic lab	Mammals	Blood	1	(Lenglos et al., 2013)
Domestic lab	Mammals	Blood	1	(Jahng et al., 2007)
Domestic lab	Mammals	Blood	1	(Armario et al., 1987)
Domestic lab	Fish	Blood	0	(Kim et al., 2014)
Domestic lab	Fish	Blood	0	(Farbridge and Leatherland, 1992)
Domestic lab	Fish	Blood	0	(Sumpter et al., 1991)
Domestic lab	Fish	Blood	0	(Pottinger et al., 2003)
Domestic lab	Fish	Blood	0	(Milne et al., 1979)
Domestic lab	Fish	Blood	1	(Abdel-Tawwab, 2016)
Domestic lab	Fish	Blood	1	(Jorgensen et al., 2002)
Domestic lab	Fish	Blood	1	(Blom et al., 2000)
Domestic lab	Fish	Blood	1	(Caruso et al., 2010)

Furthermore, we wanted to include vertebrate taxa, different study types, exposure duration and sampling methods as co-variates in order to establish whether these variables affected any putative consensus response to any of the stimuli. Because absolute CORT levels, as well as HPA-axis responsiveness, vary dramatically between species, direct comparisons of CORT response effect sizes are very difficult. We attempted to analyze differences across and within time periods for each stimulus using Chi-squared contingency tables, but sample size was very low in many categories (see Table 1), which violates the assumptions of the Chi-squared test and thus makes these tests invalid. Potential solutions to increase sample sizes for the contingency tables, such as collapsing time periods (e.g., combining Hours and Days, etc.) or CORT responses (e.g., combining no change with a decrease, etc.) are inappropriate, and in any event still leave many categories with insufficient sample sizes. In addition, such collapsing of categories would obscure details, such as studies showing responses opposite to the majority, which may provide interesting insights into specific stressors, time periods, sampling methods or taxonomic groups. We have therefore decided to focus on qualitative descriptions of the CORT responses to weather-related stimuli.

3. Responses to changes in food availability

3.1. Brief review of relationship of CORT to weather impacts on food availability

While changes in food availability are not a direct characteristic of weather, weather often affects food availability. For example, precipitation (Denlinger, 1980) and temperature (Arun and Vijayan, 2004; Chung et al., 2013) can influence food abundance or foraging opportunities both positively and negatively. There is a rich history of studying the effects of CORT with changes of food abundance. Basal levels of CORT are thought to be important for regulating normal metabolic changes (Landys et al., 2006; Sapolsky et al., 2000) and a minimum level of CORT is necessary for survival, as adrenalectomized rats cannot cope with mild stressors (Darlington et al., 1990). Consequently, we would expect basal CORT levels to change in response to periods of reduced food availability, and at least in seabirds, this appears to be the case (Sorenson et al., 2017). However, short-term (hours) and long-term (weeks, months) periods of reduced food availability are thought to be regulated differently. Prolonged food deprivation or starvation can be divided into three separate phases (Cherel et al., 1988; Goodman et al., 1980, 1981). Briefly, phase I consists of glucose metabolism, phase II shifts to fatty acid metabolism once glucose has been exhausted, and phase III shifts metabolism to protein breakdown after fatty acids are depleted (Romero and Wingfield, 2016). Mediators involved in the adaptive response to food restriction in phase I and II, such as CORT, are thought to become maladaptive in

phase III when these mediators start breaking down essential proteins (Romero, 2012; Romero et al., 2009).

Many vertebrate species undergo natural periods of fasting in response to predictable periods of low food availability (Newton, 1998), such as penguins (Groscolas and Robin, 2001) and fish (McCue, 2010). Since increased CORT levels can have negative effects on health and survival (Sapolsky et al., 2000), species undergoing such predictable fasting periods may have evolved alternative coping mechanisms and as such may actually prevent CORT levels from increasing to prevent the negative effects associated with prolonged exposure to elevated CORT levels (Romero et al., 2009). While we excluded studies that contained potentially confounding factors such as hibernation (Ultsch, 1989), we did not exclude studies of species that experience natural periods of fasting without known confounding factors, as their responses may give important insights in the role CORT plays in linking food availability to survival mechanisms.

Finally, food availability may be an important supplementary cue for timing of breeding (Young, 1994). Food availability can function as a zeitgeber for the circadian rhythm in house sparrows (*Passer domesticus*; Hau and Gwinner, 1996) and food supplementation can advance egg-laying dates in birds (Schoech and Hahn, 2008). Food availability is also often considered the limiting factor for individual breeding success, survival, and population growth and may therefore play an important role in population dynamics (Boutin, 1990). Since CORT can suppress the reproductive system (Sapolsky et al., 2000), CORT may be an important mechanism linking food availability to timing of breeding (Lattin et al., 2016). Considering the important role CORT plays in basic metabolic regulation and the effects weather has on food availability and foraging opportunities, we have therefore included food availability as one of the stimuli in this review, even though it is not a direct characteristic of weather.

The studies that examined CORT responses to different durations of exposure to reduced food availability are presented in Table 2, with studies broken down by study type and taxonomic group in Table 3. Most data points represent laboratory-based studies (56%), although there are a substantial number of captivity-based studies as well (30%; Table 3). Furthermore, most data points involve either birds (44%), fish (25%) or mammals (23%; Table 3).

3.2. Results

Results are shown in Fig. 1. Overall, CORT is increased in response to up to 24 h of reduced food availability (78%). The few studies that show no change or a decrease are some interesting exceptions. For example, in the two studies that examined fasting in a taxonomic group other than mammals or birds, 6–24 h of fasting did not cause any changes in CORT in captive fish (Barcellos et al., 2010; Hoseini et al., 2014), although CORT did increase after longer periods of fasting in

both studies. In addition, the single study (Kitaysky et al., 2005) that reported a decrease in CORT, examined captive juvenile tufted puffins (*Fratercula cirrhata*), which may be connected to a 50% decrease in metabolism in response to short-term food deprivation (Kitaysky et al., 1999). While the mechanisms for this reduction in metabolism are unclear, these chicks naturally experience periods of intermittent food availability (Kitaysky et al., 2005). Other examples would be useful to determine whether energy conserving coping mechanisms might serve as a generalized buffer for species that naturally experience forced fasts.

CORT also generally (69%) increased in response to one to seven days of reduced food availability (Fig. 1). Many of the exceptions again appear related to species adapted to short periods of fasting resulting from large variation in food availability in the natural environment. For example, CORT was found to increase in tadpoles but decrease in juvenile Western spadefoot toads (*Spea hammondii*) after 5 days of food restriction (Crespi and Denver, 2005). Whereas tadpoles would be predicted to have become adapted for rapid growth, juvenile toads likely cope with prolonged periods of fasting, and thus may be evolved towards conserving energy instead (Newman and Dunham, 1994).

The period examining the CORT response to reduced food availability for one to four weeks is the most extensively studied time frame for this stimulus. Most studies report an increase in CORT (68%), but there is more variation when compared to the shorter time periods, as several studies report no change or a decrease (Fig. 1). Laboratory-based studies generally report increased CORT, but many of the field-based studies also show CORT increases. In contrast, a similar theme to the shorter time frames (hours and days) is evident at this time frame. Many of the studies that show decreases in CORT are in species naturally exposed to fasting or intermittent food availability. These include white-tailed deer that can withstand extreme deterioration of body condition (Taillon et al., 2006) with no changes in CORT (Taillon and Cote, 2008) and seabird chicks such as penguins (Le Ninan et al., 1988a) and tufted puffins (Kitaysky et al., 2005).

Finally, the period examining the CORT response to reduced food availability for more than four weeks is also generally associated with increased CORT (76%), and while there are a few studies reporting no change, no study to date has reported a decrease in CORT (Fig. 1). Of the studies that did not show a CORT change, one is especially interesting. CORT did not change in spiny lizards (*Sceloporus jarrovii*) after 10 weeks of food restriction (Carsia et al., 2012), which is in sharp contrast with the increase found in marine iguanas (*Amblyrhynchus cristatus*) that were starving during a severe El Niño (Romero and Wikelski, 2001). The difference between these two studies suggests that the CORT response may be dependent on the severity of the food restriction. This fits with the previously described physiological changes associated with a shift from starvation phase II to starvation phase III (Romero et al., 2009).

Table 3
Food availability. Summary of the number of studies examining the effect of food availability on glucocorticoid levels in all five vertebrate taxa. Studies have further been divided into the four different study types described in the methods section. Total numbers are given for each taxonomic group and study type.

	Mammals	Birds	Fish	Reptiles	Amphibians	Study Type Totals
Field Manipulative	–	6	–	–	–	6
Field Correlational	3	13	–	1	–	17
Wild in Captivity	1	31	5	5	5	47
Domesticated Laboratory	32	20	34	–	3	89
Taxa Totals	36	70	39	6	8	159
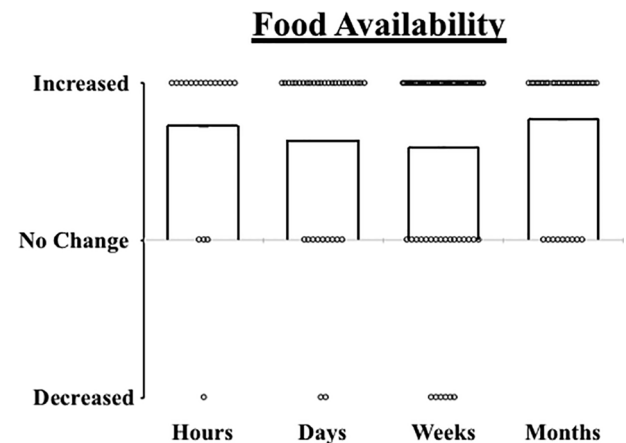
Fig. 1. Glucocorticoid responses of vertebrates to reduced food availability at four different time intervals, e.g., hours, days, weeks and months. The bars represent the average response for each time interval, while the symbols represent the direction of change for each data point for this stimulus included in this review. Glucocorticoid levels can be increased, not changed or decreased. Total number of data points is reported for each category for each time period. Some articles examined the response during multiple time periods, or for multiple species and those studies are therefore represented more than once, which means the number of data points is not a representation of the total number of articles included in the analysis.

3.3. Food addition

There are only a few studies that report CORT responses to supplemental feeding, both in birds (Clinchy et al., 2004; Lothery et al., 2014; Schoech et al., 2007, 2004) and mammals (Forristal et al., 2012; Saltz and White, 1991). Since there are so few studies of this kind, they have not been included in the larger analysis. However, there is no overall consistent response for supplemental feeding on CORT levels. For example, supplemental feeding correlated with a decrease in CORT in captive Mule deer (*Odocoileus hemionus*; Saltz and White, 1991), but an increase in free-roaming Elk (*Cervus elaphus*; Forristal et al., 2012)). Forristal et al. (2012) suggested that the increased density of Elk on the feeding grounds may lead to more intense competition or persistence of infectious diseases, leading to increases in CORT. Similarly, in both song sparrows (Clinchy et al., 2004) and Florida Scrub-jays (Schoech et al., 2004), food supplementation in the field was associated with decreased CORT, although food supplementation may only have an effect if natural food abundance is below optimum (Schoech et al., 2007), but supplementing house wrens had no impact on CORT, although supplementation also did not alter breeding success (Lothery et al., 2014).

3.4. Conclusion for impacts of food availability

Reduction in food availability generally appears to be associated with increased levels of CORT (71% of included data points), regardless of the duration (Fig. 1). The literature, therefore, clearly suggests that low food availability is perceived as a stressor by most animals. Furthermore, this supports our hypothesis that CORT may be an important physiological regulator linking changes in food availability to both stress coping mechanisms and timing of life history stages, such as breeding (Lattin et al., 2016).

The role of increased CORT during food restriction is highlighted by the exceptions. A small minority of studies show either no change or a decrease in CORT. Interestingly, many such studies examined species that experience periods of low food availability in their natural environment. This suggests that coping mechanisms for food restriction are different in these animals. The data are consistent with the hypothesis that species that experience predictable periods of low food

availability as part of their normal life history have evolved to dampen the HPA/HPI-axis during nutritional challenge. The function of this dampening could be to prevent the negative effects of prolonged exposure to increased CORT levels (Romero et al., 2009; Sapolsky et al., 2000) or to promote an energy-saving reduction in metabolism (Cherel et al., 2004) by reducing the role CORT has as an important basal metabolic regulator (Landys et al., 2006; Sapolsky et al., 2000). Clearly more work is needed in order to elucidate the role CORT plays in this context.

Furthermore, CORT responses may depend on the severity (Spencer et al., 2003; Williams et al., 2008) or the intermittent nature (Bridge et al., 2009) of the food restriction. If the restriction is not too severe, animals may be able to compensate by eating more and faster. Alternatively, prolonged reduced food availability may not require activation of the HPA-axis in order to cope with the reduced food intake in some species. There are several pieces of evidence that support the hypothesis that these species may adopt energy conserving strategies, which would reduce the need for changes in CORT, which may be important to prevent the negative effects normally associated with prolonged exposure to elevated CORT (Romero et al., 2009; Sapolsky et al., 2000). For example, after 31 days of food restriction in frogs, neither blood glucose levels, or body weight had changed (Crespi et al., 2004), suggesting these frogs successfully reduced energy metabolism. Similarly, many fish do not lose body mass during starvation, which suggests these animals have adapted to periods of fasting (Bar, 2014), as food availability can be highly variable in some environments (McCue, 2010). Short-lived fish may also down-regulate their HPI-axis to prevent CORT from intervening with breeding efforts (Gavassa and Stoddard, 2012; Wingfield and Sapolsky, 2003).

The response to reduced food availability also may be dependent on life-history stage. For example, food restriction was associated with a decrease in CORT in molting, but not in non-molting, captive European starlings (Bauer et al., 2011). The HPA-axis appears down regulated in molting starlings in general (Cyr et al., 2008), which may be important for feather quality (DesRochers et al., 2009), as CORT may have negative effects on protein synthesis, the main component of feathers (Romero et al., 2005). However, both non-molting and molting starlings increased in weight during the three weeks of intermittent food-restriction, suggesting that the birds managed to compensate for the reduced feeding time by either increasing food intake or reducing activity (Bauer et al., 2011).

Unfortunately, few studies have examined the CORT response to food restriction in amphibians and reptiles and there are no short-term studies, so it remains unclear if food removal is perceived as an acute stressor in these taxonomic groups. More work should be done before we can determine if the CORT response to reduced food availability in amphibians and reptiles are comparable to the responses found in fish, birds and mammals.

4. Responses to changes in precipitation

4.1. Brief review of relationship of CORT to precipitation

Precipitation is an important aspect of inclement weather that can affect animals both directly and indirectly. Examples of direct effects include two-fold increases in flight metabolism in bats (Voigt et al., 2011) and hummingbirds significantly changing their flight characteristics during heavy rain (Ortega-Jimenez and Dudley, 2012). Additionally, artificial rainfall induces increases in metabolism in Bald Eagles (*Haliaeetus leucocephalus*; Stalmaster and Gessaman, 1984) and American kestrels (*Falco sparverius*; Wilson et al., 2004). Finally wetting-induced hypothermia increases peak oxygen consumption in birds and may eventually lead to reduced survival (Lustick and Adams, 1977). Precipitation can also affect animals indirectly by altering foraging opportunities and prey abundance, such as insects. Consequently, unpredictable precipitation may have both direct and indirect

impacts on survival, especially in combination with low temperatures (Bumpus, 1899; Odum and Pitelka, 1939).

In contrast, predictable precipitation is often associated with positive effects. Although rain may reduce food availability in some environments, it may signal increased food availability and thus create more optimal conditions in others, such as dry or desert environments (Denlinger, 1980). As a consequence, precipitation is thought to be an important stimulus in timing of many life-history events. For example, both migration (Studds and Marra, 2011) and breeding (Zann et al., 1995) can be tied to predictable seasonal changes in precipitation. Examples like these led to the hypothesis that precipitation can act as a supplementary cue for synchronizing reproductive efforts with the most optimal breeding conditions (e.g., Wingfield and Ramenofsky, 2011). Because unpredictable and predictable precipitation have such different impacts, it is likely that there is a difference in the relationship to CORT as well.

No studies involving amphibians or fish are included in this section of the review. While precipitation may affect aquatic animals indirectly, for example by diluting pollutants or salinity, or creating a river in spate (Romero and Wingfield, 2016), these effects do not fit under any of the stimuli covered by this review and therefore are not covered here.

The studies that examined CORT responses to different durations of precipitation are presented in Table 4. While the number of studies reporting on the effects of precipitation is rather limited, the majority of data points included in the review represent field correlation studies (89%), while the rest are captivity-based (Table 5). Furthermore, most data points involve either mammals (43%) or birds (51%), with only 3 studies using reptiles (Table 5).

4.2. Results

Results are shown in Fig. 2. Short-term effects, up to 24 h, of precipitation on CORT have been studied only in birds and mammals to date. A majority of data points report CORT concentrations increasing with precipitation (64%), while five studies reported no change (Fig. 2). Four of these five studies suggest that responses could depend upon life-history stage. Three free-living arctic bird species increased CORT with precipitation while undergoing their post-breeding molt, but CORT did not increase while breeding (Romero et al., 2000). Artificial precipitation also failed to induce an increase in CORT in molting captive European starlings (de Bruijn and Romero, 2013). Although it is unclear why the CORT responses in these life-history stages were reversed in captive starlings and free-living arctic species, a consistent effect of molt suggests that animals might modulate their sensitivity to precipitation depending on life-history stage. Another factor that might modulate sensitivity to precipitation is food availability. A snowstorm was associated with increased CORT in siskins, but CORT rapidly returned to baseline after these birds spent time at a feeder (Astheimer et al., 1992).

There are only ten data points for the CORT response of vertebrates in correlation with precipitation patterns over the period of one to seven days. Only four of these report an increase in CORT, while the rest report no change (Fig. 2). The severity and duration of a storm may be important. For example, two days of light snowfall did not result in CORT changes, but a third day precipitated CORT increases and behavioral changes (Astheimer et al., 1995).

Interestingly, there is no clear pattern between changes in CORT and precipitation over a period of one to four weeks, as both increases and decreases have been reported, as well as no change (Fig. 2). This lack of a consensus response may result from the shift from negative to positive effects of precipitation occurring during this time period. Many of the studies that reported reduced CORT levels were associated with rainfall after a dry period, suggesting that for these species rainfall may reflect recovery from the stress of a drought.

Long-term precipitation patterns, over a period longer than four

Table 4

Precipitation. List of the studies that have measured CORT responses after the onset of precipitation. Papers are grouped by exposure time, study type, Taxon, and the biological matrix from which CORT was measured. See text for descriptions of Study Type (manip. = manipulative, corr. = correlational). For response, −1 = CORT decrease; 0 = no change in CORT; 1 = CORT increase.

	Study Type	Taxon	CORT matrix	Response	Reference
Hours	Field corr.	Birds	Blood	0	(Romero et al., 2000)
	Field corr.	Birds	Blood	0	(Romero et al., 2000)
	Field corr.	Birds	Blood	0	(Romero et al., 2000)
	Field corr.	Birds	Blood	0	(Astheimer et al., 1992)
	Field corr.	Birds	Blood	1	(Romero et al., 2000)
	Field corr.	Birds	Blood	1	(Romero et al., 2000)
	Field corr.	Birds	Blood	1	(Smith et al., 1994)
	Field corr.	Birds	Blood	1	(Bize et al., 2010)
	Field corr.	Birds	Blood	1	(Rogers et al., 1993)
	Field corr.	Birds	Blood	1	(Boyle et al., 2010)
	Field corr.	Birds	Blood	1	(Astheimer et al., 1992)
	Field corr.	Mammals	Feces	1	(Huber et al., 2003)
	Wild captive	Birds	Blood	0	(de Bruijn and Romero, 2013)
	Wild captive	Birds	Blood	1	(de Bruijn and Romero, 2013)
Days	Field corr.	Birds	Blood	0	(Muller et al., 2010)
	Field corr.	Birds	Blood	0	Romero et al., 2000
	Field corr.	Birds	Blood	0	Romero et al., 2000
	Field corr.	Birds	Blood	0	Romero et al., 2000
	Field corr.	Birds	Blood	0	Romero et al., 2000
	Field corr.	Birds	Blood	0	Romero et al., 2000
	Field corr.	Birds	Blood	1	Romero et al., 2000
	Field corr.	Birds	Blood	1	(Astheimer et al., 1995)
	Field corr.	Mammals	Blood	1	(Bauer et al., 2013)
	Wild captive	Mammals	Blood	1	(Meza-Herrera et al., 2007)
Weeks	Field corr.	Birds	Feces	0	(Pereira et al., 2010)
	Field corr.	Birds	Feather	−1	(Treen et al., 2015)
	Field corr.	Mammals	Feces	−1	(Lynch et al., 2002)
	Field corr.	Mammals	Feces	−1	(Foley et al., 2001)
	Field corr.	Mammals	Feces	−1	(Schoof et al., 2016)
	Field corr.	Mammals	Feces	−1	(Littlefield, 2010)
	Field corr.	Mammals	Feces	0	(Beehner and McCann, 2008)
	Field corr.	Mammals	Feces	0	(Weingrill et al., 2004)
	Field corr.	Mammals	Feces	0	(Wilkening et al., 2016)
	Field corr.	Mammals	Feces	1	(Strier et al., 1999)
	Field corr.	Mammals	Feces	1	(Naidenko et al., 2011)
	Field corr.	Reptiles	Blood	−1	(Lance et al., 2010)
	Field corr.	Reptiles	Blood	0	(MacDonald et al., 2007)
	Wild captive	Mammals	Blood	1	(Bono et al., 1989)
Months	Field corr.	Birds	Blood	−1	(Rubenstein, 2007)
	Field corr.	Mammals	Blood	0	(Rodel and Starkloff, 2014)
	Field corr.	Mammals	Feces	−1	(Gesquiere et al., 2011)
	Field corr.	Mammals	Feces	−1	(Gesquiere et al., 2008)
	Field corr.	Mammals	Feces	−1	(Carnegie et al., 2011)
	Field corr.	Mammals	Feces	0	(Girard-Buttoz et al., 2009)
	Field corr.	Mammals	Feces	1	(Sheriff et al., 2012)
	Field corr.	Reptiles	Blood	−1	(Knapp et al., 2003)
	Wild captive	Mammals	Blood	1	(Cunha et al., 2007)

Table 5

Precipitation. Summary of the number of studies examining the effect of precipitation on glucocorticoid levels in all five vertebrate taxa. Studies have further been divided into the four different study types described in the methods section. Total numbers are given for each taxonomic group and study type.

	Mammals	Birds	Fish	Reptiles	Amphibians	Study Type Totals
Field Manipulative	–	–	–	–	–	–
Field Correlational	17	22	–	3	–	42
Wild in Captivity	3	2	–	–	–	5
Domesticated Laboratory	–	–	–	–	–	–
Taxa Totals	20	24	–	3	–	47
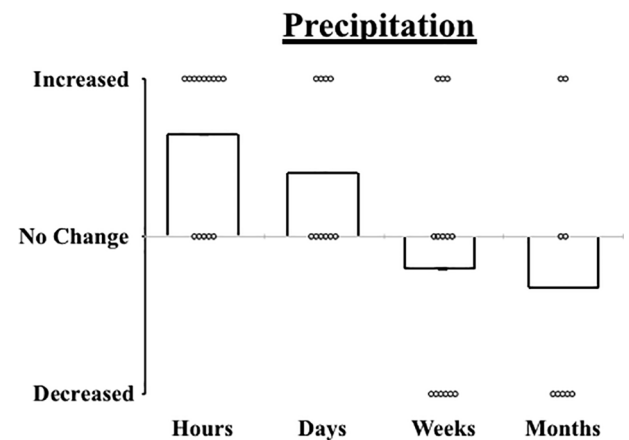
Fig. 2. Glucocorticoid responses of vertebrates to precipitation at four different time intervals, e.g., hours, days, weeks and months. See Fig. 1 for further details.

weeks, are mostly negatively correlated with CORT concentrations (56%), although there are relatively few data points in this category (Fig. 2). As with the 1–4 week period, the negative correlations between CORT and precipitation were associated with rainfall after a drier period and the drier periods themselves were consistently associated with higher CORT levels.

4.3. Conclusion for impacts of precipitation

Relatively short-term exposure (hours to days) to precipitation appears to mostly correlate with increased CORT levels. This supports our hypothesis that CORT may be an important physiological regulator linking precipitation to stress coping mechanisms. It appears, however, that the correlation may depend on the severity and duration of the precipitation, as well as the specific life-history stage when the precipitation occurs.

In contrast, there does not appear to be a consistent correlation between CORT and relatively long-term precipitation patterns (days, weeks, or months). In many ways, this is not surprising. Sustained precipitation for days or weeks might result in different responses than for a short rainstorm that lasts a few hours. The CORT response at time spans of days and weeks might better resemble responses to chronic stress. On the other hand, sustained precipitation, or lack thereof, for months generally reflects predictable seasonal changes that are a part of climate. The lack of clear correlations with precipitation at these time spans is likely related to the ultimate interpretation of precipitation by the animal; is precipitation acting as a stressor, for example by limiting foraging opportunities, or is precipitation acting as a signal to initiate a new life-history stage, such as improved food availability for breeding?

As a consequence, it is possible that correlations between precipitation and seasonal changes in CORT are not directly driven by precipitation itself but may be a response to varying life-history conditions.

An example of precipitation acting as a stressor may be the increased CORT during the rainy season in goats (*Capra aegagrus hircus*) that correlates with decreases in body condition and blood glucose levels (Meza-Herrera et al., 2007). Similarly, CORT levels are highest in Siberian tigers (*Panthera tigris altaica*) during the winter, coinciding with deep snow cover, which makes hunting more difficult (Naidenko et al., 2011). In contrast, precipitation may drive altitudinal migration in birds (Boyle et al., 2010; Breuner and Hahn, 2003) and increased CORT during the rainy season may be a supplemental cue that allows common marmosets to synchronize their reproductive efforts with the most optimal period for breeding (Cunha et al., 2007).

While there is an increasing body of literature showing correlations between precipitation and CORT levels, very few studies have actually isolated the effects of precipitation from the effects of a multitude of other stimuli that often accompany precipitation, such as temperature changes, barometric pressure changes and strong winds. It remains unclear, therefore, whether precipitation is actually the driving stimulus in many of these studies. Laboratory studies have shown that artificial rain induces increased metabolism (Stalmaster and Gessaman, 1984; Wilson et al., 2004) and CORT release (de Bruijn and Romero, 2013), suggesting that CORT may be an important mechanism through which animals respond to precipitation, but to date this has not been tested in the field.

In summary, precipitation is generally correlated with changes in CORT, but the direction of this change appears to depend on both the duration and the life-history context in which the precipitation is experienced. Perhaps under most circumstances rainfall may simply be an indicator of changes in food availability, which may explain the more complicated changes in CORT associated with longer-term or even seasonal patterns in precipitation. The effects of food availability on stress physiology were discussed in a previous section. Unfortunately, no studies to date have manipulated precipitation in the field directly, which makes it difficult to tease apart any direct and indirect effects. While technologically challenging, such studies could provide valuable insights into the mechanisms linking precipitation to the behavior and physiology of free-roaming animals. Finally, very little has been done to study the effects of repeated or prolonged exposure to precipitation in a more controlled setting. Artificial rain was used as one of a set of rotating weather-related stressors in captive European starlings. However, this did not appear to induce symptoms of chronic stress (de Bruijn et al., 2017), despite evidence that artificial precipitation induces an acute response (de Bruijn and Romero, 2013). Overall, evidence from the literature indicates that animals appear to detect and respond to precipitation with increased CORT levels in the short-term, but the response to long-term precipitation patterns appears to be dependent on context.

Note that we did not attempt to explore the relationship between a lack of precipitation (i.e., drought) and CORT. Even though drought can clearly be a stressor to many animals, defining the onset of drought is subjective. Whereas the onset of precipitation is easy to define, it is not possible to define the onset of a lack of precipitation. Consequently, drought is not amenable to the type of analysis performed here. Ideally, there would need to be time-course studies that measured CORT as a lack of precipitation continued, but we were unable to find any such studies in the literature.

5. Responses to changes in temperature

5.1. Brief review of relationship of CORT to temperature changes

Maintaining optimal temperature is critical for many physiological processes. Changes in environmental temperature, therefore, pose serious challenges to all vertebrates. Animals can cope with changes in temperature by either behavioral (Crawshaw, 1980) or physiological (Tattersall et al., 2012) adaptations. Behavioral thermoregulation allows animals to adjust to environmental temperatures through specific behaviors, such as huddling, or by finding areas with more optimal temperatures, such as a shelter (Crawshaw, 1980). Alternatively, physiological adjustments to temperature changes in endotherms often involve adaptations aimed at either decreasing or increasing heat production to protect body temperature. In ectotherms however, adaptations often involve biochemical changes aimed at supporting metabolism at different temperatures, such as expressing alternative enzymes or even antifreezes, which allow ectotherms to operate despite the fact that they may not be able to maintain a regular body temperature (Tattersall et al., 2012). CORT may play an important role in both endotherm and ectotherm coping strategies. CORT at baseline levels is an important metabolic regulator (Landys et al., 2006; Sapolsky et al., 2000) and as such may be important in either decreasing or increasing heat production in response to changes in temperature. Furthermore, CORT directly influences behavior (Haller et al., 1998) and thus may be a driving factor in behavioral thermoregulation. Finally, behavioral thermoregulation often comes with a cost. For example, finding shelter from heat often decreases time available for foraging (Haller et al., 1998), which may connect CORT to adaptations to temperature changes through a need to adjust metabolism in response to reduced foraging.

The relationship between temperature and CORT release, however, can be complex. In ectotherms, and to some extent endotherms as well, body temperature can have a profound impact on baseline CORT concentrations and the ability of an animal to mount a CORT response to other stressors (Jessop et al., 2016). In addition, stressor exposure can also induce hypothermia in some species (Bittencourt et al., 2015; Jerem et al., 2015). How to integrate these two responses into our understanding of the impact of temperature changes on CORT release is not presently clear.

As with precipitation, temperature may also impact animals indirectly, for example by affecting food availability (Arun and Vijayan, 2004; Chung et al., 2013). Temperature also may be an important supplementary cue for timing of migration (Hurlbert and Liang, 2012; Tottrup et al., 2010) and breeding (e.g., Visser et al., 2009). Additionally, temperature changes may indirectly affect survival. For example, temperature affects escape performance in ectothermic vertebrates. They respond slower at lower body temperatures (Cooper, 2000), potentially making them more at risk for predation.

Because heat and cold elicit different physiological responses, we chose to analyze them separately. The studies that examined CORT responses to different durations of cold are presented in Table 6. Many of the data points for decreased temperature are laboratory-based (46%), although there are a substantial number of field correlational and captivity-based studies as well (Table 7). Furthermore, mammals (40%) are the most studied, followed by birds (32%; Table 7). The studies that examined CORT responses to different durations of heat exposure are presented in Table 8. Most data points for increased temperature are laboratory-based (60%) and involve a wider distribution of taxa than the other weather-related stimuli (Table 9).

5.2. Results for decreased temperature

Fig. 3 indicates that CORT is generally increased in response to up to 24 h of reduced temperature (80%), while 10 data points show no change. The exceptions to the general trend suggest that life-history stage may again influence the response. In several bird species, breeding and molting birds differ in their responses to decreases in temperature (Romero et al., 2000). In addition, Amazon river fish don't alter CORT when put in colder water, but since these species rarely experience decreases in temperature in the Amazon, they may not have evolved a sensitivity to decreases in temperature (Inoue et al., 2008). Only one fish study to date has reported a decrease (Jaxion-Harm and Ladich, 2014), but CORT was measured from hormone excreted into the

Table 6

Decrease in temperature. List of the studies that have measured CORT responses after a decrease in temperature. Papers are grouped by exposure time, study type, Taxon, and the biological matrix from which CORT was measured ("water" indicates CORT was measured from the water bathing the fish). See text for descriptions of Study Type (manip. = manipulative, corr. = correlational). For response, −1 = CORT decrease; 0 = no change in CORT; 1 = CORT increase.

	Study Type	Taxon	CORT matrix	Response	Reference
Hours	Field corr.	Birds	Blood	0	(Romero et al., 2000)
	Field corr.	Birds	Blood	0	(Romero et al., 2000)
	Field corr.	Birds	Blood	0	(Romero et al., 2000)
	Field corr.	Birds	Blood	0	(Astheimer et al., 1992)
	Field corr.	Birds	Blood	1	(Schwabl et al., 1985)
	Field corr.	Birds	Blood	1	(Romero et al., 2000)
	Field corr.	Birds	Blood	1	(Romero et al., 2000)
	Field corr.	Birds	Blood	1	(Romero et al., 2000)
	Field corr.	Birds	Blood	1	(Rogers et al., 1993)
	Field corr.	Birds	Blood	1	(Astheimer et al., 1992)
	Field corr.	Birds	Blood	1	(Jenni-Eiermann et al., 2008)
	Field corr.	Birds	Blood	1	(Knutie and Pereyra, 2012)
	Field corr.	Birds	Feces	1	(Frigerio et al., 2004)
	Field corr.	Mammals	Feces	1	(Huber et al., 2003)
	Wild captive	Birds	Blood	0	(Angelier et al., 2016)
	Wild captive	Birds	Blood	0	(de Bruijn and Romero, 2013)
	Wild captive	Birds	Blood	1	(Pilo et al., 1985)
	Wild captive	Birds	Blood	1	(de Bruijn and Romero, 2013)
	Wild captive	Birds	Blood	1	(de Bruijn and Romero, 2011)
	Wild captive	Mammals	Blood	1	(Werner and Venscappell, 1985)
	Wild captive	Mammals	Urine	1	(Saltz and White, 1991)
	Wild captive	Reptiles	Blood	0	(Li et al., 2011)
	Wild captive	Reptiles	Blood	1	(Dauphin-Villemant et al., 1990)
	Wild captive	Reptiles	Blood	1	(Grassman and Crews, 1990)
	Wild captive	Fish	Water	−1	(Jaxion-Harm and Ladich, 2014)
	Wild captive	Fish	Blood	0	(Bermejo-Nogales et al., 2014)
	Wild captive	Fish	Blood	0	(Szekeres et al., 2014)
	Domestic lab	Birds	Blood	1	(Etches, 1976)
	Domestic lab	Birds	Blood	1	(Jeronen et al., 1976)
	Domestic lab	Birds	Blood	1	(el-Halawani et al., 1973)
	Domestic lab	Mammals	Blood	1	(Vernikos et al., 1982)
	Domestic lab	Mammals	Blood	1	(Dantzer and Mormede, 1983)
	Domestic lab	Mammals	Blood	1	(Noh et al., 2012)
	Domestic lab	Mammals	Blood	1	(Slađana and Ljubica, 2005)
	Domestic lab	Mammals	Blood	1	(Adels et al., 1986)
	Domestic lab	Mammals	Blood	1	(Djordjevic et al., 2003)
	Domestic lab	Mammals	Blood	1	(Kizaki et al., 1997)
	Domestic lab	Mammals	Blood	1	(Lenox et al., 1980)
	Domestic lab	Mammals	Blood	1	(Yahata et al., 1987)
	Domestic lab	Mammals	Blood	1	(Yahata and Kuroshima, 1989)
	Domestic lab	Mammals	Blood	1	(Jobin et al., 1976)
	Domestic lab	Mammals	Blood	1	(Palma et al., 2000)
	Domestic lab	Mammals	Blood	1	(Hauger and Aguilera, 1992)
	Domestic lab	Mammals	Blood	1	(Bocheva et al., 2008)
	Domestic lab	Mammals	Blood	1	(Bramham et al., 1998)
	Domestic lab	Mammals	Blood	1	(Becker et al., 1997)
	Domestic lab	Mammals	Blood	1	(Sesti-Costa et al., 2010)
	Domestic lab	Mammals	Blood	1	(Tang et al., 1984)
	Domestic lab	Reptiles	Blood	1	(Lance and Elsey, 1999)
	Domestic lab	Fish	Blood	0	(Inoue et al., 2008)
	Domestic lab	Fish	Blood	1	(Rombenso et al., 2015)
	Domestic lab	Fish	Blood	1	(He et al., 2015)
	Domestic lab	Fish	Blood	1	(Barton and Peter, 1982)
	Domestic lab	Fish	Blood	1	(Tanck et al., 2000)
	Domestic lab	Fish	Blood	1	(Chebaani et al., 2014)
	Domestic lab	Fish	Blood	1	(Chen et al., 2002)
Days	Field corr.	Birds	Blood	0	(Romero et al., 2000)
	Field corr.	Birds	Blood	0	(Romero et al., 2000)
	Field corr.	Birds	Blood	0	(Astheimer et al., 1995)
	Field corr.	Birds	Blood	1	(Romero et al., 2000)
	Field corr.	Birds	Blood	1	(Romero et al., 2000)
	Field corr.	Birds	Blood	1	(Romero et al., 2000)
	Field corr.	Birds	Blood	1	(Romero et al., 2000)
	Wild captive	Fish	Blood	1	(Shahjahan et al., 2017)
	Wild captive	Fish	Blood	1	(Pribyl et al., 2016)
	Domestic lab	Birds	Blood	1	(el-Halawani et al., 1973)
	Domestic lab	Mammals	Blood	1	(Daniels-severs et al., 1973)
	Domestic lab	Mammals	Blood	1	(Hayashi et al., 1993)
	Domestic lab	Mammals	Blood	1	(Vernikos et al., 1982)
	Domestic lab	Mammals	Blood	1	(Bligh-Tynan et al., 1993)
	Domestic lab	Reptiles	Blood	0	(Avila-Mendoza et al., 2016)

Table 6 (*continued*)

	Study Type	Taxon	CORT matrix	Response	Reference
	Domestic lab	Reptiles	Blood	1	(Dupoue et al., 2013)
	Domestic lab	Fish	Blood	1	(Chen et al., 2002)
	Domestic lab	Fish	Blood	1	(Chen et al., 1996)
	Domestic lab	Fish	Blood	1	(He et al., 2015)
Weeks	Field corr.	Birds	Blood	0	(Bears et al., 2003)
	Field corr.	Birds	Feces	0	(Pereira et al., 2010)
	Field corr.	Birds	Feces	1	(Lopez-Jimenez et al., 2016)
	Field corr.	Mammals	Blood	1	(Lee et al., 1976)
	Field corr.	Mammals	Feces	1	(Naidenko et al., 2011)
	Field corr.	Mammals	Feces	1	(Weingrill et al., 2004)
	Field corr.	Mammals	Feces	1	(Corlatti et al., 2011)
	Field corr.	Mammals	Feces	1	(Beehner and McCann, 2008)
	Wild captive	Reptiles	Blood	1	(Bonnet et al., 2013)
	Wild captive	Amphibian	Blood	0	(Xia and Li, 2010)
	Domestic lab	Birds	Blood	0	(Goymann et al., 2006)
	Domestic lab	Birds	Feces	−1	(Goymann et al., 2006)
	Domestic lab	Mammals	Blood	0	(Bhatnagar et al., 1995)
	Domestic lab	Reptiles	Blood	0	(Callard et al., 1975)
	Domestic lab	Reptiles	Blood	1	(Brischoux et al., 2016)
	Domestic lab	Reptiles	Blood	1	(Avila-Mendoza et al., 2016)
	Domestic lab	Fish	Blood	0	(Chen et al., 1996)
	Domestic lab	Fish	Blood	1	(Chen et al., 2002)
Months	Field corr.	Mammals	Feces	0	(Khonmee et al., 2016)
	Field corr.	Mammals	Feces	1	(Sheriff et al., 2012)
	Wild captive	Mammals	Blood	−1	(Xu and Hu, 2017)
	Wild captive	Fish	Blood	−1	(Alzaid et al., 2015)
	Wild captive	Mammals	Blood	0	(Xu and Hu, 2017)
	Wild captive	Mammals	Blood	0	(Monfort et al., 1993)
	Wild captive	Mammals	Blood	0	(Bubenik and Brown, 1989)
	Wild captive	Mammals	Blood	1	(Cunha et al., 2007)
	Wild captive	Mammals	Blood	1	(Bubenik et al., 1983)
	Wild captive	Mammals	Blood	1	(Reyes et al., 1997)
	Wild captive	Mammals	Blood	1	(Yousef et al., 1971)
	Domestic lab	Mammals	Blood	1	(Demas and Nelson, 1996)
	Domestic lab	Fish	Blood	1	(Tanck et al., 2000)

water and thus may represent a temperature-induced decrease in excretion rather than a decrease in plasma levels. Finally, we were unable to find any studies examining the acute CORT response of amphibians to decreased temperatures.

Although there are relatively few studies on cold exposures from one to seven days, most studies (79%) to date report that CORT is increased (Fig. 3). As with the "hours" category, the exceptions suggest that life-history stage plays a role. Once again, we were unable to find any studies examining the CORT response of amphibians to decreased temperatures.

While we found a relatively clear pattern for both shorter time periods, there is more variation with cold exposure lasting weeks. While a number of studies report an increase in CORT (56%), there are a substantial number of studies that report no change (39%) and a single study that reports a decrease (Fig. 3). There were no clear trends that might explain the differences between these responses.

There are relatively few data points for cold exposure lasting a month or longer, and no long-term cold exposure studies have been done in amphibians, reptiles or birds. A bare majority of the studies report an increase in CORT in this category (54%), with 4 studies showing no correlation and 2 studies reporting a decrease in CORT (Fig. 3). There was a suggestion that seasonal differences, perhaps reflecting differences in life-history stages, could explain the variability. In several captive studies, responses differed depending upon whether animals were held on short-day or long-day photoperiods (Xu and Hu, 2017), suggesting that winter adapted animals might not perceive cold as a stressor (Demas and Nelson, 1996).

5.3. Results for increased temperature

Exposure of up to 24 h of increased temperature is generally associated with an increase in CORT (87%), while 4 studies report no change, and another a decrease in CORT (Fig. 4). One study on three Australian desert birds suggest species differences in sensitivity to heat stressors. Laboratory-raised budgerigars (*Melopsittacus undulatus*) and zebra finches (*Taeniopygia guttata*) exposed to 1 h of heat failed to alter CORT release even though diamond doves did increase CORT (Xie

Table 7
Temperature – cold. Summary of the number of studies examining the effect of decreased temperature on glucocorticoid levels in all five vertebrate taxa. Studies have further been divided into the four different study types described in the methods section. Total numbers are given for each taxonomic group and study type.

	Mammals	Birds	Fish	Reptiles	Amphibians	Study Type Totals
Field Manipulative	–	–	–	–	–	–
Field Correlational	8	23	–	–	–	31
Wild in Captivity	10	5	6	5	–	26
Domesticated Laboratory	24	6	13	5	1	49
Taxa Totals	42	34	19	10	1	106

et al., 2017). Interestingly, these three species differ in the physiological mechanisms of how they cope with heat, even though they occupy the same habitat.
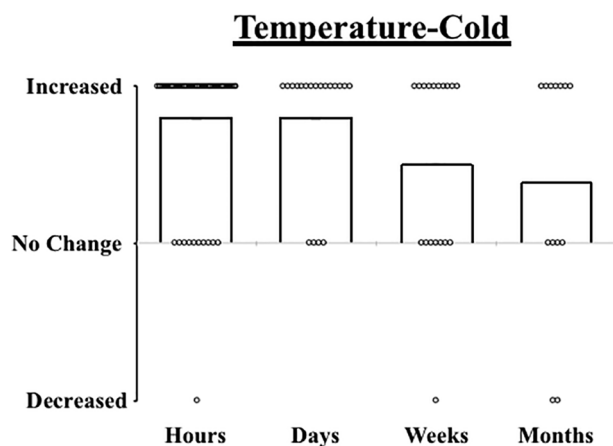
Table 8

Increases in temperature. List of the studies that have measured CORT responses after an increase in temperature. Papers are grouped by exposure time, study type, Taxon, and the biological matrix from which CORT was measured ("body" indicates CORT was measured from the entire body of the individual). See text for descriptions of Study Type (manip. = manipulative, corr. = correlational). For response, −1 = CORT decrease; 0 = no change in CORT; 1 = CORT increase.

	Study Type	Taxon	CORT matrix	Response	Reference
Hours	Field manip.	Fish	Body	1	(Quigley and Hinch, 2006)
	Field corr.	Birds	Blood	0	(Viblanc et al., 2014)
	Field corr.	Mammals	Feces	1	(Millspaugh et al., 2001)
	Field corr.	Amphibian	Blood	1	(Jessop et al., 2013)
	Wild captive	Birds	Blood	1	(Pilo et al., 1985)
	Wild captive	Birds	Feces	1	(Ozella et al., 2017)
	Wild captive	Mammals	Blood	1	(Miller and Alliston, 1974)
	Wild captive	Mammals	Blood	1	(Christison and Johnson, 1972)
	Wild captive	Reptiles	Blood	1	(Gangloff et al., 2016)
	Wild captive	Fish	Blood	1	(Mesa et al., 2002)
	Wild captive	Amphibian	Urine	1	(Narayan and Hero, 2014a)
	Domestic lab	Birds	Blood	0	(Xie et al., 2017)
	Domestic lab	Birds	Blood	0	(Xie et al., 2017)
	Domestic lab	Birds	Blood	1	(Jeronen et al., 1976)
	Domestic lab	Birds	Blood	1	(Iqbal et al., 1990)
	Domestic lab	Birds	Blood	1	(Edens and Siegel, 1975)
	Domestic lab	Birds	Blood	1	(Xie et al., 2017)
	Domestic lab	Birds	Blood	1	(el-Halawani et al., 1973)
	Domestic lab	Birds	Blood	1	(Beuving and Vonder, 1978)
	Domestic lab	Mammals	Blood	−1	(Rhynes and Ewing, 1973)
	Domestic lab	Mammals	Blood	0	(Olsson et al., 1995)
	Domestic lab	Mammals	Blood	1	(Nabeshima et al., 1982)
	Domestic lab	Mammals	Blood	1	(Jasnic et al., 2010)
	Domestic lab	Mammals	Blood	1	(Jasnic et al., 2013)
	Domestic lab	Mammals	Blood	1	(Djordjevic et al., 2003)
	Domestic lab	Mammals	Blood	1	(Harikai et al., 2003)
	Domestic lab	Mammals	Blood	1	(Abilay et al., 1975)
	Domestic lab	Mammals	Blood	1	(Abilay et al., 1975)
	Domestic lab	Mammals	Blood	1	(Bocheva et al., 2008)
	Domestic lab	Mammals	Blood	1	(Koko et al., 2004)
	Domestic lab	Mammals	Blood	1	(Alvarez and Johnson, 1973)
	Domestic lab	Mammals	Blood	1	(Besch and Brigmon, 1991)
	Domestic lab	Mammals	Blood	1	(Dantzer and Mormede, 1983)
	Domestic lab	Mammals	Blood	1	(Becker et al., 1997)
	Domestic lab	Mammals	Blood	1	(Cure, 1989)
	Domestic lab	Fish	Blood	1	(Roche and Boge, 1996)
	Domestic lab	Fish	Blood	1	(Li et al., 2016)
	Domestic lab	Fish	Blood	1	(Habte-Tsion et al., 2017)
Days	Wild captive	Reptiles	Blood	1	(Cash and Holberton, 2005)
	Wild captive	Reptiles	Blood	0	(Shahjahan et al., 2017)
	Wild captive	Fish	Blood	0	(Pribyl et al., 2016)
	Wild captive	Amphibian	Urine	1	(Narayan et al., 2012)
	Domestic lab	Birds	Blood	1	(el-Halawani et al., 1973)
	Domestic lab	Mammals	Blood	0	(Ei-Nouty et al., 1978)
	Domestic lab	Mammals	Blood	1	(Gwosdow et al., 1985)
	Domestic lab	Mammals	Blood	1	(Hayashi et al., 1993)
	Domestic lab	Fish	Blood	1	(Frost et al., 2013)
	Domestic lab	Fish	Blood	1	(Habte-Tsion et al., 2017)
	Domestic lab	Fish	Blood	1	(Choi et al., 2007)
Weeks	Field manip.	Birds	Feather	1	(Fairhurst et al., 2012)
	Field corr.	Mammals	Blood	−1	(Lee et al., 1976)
	Field corr.	Mammals	Feces	0	(Schoof et al., 2016)
	Field corr.	Fish	Blood	1	(Chadwick et al., 2015)
	Wild captive	Amphibian	Blood	0	(Xia and Li, 2010)
	Wild captive	Amphibian	Urine	1	(Narayan et al., 2012)
	Wild captive	Amphibian	Urine	1	(Narayan and Hero, 2014b)
	Domestic lab	Birds	Blood	1	(Geraert et al., 1996)
	Domestic lab	Mammals	Blood	−1	(Alvarez and Johnson, 1973)
	Domestic lab	Mammals	Blood	1	(Magal et al., 1981)
	Domestic lab	Fish	Blood	1	(Perez-Casanova et al., 2008)
	Domestic lab	Fish	Blood	1	(Cataldi et al., 1998)
	Domestic lab	Fish	Blood	1	(Eissa and Wang, 2013)
Months	Field corr.	Mammals	Blood	1	(Nilssen et al., 1985)
	Field corr.	Mammals	Feces	0	(Gesquiere et al., 2011)
	Field corr.	Mammals	Feces	1	(Gesquiere et al., 2008)
	Field corr.	Mammals	Feces	1	(Wilkening et al., 2015)
	Field corr.	Fish	Blood	1	(Mills et al., 2015)
	Wild captive	Fish	Blood	1	(Planas et al., 1990)
	Domestic lab	Birds	Blood	1	(El-Tarabany, 2016)
	Domestic lab	Fish	Blood	1	(Lyytikainen et al., 2002)

Table 9

Temperature – heat. Summary of the number of studies examining the effect of increased temperature on glucocorticoid levels in all five vertebrate taxa. Studies have further been divided into the four different study types described in the methods section. Total numbers are given for each taxonomic group and study type.

	Mammals	Birds	Fish	Reptiles	Amphibians	Study Type Totals
Field Manipulative	–	1	1	–	–	2
Field Correlational	7	1	2	–	1	11
Wild in Captivity	2	2	4	2	5	15
Domesticated Laboratory	21	11	10	–	–	42
Taxa Totals	30	15	17	2	6	70

Temperature-Heat

Fig. 4. Glucocorticoid responses of vertebrates to increased temperature at four different time intervals, e.g., hours, days, weeks and months. See Fig. 1 for further details.

Temperature-Cold

Fig. 3. Glucocorticoid responses of vertebrates to decreased temperature at four different time intervals, e.g., hours, days, weeks and months. See Fig. 1 for further details.

While relatively few studies exposed animals to heat for one to seven days, out of 11 studies, 8 reported an increase in CORT (73%), while 3 studies report no change (Fig. 4). There were no identifiable differences in these studies.

The majority of studies examining the CORT response to weeks of heat exposure report an increase (69%), although there are relatively few studies. In contrast, there are two studies reporting no change, and another two studies report a decrease (Fig. 4). One feature that stands out is the responses in large mammals. A decrease in CORT found in cattle (Alvarez and Johnson, 1973; Lee et al., 1976) may reflect acclimation to heat by decreasing metabolism and thereby heat production. Since cattle are rather large animals and there may be few opportunities to behaviorally adjust to heat exposure, e.g., by finding shelter, down regulating metabolism may help prevent overheating (Alvarez and Johnson, 1973).

Exposure to increased temperatures for more than a month has been studied mostly in mammals and fish, with one bird study. While seven studies report an increase in CORT (88%), one study reports no change (Fig. 4). The reason for the one study in baboons showing no change is unclear, but Gesquiere et al. (2011) suggest that males are either better adapted physiologically to heat (lower surface area to body mass ratio) or that competitive exclusion of females may allow them to spend comparatively more time in the shade.

5.4. Conclusion to temperature changes

In general, exposure to both decreased and increased temperatures is associated with increased CORT levels (76% of studies for both combined). Only 4% of studies report decreased CORT levels associated
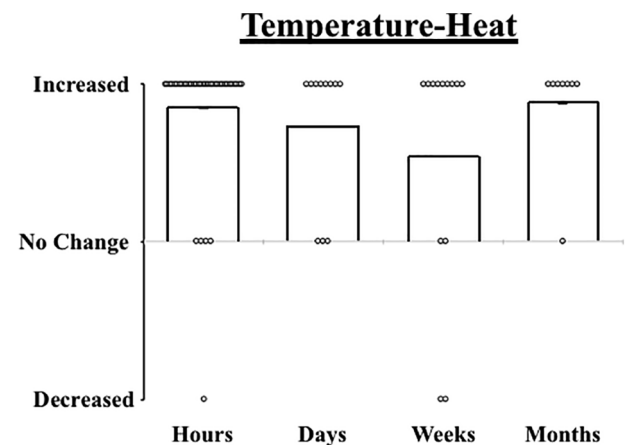
with temperature changes, and those that do are concentrated primarily at the longer exposure times. This suggests that certain animals adjust their metabolism in response to prolonged exposure, which may prevent overheating (Alvarez and Johnson, 1973).

A substantial minority of studies report no changes in CORT associated with either decreased (25 out of 106 studies) or increased temperatures (10 out of 70). It is not always clear why no CORT response was found. However, several of these studies report that the temperature change fell within the normal range of temperatures that these animals experience in their natural environments. This suggests that the lack of a response may indicate that the animals had acclimatized to the temperature change and consequently did not perceive the change as stressful. In other words, the animals were capable of adjusting to the temperature change in ways that did not require CORT-regulated pathways. For example, while no change in CORT was found in response to both decreased and increased temperatures in salamanders, temperature change was associated with a decrease in blood glucose levels which suggests activation of non-CORT mechanisms for adjusting to the temperature changes (Xia and Li, 2010). Additionally, the response to changes in temperatures over different time periods in the common carp shows that while short-term exposure is associated with increased CORT levels, hormone levels return to baseline after prolonged exposure (Chen et al., 1996). This supports the hypothesis that some species may be able to acclimatize to such temperature changes, at least if the temperatures fall within the normal range. Furthermore, preventing CORT increases in response to prolonged periods of exposure to temperature changes may be an important adaptation to prevent the negative effects associated with elevated CORT (Sapolsky et al., 2000). Unfortunately, there are no field manipulation studies examining changes in CORT in response to decreases in temperature. However, cooling of nest boxes can impact parental behavior and resulted in reduced growth and innate immunity in nestlings (Ardia et al., 2010). Whether or not these cooling-induced responses are regulated by CORT is currently unknown, but the results presented here suggest that it is likely.

To summarize, changes in temperature are generally associated with increased CORT levels, especially during short exposure. We therefore conclude that changes in temperature are perceived as a stressor by most animals. While the pattern mostly holds for longer exposure, there is more variability in the response, which suggests that many animals may be able to adjust to such prolonged exposure, provided the changes fall within the range of temperatures experienced in their natural environment.

6. Responses to change in barometric pressure

6.1. Brief review of relationship of CORT to barometric pressure changes

Barometric pressure has been suggested as a potentially reliable cue by which animals can detect and respond to inclement weather (Breuner et al., 2013). Changes in weather are generally preceded by relatively minor changes in barometric pressure, where a decrease in pressure is thought to predict inclement weather, while an increase in pressure is thought to predict clear weather. Depending upon the severity of an oncoming storm, pressure can decrease by up to 12 kPa (Saucier, 2003), but often the changes are much smaller. Additionally, the weather-driven changes in barometric pressure are much smaller than pressure changes related to altitude or depth. Such dramatic changes in pressure as experienced when under water are a very different type of stimulus and in itself not related to weather-related events. Therefore, these types of pressure effects are not part of this review, and this section instead focuses solely on effects of barometric pressure. Little is known about whether animals can detect such minor changes in barometric pressure, but it has been hypothesized that the amniote paratymic organ found in birds, which may be a homologue with the anamniote spiracular organ in fish, is able to detect changes in pressure (O'Neill, 2013) and may thus function as a barometer. It remains unclear if such organs exist in other groups of vertebrates, but there is some evidence that some species of bat have a similar organ (Paige, 1995).

Despite unknown mechanisms, a growing body of literature describes a variety of behavioral changes correlated with pressure changes in all groups of vertebrates. For example, barometric pressure appears correlated with the calling frequency of some species of anurans (Oseen and Wassersug, 2002). In breeding loggerhead turtles (*Caretta caretta*), variability in breeding area home range and frequency of forays outside of core breeding areas appear correlated to barometric pressure across a decade of study (Schofield et al., 2010). Somewhat similarly, barometric pressure has long been suggested as an important factor in bird migration patterns (Bagg et al., 1950). Barometric pressure has also been suggested as a reliable cue for cave-dwelling bats in determining insect availability, as insect abundance is negatively correlated with barometric pressure, while simultaneously the number of bats exiting the cave is positively correlated with pressure (Paige, 1995). Finally, blacktip sharks (*Carcharhinus limbatus*) move to deeper water prior to tropical storms, and this migration coincides with a period of decreasing barometric pressure in the hours before the storm makes landfall (Heupel et al., 2003). The behavioral data thus clearly suggest that barometric pressure can potentially be an important and reliable stimulus through which vertebrates might predict incipient weather changes, and the correlation between barometric pressure and potentially stressful events suggests that CORT would be a logical candidate for study.

6.2. Results for changes in barometric pressure

Very little work to date has examined the role of stress physiology in the behavioral responses to barometric pressure changes. The few studies that do exist paint an inconsistent picture. In Greylag geese (*Anser anser*), fecal CORT levels decrease with lower barometric pressure of the previous day, which would be a predictor of an oncoming storm. One possible explanation suggested by the authors is that Greylag geese down-regulate their activity levels by "hunkering down" in order to prepare for the change in weather (Frigerio et al., 2004). In contrast, no correlation was found between barometric pressure and CORT in white-crown sparrows, either in the field or in a laboratory study where barometric pressure was directly manipulated (Breuner et al., 2013). Interestingly, when confronted with decreasing barometric pressure and despite a lack of changes in either metabolic rate or stress physiology, captive birds showed increased food intake, suggesting that

CORT is not the main mediator of these behavioral responses (Breuner et al., 2013).

6.3. Conclusion to barometric pressure changes

Overall, barometric pressure should be a reliable stimulus that allows animals to predict the onset of changes in weather, which may be important in breeding, migration and survival (Wingfield, 2013). However, while a wide variety of vertebrates show behavioral responses to changes in barometric pressure (see above), very little is known about the physiological mechanisms that underlie those behavioral responses. Based on the limited data available, these behavioral adaptations do not appear to be mediated through CORT. It is possible that the fight-or-flight response, acting through catecholamines, drives this correlation, however no studies have examined this to date.

7. Overall conclusions

Regardless of the type of weather-related stimulus or taxa investigated, short-term exposure of 24 h or less is strongly associated with increased CORT levels (79% of studies – see Figs. 1–4). This suggests that stimuli such as precipitation, reductions in food availability and temperature changes are perceived as stressors by most animals studied to date. Furthermore, this response is consistent across study type, sampling method and taxonomic group. Therefore, we conclude that there is a general consensus stress response to acute changes in these weather-related stimuli.

However, a bit of caution is warranted in making this conclusion. Tables 2–9 clearly indicate a bias in both taxonomic coverage and study design. The studies included here have a heavy weight towards laboratory mammalian studies. Especially lacking are field studies of reptiles and amphibians. Although the consistent results reported here suggest that acute CORT increases to weather-related stimuli are robust responses, future work on other taxa, and especially field-based studies, would be especially valuable.

In contrast to acute exposure, there is considerably more variation in CORT levels after prolonged exposure (over 24 h) to weather-related stressors. A smaller majority of studies report increased CORT levels (64%) compared to acute exposure. Several factors may have contributed to this increased variation. First, if the prolonged exposure to change in a weather-related parameter is a predictable occurrence in the life history of an animal, such as fasting in several species of fish and birds, it seems likely that these animals have evolved adaptations to cope with such events and as such may no longer perceive them as stressors.

Second, the effects of a particular weather-related parameter will also depend on the environment in which the animal experiences it. For example, precipitation may signal an increase in food availability in a desert environment, while it may limit foraging opportunities in other circumstances. This strongly suggests that the life history and environmental context in which any changes in weather-related parameters are experienced is critical for whether or not such a change is perceived as stressful or not. Consequently, we suggest that it is important for future studies investigating weather-related stress to report details on life history and environment, so that behavioral and physiological responses can be considered carefully within the parameters of the natural context of that animal.

Third, prolonged exposure to a stimulus can push an animal into allostatic overload (McEwen and Wingfield, 2003). Recently, a new model was introduced that helps explain the complex roles CORT plays at baseline and stress induced levels, the reactive scope model (Romero et al., 2009). In short, normal circadian and seasonal changes in CORT fall under a predictive homeostasis range. Fluctuations in CORT within this range are thought to fall within the normal basal concentrations, at which levels CORT is thought to drive day-to-day homeostatic regulation. The adaptive increase in CORT in response to a stressor falls under

the reactive homeostasis range, where CORT pushes the animal into the emergency life history stage (Wingfield et al., 1998). While this will shift physiological processes towards survival, once the stressor is dealt with, the animal will return to the predictive homeostasis range and will resume normal activities. Finally, after prolonged or repeated exposure to increased CORT levels, the hormone itself becomes maladaptive, and the animal enters homeostatic overload. At this point, CORT will start causing problems, which may include pathology and disease and can eventually lead to death. Even if the animal survives such an episode of homeostatic overload (i.e., chronic stress), the model predicts that the prolonged exposure to CORT induces wear and tear, which may negatively affect an animal's ability to respond to additional stressors (Romero et al., 2009). It is likely that the acute (hours) responses to weather-related stimuli are pushing CORT into the reactive homeostasis range. This would explain the consistent responses reported in the literature. When the stimulus extends to days and weeks, however, homeostatic overload, or chronic stress, will occur. This would explain the increased variability in the CORT responses reported in the literature. The timing of the transition from acute to chronic responses is currently unknown and contributed to our division of the studies into groups of reported exposure durations of hours, days, weeks, and months. However, Figs. 1–4 provide suggestive evidence that the transition may occur on the order of weeks because for many of the stimuli, that is the period when reports from the literature become much more variable.

Fourth, the responses reported in the literature at the duration of months may reflect a completely different class of responses. They may reflect predictable adaptations to seasonal climate shifts rather than to weather per se. CORT concentrations, even at baseline, show seasonal variation (Romero, 2002). This makes interpretation of changes during prolonged periods more difficult. It is unclear whether a change in CORT results from prolonged exposure to the stimulus or is simply due to altered life-history demands. Depending on the species, such seasonal fluctuations may be especially noticeable in specific life-history stages, such as molt in birds, for which attenuation of the HPA-axis has been shown in several different studies (Cyr et al., 2008; Dawson and Howe, 1983; de Bruijn and Romero, 2013; Romero et al., 2000).

Finally, it is important to remember that models of climate change predict that the weather-related parameters discussed in this paper will likely become less predictable and more volatile (Romero and Wingfield, 2016; Wingfield et al., 2011, 2017). This raises interesting questions about whether animals will be able to acclimatize to such increased volatility to prevent negative effects of prolonged exposure to elevated CORT. Furthermore, and just as important, weather-related parameters are often used as cues for the timing of life history stages. Whether or not animals will be able to adjust to the increased unpredictability may depend upon the flexibility of CORT regulation.

Acknowledgement

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