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Epigenetic Potential as a Mechanism of Phenotypic Plasticity in Vertebrate Range Expansions

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Abstract

During range expansions, organisms are often exposed to multiple pressures, including novel enemies (i.e. predators, competitors and/or parasites) and unfamiliar or limited resources. Additionally, small propagule sizes at range edges can result in genetic founder effects and bottlenecks, which can affect phenotypic diversity and thus selection outcomes. Despite these obstacles, individuals in expanding populations often thrive at the periphery of a range, and this success may be mediated by phenotypic plasticity. Increasing evidence suggests that epigenetic mechanisms may underlie such plasticity because they allow for more rapid phenotypic responses to novel environments than are possible via the accumulation of genetic variation. Here, we review how molecular epigenetic mechanisms could underlie plasticity in range expansions, emphasizing the roles of DNA methylation and other epigenetic marks in the physiological regulatory networks (PRNs) that drive whole-organism performance. We focus on the hypothalamic-pituitary-adrenal (HPA) axis, arguing that epigenetically-mediated plasticity in the regulation of glucocorticoids in particular might strongly impact range expansions. We hypothesize that novel environments release or select for epigenetic potential; organisms with a greater disposition to regulate performance adaptively via GC-mediated changes in epigenetic potential are apt to be those most successful during range expansion.

Keywords: epigenetic potential, phenotypic plasticity, endocrinology, range expansions

Introduction

Environments are changing rapidly, in large part due to human activity, and it is becoming increasingly important to determine how organisms will respond (Ghalambor et al. 2007). One particularly impactful aspect of anthropogenic environmental change is the alteration of the geographical distributions of species. With increased urbanization and massive increases in global commerce, many individuals and populations are experiencing pressure to either change their native ranges or survive in novel areas (Parmesan and Yohe 2003). During such range expansions, organisms are often exposed to multiple pressures, including novel enemies (i.e. predators, competitors and/or parasites) and unfamiliar or limited resources (Wingfield et al. 2015; Martin et al. 2015). Small propagule sizes at range edges can also result in genetic founder effects and bottlenecks, which can affect phenotypic diversity and thus selection outcomes (Perez et al. 2006). Despite these obstacles, individuals in expanding populations often thrive at the periphery of a range, exhibiting extensive phenotypic differentiation from individuals near the range core, a phenomenon called a genetic paradox (Perez et al. 2006). Given the low genetic diversity of most range edge populations, high phenotypic variation at the range edge is likely partially underlain by phenotypic plasticity (Richards et al. 2006; Ghalambor et al. 2007; Martin and Liebl 2014). Phenotypic plasticity, including both irreversible (i.e. developmental plasticity—West-Eberhard 2005) and reversible (i.e. phenotypic flexibility—Piersma and Drent 2003) forms, is likely to be common at range edges because it allows for more rapid responses to novel environmental challenges than would be possible via genetic adaptation (Pigliucci 2001; Wright et al. 2010; Forsman 2014). Moreover, several studies from the plant literature suggest that epigenetic mechanisms may underlie plastic responses to novel environments (Bossdorf et al. 2008; Angers et al. 2010; Bossdorf et al. 2010; Nicotra et al. 2010; Richards et al. 2012; Zhang et al. 2013a), however, similar studies in vertebrates remain scarce.

Here, we review how molecular epigenetic mechanisms could be driving plasticity in range expansions, emphasizing the roles of DNA methylation and other epigenetic marks in the physiological regulatory networks (PRNs) that drive whole-organism performance (Cohen et al. 2012; Martin and Cohen 2014; Martin et al. 2016b). As an example, we focus on the hypothalamic-pituitary-adrenal (HPA) axis, arguing that epigenetically-mediated plasticity in the regulation of glucocorticoids, in particular, might strongly impact the outcomes of range expansions. We hypothesize that novel environments release and/or select epigenetic potential; genotypes/species with a greater disposition to regulate performance adaptively via epigenetically mediated changes in GC regulation are apt to be those comprising most new populations. Below, we first provide evidence that GCs are involved in current and ongoing changes in the distributions of species. We then introduce then discuss the novel concept of epigenetic potential, and review evidence for how GCs might be regulated by (and even regulate) epigenetic potential. We close by offering a few promising options for future research.

Glucocorticoid regulation and range expansions

Maintenance of homeostasis is crucial for survival (Wingfield 2013; Romero et al. 2009), particularly at range edges where individuals encounter novel challenges with which they have little to no evolutionary history (Liebl and Martin 2012). In vertebrates, endurance of and recovery from stressors (including novel ones) involves the coordinated regulation of glucocorticoids (GCs) by the hypothalamic-pituitary-adrenal (HPA) axis (Wingfield 2013; Romero et al. 2009). Encounters with stressors typically result in a rapid increase in circulating GCs, which act to promote short-term survival via coordination of a broad range of physiological and behavioral responses (Addis et al. 2011). Stressor-induced GCs, in particular, play a pivotal role in integrating sub-organismal processes to match an individual's physiology and behavior to their environment (Martin et al. 2011; Lema and Kitano 2013; Martin et al. 2016a; Taff and Vitousek 2016). Several studies provide support for GCs as physiological mediators of avian range expansions. For example, in a study comparing GC responses among subspecies of white crowned sparrow (*Zonotrichia leucophrys*), populations at the range-edge (and a higher altitude) had significantly higher baseline and stress-induced levels of the avian GC, corticosterone (CORT), than populations near the range core (i.e. lower altitude) (Addis et al. 2011). Moreover, several studies investigating the ongoing and recent range expansion of the introduced house sparrow (*Passer domesticus*) across Kenya found that individuals at the range-edge secreted more CORT in response to an acute stressor (Liebl and Martin 2012; Martin et al. 2013). In Kenya, range-edge birds also expressed different levels of GC receptors (i.e. mineralocorticoid receptor—MR and glucocorticoid receptor—GR) (Liebl and Martin 2013) in hippocampi compared to individuals residing near the site of introduction.

Whereas these studies are among the first to implicate GC regulation as important to range expansion success, the extent to which these patterns are influenced by inter-individual differences GC regulatory plasticity remains unclear. Selection for particular genotypes is also tenable, particularly because aspects of the HPA are heritable in vertebrates (Wust et al. 2004). However, regulatory plasticity within the HPA-axis, is likely to be of particular importance at range edges (Martin and Liebl 2014), especially for populations currently undergoing range expansion. The HPA is inherently plastic, as a critical mediator of organismal homeostasis, and plasticity can manifest much more rapidly than genetic variation, especially in the case of the oftentimes-small population sizes that occur at range edges. For example, evolutionarily unfamiliar stressors (e.g., novel foods, predators, or pathogens) may elicit a sub-optimal GC response (under- or over-exuberance) at range edges, yet high HPA plasticity may allow individuals to fine-tune their responses to the environment contingent on risk and experience. Moreover, because GCs affect learning and memory (Sweatt 2009), plasticity in HPA regulation may underlie plasticity in behaviors important for fitness in novel environments (e.g. vigilance, exploration, aggression).

Epigenetically-mediated variation within the HPA

The regulation of GCs by the HPA axis is complex, involving multiple pathways, cells, and tissues at which variation can occur (Lema and Kitano 2013). Variation in any one element can influence organismal responses, particularly the capacity of individuals to coordinate crucial physiological and/or behavioral responses (Lema and Kitano 2013; Martin and Liebl 2014). There is increasing evidence that GC regulatory plasticity is partially mediated by environmentally-induced epigenetic variation. DNA methylation, histone modification and other processes can affect nearly every component of the HPA axis (Figure 1; Supplementary Table 1). The hypothalamus plays an especially crucial role in HPA activity; it transduces sensory information (e.g. the perception of a stressor arising from the amygdala or prefrontal cortex) into a physiological response (e.g. initiation of a stress response) (Smith and Vale 2006). Activation of the HPA axis stimulates the release of corticotropin-releasing factor (CRF) and arginine vasopressin (AVP) from the hypothalamus, both of which are required for the stimulation/secretion of adrenocorticotrophic hormone (ACTH) from the anterior pituitary and subsequent synthesis and release of GCs from the adrenal cortex (Smith and Vale 2006). As emphasized in Fig. 1, epigenetic variation in either CRF or AVP (expression) could have substantial consequences for the regulation of downstream physiological and/or behavioral responses to stressors. In rodents, exposure of mothers to stressors during gestation or postnatal periods resulted in hypomethylation of the hypothalamic *CRF* (Mueller and Bale 2008; Chen et al. 2012) and *AVP* promoters (Murgatroyd et al. 2009); both changes were associated with HPA hyperactivity and altered behavior when pups reached adulthood. At the level of GC synthesis, there is also evidence for epigenetic regulation of enzymes involved in steroidogenesis (Martinez-Arguelles and Papadopoulos 2010). However, direct evidence for extrinsic environmental modulation of such regulation, as was the case for maternal adversity and CRF/AVP expression, is lacking.

Upon release of GCs from the adrenals, the pervasive physiological and behavioral actions of GCs are largely dependent upon sensitivity of target tissues (Sapolsky et al. 2000; Martin et al. 2016a), namely glucocorticoid receptor (GR) expression. Most available evidence for epigenetic modulation of HPA plasticity pertains to environmentally-induced epigenetic modifications to *GR* (Weaver et al. 2004; Zhang et al. 2013b). Such effects are not altogether surprising considering the pivotal role of GR in coordinating physiological/behavioral responses to stressors and in the resolution of stress responses (Sapolsky et al. 2000). For example, in rats, maternal dietary protein restriction resulted in hypomethylation of the hepatic *GR* promoter and a metabolic phenotype characterized by increased capacity for gluconeogenesis in offspring once they reached adulthood (Lillycrop et al. 2007). Within the hippocampus, the major site of GC negative feedback (i.e., the process by which release of GCs is ultimately reduced), numerous studies have found evidence for environmentally-mediated epigenetic regulation of *GR*. Among the most well-known examples, Liu et al. (1997) and Weaver et al. (2004) link the impacts of maternal care and offspring behavior to epigenetic programming of the HPA axis of offspring. In domesticated rats, high maternal care (e.g. licking and grooming) within the first week of life was associated with long-term hypomethylation within the hippocampal *GR* promoter, reduced plasma ACTH and CORT release in response to a restraint stressor, enhanced negative feedback sensitivity, decreased hypothalamic expression of *CRF*, and reduced anxiety-like behavior (Liu et al. 1997; Weaver et al. 2004). Taken together, these studies demonstrate that not only can the environment alter GC regulation through molecular epigenetic pathways, but they also indicate that molecular epigenetic mechanisms mediate *plasticity* in the HPA and thus how much GCs might affect phenotypes throughout an individual's life. We argue that such latent plasticity represents a form of epigenetic potential that could play a powerful role in the fine-tuning of organismal-wide phenotypic responses to various environments, including those experienced by organisms moving into previously unoccupied areas.

Defining epigenetic potential

We define epigenetic potential, within the HPA, as the capacity for environmentally-induced phenotypic change (i.e. plasticity) via epigenetic modifications of the relevant genomic elements. We expect that similar forms of epigenetic potential reside elsewhere in the genome for other physiological pathways, but we do not address them here for sake of space. Epigenetic potential can take both genetic and environmental forms. Genetically, epigenetic potential could be encoded in at least two locations in genomes: (i) enzymes that establish and maintain epigenetic marks and (ii) DNA sequence variants. First, organisms require the coordinated efforts of several enzymes to establish, maintain and/or remove epigenetic marks from the genome as cells differentiate and organisms develop. Among the most commonly studied of these enzymes are the DNA methyltransferases (DNMTs), which catalyze the transfer of a methyl group to specific sites on DNA (Morris and Monteggia 2014). In vertebrates, the three main DNMTs are DNMT1, which primarily acts as a housekeeper to maintain DNA methylation patterns through mitosis (but see Fatemi et al. 2002 for evidence of *de novo* methyltransferase capacity), and DNMT3a and DNMT3b, which are considered *de novo* DNA methyltransferases, capable of establishing methylation marks on previously unmethylated DNA regions (Morris and Monteggia 2014). Given the importance of DNMTs and other epigenetic modifying enzymes as the molecular editors of the genomic blueprint, genetic variation within the genes encoding these enzymes can lead to functional variation in their catalytic activity (Potter et al. 2013; Bjornsson 2015). In humans, genetic variation in *DNMT3b* was not only associated with altered DNA methylation patterns across 700 genes, but also with changes in function of several epigenetic enzymes involved in histone modification (Jin et al. 2008).

A second form of genetic variation in epigenetic potential includes DNA sequence variation within regulatory and non-regulatory regions of the genome. In vertebrates, DNA methylation typically occurs at cytosines in the context of CpG dinucleotides (Schrey et al. 2013; Kilvitis et al. 2014), and it is estimated that within the human genome, there are >200,000 CpG single nucleotide polymorphisms (i.e. CpG-SNPs) (Shoemaker et al. 2010). Within regulatory regions (e.g. gene promoters, enhancers), the appearance or loss of CpG sites would directly influence epigenetic potential by altering the genetic substrate upon which epigenetic variation can occur. For example, CpG-SNPs within regulatory regions, particularly at transcription factor binding sites, could disrupt the binding capacity of transcription machinery (Zhi et al. 2013; Lemire et al. 2015) and thus alter gene expression. In a study by Zhi et al. (2013), >80% of CpG-SNPs surveyed from human T-cells were methylation quantitative trait loci (meQTL), and these SNPs accounted for nearly two-thirds of the strongest meQTL signals within T-cells. There is increasing evidence to suggest that not only do CpG-SNPs affect the potential for methylation at that particular CpG site, they also can influence methylation distal (*trans*) to CpG sites (Zhi et al. 2013; Lemire et al. 2015). Although much more research is needed to determine how diverse naturally-occurring DNMTs and CpG-SNPs (and more complex genetic variants for CpG sites) are, both are tantalizing possible sources of genetic variation in epigenetic potential.

Epigenetic potential might also be environmentally-sensitive and genetically independent yet still heritable. These forms of epigenetic variation are among the most compelling eco-evolutionarily because they would represent distinct pathways whereby parentally-acquired traits could be conveyed to offspring, irrespective of genetic variation (Jablonka and Lamb 2008). Most often, such environmentally-driven forms of epigenetic variation arise in early-life, when cells have differentiated little and thus the phenotype has the greatest potential to be canalized into various forms (West-Eberhard 2003; Martin et al. 2011). Such programming of adult phenotypes during critical periods of development is widespread (West-Eberhard 2003), and increasing evidence suggests that such programming may influence pure-environmental variation in epigenetic potential (Richards 2006). For example, prenatal or postnatal exposure to certain environmental toxicants has enduring, stable effects on the expression of several epigenetic regulatory proteins (Kundakovic et al. 2013; Schneider and Anderson 2013). In rats, dietary exposure to lead (Pb) during the prenatal and postnatal periods was associated with altered hippocampal protein expression of DNMT1, DNMT3a and methyl-cytosine binding protein 2 (MeCP2) (Schneider and Anderson 2013), a protein that specifically binds to methylated DNA and recruits histone deacetylases (HDACs) to repress gene transcription (Jones et al. 1998). Moreover, prenatal rats exposed to environmentally-relevant doses of bisphenol A (BPA) had differential mRNA expression of *DNMT1* and *DNMT3a* in the prefrontal cortex, hypothalamus and hippocampus (Kundakovic et al. 2013). Interestingly, both of these studies found sex-specific and dose-dependent differences in the directionality of responses (i.e., up- or down-regulation), suggesting that the developmental programming of epigenetic potential can be fine-tuned contingent on sex as well as individual experience. Apart from early-life exposure to toxicants, maternal-offspring interactions can also have lasting effects on epigenetic potential. For example, low maternal licking and grooming within the first week of life in rats was linked to increased hippocampal expression of *DNMT1* in adulthood (Zhang et al. 2010). Maternal separation during the perinatal period in rats was associated with promoter hypermethylation and reduced expression of *MeCP2* in the germ cells of male offspring (Franklin et al. 2010). Furthermore, when investigating the transmissibility of these epigenetic marks, the authors found that *MeCP2* methylation and expression were maintained in the germ cells of males and brain (cortex) of female F2 progeny (Franklin et al. 2010), substantiating the possibility of transgenerational, yet non-genetic, inheritance of epigenetic potential.

Beyond occurrences in development, variation in epigenetic potential can also be influenced in adulthood by environmental factors. One of the best-studied examples entails modulation of the epigenome through diet. S-Adenosylmethionine (SAM) is the universal methyl-donor for histone and DNA methyltransferases, and its synthesis in the methionine cycle is facilitated by several dietary precursors (e.g. folate, methionine, choline, betaine, vitamins B_2, B_6 and B_{12}) (Zhang 2015). For example, vitamins B_2, B_6 and B_{12} are key cofactors required for the synthesis of methionine, a direct precursor of SAM (Zhang 2015). Thus, dietary deficiencies of methyl-donors directly influence the net synthesis of SAM, which has been associated with global DNA hypomethylation in rodents (Zhang 2015). In addition to regulating intracellular SAM, several dietary compounds can directly affect DNMT activity. For example, tea polyphenols (e.g., catechin) and genestein (found in soybeans) inhibit human DNMT1 activity (Zhang 2015; Fang et al. 2007). Moreover in humans, folic acid deficiency resulted in a ~50% decrease in DNMT1 expression and a concomitant 80% increase in DNMT3a expression in certain colorectal cancer cell lines (Farias et al. 2015). These studies strongly suggest that variation in the consumption of certain diet items could have profound effects on epigenetic potential, either via the modulation of methyl-donor bioavailability or the regulation of DNMT activity. Of course, diet is among the most likely factors to vary as organisms colonize new areas (Liebl and Martin 2014), implicating diet as a major factor whereby epigenetic potential mediates the outcomes of range expansions.

Glucocorticoids and epigenetic potential in range expansions

As discussed above, GCs play prominent roles as integrators (or date hubs) in physiological regulatory networks (PRNs), meaning that they have the ability to coordinate diverse physiological and/or behavioral processes that contribute to whole-organism performance (Martin et al. 2011; Cohen et al. 2012; Martin and Cohen 2014; Martin et al. 2016b). Unlike changes in PRN structure, which occur over evolutionary timescales (Martin and Cohen 2014), alterations in PRN state can occur within an individual's lifetime depending on intrinsic (e.g. life history stage) and/or extrinsic (e.g. parasite pressure or resource availability) factors (Cohen et al. 2012). During range expansions, the capacity for shifts in PRN state (i.e. PRN plasticity; Martin et al. 2016b) should be particularly important, particularly at range edges. Although never tested empirically, given the many ways that epigenetic mechanisms can alter GC regulation (Fig. 1), variation in epigenetic potential might facilitate the diversity of and/or plasticity in PRN states and hence success in new areas (Fig. 2).

Consider a hypothetical example in which a newly established range-edge population is comprised of individuals that vary genetically in epigenetic potential. In this case, individuals with the greatest number of regulatory CpGs across many HPA genes have high epigenetic potential, whereas individuals with very little regulatory CpGs across few HPA genes have low epigenetic potential (Fig. 2). Such genetic variation in epigenetic potential could influence organismal responses to stressors via the impacts of epigenetic marks on HPA regulatory flexibility (e.g. individual variation in homeostatic range/reactive scope—Romero 2009). For example, in response to an early-life stressor, the connectivity among PRN components in genotypes with low epigenetic potential may remain unchanged, thereby inhibiting HPA flexibility. In contrast, the PRN state of genotypes with modest or high epigenetic potential would be capable of responding plastically to the early-life stressor, but to varying degrees. In individuals with modest epigenetic potential, early-life stressors might alter PRN state (connectivity in Fig. 2) similarly to individuals with high epigenetic potential, however, reduced expression of genes encoding epigenetic modifying enzymes and/or dietary restriction of methyl-donors could stabilize PRN connectivity, at least compared genotypes with high epigenetic potential, which here includes exceptional reversible connectivity within PRNs.

These genetic variants could further experience environmental alterations to epigenetic potential contingent on the diets they consume or other adversity they encounter (e.g., novel parasite and predator threats). Such environmental differences, in conjunction with genetic differences, could further modify HPA flexibility, and thus coping ability with the challenges of living at range edges. For example, low epigenetic potential for HPA flexibility and the resultant limitations to PRN plasticity could result in under-exuberant responses to novel stressors (e.g. homeostatic failure—Romero et al. 2009), whereas individuals with modest epigenetic potential may result in over-exuberant responses (e.g. homeostatic overload—Romero et al. 2009). In other words, in some contexts for some (epi)genotypes, high epigenetic potential might not only enhance phenotypic adjustments to prevailing conditions and developmental experience (via the recruitment of typically unconnected PRN subnetworks), but also allow for phenotypic de-integration via the reversibility of edge formation among PRN subnetworks.

Future Directions

Here, we sought to provide evidence that epigenetic potential and its mediation of organismal-wide plastic responses might affect vertebrate range expansion success. Whereas some aspects of the concept of epigenetic potential have been alluded to previously (a Web of Science search for “epigenetic potential” on March 8, 2017 returned 17 hits), to our knowledge, this paper is among the first to define the term in regards to its genetic and environmental underpinnings, its physiological functions, and its prospective ecological and evolutionary consequences. Given the infancy of epigenetic potential as a concept, we use the remainder of our paper to highlight some promising avenues to pursue in future research on epigenetic potential.

In Fig. 1, our primary goal was to reveal where in the HPA the most epigenetic potential might lie (Fig. 1). A Web of Science search (conducted in December 2016, see Supplementary Table 1 for search terms) demonstrated that there was substantial evidence for epigenetic modulation throughout the HPA, however, particular aspects appeared disproportionally more likely to mediate epigenetic potential than others (Fig. 1; Supplementary Table 2). Indeed, to try to account for possible biases in research effort, which might obscure meaningful estimation of epigenetic potential, we quantified the number of studies reporting epigenetic effects within a particular HPA component and adjusted that count by the total number of published primary research studies on that particular HPA component. In Fig. 1 and Supplementary Table 2, we report this ratio as an estimate of epigenetic potential. Although most available data come from domesticated lab rodents, which might not represent the most evolutionarily-relevant examples, four of the top five epigenetic potential estimates in the HPA were for receptors. The only non-receptor component was the gene encoding steroidogenic acute regulatory protein (StAR or *STARD1*). StAR acts as the rate-limiting step in the synthesis of most major steroid hormones, including GCs (Christenson and Strauss 2001). Among the top four receptors, epigenetic potential rankings (highest to lowest) were as follows: CRH receptor 2 (*CRHR2*), CRH receptor 1 (*CRHR1*), ACTH receptor (*ACTHR* or *MCR2*), and glucocorticoid receptor *(GR)*.

These estimates of epigenetic potential, while unquestionably preliminary, suggest that HPA regulatory plasticity may be most common at receptors. In a sense, this outcome is unsurprising given that receptors are particularly important for the initiation of the stress response, distal actions at target tissues, and negative feedback. We also note that epigenetic potential was highest among all factors we considered for glucocorticoid response elements (GREs). However, we chose to exclude GREs from the rankings in the table because they represent a different type of GC regulation than elements of the HPA itself. It would be interesting to investigate how much epigenetic potential resides in GRE, but as these regions occur across the genome, they are harder to enumerate and inappropriate to compare to other estimates of epigenetic potential we calculated. Overall, given the rarity of studies for some HPA components, we are reluctant to conclude that our crude estimate of epigenetic potential is reflective of natural epigenetic potential in the HPA. Nonetheless, we hope it motivates other more direct efforts to measure HPA epigenetic potential. Loci with high epigenetic potential could be particularly important targets for environmental modulation of organismal-wide plasticity and selection.

A second critical research venture involving epigenetic potential and the HPA would evaluate directly the value of the PRN construct. For instance, using transcriptomics approaches, one could determine: (i) how HPA manipulations influence variation or plasticity in relevant phenotypic traits; (ii) the extent to which observed phenotypic integration and/or de-coupling is associated with changes in PRN connectivity or other network traits; and (iii) whether PRN plasticity via manipulation of GC synthesis or negative feedback is associated with epigenetic variation. An alternative approach would be to administer drugs, such as 5-aza-2'-deoxycytidine or trichostatin A (e.g., Weaver et al. 2004; 2006), or to manipulate dietary intake of methyl-donors (e.g., Waterland and Jirtle 2004), both of which alter epigenetic marks. Again, the use of transcriptomic tools could reveal whether such manipulations influences GC regulatory plasticity and if so, how this plasticity is associated with PRN states (Martin et al. 2011; Cohen et al. 2012; Martin and Cohen 2014).

Lastly, it will be useful to identify additional factors that contribute to variation in epigenetic potential. Whereas we focused primarily on how epigenetic potential acts as a source of HPA regulatory plasticity, there is some evidence that GCs can influence epigenetic potential. For example, dexamethasone (DEX) treatment reduced (human) natural killer (NK) cell cytokine expression in a dose-dependent manner, and was associated with increased cytokine promoter-specific histone deacetylation. Further, these DEX effects were reversible upon treatment with the histone deacetylase inhibitor, trichostatin A (Krukowski et al. 2011). In another study on rats, prenatal exposure to lipopolysaccharide (LPS), an immunogenic component of Gram-negative bacterial cell walls, had enduring effects on *DNMT1* and *DNMT3b* expression within the adrenal cortex (Wang et al. 2017).

Conclusion

Given increases in the occurrence of natural and especially anthropogenically-mediated species' range shifts, it is becoming increasingly important to understand the underlying mechanisms that facilitate whole-organism performance and thus mediate range expansion outcomes. Here, we highlighted a potential role of molecular epigenetic mechanisms as drivers of genotype x environment (GxE) and/or individual x environment (IxE) interactions (Nussey et al. 2007). Indeed, epigenetic potential—particularly within physiological pathways crucial for homeostasis—allows not only for rapid phenotypic adjustments in response to salient environmental cues, but also may act as an additional source of variation for overcoming genetic paradoxes. Moreover, evidence for the heritability of environmentally-induced epigenetic effects (Jablonka and Raz 2009) provides an alternate route whereby the epigenetic potential for homeostatic fine-tuning is propagated rapidly across generations. We believe epigenetic potential in HPA plasticity warrants extensive investigation in various native and non-native range expansions as well as other contexts in which populations are being forced to adjust to rapid (and often anthropogenic) environmental change.

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Figures and Tables:

Figure 1: Epigenetic regulation in the hypothalamic-adrenal-pituitary axis. The regulation of GCs by the HPA-axis is a complex process in which epigenetic mechanisms have the potential to influence multiple steps, from the upstream processes involved in initiating GC synthesis to the downstream actions of GCs on target tissues. A Web of Science search was conducted in December 2016 in order to reveal the components of the HPA-axis in which epigenetic marks have been observed and where they are most likely to occur. Each component of the HPA-axis was queried using search terms "epigenetic" and "component name" or "component abbreviation" or "associated gene" (for exact search terms see Supplementary Table 1). After filtering out document types besides peer-reviewed primary articles, studies were then sorted into categories based on content. Review or non-relevant papers were notated, as were studies that investigated epigenetic marks but found no significant patterns or relevance to functionality (i.e., gene expression, effects on behavior, etc.). Articles that reported functional impacts of epigenetic marks were categorized by mechanism (DNA methylation, histone modification, or other). Numbers in yellow burst-symbols denote epigenetic potential within each HPA component, which is calculated as: (the number of papers with evidence of functional epigenetic regulation / the total number of papers investigating that particular HPA component) x 100 (See Supplementary Table 2 for additional information).

Figure 2. Epigenetic potential as a mediator of plasticity in physiological regulatory networks (PRNs), and hence range-expansion success.

In a hypothetical, newly established range-edge population, individuals (genotypes, G1-3) will vary in PRN state (due to plasticity) and structure (due to genes or enduring epigenetic marks). Some PRN structures (G3) have limited capacity for engaging in and stopping cross-talk (plasticity mediated via connectivity) between date hubs (e.g., aspects of the HPA—red circles) and other subnetworks (blue circles) and/or party hubs. However, other individuals with many CpGs across many HPA genes (e.g., G1) have high epigenetic potential and hence a strong propensity for (reversible) plasticity. Such genetic variation in epigenetic potential could influence organismal responses to stressors via the impacts of epigenetic marks on HPA regulatory flexibility (e.g. individual variation in homeostatic range/reactive scope—Romero 2009). However, some such variation could be solely environmentally-mediated such as by exposure to an early-life stressor (lightning bolt symbol depicting early-life experience). In these cases, connectivity among PRN components in genotypes with low epigenetic potential may remain unchanged (G3), thereby inhibiting HPA flexibility. In contrast, the PRN state of genotypes with modest or high epigenetic potential (G1 and 2) would be capable of responding plastically to the early-life stressor to varying degrees. In individuals with modest epigenetic potential, early-life stressors might alter PRN connectivity similarly to individuals with high epigenetic potential, however low expression of genes encoding epigenetic modifying enzymes and/or dietary restriction of methyl-donors could stabilize connectivity within PRNs (i.e. solid black lines), at least compared genotypes with high epigenetic potential, which here involves exceptional reversible connectivity within PRNs (i.e. dashed black lines). Contingent on further experience, environmental alterations to epigenetic potential (via diet or exposure other stressors—lightning bolt) may act in conjunction with genetic differences to further modify HPA flexibility. For example, low epigenetic potential for HPA flexibility and the resultant limitations to PRN plasticity could result in under-exuberant responses to novel stressors (e.g. homeostatic failure; red lower dashed line—Romero et al. 2009) for some (epi)genotypes, whereas (epi)genotypes with modest epigenetic potential may result in over-exuberant responses (e.g. homeostatic overload; red upper dashed line—Romero et al. 2009). In other words, in some contexts for some (epi)genotypes, high epigenetic potential might not only enhance phenotypic adjustments to prevailing conditions and developmental experience (via the recruitment of typically unconnected PRN subnetworks; yellow circles), but also allow for phenotypic de-integration via the reversibility of edge formation among PRN subnetworks.

Supplementary Tables:

Supplementary Table 1: Web of Science Search Results for Epigenetic Potential among HPA Components

A Web of Science search was conducted in December of 2016 in order to reveal the components of the HPA-axis in which epigenetic marks have influenced functionality and where within the pathway epigenetic regulation is most likely to occur. Each component of the HPA-axis was queried using search terms "epigenetic" and "component name" or "component abbreviation" or "associated gene". After filtering out document types besides peer-reviewed primary articles, studies were then sorted into categories based on content. Review or non-relevant papers were notated, as were studies that investigated epigenetic marks but found no significant patterns or relevance to functionality (i.e., gene expression, effects on behavior, etc.). Articles that reported functional impacts of epigenetic marks were categorized by mechanism (DNA methylation, histone modification, or other).

Supplementary Table 2: Epigenetic Potential of Various HPA Axis Components

A Web of Science search was conducted in December of 2016 in order to reveal the components of the HPA-axis in which epigenetic marks have influenced functionality and where within the pathway epigenetic regulation is most likely to occur. Total Epigenetic Studies—each component of the HPA-axis was queried using search terms "epigenetic" and "component name" or "component abbreviation" or "associated gene" (for exact search terms see Supplemental Table 1). Total Research Effort—to account general research effort among HPA components, we also removed the search term "epigenetic" to calculate the number of studies investigating each component. Epigenetic Potential—calculated by taking the ratio of Total Epigenetic Studies to Total Research Effort (x 100). Epigenetic Potential Ranking—assigned after sorting HPA components by Epigenetic Potential value (highest to lowest). * = GREs, while facilitators of rapid genomic actions of GC-bound GR within the nucleus, are not necessarily deemed as an HPA component, as GC-bound GR can exert a variety of nongenomic effects (e.g., via membrane-bound GR). Abbreviations: CRHR2 (corticotropin-releasing hormone receptor 2); CRHR1 (corticotropin-releasing hormone receptor 1); MC2R/ACTHR (adrenocorticotropic hormone receptor); StAR (steroidogenic acute regulatory protein); GR (glucocorticoid receptor); CYP11A1/P450scc (cholesterol side chain cleavage enzyme); AVP/ADH (arginine vasopressin/antidiuretic hormone); MR (mineralocorticoid receptor); CRH/CRF (corticotropin-releasing hormone/factor); ACTH (adrenocorticotropic hormone); POMC (proopiomelanocortin); HSD3B2 (3-beta-hydroxysteroid dehydroxylase); CYP21A2/P450c21 (21-hydroxylase); CYP11B1/P45011B1 (11 β-hydroxylase); CBG (corticosteroid-binding globulin); V1bR/VPR3/AVPR3 (arginine vasopressin receptor); GRE (glucocorticoid response element).

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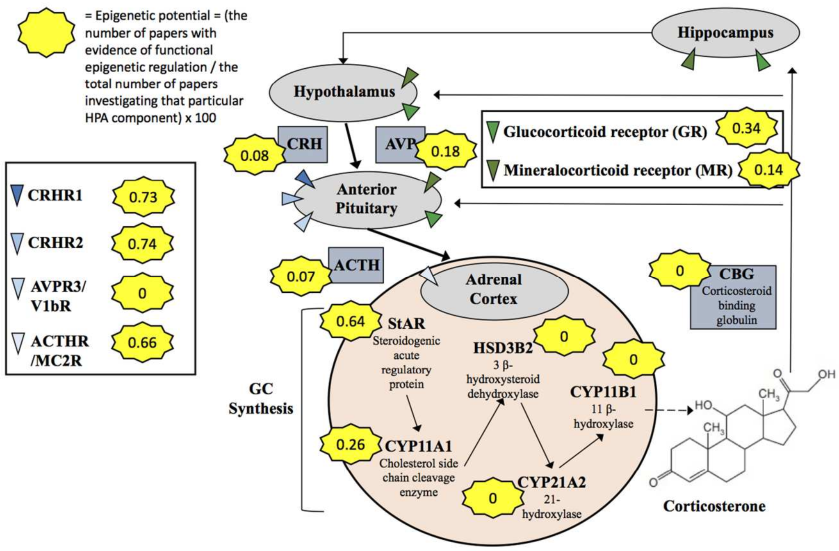

Figure 1: Epigenetic regulation in the hypothalamic-adrenal-pituitary axis. The regulation of GCs by the HPA-axis is a complex process in which epigenetic mechanisms have the potential to influence multiple steps, from the upstream processes involved in initiating GC synthesis to the downstream actions of GCs on target tissues. A Web of Science search was conducted in December 2016 in order to reveal the components of the HPA-axis in which epigenetic marks have been observed and where they are most likely to occur. Each component of the HPA-axis was queried using search terms "epigenetic" and "component name" or "component abbreviation" or "associated gene" (for exact search terms see Supplementary Table 1). After filtering out document types besides peer-reviewed primary articles, studies were then sorted into categories based on content. Review or non-relevant papers were notated, as were studies that investigated epigenetic marks but found no significant patterns or relevance to functionality (i.e., gene expression, effects on behavior, etc.). Articles that reported functional impacts of epigenetic marks were categorized by mechanism (DNA methylation, histone modification, or other). Numbers in yellow burst-symbols denote epigenetic potential within each HPA component, which is calculated as: (the number of papers with evidence of functional epigenetic regulation / the total number of papers investigating that particular HPA component) x 100 (See Supplementary Table 2 for additional information). ‼ ┼ ‼ ┼

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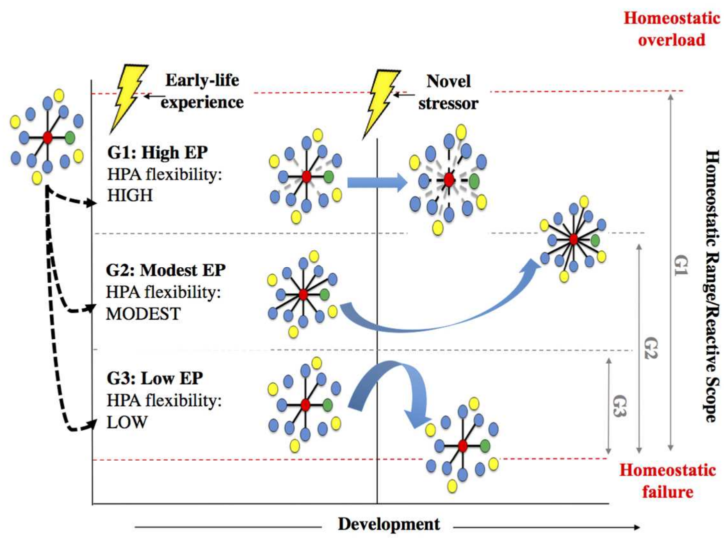

Figure 2. Epigenetic potential as a mediator of plasticity in physiological regulatory networks (PRNs), and hence range-expansion success. In a hypothetical, newly established range-edge population, individuals (genotypes, G1-3) will vary in PRN state (due to plasticity) and structure (due to genes or enduring epigenetic marks). Some PRN structures (G3) have limited capacity for engaging in and stopping cross-talk (plasticity mediated via connectivity) between date hubs (e.g., aspects of the HPA—red circles) and other subnetworks (blue circles) and/or party hubs. However, other individuals with many CpGs across many HPA genes (e.g., G1) have high epigenetic potential and hence a strong propensity for (reversible) plasticity. Such genetic variation in epigenetic potential could influence organismal responses to stressors via the impacts of epigenetic marks on HPA regulatory flexibility (e.g. individual variation in homeostatic range/reactive scope—Romero 2009). However, some such variation could be solely environmentally-mediated such as by exposure to an early-life stressor (lightning bolt symbol depicting early-life experience). In these cases, connectivity among PRN components in genotypes with low epigenetic potential may remain unchanged (G3), thereby inhibiting HPA flexibility. In contrast, the PRN state of genotypes with modest or high epigenetic potential (G1 and 2) would be capable of responding plastically to the early-life stressor to varying degrees. In individuals with modest epigenetic potential, early-life stressors might alter PRN connectivity similarly to individuals with high epigenetic potential, however low expression of genes encoding epigenetic modifying enzymes and/or dietary restriction of methyl-donors could stabilize connectivity within PRNs (i.e. solid black lines), at least compared genotypes with high epigenetic potential, which here involves exceptional reversible connectivity within PRNs (i.e. dashed black lines). Contingent on further experience, environmental alterations to epigenetic potential (via diet or exposure other stressors—lightning bolt) may act in conjunction with genetic differences to further modify HPA flexibility. For example, low epigenetic potential for HPA flexibility and the resultant limitations to PRN plasticity could result in under-exuberant responses to novel stressors (e.g. homeostatic failure; red lower dashed line—Romero et al. 2009) for some (epi)genotypes, whereas (epi)genotypes with modest epigenetic potential may result in over-exuberant responses (e.g. homeostatic overload; red upper dashed line—Romero et al. 2009). In other words, in some contexts for some (epi)genotypes, high epigenetic potential might not only enhance phenotypic adjustments to prevailing conditions and developmental experience (via the recruitment of typically unconnected PRN subnetworks; yellow circles), but also allow for phenotypic de-integration via the reversibility of edge formation among PRN subnetworks.

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HPA Component	Total Epigenetic Studies	Total Research Effort	Epigenetic Potential (%)	Epigenetic Potential Ranking
CRHR2	1	136	0.74	1
CRHR1	3	410	0.73	2
MC2R or ACTHR	2	301	0.66	3
StAR	8	1254	0.64	4
GR	123	36465	0.34	5
CYP11A1 or P450scc	5	1949	0.26	6
AVP or ADH	5	2857	0.18	7
MR	5	3673	0.14	8
CRH or CRF	19	25128	0.08	9
ACTH	30	41924	0.07	10
POMC	1	1706	0.06	11
HSD3B2	0	2594	0	N/A
CYP21A2 or P450c21	0	3041	0	N/A
CYP11B1 or P450 11B1	0	1241	0	N/A
CBG	0	2015	0	N/A
V1bR or VPR3 or AVPR3	0	97	0	N/A
*GRE	4	621	0.64	N/A

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Title	Authors	*DNA Methylation*	*Histone Modification*	*Other*	*Investigated*	*Review*
Epigenetic Changes in the Hypothalamic Proopiomelanocortin and Glucocorticoid Receptor Genes in the Ovine Fetus after Periconceptional Undernutrition	Stevens, Adam; Begum, Ghazala; Cook, Alice; Connor, Kristin; Rumball, Christopher; Oliver, Mark; Challis, John; Bloomfield, Frank; White, Anne	1	1			
Male Germline Transmits Fetal Alcohol Adverse Effect on Hypothalamic Proopiomelanocortin Gene Across Generations	Govorko, Dmitry; Bekdash, Rola A.; Zhang, Changqing; Sarkar, Dipak K.	1	1			
Epigenetic changes in fetal hypothalamic energy regulating pathways are associated with maternal undernutrition and twinning	Begum, Ghazala; Stevens, Adam; Smith, Emma Bolton; Connor, Kristin; Challis, John R. G.; Bloomfield, Frank; White, Anne	1	1			

Epigenetic changes in hypothalamic appetite regulatory genes may underlie the developmental programming for obesity in rat neonates subjected to a high-carbohydrate	Mahmood, S.; Smiraglia, D. J.; Srinivasan, M.; Patel, M. S.	1	1
Hypothalamic proopiomelanocortin promoter methylation becomes altered by early overfeeding: an epigenetic model of obesity and the metabolic syndrome	Plagemann, Andreas; Harder, Thomas; Brunn, Matthias; Harder, Anja; Roepke, Katharina; Wittrock-Staar, Manon; Ziska, Thomas; Schellong, Karen; Rodekamp, Elke;	1	
An Alu Element-Associated Hypermethylation Variant of the POMC Gene Is Associated with Childhood Obesity	Kuehnen, Peter; Mischke, Mona; Wiegand, Susanna; Sers, Christine; Horsthemke, Bernhard; Lau, Susanne; Keil, Thomas; Lee, Young-Ae; Grueters, Annette; Krude, Heiko	1	
Promoter specific DNA methylation and gene expression of POMC in acutely underweight and recovered patients with anorexia nervosa	Ehrlich, Stefan; Weiss, Deike; Burghardt, Roland; Infante-Duarte, Carmen; Brockhaus, Simone; Muschler, Marc A.; Bleich, Stefan; Lehmkuhl, Ulrike; Frieling, Helge	1	

DNA methylation of the POMC gene promoter is associated with craving in alcohol dependence	Muschler, Marc Andre Nicolas; Hillemacher, Thomas; Kraus, Cornelia; Kornhuber, Johannes; Bleich, Stefan; Frieling, Helge	1
Early-Life Stress Reduces DNA Methylation of the Pomc Gene in Male Mice	Wu, Yonghe; Patchev, Alexandre V.; Daniel, Guillaume; Almeida, Osborne F. X.; Spengler, Dietmar	1
High folate gestational and post-weaning diets alter hypothalamic feeding pathways by DNA methylation in Wistar rat offspring	Cho, Clara E.; Sanchez-Hernandez, Diana; Reza-Lopez, Sandra A.; Huot, Pedro S. P.; Kim, Young-In; Anderson, G. Harvey	1
Array-Based Profiling of DNA Methylation Changes Associated with Alcohol Dependence	Zhang, Huiping; Herman, Aryeh I.; Kranzler, Henry R.; Anton, Raymond F.; Zhao, Hongyu; Zheng, Wei; Gelernter, Joel	1

Transcriptomic and Epigenetic Changes in the Hypothalamus Are Involved in an Increased Susceptibility to a High-Fat-Sucrose Diet in Prenatally Stressed Female Rats	Paternain, L.; Batlle, M. A.; De la Garza, A. L.; Milagro, F. I.; Martinez, J. A.; Campion, J.	1
Identification of Disease-Associated DNA Methylation in B Cells from Crohn's Disease and Ulcerative Colitis Patients	Lin, Zhenwu; Hegarty, John P.; Yu, Wei; Cappel, Jon A.; Chen, Xi; Faber, Pieter W.; Wang, Yunhua; Poritz, Lisa S.; Fan, Jian-Bing; Koltun, Walter A.	1
Association of weight regain with specific methylation levels in the NPY and POMC promoters in leukocytes of obese men: A translational study	Crujeiras, Ana B.; Campion, Javier; Diaz-Lagares, Angel; Milagro, Fermin I.; Goyenechea, Estibaliz; Abete, Itziar; Casanueva, Felipe F.; Alfredo Martinez, J.	1
Leptin resistance and obesity in mice with deletion of methyl-CpG-binding protein 2 (MeCP2) in hypothalamic pro-opiomelanocortin (POMC) neurons	Wang, Xiaorui; Lacza, Zsombor; Sun, Yi E.; Han, Weiping	1

Smoking, But Not Malnutrition, Influences Promoter-Specific DNA Methylation of the Proopiomelanocortin Gene in Patients With and Without Anorexia Nervosa	Ehrlich, Stefan; Walton, Esther; Roffman, Joshua L.; Weiss, Deike; Puls, Imke; Doehler, Nico; Burghardt, Roland; Lehmkuhl, Ulrike; Hillemacher, Thomas; Muschler, Marc; Frieling,	1
Hypermethylation of Sp1 Binding Site Suppresses Hypothalamic POMC in Neonates and May Contribute to Metabolic Disorders in Adults: Impact of Maternal Dietary CLAs	Zhang, Xiaomei; Yang, Ran; Jia, Yan; Cai, Demin; Zhou, Bo; Qu, Xiaoli; Han, Huihua; Xu, Liang; Wang, Linfeng; Yao, Yanan; Yang, Guoqing	1
DNA methylation profiling in the Carolina Breast Cancer Study defines cancer subclasses differing in clinicopathologic characteristics and survival	Conway, Kathleen; Edmiston, Sharon N.; May, Ryan; Kuan, Pei Fen; Chu, Haitao; Bryant, Christopher; Tse, Chiu-Kit; Swift-Scanlan, Theresa; Geradts, Joseph; Troester, Melissa A.;	1
Nuclear factor kappa B (NF-kappa B) suppresses food intake and energy expenditure in mice by directly activating the Pomc promoter	Shi, X.; Wang, X.; Li, Q.; Su, M.; Chew, E.; Wong, E. T.; Lacza, Z.; Radda, G. K.; Tergaonkar, V.; Han, W.	1

Overweight and CpG methylation of the Pomc promoter in offspring of high-fat-diet-fed dams are not reprogrammed by regular chow diet in rats	Marco, Asaf; Kisliouk, Tatiana; Tabachnik, Tzlil; Meiri, Noam; Weller, Aron	1
Increasing vitamin A in post-weaning diets reduces food intake and body weight and modifies gene expression in brains of male rats born to dams fed a high multivitamin diet	Sanchez-Hernandez, Diana; Cho, Clara E.; Kubant, Ruslan; Reza-Lopez, Sandra A.; Poon, Abraham N.; Wang, Jingzhou; Huot, Pedro S. P.; Smith, Christopher E.; Anderson, G. Harvey	1
Regulation of hypothalamic neuropeptides gene expression in diet induced obesity resistant rats: possible targets for obesity prediction?	Cifani, Carlo; Di Bonaventura, Maria V. Micioni; Pucci, Mariangela; Giusepponi, Maria E.; Romano, Adele; Di Francesco, Andrea; Maccarrone, Mauro; D'Addario,	1
A Genome-Wide mQTL Analysis in Human Adipose Tissue Identifies Genetic Variants Associated with DNA Methylation, Gene Expression and Metabolic Traits	Volkov, Petr; Olsson, Anders H.; Gillberg, Linn; Jorgensen, Sine W.; Brons, Charlotte; Eriksson, Karl-Fredrik; Groop, Leif; Jansson, Per-Anders; Nilsson, Emma; Ronn, Tina; Vaag, Allan;	1

Maternal and post-weaning high-fat, high-sucrose diet modulates glucose homeostasis and hypothalamic POMC promoter methylation in mouse offspring	Zheng, Jia; Xiao, Xinhua; Zhang, Qian; Yu, Miao; Xu, Jianping; Wang, Zhixin; Qi, Cuijuan; Wang, Tong	1
Methylation profiling of DNA in the area of atherosclerotic plaque in humans	Nazarenko, M. S.; Puzyrev, V. P.; Lebedev, I. N.; Frolov, A. V.; Barbarash, O. L.; Barbarash, L. S.	1
Associations among child abuse, mental health, and epigenetic modifications in the proopiomelanocortin gene (POMC): A study with children in Tanzania	Hecker, Tobias; Radtke, Karl M.; Hermenau, Katharin; Papassotiropoulos, Andreas; Elbert, Thomas	1
Corticotropin releasing factor up-regulates the expression and function of norepinephrine transporter in SK-N-BE (2) M17 cells	Huang, Jingjing; Tufan, Turan; Deng, Maoxian; Wright, Gary; Zhu, Meng-Yang	1

Interindividual Variation in DNA Methylation at a Putative POMC Metastable Epiallele Is Associated with Obesity	Kuehnen, Peter; Handke, Daniela; Waterland, Robert A.; Hennig, Branwen J.; Silver, Matt; Fulford, Anthony J.; Dominguez-Salas, Paula; Moore, Sophie E.; Prentice, Andrew M.;	1	
DNA CpG Methylation (5-Methylcytosine) and Its Derivative (5-Hydroxymethylcytosine) Alter Histone Posttranslational Modifications at the Pomc Promoter,	Marco, Asaf; Kisliouk, Tatiana; Tabachnik, Tzlil; Weller, Aron; Meiri, Noam	1	
Epigenetic regulation of G protein coupled receptor signaling and its implications in psychiatric disorders	Dogra, Shalini; Sona, Chandan; Kumar, Ajeet; Yadav, Prem N.	1	
Many obesity-associated SNPs strongly associate with DNA methylation changes at proximal promoters and enhancers	Voisin, Sarah; Almen, Markus Sallman; Zheleznyakova, Galina Y.; Lundberg, Lina; Zarei, Sanaz; Castillo, Sandra; Eriksson, Fia Ence; Nilsson, Emil K.; Blueher, Matthias;		1

Epigenetics and the Environmental Regulation of the Genome and Its Function	Zhang, Tie-Yuan; Meaney, Michael J.	1
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Association of DNA Methylation with Acute Mania and Inflammatory Markers	Sabunciyan, Sarven; Maher, Brion; Bahn, Sabine; Dickerson, Faith; Yolken, Robert H.
Epigenetic regulation of nociceptin/orphanin FQ and corticotropin-releasing factor system genes in frustration stress-induced binge-like palatable food consumption	Pucci, Mariangela; Di Bonaventura, Maria Vittoria Micioni; Giusepponi, Maria Elena; Romano, Adele; Filaferro, Monica; Maccarrone, Mauro; Ciccocioppo, Roberto;
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Methylation of the Corticotropin Releasing Hormone Gene Promoter in BeWo Cells: Relationship to Gene Activity	Pan, Xin; Bowman, Maria; Scott, Rodney J.; Fitter, John; Nicholson, Richard C.; Smith, Roger; Zakar, Tamas

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Title	Authors	*DNA Methylation*	*Histone Modification*	*Other*	*Investigated*	*Review*
Sex-specific programming of offspring emotionality after stress early in pregnancy	Mueller, Bridget R.; Bale, Tracy L.	1				
Epigenetic variation during the adult lifespan: cross-sectional and longitudinal data on monozygotic twin pairs	Talens, Rudolf P.; Christensen, Kaare; Putter, Hein; Willemsen, Gonneke; Christiansen, Lene; Kremer, Dennis; Suchiman, H. Eka D.; Slagboom, P. Eline; Boomsma,	1				
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Maternal choline intake alters the epigenetic state of fetal cortisol-regulating genes in humans	Jiang, Xinyin; Yan, Jian; West, Allyson A.; Perry, Cydne A.; Malysheva, Olga V.; Devapatla, Srisatish; Pressman, Eva; Vermeylen, Francoise; Caudill, Marie A.	1				
Chronic Stress Induces Sex-Specific Alterations in Methylation and Expression of Corticotropin-Releasing Factor Gene in the Rat	Sterrenburg, Linda; Gaszner, Balazs; Boerrigter, Jeroen; Santbergen, Lennart; Bramini, Mattia; Elliott, Evan; Chen, Alon; Peeters, Bernard W. M. M.; Roubos, Eric W.; Kozicz,	1				
Importance of epigenetic mechanisms in visceral pain induced by chronic water avoidance stress	Tran, L.; Chaloner, A.; Sawaiha, A. H.; Van-Meerveld, B. Greenwood	1				

Epigenetic Upregulation of Corticotrophin-Releasing Hormone Mediates Postnatal Maternal SeparationInduced Memory Deficiency	Wang, Aiyun; Nie, Wenying; Li, Haixia; Hou, Yuhua; Yu, Zhen; Fan, Qing; Sun, Ruopeng	1
Embryonic exposure to corticosterone modifies aggressive behavior through alterations of the hypothalamic pituitary adrenal axis and the serotonergic system in the chicken	Ahmed, Abdelkareem A.; Ma, Wenqiang; Ni, Yingdong; Zhou, Qin; Zhao, Ruqian	1
Estrogens protect myocardium against ischemia/reperfusion insult by up-regulation of CRH receptor type 2 in female rats	Cong, Binhai; Zhu, Xiaoyan; Cao, Buqing; Xiao, Jian; Wang, Zhinong; Ni, Xin	1
Prenatal Maternal Stress Predicts Methylation of Genes Regulating the Hypothalamic-Pituitary-Adrenocortical System in Mothers and Newborns in the Democratic	Kertes, Darlene A.; Kamin, Hayley S.; Hughes, David A.; Rodney, Nicole C.; Bhatt, Samarth; Mulligan, Connie J.	1
Early life adversity and serotonin transporter gene variation interact to affect DNA methylation of the corticotropin-releasing factor gene promoter region in the adult rat brain	van der Doelen, Rick H. A.; Arnoldussen, Ilse A.; Ghareh, Hussein; van Och, Liselot; Homberg, Judith R.; Kozicz, Tamas	1
Bidirectional rescue of extreme genetic predispositions to anxiety: impact of CRH receptor 1 as epigenetic plasticity gene in the amygdala	Sotnikov, S. V.; Markt, P. O.; Malik, V.; Chekmareva, N. Y.; Naik, R. R.; Sah, A.; Singewald, N.; Holsboer, F.; Czibere, L.; Landgraf, R.	1
Prenatal Restraint Stress is Associated with Demethylation of Corticotrophin Releasing Hormone (CRH) Promoter and Enhances CRH Transcriptional Responses to Stress in Adolescent	Xu, Li; Sun, Yan; Gao, Lu; Cai, Yi-Yun; Shi, Shen-Xun	1

Epigenetic regulation of nociceptin/orphanin FQ and corticotropin-releasing factor system genes in frustration stress-induced binge-like palatable food	Pucci, Mariangela; Di Bonaventura, Maria Vittoria Micioni; Giusepponi, Maria Elena; Romano, Adele; Filaferro, Monica; Maccarrone, Mauro; Ciccocioppo, Roberto; Cifani,	1			
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Chronic Corticosterone Exposure Increases Expression and Decreases Deoxyribonucleic Acid Methylation of Fkbp5 in Mice	Lee, Richard S.; Tamashiro, Kellie L. K.; Yang, Xiaoju; Purcell, Ryan H.; Harvey, Amelia; Willour, Virginia L.; Huo, Yuqing; Rongione, Michael; Wand, Gary S.; Potash, James B.				1

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Increased methylation of glucocorticoid receptor gene (NR3C1) in adults with a history of childhood maltreatment: a link with the severity and type of trauma	Perroud, N.; Paoloni-Giacobino, A.; Prada, P.; Olie, E.; Salzmann, A.; Nicastro, R.; Guillaume, S.; Mouthon, D.; Stouder, C.; Dieben, K.; Huguelet, P.; Courtet, P.; Malafosse, A.
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Title	Authors	*DNA Methylation*	*Histone Modification*	*Other*	*Investigated*	*Review*
Epigenetic programming by maternal behavior	Weaver, ICG; Cervoni, N; Champagne, FA; D'Alessio, AC; Sharma, S; Seckl, JR; Dymov, S; Szyf, M; Meaney, MJ	1	1			
The transcription factor nerve growth factor-inducible protein A mediates epigenetic programming: Altering epigenetic marks by immediate-early genes	Weaver, Ian C. G.; D'Alessio, Ana C.; Brown, Shelley E.; Hellstrom, Ian C.; Dymov, Sergiy; Sharma, Shakti; Szyf, Moshe; Meaney, Michael J.	1	1			
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Epigenetic Changes in the Hypothalamic Proopiomelanocortin and Glucocorticoid Receptor Genes in the Ovine Fetus after Periconceptional	Stevens, Adam; Begum, Ghazala; Cook, Alice; Connor, Kristin; Rumball, Christopher; Oliver, Mark; Challis, John; Bloomfield, Frank; White, Anne	1	1	
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Impact of voluntary exercise and housing conditions on hippocampal glucocorticoid receptor, miR-124 and anxiety	Pan-Vazquez, Alejandro; Rye, Natasha; Ameri, Mitra; McSparron, Bethan; Smallwood, Gabriella; Bickerdyke, Jordan; Rathbone, Alex; Dajas-	1		1
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Prenatal exposure to maternal depression, neonatal methylation of human glucocorticoid receptor gene (NR3C1) and infant cortisol stress	Oberlander, Tim F.; Weinberg, Joanne; Papsdorf, Michael; Grunau, Ruth; Misri, Shaila; Devlin, Angela M.	1
Reversal of maternal programming of stress responses in adult offspring through methyl supplementation: Altering epigenetic marking later in	Weaver, ICG; Champagne, FA; Brown, SE; Dymov, S; Sharma, S; Meaney, MJ; Szyf, M	1
Sex-specific programming of offspring emotionality after stress early in pregnancy	Mueller, Bridget R.; Bale, Tracy L.	1
Induction of altered epigenetic regulation of the hepatic glucocorticoid receptor in the offspring of rats fed a protein-restricted diet during pregnancy	Lillycrop, Karen A.; Slater-Jefferies, Jo L.; Hanson, Mark A.; Godfrey, Keith M.; Jackson, Alan A.; Burdge, Graham C.	1

Dietary protein restriction of pregnant rats in the F-0 generation induces altered methylation of hepatic gene promoters in the adult male offspring in the F-1 and F-2	Burdge, Graham C.; Slater-Jefferies, Jo; Torrens, Christopher; Phillips, Emma S.; Hanson, Mark A.; Lillycrop, Karen A.	1
Childhood Adversity and Epigenetic Modulation of the Leukocyte Glucocorticoid Receptor: Preliminary Findings in Healthy Adults	Tyrka, Audrey R.; Price, Lawrence H.; Marsit, Carmen; Walters, Oakland C.; Carpenter, Linda L.	1
Folic Acid Supplementation during the Juvenile-Pubertal Period in Rats Modifies the Phenotype and Epigenotype Induced by Prenatal Nutrition	Burdge, Graham C.; Lillycrop, Karen A.; Phillips, Emma S.; Slater-Jefferies, Joanne L.; Jackson, Alan A.; Hanson, Mark A.	1
Increased methylation of glucocorticoid receptor gene (NR3C1) in adults with a history of childhood maltreatment: a link with the severity and type of trauma	Perroud, N.; Paoloni-Giacobino, A.; Prada, P.; Olie, E.; Salzmann, A.; Nicastro, R.; Guillaume, S.; Mouthon, D.; Stouder, C.; Dieben, K.; Huguelet, P.;	1
Conserved epigenetic sensitivity to early life experience in the rat and human hippocampus	Suderman, Matthew; McGowan, Patrick O.; Sasaki, Aya; Huang, Tony C. T.; Hallett, Michael T.; Meaney, Michael J.; Turecki, Gustavo; Szyf,	1

Chronic Corticosterone Exposure Increases Expression and Decreases Deoxyribonucleic Acid Methylation of Fkbp5 in Mice	Lee, Richard S.; Tamashiro, Kellie L. K.; Yang, Xiaoju; Purcell, Ryan H.; Harvey, Amelia; Willour, Virginia L.; Huo, Yuqing; Rongione, Michael; Wand, Gary S.;	1
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Metabolic Programming of MEST DNA Methylation by Intrauterine Exposure to Gestational Diabetes Mellitus	El Hajj, Nady; Pliushch, Galyna; Schneider, Eberhard; Dittrich, Marcus; Mueller, Tobias; Korenkov, Michael; Aretz, Melanie; Zechner, Ulrich; Lehnen,	1
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Investigating the influence of maternal cortisol and emotional state during pregnancy on the DNA methylation status of the glucocorticoid receptor gene	Hompes, Titia; Izzi, Benedetta; Gellens, Edith; Morreels, Maarten; Fieuws, Steffen; Pexsters, Anne; Schops, Ganel; Dom, Myriam; Van Bree, Rieta;	1
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Influences of Maternal and Paternal PTSD on Epigenetic Regulation of the Glucocorticoid Receptor Gene in Holocaust Survivor Offspring	Yehuda, Rachel; Daskalakis, Nikolaos P.; Lehrner, Amy; Desarnaud, Frank; Bader, Heather N.; Makotkine, Iouri; Flory, Janine D.; Bierer, Linda M.; Meaney,	1
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Maternal choline intake alters the epigenetic state of fetal cortisol-regulating genes in humans	Jiang, Xinyin; Yan, Jian; West, Allyson A.; Perry, Cydne A.; Malysheva, Olga V.; Devapatla, Srisatish; Pressman, Eva; Vermeylen, Francoise; Caudill, Marie A.	1
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Epigenetic changes in fetal hypothalamic energy regulating pathways are associated with maternal undernutrition and twinning	Begum, Ghazala; Stevens, Adam; Smith, Emma Bolton; Connor, Kristin; Challis, John R. G.; Bloomfield, Frank; White, Anne	1

An unbalanced maternal diet in pregnancy associates with offspring epigenetic changes in genes controlling glucocorticoid action and foetal growth	Drake, Amanda J.; McPherson, Rhoanne C.; Godfrey, Keith M.; Cooper, Cyrus; Lillycrop, Karen A.; Hanson, Mark A.; Meehan, Richard R.; Seckl, Jonathan	1
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Maternal separation is associated with strain-specific responses to stress and epigenetic alterations to Nr3c1, Avp, and Nr4a1 in mouse	Kember, R. L.; Dempster, E. L.; Lee, T. H. A.; Schalkwyk, L. C.; Mill, J.; Fernandes, C.	1
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Increased DNA methylation of neuropsychiatric genes occurs in borderline personality disorder	Dammann, Gerhard; Teschler, Stefanie; Haag, Tanja; Altmueller, Franziska; Tuczek, Frederik; Dammann, Reinhard H.	1

Genetic and Epigenetic Variation of the Glucocorticoid Receptor (NR3C1) in Placenta and Infant Neurobehavior	Bromer, Cailey; Marsit, Carmen J.; Armstrong, David A.; Padbury, James F.; Lester, Barry	1
Importance of epigenetic mechanisms in visceral pain induced by chronic water avoidance stress	Tran, L.; Chaloner, A.; Sawaiha, A. H.; Van-Meerveld, B. Greenwood	1
Methylation of the glucocorticoid receptor gene promoter in bulimic women: Associations with borderline personality disorder, suicidality, and exposure to	Steiger, Howard; Labonte, Benoit; Groleau, Patricia; Turecki, Gustavo; Israel, Mimi	1
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Epigenetic regulation of the glucocorticoid receptor promoter 1(7) in adult rats	Witzmann, Simone R.; Turner, Jonathan D.; Meriaux, Sophie B.; Meijer, Onno C.; Muller, Claude P.	1
Epigenetic Modification of the Glucocorticoid Receptor Gene Is Linked to Traumatic Memory and Post-Traumatic Stress Disorder Risk in Genocide Survivors	Vukojevic, Vanja; Kolassa, Iris-T.; Fastenrath, Matthias; Gschwind, Leo; Spalek, Klara; Milnik, Annette; Heck, Angela; Vogler, Christian; Wilker, Sarah;	1
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The Tutsi genocide and transgenerational transmission of maternal stress: epigenetics and biology of the HPA axis	Perroud, Nader; Rutembesa, Eugene; Paoloni-Giacobino, Ariane; Mutabaruka, Jean; Mutesa, Leon; Stenz, Ludwig; Malafosse, Alain; Karege, Felicien	1
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Association between methylation of the glucocorticoid receptor gene, childhood maltreatment, and clinical severity in borderline	Martin-Blanco, Ana; Ferrer, Marc; Soler, Joaquim; Salazar, Juliana; Vega, Daniel; Andion, Oscar; Sanchez-Mora, Cristina; Jesus Arranz, Maria;	1
Genome-wide DNA methylation in neonates exposed to maternal depression, anxiety, or SSRI medication during pregnancy	Non, Amy L.; Binder, Alexandra M.; Kubzansky, Laura D.; Michels, Karin B.	1
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Maternal smoking during pregnancy and infant stress response: Test of a prenatal programming hypothesis	Stroud, Laura R.; Papandonatos, George D.; Rodriguez, Daniel; McCallum, Meaghan; Salisbury, Amy L.; Phipps, Maureen G.; Lester, Barry;	1
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The Contributions of Maternal Sensitivity and Maternal Depressive Symptoms to Epigenetic Processes and Neuroendocrine Functioning	Conradt, Elisabeth; Hawes, Katheleen; Guerin, Dylan; Armstrong, David A.; Marsit, Carmen J.; Tronick, Edward; Lester, Barry M.	1
Prenatal predictors of infant self-regulation: the contributions of placental DNA methylation of NR3C1 and neuroendocrine activity	Conradt, Elisabeth; Fei, Mary; LaGasse, Linda; Tronick, Edward; Guerin, Dylan; Gorman, Daniel; Marsit, Carmen J.; Lester, BarryM.	1
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Methylation of NR3C1 is related to maternal PTSD, parenting stress and maternal medial prefrontal cortical activity in response to child separation among	Schechter, Daniel S.; Moser, Dominik A.; Paoloni-Giacobino, Ariane; Stenz, Ludwig; Gex-Fabry, Marianne; Aue, Tatjana; Adouan, Wafae; Cordero,	1
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Epigenetic Regulation of Placental NR3C1: Mechanism Underlying Prenatal Programming of Infant Neurobehavior by Maternal Smoking?	Stroud, Laura R.; Papandonatos, George D.; Salisbury, Amy L.; Phipps, Maureen G.; Huestis, Marilyn A.; Niaura, Raymond; Padbury, James	1
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An investigation of child maltreatment and epigenetic mechanisms of mental and physical health risk	Cicchetti, D (Cicchetti, Dante)[1,2] ; Hetzel, S (Hetzel, Susan)[1] ; Rogosch, FA (Rogosch, Fred A.)[2] ; Handley, ED (Handley, Elizabeth D.)[2]	1
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Epigenetic modulation of glucocorticoid receptors in posttraumatic stress disorder	Labonte, B.; Azoulay, N.; Yerko, V.; Turecki, G.; Brunet, A.	1
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EPIGENETIC EFFECTS OF SHIFTWORK ON BLOOD DNA METHYLATION	Bollati, Valentina; Baccarelli, Andrea; Sartori, Samantha; Tarantini, Letizia; Motta, Valeria; Rota, Federica; Costa, Giovanni	1
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DNA methylation profiling of ovarian carcinomas and their in vitro models identifies HOXA9, HOXB5, SCGB3A1, and CRABP1 as novel targets	Wu, Qinghua; Lothe, Ragnhild A.; Ahlquist, Terje; Silins, Ilvars; Trope, Claes G.; Micci, Francesca; Nesland, Jahn M.; Suo, Zhenhe; Lind, Guro E.	1
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A calcium-deficient diet in pregnant, nursing rats induces hypomethylation of specific cytosines in the 11 beta-hydroxysteroid dehydrogenase-1 promoter	Takaya, Junji; Iharada, Anna; Okihana, Hiroyuki; Kaneko, Kazunari	1
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In vitro maturation of oocytes is not associated with altered deoxyribonucleic acid methylation patterns in children from in vitro	Pliushch, Galyna; Schneider, Eberhard; Schneider, Tamara; El Hajj, Nady; Roesner, Sabine; Strowitzki, Thomas; Haaf, Thomas	1

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Magnesium deficiency in pregnant rats alters methylation of specific cytosines in the hepatic hydroxysteroid dehydrogenase-2 promoter	Takaya, Junji; Iharada, Anna; Okihana, Hiroyuki; Kaneko, Kazunari	1	
Maternal psychosocial stress during pregnancy alters the epigenetic signature of the glucocorticoid receptor gene promoter in their offspring: a meta-analysis	Palma-Gudiel, H.; Cordova-Palomera, A.; Eixarch, E.; Deuschle, M.; Fananas, L.		1
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Epigenetic mechanisms in stress-related memory formation	Reul, Johannes M. H. M.; Chandramohan, Yalini	1
Acetylation-mediated epigenetic regulation of glucocorticoid receptor activity: Circadian rhythm-associated alterations of glucocorticoid actions in	Kino, Tomoshige; Chrousos, George P.	1
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Supplementary Table 1: Web of Science Search Results for Epigenetic Potential among HPA Components

A Web of Science search was conducted in December of 2016 in order to reveal the components of the HPA-axis in which epigenetic marks have influenced functionality and where within the pathway epigenetic regulation is most likely to occur. Each component of the HPA-axis was queried using search terms "epigenetic" and "component name" or "component abbreviation" or "associated gene". After filtering out document types besides peer-reviewed primary articles, studies were then sorted into categories based on content. Review or non-relevant papers were notated, as were studies that investigated epigenetic marks but found no significant patterns or relevance to functionality (i.e., gene expression, effects on behavior, etc.). Articles that reported functional impacts of epigenetic marks were categorized by mechanism (DNA methylation, histone modification, or other).

Supplementary Table 2: Epigenetic Potential of Various HPA Axis Components

A Web of Science search was conducted in December of 2016 in order to reveal the components of the HPA-axis in which epigenetic marks have influenced functionality and where within the pathway epigenetic regulation is most likely to occur. Total Epigenetic Studies—each component of the HPA-axis was queried using search terms "epigenetic" and "component name" or "component abbreviation" or "associated gene" (for exact search terms see Supplemental Table 1). Total Research Effort—to account general research effort among HPA components, we also removed the search term "epigenetic" to calculate the number of studies investigating each component. Epigenetic Potential—calculated by taking the ratio of Total Epigenetic Studies to Total Research Effort (x 100). Epigenetic Potential Ranking—assigned after sorting HPA components by Epigenetic Potential value (highest to lowest). * = GREs, while facilitators of rapid genomic actions of GC-bound GR within the nucleus, are not necessarily deemed as an HPA component, as GC-bound GR can exert a variety of nongenomic effects (e.g., via membrane-bound GR). Abbreviations: CRHR2 (corticotropin-releasing hormone receptor 2); CRHR1 (corticotropin-releasing hormone receptor 1); MC2R/ACTHR (adrenocorticotropic hormone receptor); StAR (steroidogenic acute regulatory protein); GR (glucocorticoid receptor); CYP11A1/P450scc (cholesterol side chain cleavage enzyme); AVP/ADH (arginine vasopressin/antidiuretic hormone); MR (mineralocorticoid receptor); CRH/CRF (corticotropin-releasing hormone/factor); ACTH (adrenocorticotropic hormone); POMC (proopiomelanocortin); HSD3B2 (3-beta-hydroxysteroid dehydroxylase); CYP21A2/P450c21 (21-hydroxylase); CYP11B1/P45011B1 (11 β-hydroxylase); CBG (corticosteroid-binding globulin); V1bR/VPR3/AVPR3 (arginine vasopressin receptor); GRE (glucocorticoid response element).